

BARRIERS TO GROWTH:  
TRANSGENIC MANIPULATION OF SUCROSE TRANSPORT GENES ON  
BIOMASS YIELD AND CARBON PARTITIONING IN *POPULUS* & THE  
INFLUENCE OF NEGATIVE MENTORING EXPERIENCES ON DOCTORAL  
STUDENTS' CAREER AND PSYCHOSOCIAL DEVELOPMENT

by

TREVOR TREE TUMA

(Under the Direction of Chung-Jui Tsai and Erin L. Dolan)

ABSTRACT

My dissertation is comprised of dual research in tree biology and biology education. The first part presents my molecular tree biology research which sought to elucidate how sucrose trafficking influences carbohydrate remobilization in *Populus*. The second chapter focuses on a tonoplast sucrose transport protein (SUT4), a transmembrane protein that facilitates subcellular sucrose transport. By using transgenic mutants and coppicing experiments conducted under contrasting seasons, the study explored how trees allocate, store, and mobilize carbohydrate reserves to sustain growth and protection in an environmentally conditioned manner. The results suggest that carbohydrate reserves were maintained following coppicing and not completely depleted to sustain new tissue growth. The third chapter examined the importance of winter-biased sucrose transporters for carbohydrate allocation, phenology, and biomass accrual in hybrid poplar under a multi-season field trial. Despite their similar winter-biased expression, *SUT4* appeared to

have a greater role than *SUT5* and *SUT6* on environmental sensing, leaf area duration, and protective metabolism during the winter for woody perennials. Taken together, the findings highlight an environmentally conditioned role for sucrose transporters in the perennial growth cycle. The second part of this dissertation investigated how mentoring relationships contribute to or hinder STEM graduate student development. The fourth chapter defined and characterized graduate students negative mentoring experiences during their graduate education. The findings suggest that graduate students experience negative mentoring from multiple, interacting levels which hinders their career and psychosocial outcomes. The fifth chapter extended these findings by developing a psychometrically sound scale to measure negative mentoring experiences in STEM graduate education. The work provided rigorous validation evidence in support of the scale to measure these destructive experiences and relate them to graduate student outcomes. Finally, the sixth chapter tested the influence of variables theorized to predict mentorship quality. Despite an abundance of lore, little evidence supported the widely held beliefs that matching based on demographics and career stage promotes higher quality mentorship. The results of this study provided the most robust evidence to date on how to match graduate students and faculty mentors to promote effective and supportive mentoring relationships.

INDEX WORDS: SUT, sucrose, transport protein, *Populus*, metabolism, CRISPR, bioenergy, perennial, carbohydrates, wood development, mentoring, career development, well-being, psychosocial, STEM education, discipline-based education research

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## DEDICATION

This dissertation is dedicated to my parents, Kathleen & Doug. Thank you for your endless support, encouragement, and love.

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## CHAPTER 1

### INTRODUCTION AND LITERATURE REVIEW

#### *Summary and Scope of Dissertation*

This chapter outlines the structure of my dual dissertation and provides a broad overview of relevant background information. The first section describes my experiences prior to graduate education and my motivation for pursuing dual training in tree biology and biology education. The second section is a description of the role of sucrose transport proteins in the intracellular trafficking of sucrose in trees with a particular focus on their roles in processes that require non-structural carbohydrate remobilization from reserves. The third section includes an overview of the role of mentoring relationships in promoting the development and training of students in STEM fields and how mentoring relationships have the potential to be ineffective or dysfunctional. Together, my overall dissertation reflects my dual training in tree biology and biology education research.

#### *Dual training, dual expertise, and dual expectations*

I first discovered my interests in teaching, mentoring, and education research during my undergraduate education. After taking a course on evidence-based teaching, I began volunteering in middle school science classrooms. The experience was transformative. I left the science classrooms feeling fulfilled in part because I was having a positive impact on students' learning of complex science topics. It also made me astutely aware of many of the challenges facing United States educational system and the challenges associated with science instruction. Because of my experiences volunteering

in science classrooms and my undergraduate research experiences in both basic biology and science education, I was motivated to pursue graduate studies. I aspired to continue my development and training in both science research and science education research.

Few graduate programs in the United States offer interdisciplinary degrees that aligned with both of my academic interests. I chose to attend the University of Georgia (UGA) because they provided such training experiences. At UGA I was in a unique position where I would be trained as both a scientific and education researcher while pursuing my professional and personal goals in both fields. UGA is widely recognized to be home to many of the leaders in biology education in the nation. I was also attracted to UGA because of the high-quality research and broad research focus in agriculture and, specifically, in plant science research. In 2018 I enrolled in the Integrated Life Sciences program, where I joined the labs of Drs. CJ Tsai and Erin Dolan. I pursued my tree biology research in the Tsai lab and my biology education research in the Dolan lab, each of which is discussed further below.

## PART 1

### *Poplar as a model system for tree biology*

Wood is one of the most abundant natural materials produced in the world (Calvo-Flores & Dobado, 2010). Consequentially, trees represent a promising source of lignocellulosic biomass that can be utilized for the production of biofuels, bioproducts, and biopower. The United States Department of Energy has committed billions of dollars in grant funding over the past several decades to develop technologies that enable the sustainable production of clean and affordable energy through the utilization of non-food biomass resources, such as woody trees (Bryant et al., 2020). Members of the genus

*Populus* (e.g., poplar, aspen, cottonwood, and their hybrids) are used for lignocellulosic biomass feedstock (Ragauskas et al., 2006), making them economically important as one of the leading woody biomass feedstocks in the United States (Bryant et al., 2020).

*Populus* is also the model system for basic research in forest biology because of its rich genomic resources and genetic transformation ability, which have allowed for advances in our understanding of wood formation, perennial growth processes, and carbohydrate partitioning (Jansson & Douglas, 2007). Carbohydrate partitioning is critical for the perennial growth cycle and in determining tree growth, development, and biomass accumulation (Kozlowski, 1992; Rohde & Bhalerao, 2007; Traversari et al., 2018).

Therefore, understanding the mechanisms underlying carbohydrate allocation is critical for optimizing trees for use as a sustainable bioenergy source.

Recent advances in functional genomics and the application of the CRISPR/Cas9 mutagenesis in woody perennial species (Bewg et al., 2018) have provided unprecedented opportunities to understand the molecular mechanisms and regulatory networks responsible for carbohydrate allocation, storage, and utilization in woody trees. Uncovering the processes responsible for carbohydrate partitioning can ultimately be leveraged to improve the formation of wood, a carbon-demanding process reliant on carbohydrate assimilation (Mahboubi et al., 2013). For instance, in *Populus*, sucrose transporter genes (*SUTs*) are abundantly expressed in the wood-forming tissues used as feedstock for biofuel production (Payyavula et al., 2011). Given that sucrose is the predominant form into which photosynthate is assimilated, understanding the dynamics of carbohydrate allocation, and in particular sucrose transporter involvement, may provide insights that could be leveraged to maximize biomass production. To this end, the

present research aimed to elucidate the role of sucrose transport proteins during processes that require carbohydrate remobilization using the model woody perennial tree species *Populus* as a study system.

### *Translocation of Solutes in the Phloem*

In many higher plants, photosynthetically fixed carbon is transported primarily as sucrose in the phloem from sites of synthesis in the source leaves (e.g., mature leaves) to sink tissues (e.g., roots, bark, immature leaves, xylem) for utilization and storage (Kühn & Grof, 2010; Ayre, 2011). Following transport, sucrose is utilized for key metabolic processes such as growth and for usage as an energy source (e.g., carbon skeletons), development, abiotic stress response, cold tolerance, signaling, or can also be stored as starch for future utilization. Transmembrane sucrose transporter proteins (referred to as SUTs or SUCs throughout) play an important role in facilitating the phloem loading and efficient long distance transport of sucrose from source to sink tissues (Ayre, 2011; Braun et al., 2014). To date, three different mechanisms have been proposed for facilitating sucrose loading in to the phloem: apoplastic loading, polymer trapping, and symplastic diffusion (Rennie & Turgeon, 2009; Fu et al., 2011). These physiological processes differ between herbaceous annuals and woody perennials (Rennie & Turgeon, 2009).

Many herbaceous crop species have little symplastic continuity between the phloem companion cells and the photosynthetic mesophyll. In these species, phloem loading is facilitated by an active loading step with plasma-membrane SUTs and energized by the proton motive force (i.e., apoplastic loading) (Turgeon, 2010; Ayre, 2011; Liesche, 2017). Relatively few species (e.g., Cucurbitaceae, Oleaceae) are thought to use an alternative active mechanism, where sucrose diffuses into companion cells in

the phloem through specialized plasmodesmata and is converted into raffinose family oligosaccharides (RFOs) (e.g., raffinose, stachyose). Since the RFOs are larger than sucrose, they are unable to diffuse back into the mesophyll and consequently they accumulate or become “trapped” in the phloem (i.e., polymer trapping) (Turgeon, 1996; Rennie & Turgeon, 2009; Zhang & Turgeon, 2018). However, several functional studies suggest that woody and perennial species do not rely on active transmembrane transport for phloem loading, but instead may utilize a passive mechanism (i.e., symplastic diffusion) (Fu et al., 2011; Payyavula et al., 2011; Zhang et al., 2014). In these species, sucrose passively moves down a concentration gradient from high concentrations in the mesophyll and travels through dense numbers of plasmodesmata to areas of lower concentrations. Plants utilizing passive transport are believed to maintain a high cytosolic sucrose concentration in order to drive the long-distance transport and diffusion created by the Munch pressure flow, thereby alleviating the need for thermodynamically active loading (Slewiniski et al., 2013). In poplar, sucrose is believed to migrate passively through the abundant plasmodesmata that are typically present in species utilizing symplastic transport (Zhang et al., 2014). Additional research has revealed that many tree species, such as beech (*Fagus sylvatica*), walnut (*Juglan ailantifolia*), oak (*Quercus coccinea*), and willow (*Salix babylonica*), also utilize passive symplastic transport (Turgeon & Medville, 1998; Fu et al., 2011). However, relative to species that utilize apoplastic loading, the processes responsible for carbohydrate transport and allocation are under-studied in species with symplastic sucrose transport.

*Membrane proteins controlling sucrose trafficking*

Sucrose is a large polar compound that requires proteins to mediate its transport across cellular organelles (Ayre, 2011). After being produced in the cytosol, sucrose can either enter the vacuole or be transported across the plasma membrane to apoplastic space (Ayre, 2011). In most photosynthetic tissues, sucrose accumulation follows a diurnal pattern where it is stored in the vacuoles during the day and then exported to reserves at night (Martinoia et al., 2007). Movement across either the tonoplast or the plasma membrane requires proteins (i.e., sucrose transporters) to catalyze transport in an energy-dependent manner (Kühn & Grof, 2010). SUTs are sucrose/H<sup>+</sup> symporters that utilize the proton motive force to move sucrose against its concentration gradient into the phloem to allow for this (Lalonde et al., 2004; Reinders et al., 2012). In addition to transporting sucrose across the plasma membrane, SUTs are also implicated in controlling sucrose efflux across the tonoplast and into the cytosol (Payyavula et al., 2011; Schulz et al., 2011; Reinders et al., 2012; Schneider et al., 2012).

SUTs are encoded by small gene families in the genomes of almost all apoplastic and symplastic transport species, with distinct spatiotemporal expression among isoforms (Aoki et al., 2003; Sauer, 2007; Peng et al., 2014). An updated phylogenetic tree based on 41 sequenced plant genomes revealed four distinct *SUT* groups and their origin from two ancient clades (AG1 and AG2) (Peng et al., 2014). AG1, which is nearly twice as large as AG2, contains two branches of functionally distinct sub-groups, Type I and Type III. Type I SUTs are eudicot specific and localized to the plasma-membrane to facilitate apoplastic phloem loading. Type III *SUTs* are present in both monocots and eudicots and localized to the tonoplast to facilitate vacuolar sucrose efflux. The smaller clade, AG2, comprises Type II *SUTs* and are found in both eudicots and monocots. Type II SUTs

have an extended cytoplasmic loop and are localized to the plasma-membrane, yet very little is known about their function (Reinders et al., 2012; Peng et al., 2014). Type IIB *SUTs* are also localized to the plasma-membrane and thought to function in the apoplastic loading of monocot species. Type I *SUTs* display a greater tendency for gene duplication, resulting in multiple isoforms with either unique or overlapping expression patterns and often functional redundancy (Reinders et al., 2012; Peng et al., 2014). In contrast, Type III tonoplast *SUTs* typically occur as a single isoform in most taxa. The functional diversification of the *SUT* gene family may have occurred from phloem evolution and be associated with different phloem loading strategies (Peng et al., 2014).

#### *The underappreciated role of tonoplast SUTs*

Intracellular sucrose trafficking was thought to be primarily controlled by plasma membrane-localized *SUTs* (Ayre, 2011), but some evidence suggests that tonoplast-localized *SUTs* also contribute (Turgeon & Medville, 1998). Differential expression of various *SUTs* may be associated with their distinct transport mechanism (e.g., symplastic vs. apoplastic). For example, in *Arabidopsis*, an apoplastic loader, plasma membrane *SUTs* exhibit high expression in comparison to the tonoplast *SUT*, *AtSUT4*, which represents less than 5% of the leaf *SUT* transcript abundance (Lloyd & Zakhleniuk, 2004; Schulz et al., 2011). In contrast, in the poplar hybrid clone, *Populus tremula* × *alba* INRA 717-1B4, the tonoplast localized *PtaSUT4* is the most highly expressed *SUT* in leaves and its expression is detected throughout all tissues (Payyavula et al., 2011). In *Zea mays* (maize) and *Oryza sativa* (rice), the *SUT4* ortholog represents a much larger percentage of the *SUT* expression in leaves in comparison to other *SUTs* (Xu et al., 2018),

providing evidence that tonoplast *SUTs* may have expression specificity and functionality in several species.

A handful of studies have characterized the roles of tonoplast localized *SUTs* in several plant species. Knock-down (KD) and knock-out (KO) of vacuolar *PtaSUT4* in hybrid *Populus tremula* × *alba* led to constitutively elevated levels of sucrose in transgenic leaf, bark, and xylem tissues, consistent with vacuolar compartmentalization of sucrose throughout the plant and increased vacuolar sucrose sequestration (Payyavula et al., 2011; Harding et al., 2020). *SUT4* silencing also led to striking changes in the vacuole size and overall cell packing of mesophyll cells in source leaves, providing evidence that *SUT4* may also be responsible for maintaining vacuolar turgor necessary for sustaining normal leaf hydraulic properties (Harding et al., 2020). *SUT4*-KD mutants also exhibited altered drought transcriptomes, with the largest magnitude of differential expression occurring in the root tips (Xue et al., 2016). Subtle changes to shoot biomass allocation patterns and water content have also been reported in the *SUT4*-KD poplar (Payyavula et al., 2011; Frost et al., 2012). However, these phenotypic changes occurred independently from changes in the rate of carbon fixation because photosynthetic rates were not affected in the *SUT4*-KD poplar (Frost et al., 2012). Furthermore, in rice (*Oryza sativa*), gene silencing of tonoplast localized *OsSUT2* led to mutants with reduced tiller numbers, height, and grain and root mass compared to the wild-type (Eom et al., 2011, 2012). Increased sucrose content in the mutant source leaves was also reported, suggesting that *OsSUT2* is involved in transporting sucrose across the tonoplast from the vacuole into the cytosol (Eom et al., 2011, 2012). These findings were echoed in maize (*Zea mays*) and potato (*Solanum tuberosum*), where tonoplast *SUT* loss of function

mutants exhibited vacuolar sequestration of sucrose in the source leaves and reductions to growth and biomass allocation patterns (Chincinska et al., 2008; Leach et al., 2017).

These findings are largely in contrast to species utilizing apoplastic loading, where compromised plasma-membrane SUT function impairs plant growth severely (Gottwald et al., 2000; Hackel et al., 2006; Slewinski et al., 2009).

SUTs are well recognized for their role in mediating subcellular sucrose trafficking in source organs (e.g., mature leaves) and numerous studies have established a critical role for their involvement in abiotic stress response (Ayre, 2011; Secchi & Zwieniecki, 2016; Liesche, 2017; Xu et al., 2018; Harding et al., 2022). Carbohydrate dynamics from reserve organs is likely necessary for the seasonal survival of perennial trees or during periods where sink-source relationships are unbalanced. For example, perturbation to intracellular sucrose dynamics has been shown to alter bud and vegetative tissue growth, particularly following defoliation or sink-source manipulation (Park et al., 2009; Falk et al., 2020). Furthermore, temperate woody trees experience seasonal fluctuations of nonstructural carbohydrate reserves following periods of dormancy (Kozlowski, 1992; Hartmann & Trumbore, 2016; Dobbelstein et al., 2019). These metabolic changes have been linked to the contrasting seasonal expression patterns of genes involved in carbohydrate biosynthesis, transport, and catabolism (Ko et al., 2011). However, given the various routes available for sucrose trafficking and catabolism, the role of SUT4-mediated intracellular sucrose movement for modulating these changes remains unclear.

The first half of this dissertation utilized a sink-source manipulation strategy (i.e., coppicing) and natural field experiments to characterize how altered sucrose trafficking

affects processes requiring carbohydrate remobilization from sink tissues in the temperate tree species *Populus tremula* × *alba*. The study used CRISPR/Cas9-derived transgenic poplar mutant trees with altered intracellular pools of sucrose to determine how perturbed sucrose transport impacts tree growth and carbohydrate allocation. Chapter 2 investigated the contribution of intracellular sucrose trafficking on tree regrowth following coppicing. Chapter 3 examined the mutational response of winter-biased *SUT* genes on seasonal growth, biomass accrual, phenology, and cell wall composition in field-grown trees.

## PART 2

### *Challenges facing the STEM enterprise*

Important global and societal problems (e.g., climate change, developing sustainable agricultural practices, health disparities) have necessitated the development of a robust workforce in science, technology, engineering, and mathematics (STEM) disciplines. To meet the demands of the economy, the President’s Council of Advisors on Science and Technology suggested that the United States needs to produce one million more college graduates in STEM fields (Olson & Riordan, 2012). Yet, less than 40% of undergraduates who intend to obtain a degree in a STEM field actually do so (Hill et al., 2010; Chen, 2013; Sowell et al., 2015). These trends persist in graduate education where nearly half of doctoral students in STEM graduate programs leave before completing their intended degree. Furthermore, many STEM fields have low levels of diversity across multiple socio-demographic groups (e.g., gender, race/ethnicity, socioeconomic status) (National Center for Science and Engineering Statistics (NCSES), 2023), which has the potential to magnify societal and economic inequalities. These disparities persist and are further widened at each level of higher education (Matias et al., 2022; National

Center for Science and Engineering Statistics (NCSES), 2023). Although the reasons behind these inequities are complex, such statistics suggest that students are not integrating into STEM fields. Despite the pressing need for a strong STEM workforce, future potential STEM professionals are currently being drawn from a limited talent pool because over half of the potential capable and interested individuals chose to opt out of STEM disciplines (Tabak & Collins, 2011; Valantine & Collins, 2015). The lack of diversity in STEM has suppressed problem solving and innovation (McGee, 2020), resulting in a less productive and creative workforce. In response to these substantial concerns, national calls have advocated for a renewed focus on mentoring relationships as a strategy for ameliorating these problems and to broaden STEM participation (National Academies of Sciences, Engineering, and Medicine., 2018).

#### *Mentoring in graduate education*

Mentorship has most recently been defined as a professional, working alliance in which a more experienced individual (the mentor) acts as a guide, role model, and sponsor to support the personal and professional growth, development, and success of a less experienced individual (the mentee) (NASEM, 2019). Mentorship relies on career (e.g., career guidance, sponsorship, advancement) and psychosocial support (e.g., counseling, encouragement, role modeling, acceptance) and the provision of such support is thought to lead to many desirable outcomes (Eby et al., 2013; Eby & Robertson, 2020). Mentoring is thought to be a key component of academic training in STEM fields (Lunsford, 2012). Indeed, quality mentorship during graduate education is positively related to graduate students' persistence in academic research (McGee & Keller, 2007; Williams et al., 2016), scholarly productivity (Cronan-Hillix et al., 1986; Lunsford, 2012;

Paglis et al., 2006; Steiner et al., 2002, 2004; Tenenbaum et al., 2001), research self-efficacy (Paglis et al., 2006; Tenenbaum et al., 2001), rate of degree completion (Lunsford, 2012), and program satisfaction (Lunsford, 2012; McAllister et al., 2009). As a result, mentorship has been touted as a national priority (Crisp et al., 2017) and is thought to serve an essential role in training STEM professionals (National Academies of Sciences, Engineering, and Medicine., 2019).

Mentorship is believed to lead to a wide range of attitudinal, behavioral, career, health, and motivational outcomes (Allen et al., 2004; Eby et al., 2008; Kammeyer-Mueller & Judge, 2008; Eby et al., 2013). Indeed, individuals with a mentor and who perceive receiving greater career support, psychosocial support, and relationship quality experience greater personal and professional outcomes than those without a mentor (Eby et al., 2008; Eby et al., 2013). Yet, the effect sizes are small to moderate in magnitude ( $\rho$  ranging from 0.03 to 0.41) (Eby et al., 2013). Furthermore, there is substantial heterogeneity in the effect sizes from these meta-analyses, which suggests that the outcomes associated with mentorship are quite varied and may be overemphasized (Eby et al., 2008). These findings also suggest that moderating variables may influence why the effects of mentorship can lead to many beneficial outcomes in some cases but not others.

*Why does mentoring not always have a positive effect?*

Mentoring is commonly assumed to be critical for success. However, mentoring relationships may not always have a positive influence, and some may even be negative or destructive in nature. Mentoring, like any other prolonged interpersonal relationship, can have negative elements (Duck, 1994; Scandura, 1998). Scholars collectively refer to

the dysfunctional elements of mentoring relationships or less than favorable interactions with mentors as “negative mentoring experiences” (Eby et al., 2000, 2004; Limeri et al., 2019; Scandura, 1998; Tuma et al., 2021). However, the occurrence of a negative experience does not necessarily indicate that the entire mentoring relationship is negative or harmful. Instead negative mentoring experiences can include problematic aspects of an otherwise positive or healthy relationship (Scandura, 1998; Simon & Eby, 2003). In fact, an extensive body of research on intense interpersonal relationships has shown that dysfunctional, unpleasant or problematic events are likely to occur in any prolonged relationship (Duck, 1994; Kram, 1983). Such variation in the mentorship quality is one possible explanation for the modest effect sizes reported for mentoring outcomes (Eby et al., 2008; Eby et al., 2013). Yet, little research has investigated the influence of negative mentoring experiences in student-faculty mentoring relationships.

The majority of research on academic-mentoring relationships suggests that mentoring is critical for success and development, particularly for individuals from marginalized and minoritized backgrounds in STEM fields (NASEM, 2019). However, prior research has not acknowledged the possibility that not all mentoring relationships may be beneficial or positive. This omission has the potential to paint an inaccurate picture of the dynamics that may occur in a mentoring relationship by minimizing the possibility that the relationship may be ineffective or destructive in nature. This is concerning because of their potential to cause harm, particularly for individuals from historically or currently marginalized groups. Thus, ineffective mentoring relationships have the potential to exacerbate disparities in STEM graduate education, rather than contributing to the integration of individuals who are most likely to opt out of STEM.

The second half of this dissertation aims to determine the extent to which graduate students in STEM fields experience negative mentoring with their graduate research mentors. Chapter 4 is a study aimed at delineating and operationalizing the construct of negative mentoring experiences in STEM graduate education. Chapter 5 seeks to develop a psychometrically sound scale to measure negative mentoring experiences in graduate education and relate to graduate student mentee outcomes. Finally, Chapter 6 tests the influence of a variety of antecedent variables theorized to predict graduate student mentee perceptions of high-quality mentorship.

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## CHAPTER 2

# FROM SUGARS TO SHOOTS: THE INFLUENCE OF SUCROSE TRANSPORTER PERTURBATION ON CARBON PARTITIONING IN COPPICED POPLAR <sup>1</sup>

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## ABSTRACT

Perennial woody trees grown for short-rotation bioenergy production are often maintained by coppicing. The mobilization of non-structural carbohydrate reserves is thought to contribute to regrowth, with multiple molecular mechanisms responsible for remobilizing stored carbohydrates. Tonoplast sucrose transport proteins (SUT4) are known for their role in mediating vacuolar sucrose efflux and thereby the export of sucrose from source leaves in trees. However, sucrose transporter involvement in carbohydrate remobilization from sink tissues remains less explored. Here, we used *PtaSUT4*-knockout mutants of *Populus tremula* × *alba* (INRA 717-1B4) and glasshouse coppicing experiments in contrasting seasons to examine the role of SUT4 in carbohydrate reserve allocation. We show that epicormic bud emergence was delayed and subsequent growth reduced in the mutants when coppicing took place during the winter but not in the summer. Sink (bark, wood, and root) carbohydrate reserve depletion during post-coppice regrowth was not impaired in the *sut4* mutants under winter or summer glasshouse conditions, but root sucrose levels were less depleted in the mutants. Both xylem and root hexose levels increased during the post-coppicing growth in the winter when osmoprotection is critical, but the increases were attenuated in the mutants. Similarly, bark accrual of abundant defense metabolites, including salicinoids, chlorogenic acids, and flavonoid products were sustained post coppicing, but were lower in mutants than controls. Together, our results point to seasonal-sensitive competing shoot processes for carbohydrate utilization that resulted in the delayed bud release and growth following winter coppicing in the *sut4* mutants. In summary, this work highlights a role for SUT4 in reserve mobilization under carbon-limiting growth conditions.

## INTRODUCTION

Properly managed, fast-growing, short rotation trees can be utilized for the production of carbon-neutral renewable energy. Energy produced from tree crops is therefore expected to play a critical role in reducing fossil fuel use and mitigating greenhouse gas emissions responsible for global warming (Dhillon & Von Wuehlisch, 2013; Li et al., 2008; Nieminen et al., 2012). *Populus* species (e.g., poplar, aspen, cottonwood, and their respective hybrids) have been promoted as a sustainable feedstock for bioenergy production due to their fast growth, high biomass production, and ability to grow in marginal environments (Bryant et al., 2020; Chudy, 2019; Kauter et al., 2003). Coppicing is a common silvicultural practice for short rotation woody biomass production where trees are harvested near ground level, and new shoots regenerate from the stool for additional harvesting without replanting (Tschaplinski & Blake, 1989). Coppicing of woody plants destined for bioenergy has potential to increase the biomass yield compared to trees grown from seedlings or cuttings (Ceulemans et al., 1996; Sennerby-Forsse & Zsuffa, 1995).

The success of coppicing for short rotation biomass production is dependent in part on non-structural carbohydrate reserves, such as sugars and starch, which influence the growth of new sprouts (Karp & Shield, 2008; Kauter et al., 2003). Much of what is known about mobilization of carbohydrate reserves in trees comes from the study of new shoot growth in the spring before source organ photosynthesis becomes active, or after abiotic/biotic stress events that lead to defoliation (Falk et al., 2020; Gleason & Ares, 2004). Yet, the molecular mechanisms by which non-structural carbohydrates contribute to tree regrowth following coppicing remain underexplored.

Starch reserves are thought to be critical for remobilization when demand for photoassimilate exceeds assimilation and are regulated diurnally in many plant species (Hartmann & Trumbore, 2016; Klein & Hoch, 2015; Noronha et al., 2018). However, recent evidence suggests that starch reserves are not vital to growth of aspen under non-stressed conditions (Wang et al., 2022). Significant diurnal fluctuations in leaf sucrose reserves relative to starch have been reported for *Populus* (Wang et al., 2022; Zhang et al., 2014). It has also been shown that trees actively store starch and other soluble sugars even under extreme carbon limitation and at the expense of growth (Huang et al., 2021; Piper & Fajardo, 2016; Sala et al., 2012; Wang et al., 2022; Wiley et al., 2019). In addition to stored soluble carbohydrate pools, trees may rely on alternative substrates such as lipids (Fischer et al., 2015; Huang et al., 2021) and hemicelluloses (Schadel et al., 2009) to sustain respiration and growth under such conditions. However, not all carbohydrate-rich compounds are utilized or remobilized for growth. For instance, salicinoid phenolic glycosides, which are abundant defense compounds in *Populus* species, were found not to be metabolized during severe carbon deprivation (Hillabrand et al., 2023). Given that the majority of plant biochemical compounds are ultimately derived from sucrose, its trafficking between the vacuole and the cytosol in relation to external cues potentially conditions the dynamic balance between growth and defense.

Transmembrane sucrose transport proteins (i.e., SUTs) facilitate energized movement of sucrose between cellular compartments (Ayre, 2011; Lalonde et al., 1999). Both Type I and Type II SUTs mediate sucrose transport across plasma membrane, whereas Type III tonoplast SUT4 facilitates the subcellular export of sucrose from the vacuole to the cytosol (Eom et al., 2012; Peng et al., 2018; Reinders et al., 2012). *SUT*

expression varies among family members and across species (Payyavula et al., 2011; Reuscher et al., 2014; Schneider et al., 2012; Xu et al., 2018). For instance, plasma-membrane isoforms dominate *SUT* transcript abundance in source leaves of apoplastic loading herbaceous species (i.e., *Arabidopsis*), with the tonoplast-localized *SUT4* expressed at low levels (Lloyd & Zakhleniuk, 2004; Schulz et al., 2011). The reverse is true in poplar where *SUT4* is constitutively expressed in all source and sink tissues (Payyavula et al., 2011; Weise et al., 2000; Xu et al., 2018).

Environmental changes and stressors are also known to affect *SUT* expression and alter intracellular sucrose trafficking (Ayre, 2011; Liesche, 2017; Xu et al., 2018). For example, *SUTs* have been implicated in detecting and refilling embolized xylem vessels of walnut trees during winter (Decourteix et al., 2006; Secchi & Zwieniecki, 2011). Moreover, *PtaSUT4*-downregulated poplars exhibit altered turgor control and transpiration rates in response to sink-source manipulations (Harding et al., 2020). It is also plausible that intracellular sucrose trafficking may have an important role in carbohydrate access and growth under carbon-limiting conditions. Sucrose concentrations have been reported to fluctuate during vegetative bud outgrowth in sink-source manipulation studies (Fichtner et al., 2017; Mason et al., 2014). In addition, increased abundance of sucrose supply, either through exogenous application or by reducing competition between sinks, increased axillary bud outgrowth of pea (*Pisum sativum*), rose (*Rosa hybrida*), and *Arabidopsis thaliana* (Barbier et al., 2015; Fichtner et al., 2017). While carbon-rich compounds, such as sucrose, can promote metabolism, development, signaling, and regrowth under carbohydrate-limited conditions, the contribution of *SUTs*

to the provisioning of growth and potentially competing processes has received modest investigation.

Here, we investigated the contribution of intracellular sucrose trafficking to tree regrowth following coppicing in hybrid poplar *Populus tremula* × *P. alba* (INRA 717-1B4, hereon referred to as 717). We made use of *SUT4*-knockout (KO or *sut4*) poplar with increased sucrose accumulations (Harding et al., 2022) to test the extent to which sucrose trafficking influences coppicing responses. We compared the biomass, growth rate, metabolite abundances, photosynthetic parameters, and osmotic adjustments at different developmental stages of bud regrowth in coppiced wild-type and *sut4* poplar during summer and winter glasshouse conditions.

## MATERIALS & METHODS

**Plant production and maintenance.** *PtaSUT4*-KO mutants and *Cas9* empty vector control used in this study were generated by CRISPR/Cas9 mutagenesis as reported previously (Harding et al., 2022; Zhou et al. 2015) and grown in a glasshouse located in the Whitehall Forest at the University of Georgia. Supplemental LED lighting was used to maintain a 16-hour photoperiod, with photosynthetic photon flux density (PPFD) of at least 600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  at mid canopy. Plants were propagated by single-node cuttings as described (Frost et al., 2012) year-round for the experiments. Once established, rooted propagules were transferred to 1-gallon pots containing commercial soil mix (Fafard 3B) supplemented with Osmocote (15-9-12, NPK 6-month slow release) and maintained with daily watering until coppicing.

**Coppicing regrowth experiments.** For the winter coppicing experiment (January), twelve control (six wild-type [WT] and six *Cas9*) and twelve *sut4* mutants

(four plants each of three independent events: KO-18, KO-25, and KO-51), were equally and randomly spaced on the floor of the glasshouse. Ten days prior to coppicing, the number of fully expanded leaves was reduced to forty for each plant to minimize differences in water uptake and photosynthetic capacity. Plants ~1.5 m in height were then coppiced (Julian Day 18) to ~25 cm stumps and any remaining leaves were removed. Watering was reduced after coppicing to avoid root anoxia. Outdoor temperatures during the duration of the winter coppicing experiment ranged from -5°C to 16°C, with an average of 6.5°C. Day length ranged from 10.2 hours to 10.7 hours. Supplemental gas heating prevented indoor glasshouse temperatures from dropping below 10°C.

For the summer coppicing experiment (August), plants were managed as described above and were approximately the same height at coppicing as those in the winter experiment. Ten control (six WT and four *Cas9*) and twelve *sut4* mutants (four plants each of KO-18, KO-25, and KO-51 as above), were coppiced (Julian Day 228). Outdoor temperatures during the duration of the summer coppicing experiment ranged from 20°C to 33°C, with an average of 26°C. Day length ranged from 13.4 hours to 12.9 hours. Evaporative cooling prevented glasshouse temperatures from exceeding a high of 35°C during the day.

**Pre- and post-coppice sampling.** Immediately before coppicing, two adjacent fully-expanded source leaves, *i.e.*, Leaf Plastochron Index (LPI) 15-16, were collected; one was used for relative water content measurement and the other flash frozen in liquid N for analytical analyses after separating the lamina from the petiole and midvein. Immediately after coppicing ( $t=0$ ), xylem sap was collected from the cut surfaces of the

stools. Bark and xylem tissues were collected from the top of the stump immediately after sap collection (t=0; Supplemental Figure 1) and again at the date epicormic bud elongation was measured (t=1; Supplemental Figure 1). The third and final sampling (t=2) took place during shoot extension. At t=2, root samples (terminal 6 cm of elongating roots excluding root tips) were rapidly washed in deionized water, dried, and snap frozen in liquid N. The largest (dominant) epicormic bud that emerged after coppicing of each tree was photographed and its length determined at t=1 using the ImageJ software package (<https://imagej.net/ij/index.html>). The coppicing experiments were carried out twice to ensure sure reproducibility. Results from the most comprehensive of the two experiments are reported here. Due to seasonal growth differences, sampling at times t=1 and t=2 was carried out 10 and 16 days after summer coppicing and 11 and 20 days after winter coppicing (Supplemental Figure S2). All tissue sampling occurred under sunny conditions between 11AM – 2PM.

**Biomass.** Independently of the coppicing experiments described above, cohorts of mature (~1.5 m) control and *sut4* mutant plants ( $n = 8 - 14$  plants) were harvested in mid-winter (January) and mid-summer (July-August) for dry biomass analysis. Plant height and stem diameter were measured at harvest, and leaves (including petiole), phloem (bark), and xylem (de-barked stem) were collected to determine biomass allocation patterns. Root tissues were washed in deionized water and dried. After subjecting the trees to the same conditions outlined above, a third cohort of ~1.0 m plants ( $n = 6 - 12$ ) were coppiced in winter (December) and summer (June). Biomass produced from 25 cm stumps ~1 month after coppicing was collected. Tissues were dried in a forced air oven for 48 hours at 60°C. Total dry biomass was calculated as the sum of all tissues per plant.

**Xylem sap.** Immediately after coppicing ( $t=0$ ), xylem sap was collected from the stumps following the published approach (Schenk et al., 2017). Bark was removed from the top 4 cm of the stump to expose the xylem cylinder and to avoid mixing of phloem and xylem sap during collection. The razor-cut surface of the wood was tamped with a damp kimwipe to remove cell debris and cytoplasmic contamination. The first 400  $\mu$ l of xylem sap was removed with a kimwipe and discarded. Over the next 45 min,  $\sim$ 100-200  $\mu$ l of xylem sap was collected with a pipette from each stump and snap frozen in liquid nitrogen. Frozen sap was stored at  $-80^{\circ}\text{C}$ , thawed on ice just before analysis, mixed, and aliquots derivatized after drying in glass inserts for metabolite analysis as described below.

**Metabolic analysis.** Tissues were lyophilized for 48 hours (FreezeZone 2.5, Labconco), ground through a 40-mesh sieve using a Wiley Mill (Thomas Scientific), and further ball-milled at 1500 rpm in a S1600 Mini G Bead-beater (Spex SamplePrep; Metuchen, New Jersey) to a fine powder for metabolite profiling by Gas Chromatography-Mass Spectrometry (GC-MS) and Ultra-Performance Liquid Chromatography coupled with Quadrupole Time-of-Flight Mass Spectrometry (UPLC-QTOF).

For GC-MS, tissue powders ( $10.0 \pm 0.5$  mg) were sonicated in a pre-chilled water bath ( $4^{\circ}\text{C}$ ) for 15 minutes in 500  $\mu$ l methanol:chloroform (1:1, v/v), with adonitol (Sigma-Aldrich) added as an internal standard. Following the addition of 200  $\mu$ l of water, extracts were vortexed and centrifuged at 14,500 rpm for 5 min. The upper aqueous-methanol phase (10  $\mu$ l) was evaporated to dryness in a centrifugal vacuum concentrator (Centrivap, Labconco) and derivatized. Carbonyl moieties were methoximated in 15  $\mu$ l of

methoxyamine hydrochloride/pyridene (20mg/ml) for 30 minutes at 30°C and silyated with 30 µl of *N*-methyl-*N*-(trimethylsilyl) trifluoroacetamide (MSTFA; Sigma Aldrich) for 90 minutes at 60°C as described previously (Jeong et al., 2004). Samples were analyzed on an Agilent 7890A GC coupled to an Agilent 5975C single quadrupole MS detector (Agilent Technologies, Wilmington, DE). Following sample randomization, 1 µl of the derivatized extract was injected in splitless or split (25:1) modes onto a DB-5MS column (30 m x 0.25 mm, with a 0.25-µm film DuraGuard pre-column). Helium flow rate was 1 ml/min. Following a 1-min. hold at 80°C, oven temperature increased at a rate of 20°C/min to 200°C, then at 10°C/min to 320°C with a final 6.5 min hold at 320°C. Mass spectra (*m/z* 50-500) were collected using Chemstation (Agilent Technologies). Peaks were deconvoluted using AnalyzerPro (SpectralWorks) and peak identities were assigned based on the NIST08, the Fiehnlab (Agilent) plant metabolite library, and an in-house library of authentic standards (Bowsher et al., 2015; Frost et al., 2012; Jeong et al., 2004; Xue et al., 2013). A standard mix containing succinic acid, sucrose, glutamic acid, fructose, glucose, and ascorbic acid was loaded at the beginning and end of each sample set to monitor derivatization and instrument performance.

For UPLC-QTOF, tissue powders ( $5.0 \pm 0.5$  mg) were extracted as above with the exception that  $^{13}\text{C}_6$ -cinnamic acid and  $\text{D}_5$ -benzoic acid were included as internal standards. Supernatants were then filtered through a 0.20 µm PTFE filter (P.N. 5191-5912; Agilent Technologies) and analyzed on an Agilent 1290 Infinity II UPLC coupled to an Agilent 6546 LC/Q-TOF tandem MS. Extracts were resolved on a reverse phase C18 column (Agilent Zorbax Eclipse Plus C18, 2.1 x 50mm, 1.8 micron) with mobile solvent (A) comprised of water and 0.1% formic acid and mobile solvent (B) comprised

of acetonitrile with 0.1% formic acid at a flow rate of 0.5 mL/min. The elution gradient was 3% B from 0 – 0.5 min, linear gradient to 15% B over 3.50 min, isocratic at 30% B over 4.50 min, linear gradient to 50% B over 5.50 min, and then to 100% B over 7 min, followed by 3-min post run. Column temperature was 45 °C. Masses were acquired in negative mode with the following parameters: gas temperature, 250 °C; nebulizer gas, 40 psi; nozzle voltage, 500 V; and capillary voltage, 400 V. Data were processed using the MassHunter software suite Version 11.0 (Agilent). Peak identities were confirmed using an in-house library of authentic standards, and by accurate-mass-predicted formula match scores. The highest database match score obtained was used to support the putative identity of the QTOF metabolites. In general, match scores were over 85% for the majority of reported metabolites (Supplemental Table 1).

GC-MS and LC-QTOF peak intensities were normalized by their respective internal standards and sample dry weight, with the exception of sucrose and hexoses (e.g., fructose, glucose) which are reported as µg/mg dry weight based on their respective calibration curves. The final peak intensity is referred to as normalized peak area.

**Starch.** Starch content was determined by enzymatic digestion with  $\alpha$ -amylase and amyloglucosidase (Chow & Landhausser, 2004). In brief, 10 mg of lyophilized, Wiley- and ball-milled tissue (e.g., leaf, bark, root, xylem) powder was pre-extracted three times with vortexing and sonication with 1 ml of methanol. The tissue pellet was resuspended in 0.5 ml of buffer (0.1 M sodium acetate, pH 5.0, with 5 mM CaCl<sub>2</sub>) containing 500 U of  $\alpha$ -amylase (Sigma A4551). Following a 2-hour incubation at 65°C, samples were cooled and 10 µl of sodium acetate buffer (pH 5.0) containing 5 U amyloglucosidase (Sigma A1602) was added to each digest. The digest was then

incubated at 50°C for 48 hours with shaking. Digests were then diluted with 500 µl of H<sub>2</sub>O, vortexed and centrifuged. Twenty microliters of the diluted supernatant were dried and derivatized for GC-MS as described above. Total starch content (expressed as µg starch per mg of dry tissue) was calculated based on a glucose standard curve.

Chromatograms contained only glucose and adonitol loading standard peaks.

**Condensed tannins.** Freeze dried tissue powder (10 mg) was extracted in 600 µl of methanol for 15 minutes in a sonicator bath to extract interfering chlorophyll. The depigmented pellet was dried in a Centrivap, and pellet-bound condensed tannin (CT) content estimated using the butanol-HCl method (Harding et al., 2005; Porter et al., 1985). Pellets were incubated and hydrolyzed at 95°C for 20 minutes in 1 ml of a butanol-5% hydrochloric acid solution containing ferric ammonium sulfate. CT absorbance was read at  $A_{550}$  (SpectraMax M2; Molecular Devices) and quantified against aspen leaf CT standards.

**Chlorophyll content.** Ten mg of freeze-dried powder was extracted twice in 750 µl of cold 90% acetone – 10% water, with sonication and centrifugation. Absorbances at  $A_{645}$  and  $A_{663}$  were used to determine chlorophyll *a*, chlorophyll *b*, and total chlorophyll content (µg g<sup>-1</sup> DW) as described by Lichtenthaler (1987) .

**Water content.** Leaf, bark, and wood total water content (TWC) and leaf relative water content (RWC) were determined throughout the course of the coppicing experiments. For RWC, a mature, healthy leaf (i.e., LPI-15) was removed with petiole attached using a razor blade, weighed, and petiole end inserted into a 50 ml Falcon tube filled with dH<sub>2</sub>O. Tubes with leaves were transported in closed styrofoam boxes to laboratory facilities and transferred into a dark humid chamber for hydration. After 4

hours, leaf surfaces were blotted dry, and hydrated weight was recorded. For TWC, 2.5cm of stem tissue was excised with a razor blade, debarked and fresh weights of bark and wood tissues obtained. Bark, wood and leaf dry weights were obtained following 36 hours in a 55°C forced air oven. Leaf RWC was calculated as (fresh weight – dry weight) / (hydrated weight – dry weight), and TWC of all tissues was calculated as (fresh weight – dry weight) / fresh weight.

**RNA-sequencing analysis.** Wild-type *Populus tremula* × *alba* (717-1B4 clone) were grown from single-node cuttings before being transplanted to 10-gallon pots and moved outdoors to the Whitehall Forest at the University of Georgia. For seasonal transcriptional profiling, stem xylem and phloem with bark were collected 60 cm above soil level from four plants (~1.5 m in height) in the Winter (February) and Summer (July). The average day time temperature in the Winter was 12°C and 28°C in the Summer, and the approximate day lengths were 10.5 hours and 14 hours, respectively. All sampling occurred between 11 am – 1 pm and under sunny conditions. Samples were snap frozen and ground under liquid N<sub>2</sub> to a fine powder. Total RNA was extracted using the PureLink Plant RNA Reagent (Invitrogen) and Direct-zol RNA MiniPrep kit (Zymo Research). Libraries were prepared using the Mercurius BRB-seq library preparation kit (Alithea Genomics) and Illumina NextSeq 200 sequencing was performed at the Georgia Genomics and Bioinformatics Core. We obtained 6.8-12.6 million SE50 reads per summer sample and 9.7-24.6 M reads per winter sample. The nf-core/rnaseq software suite was used for data processing and read mapping to the haplotype-resolved *Populus tremula* × *alba* genome (Phytozome v13). Transcript abundance was estimated and expressed as TPM (transcripts per million).

**Statistics.** Repeated measures analysis of variance (ANOVA) was used to determine significant differences at each stage of coppicing re-growth over time, between genotypes, and their interactions using R version 4.1.0 (R Core Team, 2016) in Rstudio (version 2022.12.353) . Linear regression was used to test for the relationships between sucrose (or) starch depletion and bud elongation of wild type or *sut4* mutants between t=0 and t=1 of the winter and summer coppicing experiments.

## RESULTS

### *Seasonal variation of PtaSUT4-knockout mutant growth and PtaSUT4 expression*

We previously generated *PtaSUT4*-KO plants by CRISPR/Cas9 mutagenesis (Harding et al. 2022), which accumulated higher levels of sucrose in all organs examined (Supplemental Figure 2). During routine plant propagation (see Methods), we observed slower bud release following cutback and slower growth of rooted cuttings of *sut4* mutants than the controls under winter glasshouse conditions (Figure 1A). To probe this further, we compared growth of mutant and control plants in summer and winter months under glasshouse conditions. The *sut4* mutants displayed subtle growth differences compared to control plants in the summer, similar to those reported for *PtaSUT4*-RNAi knockdown lines (Frost et al., 2012; Payyavula et al., 2011). However, multiple mutant growth parameters were significantly changed in winter. These included reductions in height, increased leaf number and mass, and a reduction in wood mass (Table 1). Such findings suggest a potential sensitivity of *PtaSUT4* perturbation to seasonal differences.

Carbohydrate metabolism genes including *SUT4* have been shown to exhibit seasonal variation in their expression in perennial trees (Dobbelstein et al., 2019; Ko et al., 2011). To ascertain seasonal *SUT4* transcriptional responses in 717, we performed

RNA-seq of xylem (debarked stem) and bark samples collected during the summer and winter from outdoor grown plants. Transcript levels of *PtaSUT4* were substantially higher during the winter in both xylem and bark (Figure 1B), consistent with previous results from field-grown *P. trichocarpa* stem (Ko et al., 2011). These findings, along with effects of *PtaSUT4* knockout or knockdown on starch utilization and osmotic responses to water stress (Harding et al., 2022), motivated a series of glasshouse coppicing experiments to investigate SUT4 relevance to carbohydrate access and growth following coppicing.

#### *Seasonal coppicing response of sut4 mutants*

The rate at which new epicormic buds appeared on stumps after coppicing was similar between genotypes under the summer glasshouse conditions (Figure 2A). The total biomass of new shoots at t=2 in the *sut4* plants in the summer was also similar to the controls despite slower bud elongation in *sut4* mutants (Figure 2). By contrast, epicormic bud release was delayed by several days in *sut4* mutants compared to controls in the winter but attained the same number of emerged buds by t=2 (Figure 2A-B). Bud elongation was slower and total final biomass was reduced in the *sut4* mutants compared to control lines following winter coppicing (Figure 2C-D). However, during the summer bud elongation was faster in the *sut4* mutants than the controls; yet total final biomass did not differ between genotypes (Figure 2C-D). A replicate experiment was conducted to examine the biomass partitioning of fully-grown new shoots 32 and 40 days after winter and summer coppicing. Total leaf, stem, and root dry mass trended lower, but not significantly, in *sut4* than in control plants in the winter (Table 2). However, *sut4* mutants had significantly higher shoot (leaf and stem) biomass under summer conditions (Table

2). As a result, the leaf:root and stem:root ratios were both higher in summer-coppiced mutants than control (Table 2).

#### *Sink carbohydrate reserves*

Non-structural carbohydrate reserves support post-coppice sprout initiation and early growth (Smith & Stitt, 2007; Tixier et al., 2017). To further assess SUT4's role in this process, we quantified levels of sucrose, hexoses (i.e., glucose, fructose), and starch before and after coppicing in the control and *sut4* mutant lines. Prior to summer or winter coppicing, sucrose contents were higher in all sampled organs of the *sut4* mutants when compared to the controls (Figure 3 and Supplemental Figures S2 and S3). Following coppicing, bark and xylem sucrose decreased in abundance in both WT and *sut4* mutants in both the summer and winter (Figure 3). While sucrose remained substantially more abundant in *sut4* than control lines by t=2 of the summer experiment, sucrose was depleted to approximately the same low abundance in both genotypes under winter conditions (Figure 3 A, D, J, M). In contrast to shoot organs, sucrose was not depleted in roots of *sut4* mutant or control lines after coppicing and remained higher in *sut4* than control lines at t=2 especially in the summer (Figure 3 G, P).

Bark hexose (sum of fructose and glucose) levels differed little between genotypes and decreased by t=2 in both the summer and the winter (Figure 3 B, K). In contrast, xylem hexose levels increased in both lines in the winter, but eventually decreased in the summer by t=2 (Figure 3, E, N). In both seasons, xylem hexose levels were higher in control than *sut4* mutants. Root hexose levels increased after coppicing and were higher in the controls than the *sut4* mutants in winter but not in the summer (Figure 3 H, Q).

Starch levels in the bark and xylem were higher in control than *sut4* plants in both the summer and winter, and remained so as starch became depleted through t=1 (Figure 3 C, F, L, O). Bark and xylem starch was depleted to similarly low levels in all genotypes by t=2, suggesting that starch abundance there had reached a minimum. Root starch content was detected at a similar level in both lines after coppicing but were reduced to a far greater level in the summer than the winter (Figure 3 I, R). Together, the data suggest a depletion of non-structural carbohydrates to less than 15% of pre-coppice levels for the major reserves, starch and sucrose, in shoot organs. In contrast, root reserves with the exception of winter sucrose were much less reduced.

#### *Sucrose and starch utilization for bud growth*

The sprout emergence and growth differential between *sut4* mutant and wild-type trees following winter coppicing led to a closer examination of the epicormic bud expansion and carbohydrate depletion data (Figures 3 and 4). We tested whether sucrose and/or starch depletion in the bark between t=0 and t=1 predicted the size of the emerged, elongating, and dominant epicormic bud length at t=1. Under winter conditions, dominant epicormic bud size correlated with sucrose depletion in the *sut4* mutant trees ( $r^2 = 0.39, p = 0.03$ ) but not the controls ( $r^2 = 0.16, p = 0.19$ ). However, bud size did not correlate with sucrose depletion in the summer in either genotype (*sut4*:  $r^2 = 0.17, p = 0.21$ , control:  $r^2 = 0.06, p = 0.49$ ). Bud expansion did not correlate with changes in starch content under winter (*sut4*:  $r^2 = 0.00, p = 0.99$ , control:  $r^2 = 0.04, p = 0.54$ ) or summer (*sut4*:  $r^2 = 0.02, p = 0.68$ , control:  $r^2 = 0.12, p = 0.439$ ) conditions. Taken together, our results suggest that the *sut4* mutant bud expansion in the winter correlated with depletion of sink sucrose but not of sink starch. While bud growth was slower in *sut4* than control

plants in the winter, it did not appear that depletion of bark sucrose (or starch) reserves was negatively impacted in *sut4* mutants.

#### *Xylem sap and root metabolism*

Xylem sap serves an essential function by transporting nitrogen and other nutrients from soil to the transpiring leaves (Grassi et al., 2002). Given that nitrogen assimilation depends on carbon skeletons in the assimilating organ, in this case roots, a comparison of xylem sap contents could reveal seasonal and genotypic differences in systemically available carbon from the roots. Xylem sap sucrose differed little between genotype and in the summer and winter (Supplemental Figure 4). Hexose levels in the xylem sap did not differ between the genotypes in the summer but were reduced in the *sut4* plants compared to the controls (Supplemental Figure 4). Krebs cycle intermediates malate and citrate comprised most of the xylem sap metabolic load in both summer and winter, being most abundant in *sut4* xylem saps (Figure 5A-B and Supplemental Figure 5). Two of the next three most abundant sap metabolites were amino acids glutamine and glutamate. Both were significantly more abundant in *sut4* than control xylem sap in the summer, but less abundant in the *sut4* than control sap in the winter (Figure 5A-B and Supplemental Figure 5). These five metabolites were also among the most abundant in root tissues (Supplemental Figure 6). Malate was by far the most abundant, with *sut4* levels exceeding control root levels in a similar manner observed in the xylem saps (Supplemental Figure 6). In contrast to the genotype differences observed in the saps, root concentrations of other metabolites did not differ between *sut4* and control, with the exception of glutamine in the summer (Supplemental Figure 6).

#### *Bark and xylem metabolism*

Xylem sap amino acid and Krebs cycle intermediate abundance differentials between mutant and control lines roughly paralleled those observed in bark and xylem tissue at  $t=0$  (Figure 6A-B). Bark and xylem amino acid levels were higher in the *sut4* mutant than control plants during bud expansion ( $t=1$ ) and markedly higher in mutants at  $t=2$  of the summer experiment (Figure 6A-B). Phenylpropanoid pathway precursors (e.g., quinic acid, shikimic acid), hydroxycinnamates (e.g., *p*-coumaric acid), and phenylpropanoid products (e.g., catechin) were detected at comparatively low levels in the bark of the mutants throughout the course of both experiments. Finally, sugar alcohols (e.g., galactinol, myo-inositol) were generally more abundant in the bark of mature *sut4* plants ( $t=0$ ) but were detected at considerably lower levels than in controls by  $t=2$  in the summer while displaying increases in the winter experiments.

#### *Secondary metabolism*

Growth and the provisioning of large magnitude nonstructural metabolic sinks related to plant fitness and defense depend on carbohydrate transport and trafficking (Harding et al., 2005; Kleiner et al., 1999; Kosonen et al., 2012). The most well-known of such sinks in *Populus* (cottonwoods, aspens, and poplars) and closely related taxa, including *Salix* (willow) and *Betula* (birch), are comprised of shikimate and phenylpropanoid derived chlorogenic acids, hydroxycinnamate derivatives, flavonoids and their polymers (condensed tannins or CTs), and salicinoids, such as salicortin, salicin, and tremulacin (Harding et al., 2005; Tsai et al., 2006; Zhang et al., 2018). The abundant chlorogenic acids (i.e., caaffeoylquinic acid isomers) exhibited reduced levels in *sut4* relative to control stumps at all time points in both the summer and winter experiments (Figure 7A-B). The stress hormone, salicylic acid (SA), and its conjugate, salicylic acid glucoside

(SAG), were significantly lower in the bark of the *sut4* mutants during the summer (Figure 7C). In the winter, SA levels remained lower in the *sut4* mutants, but the levels of SAG were higher than in control lines through t=1 (Figure 7D).

By far, the most abundant of the nonstructural phenylpropanoid end products observed in the coppiced stools were the phenolic glycoside salicinoids, especially salicortin (Figure 7E-F). Bark salicortin abundance was substantially lower in the *sut4* mutants than control during the summer (Figure 7E) but did not differ between genotypes during the winter (Figure 7F). The closely related salicinoid, tremulacin showed a similar pattern, being significantly lower in mutant bark during summer (Figure 6E). Salicin differed little between genotype and season (Figure 7E-F).

The levels of flavonoid-derived CTs were lower in bark of the *sut4* lines across both seasons compared to the controls (Figure 7G-H). CT levels were higher in the leaves of the *sut4* mutants during the summer but were higher than the controls in the winter (Supplemental Figure 7A). CT levels in the roots did not differ between genotypes but were generally reduced in the winter than the summer (Supplemental Figure 7B). Consistent with bark CT trends, levels of the CT precursors catechin and epigallocatechin were also lower in mutant bark across both seasons (Figure 7I-L). Rutin abundance did not differ in the bark between genotypes in the summer but was greater in the bark of the *sut4* mutants than the controls during the winter (Figure 7K-L). Naringenin-7-O-glucoside was reduced in the mutant bark relative to the controls during the summer (Figure 7K-L). Levels of luteolin, a flavone, were reduced in the *sut4* lines during the winter but not in the summer (Figure 7K-L). Levels of the flavonols, quercetin, taxifolin, and Naringenin-5-O-glucoside did not differ between genotypes or seasons

(Supplemental Figure 8). Finally, levels of the hydroxycinnamic acid glycoside, 1-Caffeoyl-beta-D-glucose, and additional phenylpropanoid metabolites (e.g., 4-( $\beta$ -D-Glucosyloxy)benzoate and O-Feruloylgalactarate) displayed modest effects between the *sut4* and control lines during coppicing (Supplemental Figure 8).

#### *Tissue water relations*

In addition to its role in energy metabolism, sucrose also acts as an osmolyte and its subcellular compartmentalization influences osmotic adjustments to stress (Harding et al., 2022; Ozturk et al., 2021; Secchi & Zwieniecki, 2016). RWC did not differ in the mature leaves between the genotypes under either summer or winter conditions prior to coppicing at t=0 (Supplemental Figure 9). TWC in the bark and xylem was similar between genotypes at the start of the experiment but was higher in the *sut4* mutants than in the controls during bud expansion and shoot extension (Figure 8). A sharp decline in bark but not xylem TWC was observed in all plants at t=1 in the summer experiment (Figure 8A). Xylem TWC was higher in the *sut4* mutants, and trended higher in the *sut4* mutants during bud expansion (Figure 8 B, D).

#### *Chlorophyll content*

We also examined leaf and bark chlorophyll contents as proxies for photosynthetic capacity before and after coppicing. Leaf chlorophyll content was higher in summer than winter-grown plants (Supplemental Figure 10). While leaf chlorophyll content did not differ between *sut4* and control in the summer, it was substantially lower in *sut4* than control plants in the winter prior to coppicing (Supplemental Figure 10). Bark chlorophyll content, and thus expected stool photosynthetic capacity, was similar in

winter and summer plants and differed very little between lines in either coppicing experiment (Figure 9).

## DISCUSSION

Under normal growth conditions, trees store large amounts of nonstructural carbohydrates to sustain respiration, osmoregulation and other metabolic processes for when photosynthesis or sugar transport is limited. For example, Norway spruce (*Picea abies*) exhibited upregulation of genes encoding starch degradation enzymes (e.g.,  $\alpha$ - and  $\beta$ -amylases) and enzymes involved in with the catabolism of cell wall polysaccharides to maintain sugar solute levels under environmental stress (Huang et al., 2021). The utilization of such reserves vary seasonally, across species, and within species of poplar (Sevanto et al., 2014; Blumstein et al., 2020; Furze et al., 2019; Martínez-Vilalta et al., 2016). Under post-coppice conditions in the present study, shoot starch and sucrose were reduced to less than 15% of their initial levels, but not to complete exhaustion (Figures 3 and 4). These results imply that following coppicing, aspen trees prioritize carbohydrate reserves to fuel respiration or growth (Huang et al., 2021; Kozłowski, 1992; Sala et al., 2012; Wang et al., 2022), and that such reserves are not completely depleted even under extreme carbon limiting conditions. The utilization of *sut4* mutant poplar and a coppicing treatment for source removal allowed us to explore the idea that within limits, intracellular trafficking of vacuolar sucrose conditionally influences carbohydrate mobilization from sink reserves. The importance of this in relation to other carbohydrate reserves was illustrated by our observation that epicormic bud expansion after coppicing correlated with sucrose but not starch depletion. The utilization of sucrose and starch

reserves under conditions of carbon limitation may therefore differ with regard to subsequent partitioning or allocation (Dietze et al., 2014). Furthermore, the constitutive maintenance of such nonstructural carbohydrate reserves may also reflect their multifaceted roles in metabolism, osmoregulation, and signaling (Goetz et al., 2021; Weber et al., 2018; Wiley et al., 2019).

Bud release was delayed in addition to slower bud growth after winter coppicing in the *sut4* lines. Interestingly, shoot organ sucrose was depleted to similar levels in *sut4* and control plants during this period of epicormic bud appearance and growth, despite *sut4* mutants having higher levels of sucrose to begin with. Reduced *sut4* growth may therefore suggest that sucrose allocation for bud expansion was a lower priority in the coppiced stump than some other process, and that sucrose utilization was somehow limiting for *sut4* bud growth. Along those lines, we observed that xylem hexose levels were sustained throughout the post coppicing period in *sut4* and controls during the winter but not the summer experiment. The provisioning of hexose osmolytes in the xylem could therefore represent a high priority allocation of nonstructural carbohydrates for winter protection. This is consistent with the previously established roles of sugar osmolytes in protecting against reactive oxygen species scavenging, cold tolerance, and embolism refilling during winter (Charrier et al., 2018; Tarkowski & Van den Ende, 2015).

Our results also raise the question of whether the maintenance of large winter defense metabolite reserves (e.g. CTs, salicinoids, chlorogenic acids, and flavonols) were prioritized in the bark and contributed negatively to post coppice bud growth in the *sut4* plants. Similar to the winter provisioning of hexoses in the xylem, salicinoid accrual was

sustained equally in *sut4* and control bark. In sharp contrast to the winter scenario, salicinoid levels were much higher in control than *sut4* lines in the summer when post coppice bud growth was slightly less in control than in *sut4*. Based on these results, it appears that growth was more penalized in winter in the *sut4* mutants while defense compound abundance was more penalized in summer in the *sut4* mutants. Aspen maintain constitutive levels of salicinoids even under severe carbon limitation (Fabisch et al., 2019; Hillabrand et al., 2023), but our results suggest their abundance may be dependent on seasonal conditions. Furthermore, carbon allocations for defense compounds such as salicinoids in aspen are significant and exhibit complicated regulation in relation to timing and intensity of responses to defoliation (Stevens & Lindroth, 2005). A ramification of the present findings is that SUT4 can contribute to the modulation of important allocations for defense and growth in line with carbon availability and other sink organ demands.

A potentially key observation with respect to the importance of SUT4 in systemic carbon provisioning was that hexose levels in winter xylem sap were substantially lower in *sut4* than control stumps (Supplemental Figure 5). Amino acids were also relatively depleted in winter xylem sap of *sut4* mutants despite there being no difference between *sut4* and control lines with regard to root levels of sucrose or amino acids (Supplemental Figure 5). It appears that over the entire course of the experiment, from t=0 to t=2, root sucrose was substantially less depleted (i.e., more abundant at harvest) in *sut4* than control lines, although root starch and shoot sucrose were equally drawn down in all lines during the winter. In the case of winter coppicing, therefore, bud growth may have been more supplemented by root sucrose in control than in *sut4* lines given the competing

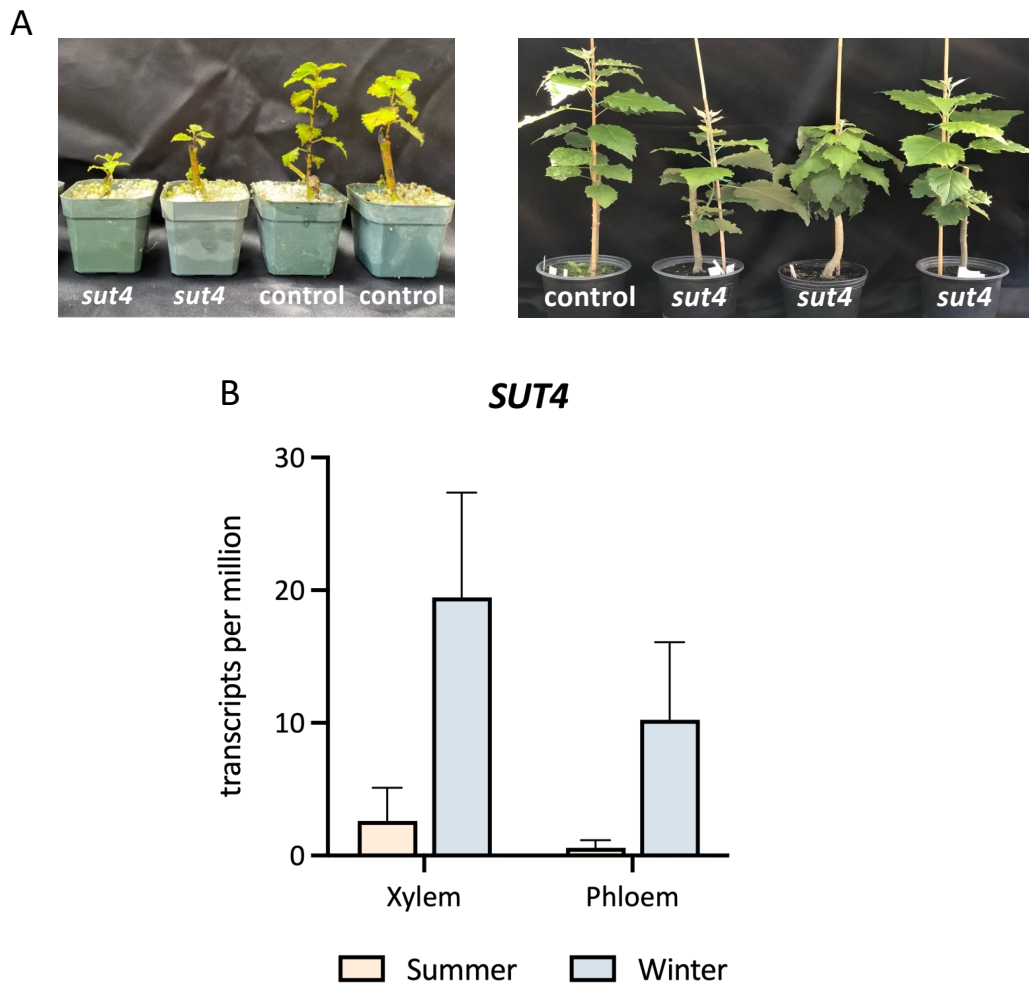
shoot processes such as provisioning of hexose in the xylem and accrual of abundant defense metabolites in the bark for winter protection.

It is also possible that SUT4 perturbation was more limiting for sucrose mobilization from the roots than other organs, and that such mobilization could have been influenced by a greater involvement of invertases in the *sut4* lines. Root hexose levels were equal in *sut4* and control lines at the time of coppicing but were detected at higher levels in controls in the winter at  $t=2$ . These results suggest that sucrose was more robustly converted to hexose in controls than in *sut4* following coppicing. Sucrose that is exported from the vacuole is subject to hydrolysis to hexoses by cytosolic and apoplastic cell wall invertases. The utilization of sucrose that is still in the vacuole also depends on the activity of vacuolar invertase and tonoplast hexose transporters (Etxeberria & Gonzalez, 2003; Koch, 2004). Therefore depending on SUT4 activity, sucrose will have varying exposure to several invertases which may be differentially regulated by environmental cues (Roitsch & González, 2004; Ruan, 2014). For example, expression of vacuolar invertases was much more sensitive than other invertases to drought in poplar, increasing sharply in roots and decreasing in xylem (Xue et al., 2016). It is also possible for coppiced stumps to exhibit reduced soil drying after watering, which could have led to cooler, damper soil with reduced aeration and oxygenation in the winter. In potato, low storage temperatures increased total invertase activity (Pressey & Shaw, 1966). Other studies suggest that invertase activity is reduced under water-logging conditions (Kreuzwieser et al., 2009; Peng et al., 2018). An environmentally dictated difference in root invertase activities between winter and summer conditions might therefore contribute to a seasonal difference in the dependence on SUT4 for root sugar utilization.

In accordance with our data pointing toward higher residual sucrose and lower residual hexose in *sut4* roots post winter coppicing, this highlights the potential for an environmentally conditioned role for SUT4.

In summary, *PtaSUT4* was revealed through seasonal changes in the coppicing responses of *sut4* mutant lines to have a role in nonstructural carbohydrate allocations for growth and protection from environmental stressors under carbon limiting conditions in trees. During the winter, *PtaSUT4* appears to contribute to sucrose mobilization from roots under conditions that might reduce invertase activities. During the summer, prioritization of defense pools relative to growth was more evident than in winter, and that shift in prioritizations was less evident in *sut4* than control lines. Accordingly, these findings suggest that carbohydrate utilization may not be a limiting factor in the growth response of trees following coppicing. Finally, the present work raises enticing questions about how trees allocate, store, and mobilize carbohydrate reserves when faced with carbon limiting and changing environmental conditions.

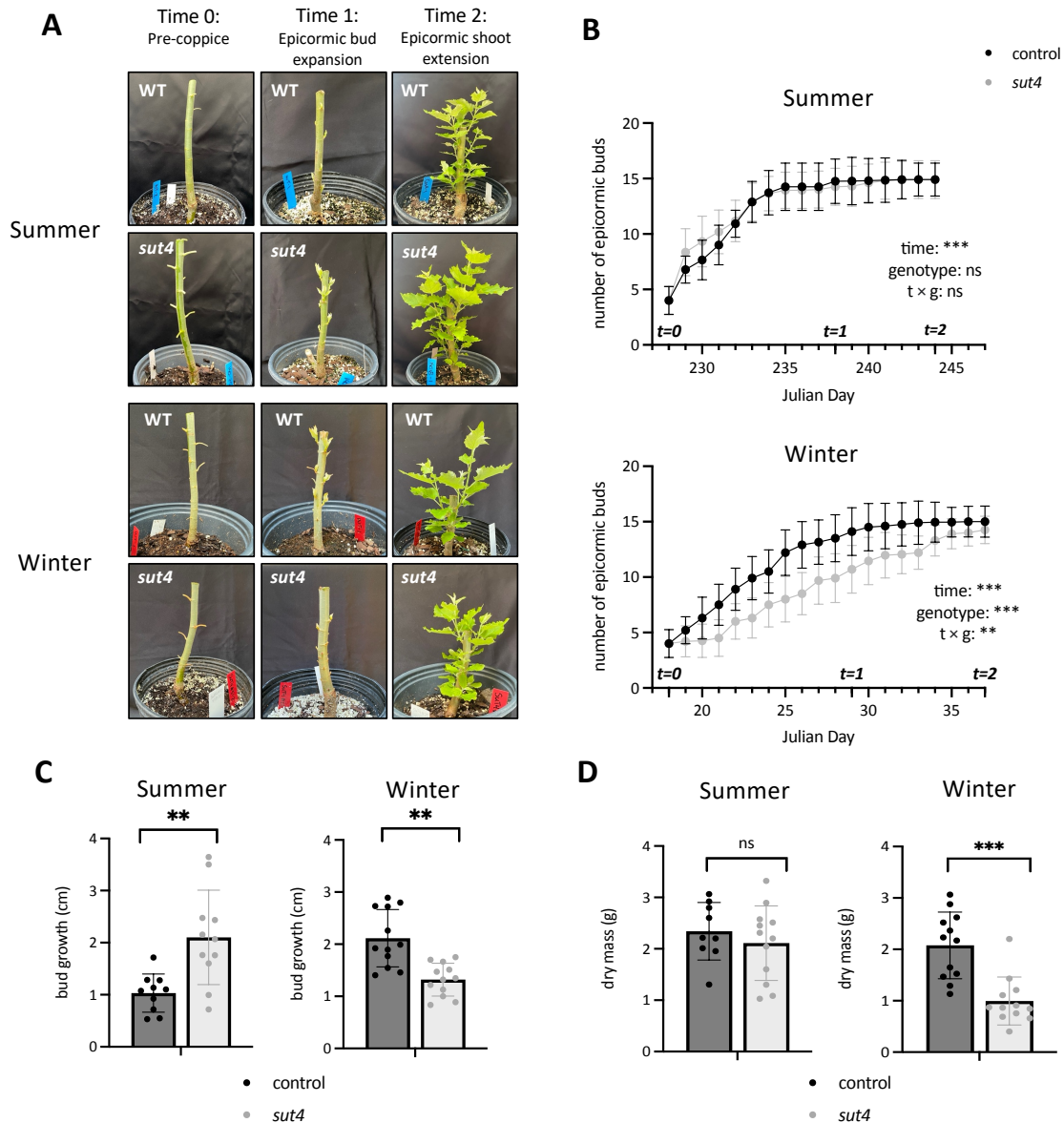
## FIGURES, TABLES, AND LEGENDS



**FIGURE 2.1: Seasonal variation of *PtaSUT4*-knockout mutant growth and *PtaSUT4* expression.**

(A) The corresponding growth of the *sut4* mutants under winter conditions as vegetative cuttings (left) and coppiced plants (right).

(B) Expression of *SUT4* (Potri.002G106900) transcript levels in xylem and phloem of wild-type *Populus tremula* x *alba* during the Summer and Winter. Bars represent the mean with standard error ( $n = 3$ ). Yen-Ho Chen generated mRNA-sequencing libraries and Chen Hsieh provided bioinformatic support.



**FIGURE 2.2: Epicormic bud expansion and shoot extension following coppicing.**

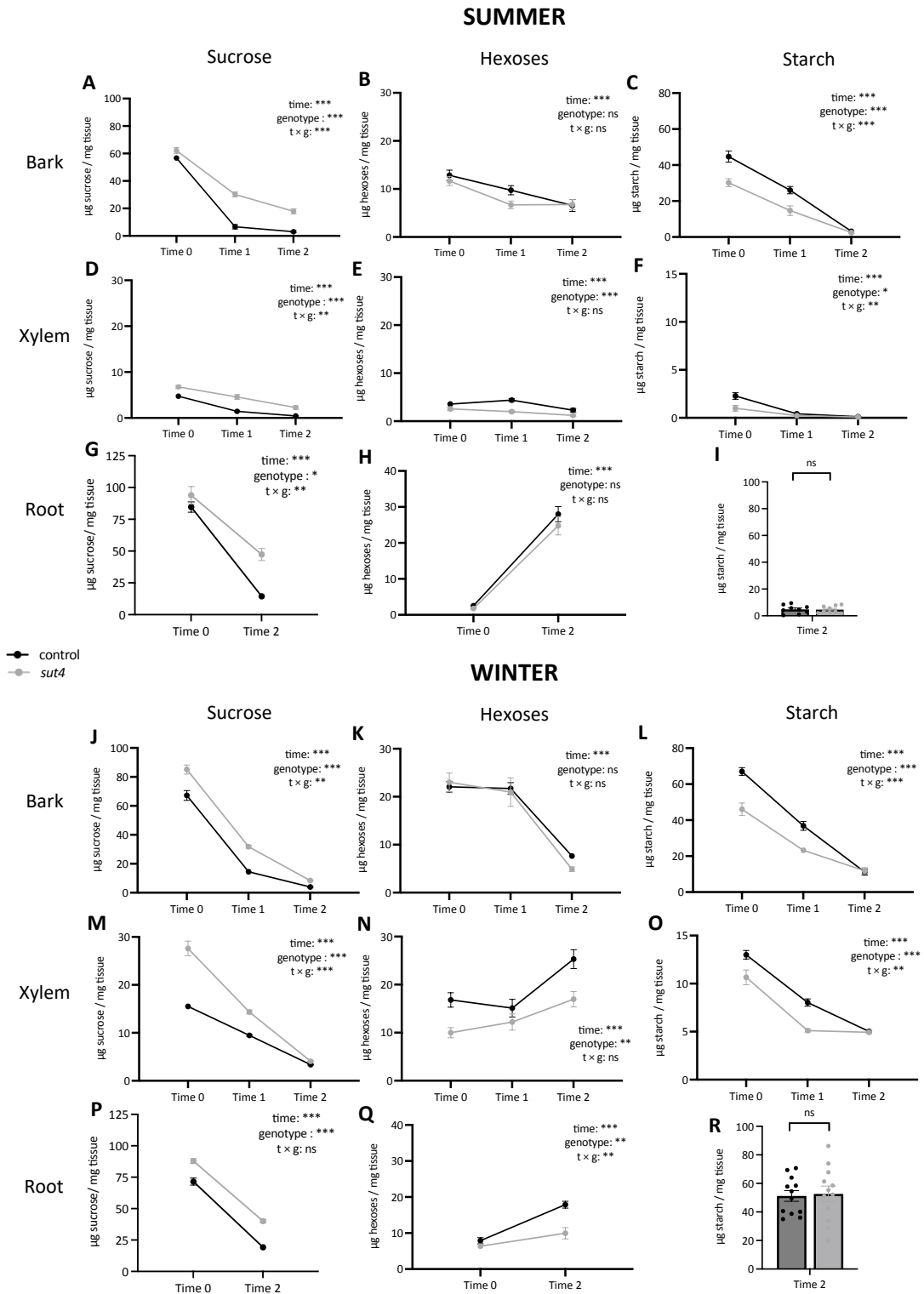
(A) Representative images of *sut4* and control poplar stools under Summer (top two rows) and Winter (bottom two rows) conditions just after coppicing (time = 0; left column), during epicormic bud expansion (time = 1; middle column), and during sprout growth (time = 2; right column).

(B) Bud emergence was monitored daily and scored throughout the course of the summer and winter experiments. Black and grey are for control and *sut4* plants, respectively.

Values are means  $\pm$  SD of bud number from  $n = 8$  biological replicates. The effects of genotype or time were assessed by a repeated measures two-way ANOVA and indicated by P values. t, time; g, genotype; t x g, time x genotype interaction; ns, nonsignificant; \*,  $P \leq 0.05$ ; \*\*\*,  $P \leq 0.001$ .

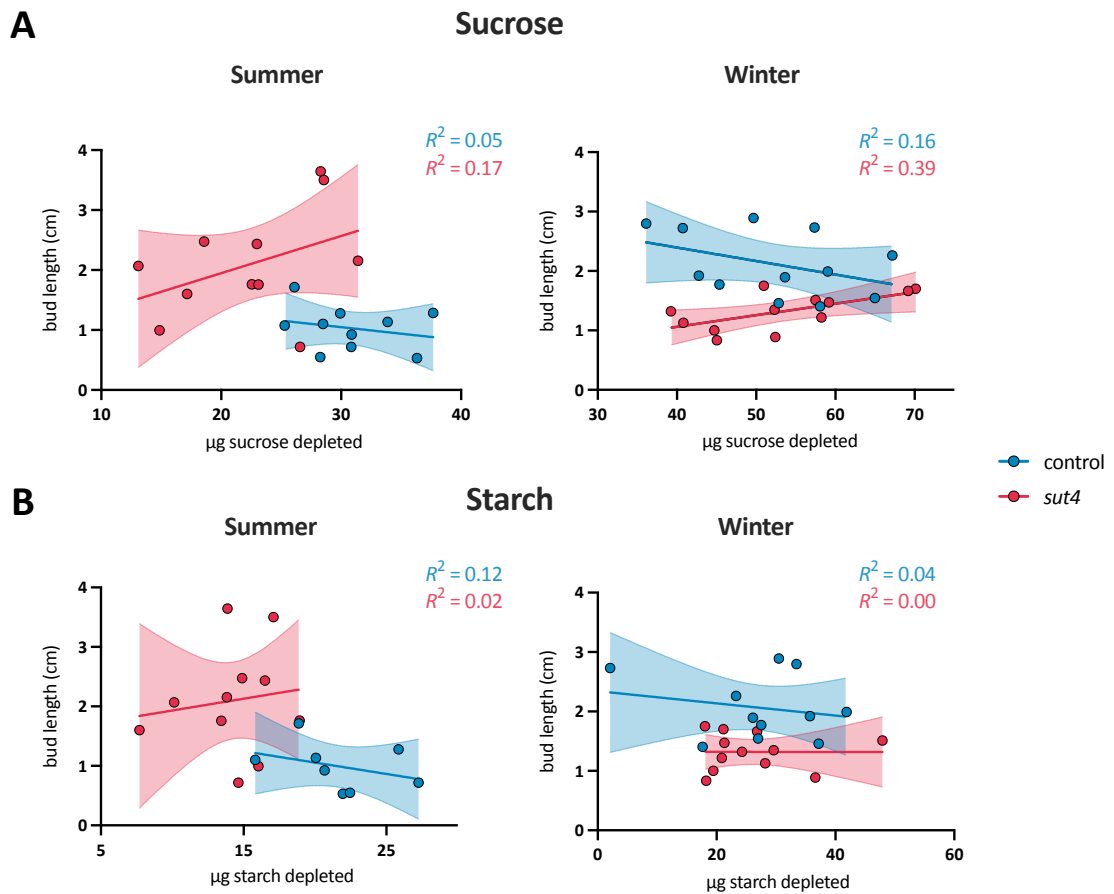
(C) Length of largest (dominant) and emerging epicormic bud at  $t=1$ . Data are mean  $\pm$  standard error from 8 - 12 biological replicates for control and *sut4* lines. Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).

(D) Total new aboveground shoot biomass produced following shoot extension at  $t=2$ . Data are mean  $\pm$  standard error from 8 - 12 biological replicates for control and *sut4* lines. Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).

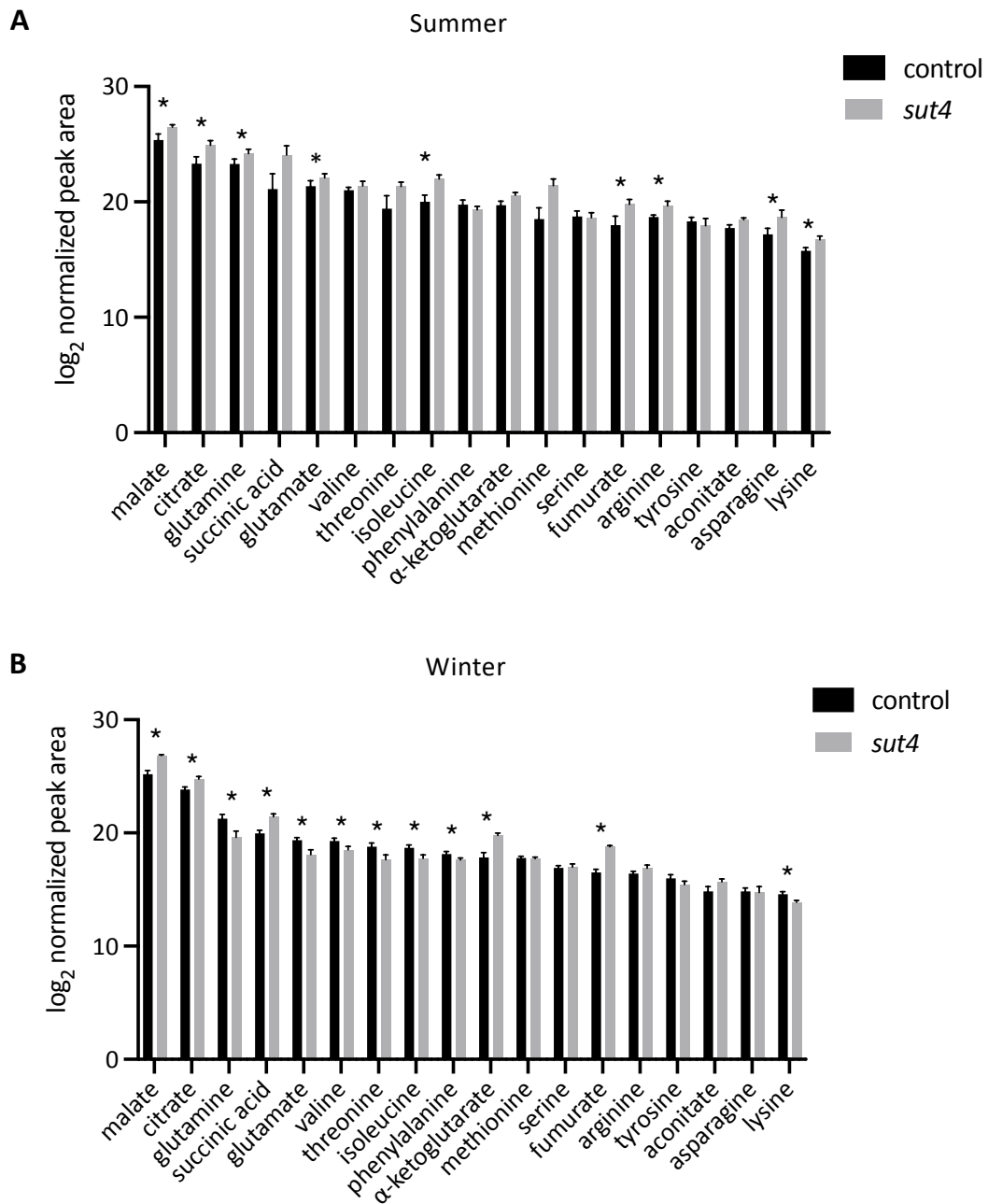


**FIGURE 2.3: Non-structural carbohydrate levels at the time of coppicing and during post-coppice sprouting.**

(A, D, G, J, M, P) Sucrose, (B, E, H, K, N, Q) Hexose (sum of fructose & glucose), and (C, F, I, L, O, R) Starch levels are depicted for the bark (A-C) Bark, (D-F) Xylem, (G-I) Root in the summer and for the (J-L) Bark, (M-O) Xylem, (P-R) Root in the winter. Black and grey are for control and *sut4* plants, respectively. Data are mean  $\pm$  standard error from 10 biological replicates for control and *sut4* lines, respectively. The effects of genotype or time were assessed by a repeated measures two-way ANOVA and indicated by P values. t, time; g, genotype; t x g, time x genotype interaction; ns, nonsignificant; \*,  $P \leq 0.05$ ; \*\*\*,  $P \leq 0.001$ . Statistical significance for root starch levels at t=2 was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).



**FIGURE 2.4: Epicormic bud length as a function of bark sucrose or starch depletion between  $t=0$  and  $t=1$  under summer and winter conditions.** (A) Bud length versus sucrose; (B) Bud length versus starch. Linear regression trendlines are depicted in blue for control; red for *sut4*. Shading highlights the 95% confidence intervals.



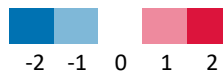
**FIGURE 2.5: Relative metabolite abundances of xylem sap in the summer and winter.**

(A) Overall relative abundance of normalized,  $\log_2$ - transformed peak areas of steady state Krebs cycle intermediates and amino acids in control and *sut4* plants in Summer (A) and Winter (B) Data are presented as the mean  $\pm$  SE ( $n = 8-10$ ). Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ )

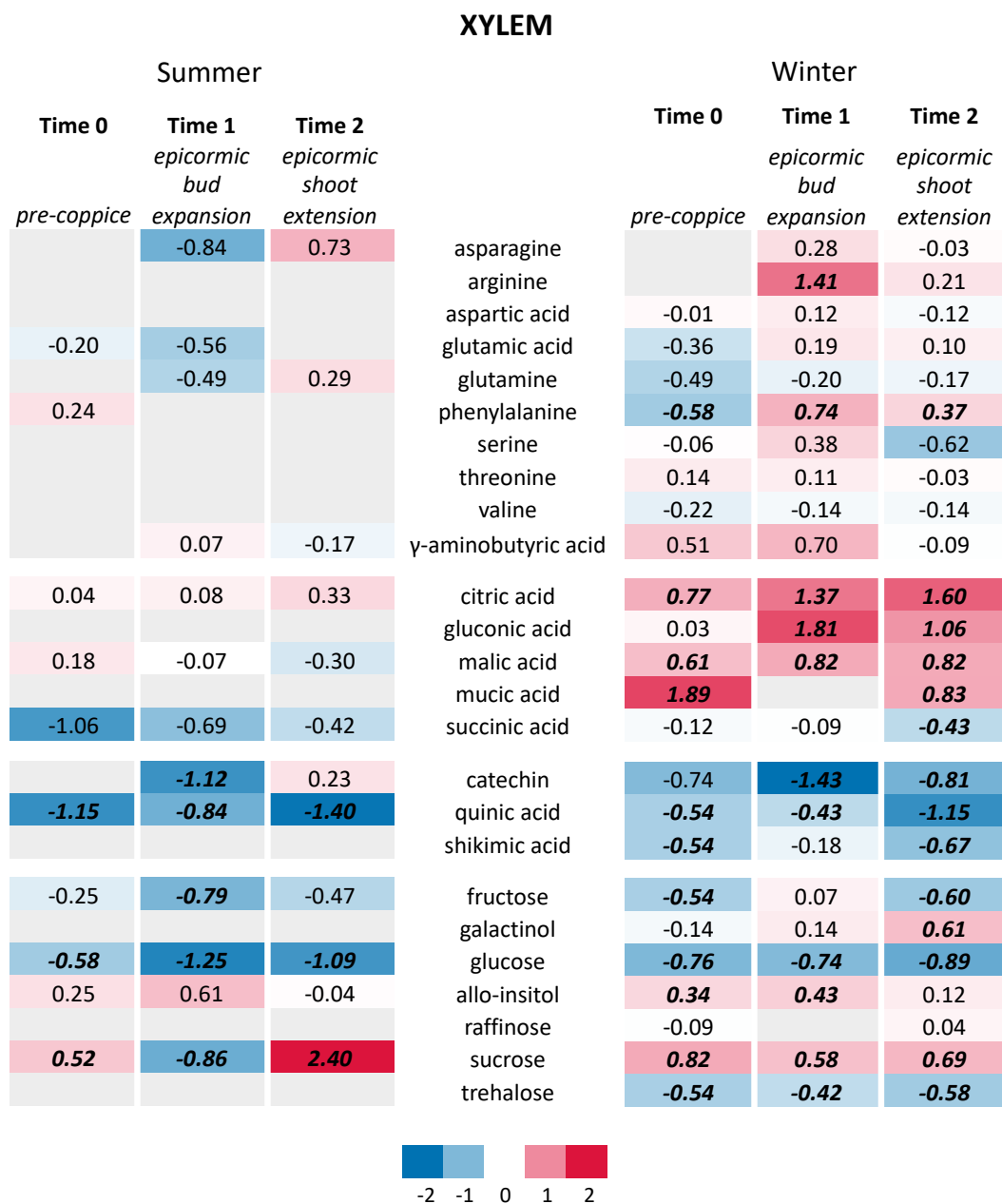
A

BARK

Summer			Winter			
Time 0	Time 1	Time 2		Time 0	Time 1	Time 2
	<i>epicormic bud</i>	<i>epicormic shoot</i>			<i>epicormic bud</i>	<i>epicormic shoot</i>
<i>pre-coppice</i>	<i>expansion</i>	<i>extension</i>		<i>pre-coppice</i>	<i>expansion</i>	<i>extension</i>
	1.13	1.11	asparagine		0.79	-0.38
0.77	0.53	0.71	aspartic acid	-0.07	0.54	-0.66
-0.01	0.03	0.34	glutamic acid	-0.74	0.73	0.84
	-0.09	0.70	glutamine	-0.04	0.33	0.21
	0.18	0.54	lysine	-0.18	-0.18	0.52
	0.30	0.73	serine	-0.22	-0.04	0.1
	-0.01	0.58	threonine	-0.15	-0.06	0.77
	0.18	0.67	valine	-0.42	0.29	0.65
0.78	0.36	0.61	γ-aminobutyric acid	0.45	0.49	0.37
0.34	-0.03	0.11	citric acid	0.51	0.58	1.56
-0.22			gluconic acid	1.24	1.16	0.43
-0.10	0.00	0.01	malic acid	0.07	0.53	0.5
0.06	-0.07	-0.01	mucic acid	1.17	1.70	1.05
-0.01	0.25	0.11	succinic acid	-0.40	-0.17	0.18
-0.74	-0.62	-0.40	catechin	-0.58	-0.20	0.03
			<i>p</i> -coumaric acid	-0.17	-0.6	-1.40
-0.92	-1.03	-0.76	quinic acid	-0.76	-0.76	-0.74
0.42	-0.64	-0.71	shikimic acid	0.15	-0.43	-0.49
0.12	0.28	0.24	trans-cinnamic acid	0.25	0.43	-0.03
0.07	0.34	0.28	arabinofuranose	0.24	0.18	0.31
0.03	-0.12	0.40	fructose	0.23	0.29	-0.17
0.30	-0.18	-1.15	galactinol	0.46	0.11	0.48
-0.20	-1.09	-0.49	glucose	-0.09	-0.74	-1.15
-0.32	-0.43	-0.71	lactose	-0.40	-0.36	-0.71
-0.06	0.08	0.04	melezitose	-0.76	0.56	0.57
0.33	-0.04	-0.22	myoinositol	0.28	-0.14	-0.42
1.06	-0.54	-1.25	raffinose	-0.39	2.89	-1.15
0.07	-0.17	0.19	sorbose	-0.14	0.56	
0.38	0.80	1.15	sucrose	0.33	1.07	1.07
-1.09	-0.94	-0.89	trehalose	0.16	0.06	-0.76
-0.15	-0.32	0.06	treonic acid	-0.32	-0.18	

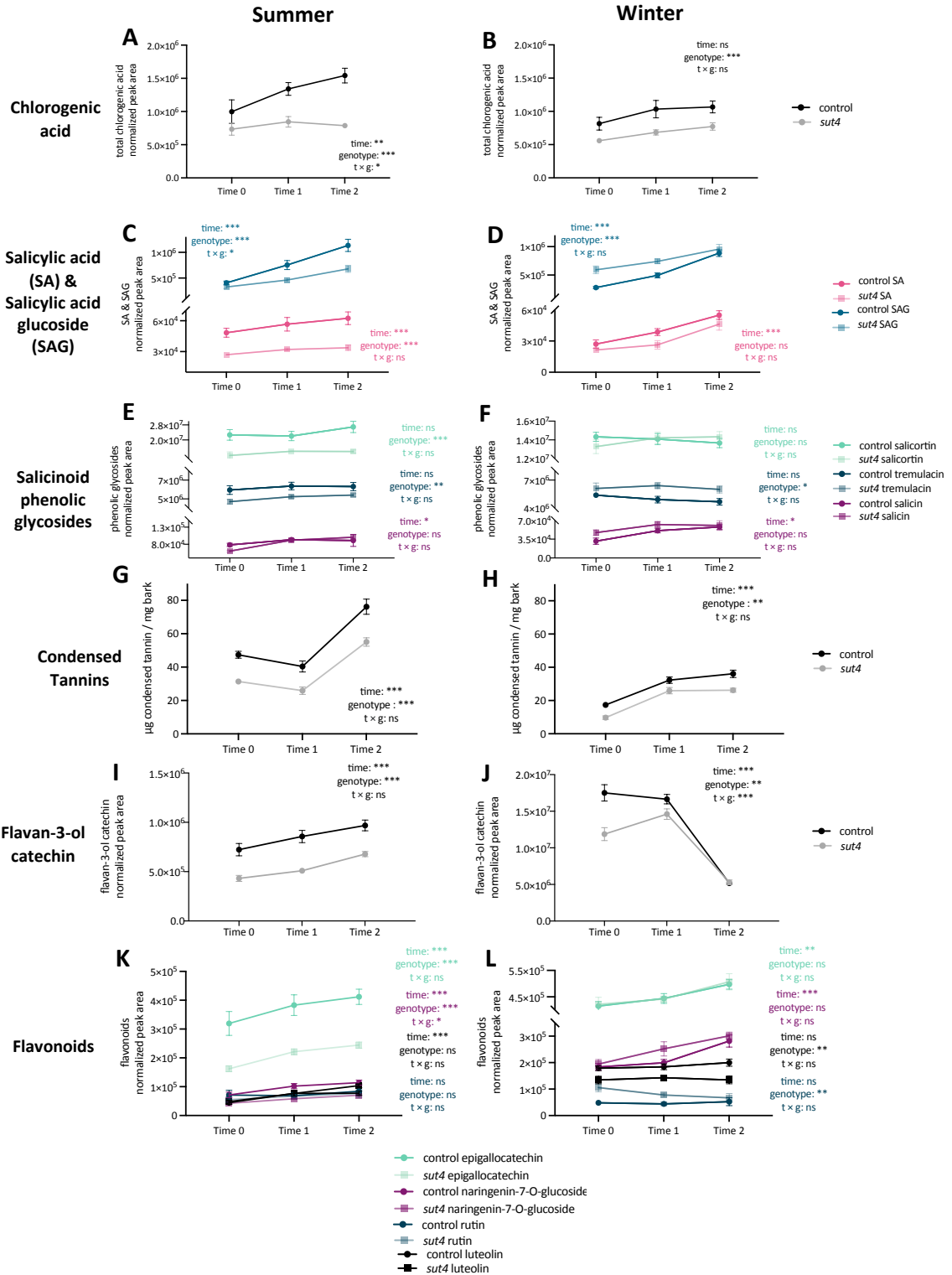


**B**



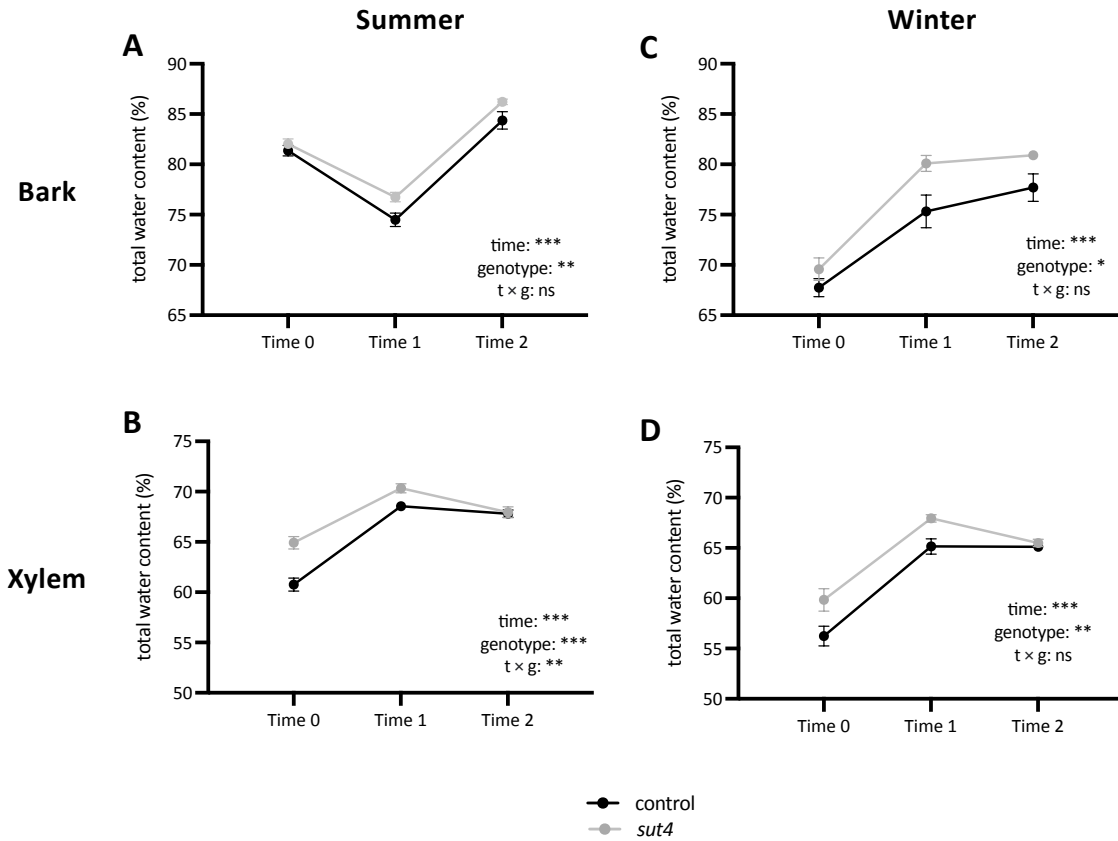
**FIGURE 2.6: Relative metabolite abundances of bark and xylem in summer and winter.**

(A) Bark and (B) Xylem metabolite abundance. Metabolite averages ( $n = 10$  and  $12$  for control and *sut4*, respectively), were converted to response ratio (*sut4*/control) and log<sub>2</sub>-transformed for heat maps occurring in the Summer (left) and Winter (right) experiments. Blue and red colors indicate decreased or increased metabolite abundance in mutants, while grey indicates no change. Significance between genotypes was obtained by the two-sample *t*-test and is indicated in bold, italic font ( $P < 0.05$ ).



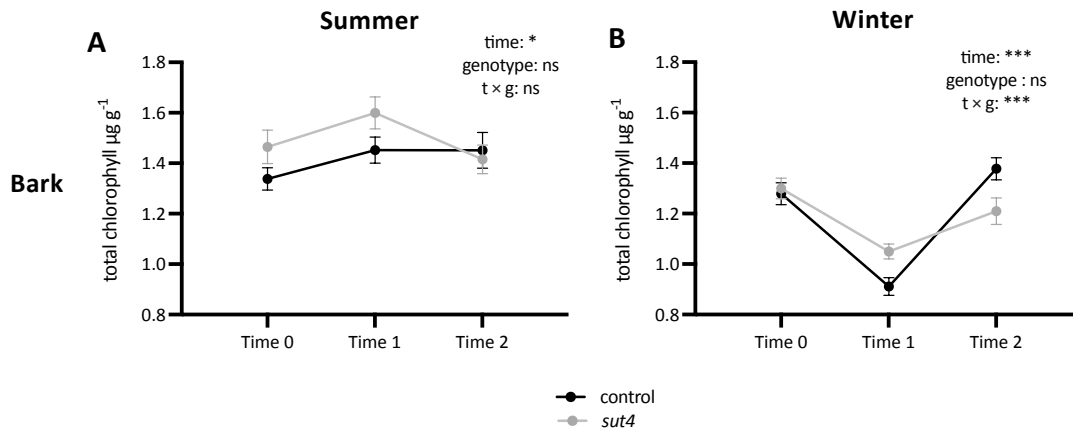
**FIGURE 2.7: Defense and phenylpropanoid metabolism response in bark of *sut4* coppiced poplar.**  
 (A-B), relative abundance of total chlorogenic acid in summer (A) and winter (B).

(C-D), relative abundance of salicylic acid (SA) and salicylic acid glucoside (SAG) in summer (C) and winter (D).  
(E-F), relative abundance of salicinoid phenolic glycosides (i.e., salicortin, tremulacin, and salicin) in summer (E) and winter (F).  
(G-H), condensed tannin abundance in summer (G) and winter (H).  
(I-J), relative abundance of flavan-3-ol catechin in summer (I) and winter (J).  
(K-L), relative abundance of flavonoids (i.e., epigallocatechin, naringenin-7-O-glucoside, rutin, and luteolin) in summer (K) and winter (L). Black and grey are for control and *sut4* plants, respectively. Values represent the normalized peak area of mean  $\pm$  standard error of ( $n = 8$  for control and *sut4* plants). The effects of genotype or time were assessed by a repeated measures two-way ANOVA and indicated by P values. t, time; g, genotype; t x g, time x genotype interaction; ns, nonsignificant; \*,  $P \leq 0.05$ ; \*\*\*,  $P \leq 0.001$ .



**FIGURE 2.8: Plant water status.**

(A-D) Bark and xylem water content (TWC) in Summer (A-B) and Winter (C-D). Black and grey are for control and *sut4* plants, respectively. Data were analyzed with a repeated measures two-way ANOVA. Data are presented as the mean  $\pm$  SE ( $n = 10$ ). t, time; g, genotype; t x g, time x genotype interaction; ns, nonsignificant; \*,  $P \leq 0.05$ ; \*\*\*,  $P \leq 0.001$ .



**FIGURE 2.9: Bark chlorophyll content.**

(A-B) Changes in bark chlorophyll following Summer (A) and Winter (B) coppicing. Black and grey are for control and *sut4* plants, respectively. Data were analyzed with a repeated measures two-way ANOVA. Data are presented as the mean  $\pm$  SE ( $n = 10$ ). t, time; g, genotype; t x g, time x genotype interaction; ns, nonsignificant; \*,  $P \leq 0.05$ ; \*\*\*,  $P \leq 0.001$ .

**TABLE 2.1: Growth of mature control and *sut4* mutant poplar.**

	Summer		Winter	
	Control	<i>sut4</i>	Control	<i>sut4</i>
Height (cm)	204.8 ± 15.8	197.1 ± 10.6	187.75 ± 6.77	182.33 ± 8.44**
Number of leaves	44.9 ± 2.4	48.1 ± 3.9**	43.75 ± 1.79	45.33 ± 2.23**
Leaf mass (g)	29.4 ± 4.3	35.3 ± 7.3*	30.97 ± 3.24	34.32 ± 3.33**
Bark mass (g)	9.6 ± 2.6	9.88 ± 1.4	9.35 ± 1.88	9.58 ± 1.61
Wood mass (g)	38.38 ± 7.46	30.9 ± 4.9*	32.93 ± 6.90	29.28 ± 4.32*
Stem mass (wood + bark) (g)	46.5 ± 9.72	40.8 ± 6.1	42.29 ± 8.79	38.86 ± 5.93
Root mass (g)	11.57 ± 2.54	10.28 ± 2.27	10.53 ± 2.30	9.67 ± 1.31

Values represent mean and SD of  $n = 8 - 14$  biological replicates. Student's  $t$ -test was used to determine statistical significance between genotypes. Significance is denoted by \*\* ( $P \leq 0.001$ ) or \* ( $P \leq 0.05$ ).

**TABLE 2.2: Total biomass of new sprout growth following coppicing in control and *sut4* poplar.**

	Summer		Winter	
	Control	<i>sut4</i>	Control	<i>sut4</i>
Tissue dry mass (g)				
Total aboveground	16.25 ± 4.20	24.12 ± 4.8*	15.57 ± 2.52	13.59 ± 2.53
Leaf	10.97 ± 2.8	16.56 ± 3.54*	10.35 ± 1.56	9.54 ± 1.75
Stem	5.28 ± 1.42	7.56 ± 1.67*	5.22 ± 0.96	4.05 ± 0.78
Root	11.46 ± 2.36	11.55 ± 2.76	10.87 ± 1.17	9.42 ± 1.41
Tissue mass ratio				
Leaf:Stem	2.05 ± 16	2.21 ± 0.35*	1.99 ± 0.10	1.95 ± 0.18
Leaf:Root	0.95 ± 0.13	1.42 ± 0.23*	0.94 ± 0.08	1.01 ± 0.13
Stem:Root	0.47 ± 0.09	0.66 ± 0.14*	0.47 ± 0.04	0.47 ± 0.04

Values represent mean and SD of  $n = 6 - 12$  biological replicates. Student's  $t$ -test was used to determine statistical significance between genotypes. Significance is denoted by \* ( $P \leq 0.05$ ).

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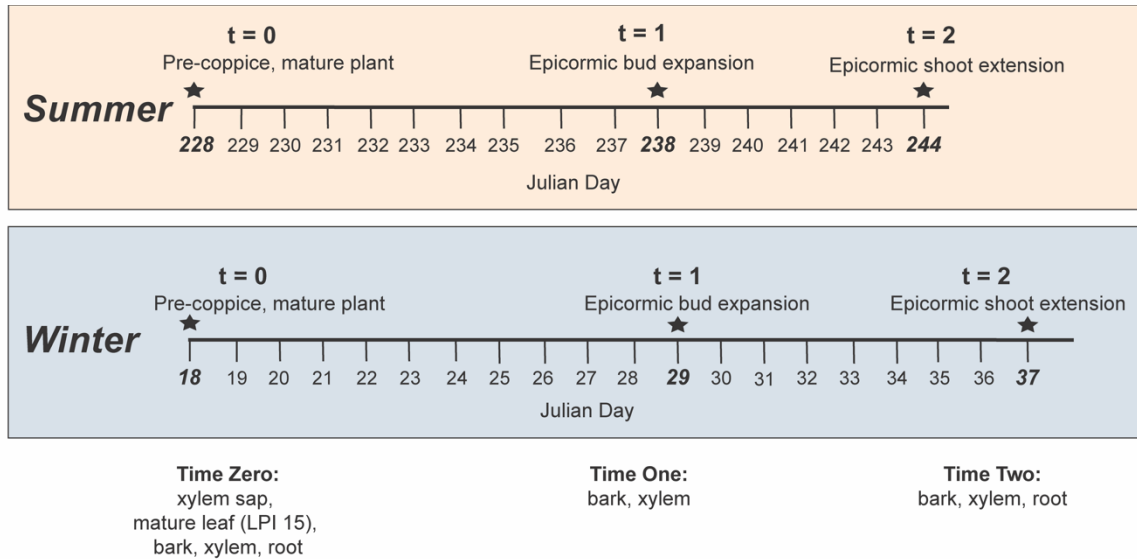
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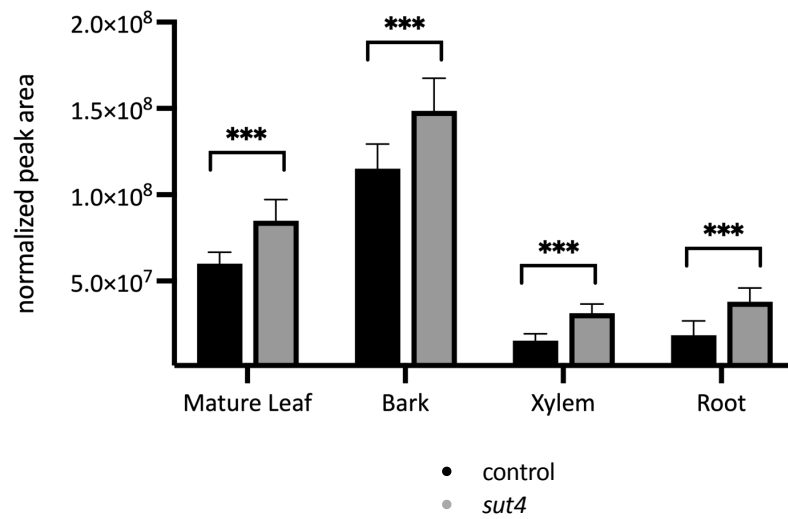
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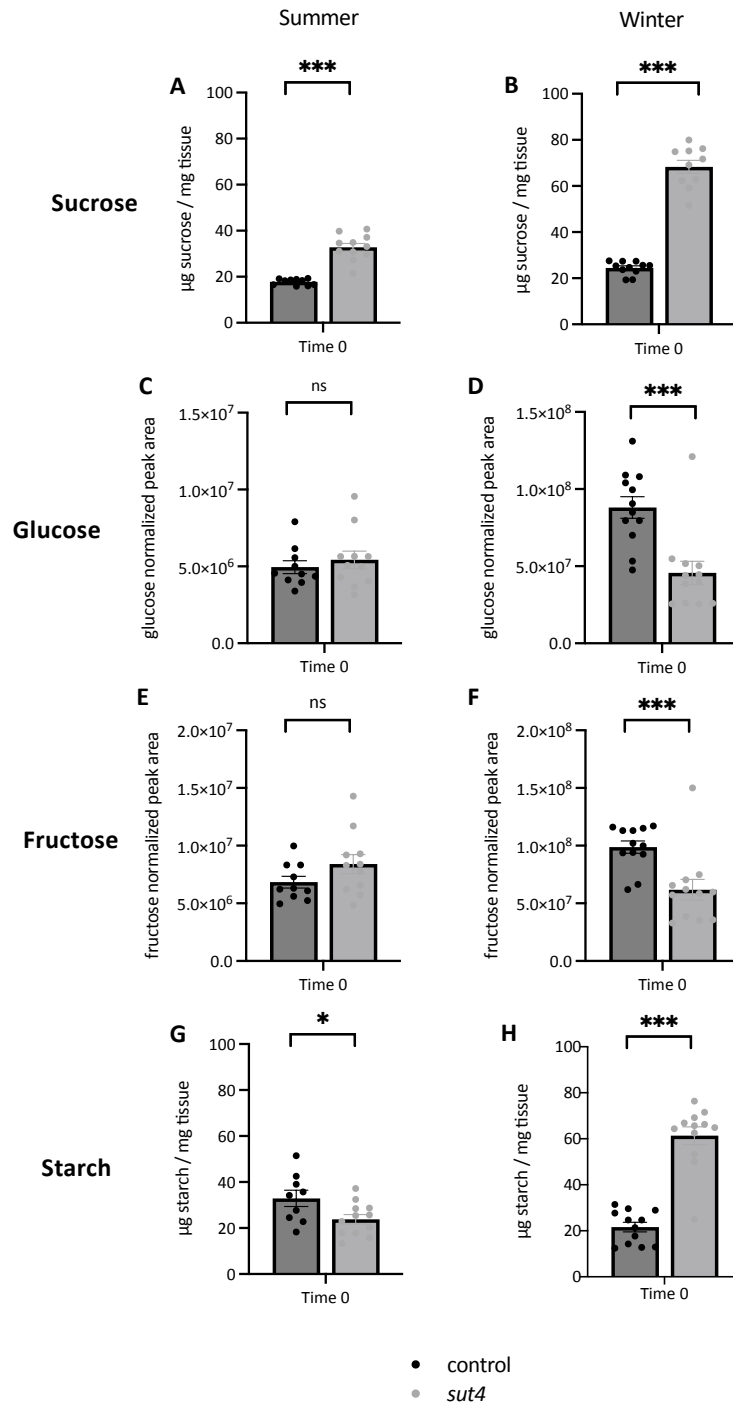
**SUPPLEMENTAL FIGURE 2.S1: Schematic of experimental design and sampling dates.**

Two coppicing experiments were conducted, one in Summer (August) and one in Winter (January). Bark and xylem of the coppiced stem were sampled from the coppiced stool  $t=0, 1, 2$ , with  $t=0$  corresponding to the date of coppicing. For epicormic bud expansion measurements, the length of the largest (dominant) epicormic bud on each stool at  $t=1$  was obtained by Image J software. Days until post-coppice sampling at  $t=1$  and  $2$  differed between the winter and summer experiments in order to normalize for seasonal effects on bud emergence and sprout growth rates.



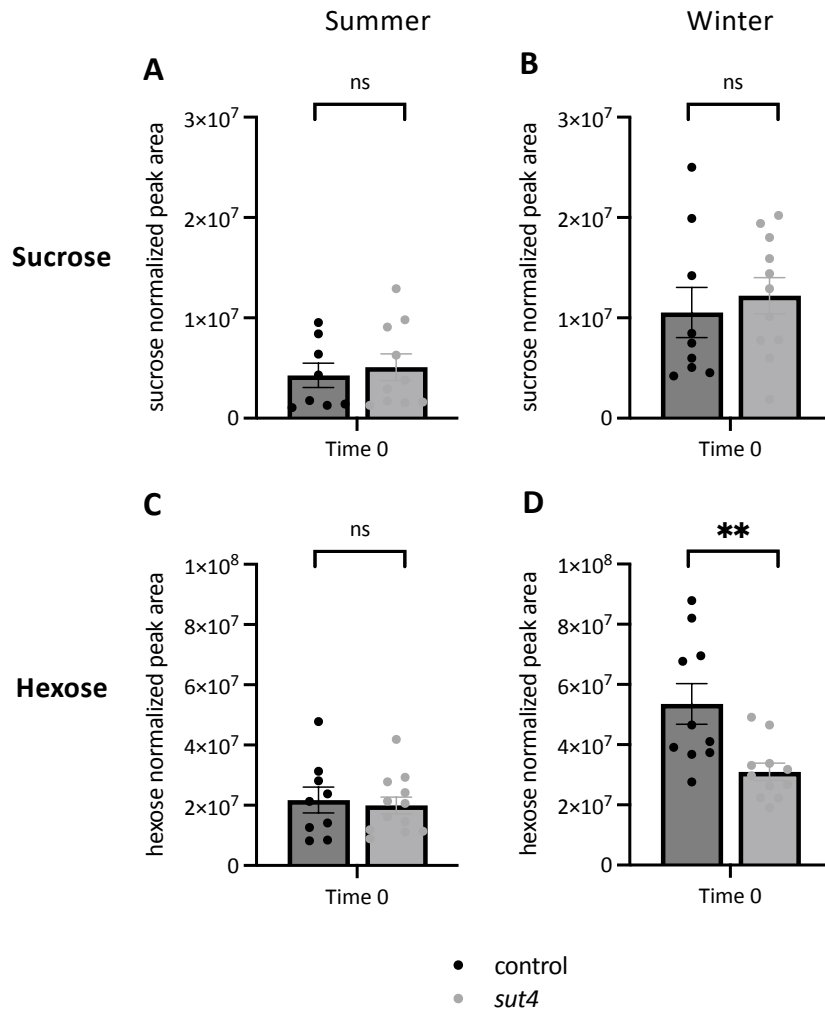
**SUPPLEMENTAL FIGURE 2.S2: Sucrose content in mature source leaf, bark, xylem, and root of control and *sut4* poplar.**

Data represent mean  $\pm$  SD of 8 biological replicates. \*\*\*  $P < 0.001$  according to Student's t test.



**SUPPLEMENTAL FIGURE 2.S3: Steady state non-structural carbohydrate levels in mature leaves prior to coppicing.**

Sucrose (A-B), Glucose (C-D), Fructose (E-F), and Starch (G-H) levels in the Summer (A, C, E, G) and Winter (B, D, F, H). Data are mean  $\pm$  standard error from  $n = 8 - 12$  biological replicates for control and *sut4* lines. Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).

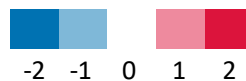


**SUPPLEMENTAL FIGURE 2.S4: Steady state non-structural carbohydrate levels in xylem sap prior to coppicing.**

Sucrose (A-B) and Hexose (Glucose + Fructose) (C-D) normalized peak areas levels in the Summer (A, C) and Winter (B, D). Data are mean  $\pm$  standard error from  $n = 8 - 12$  biological replicates for control and *sut4* lines. Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).

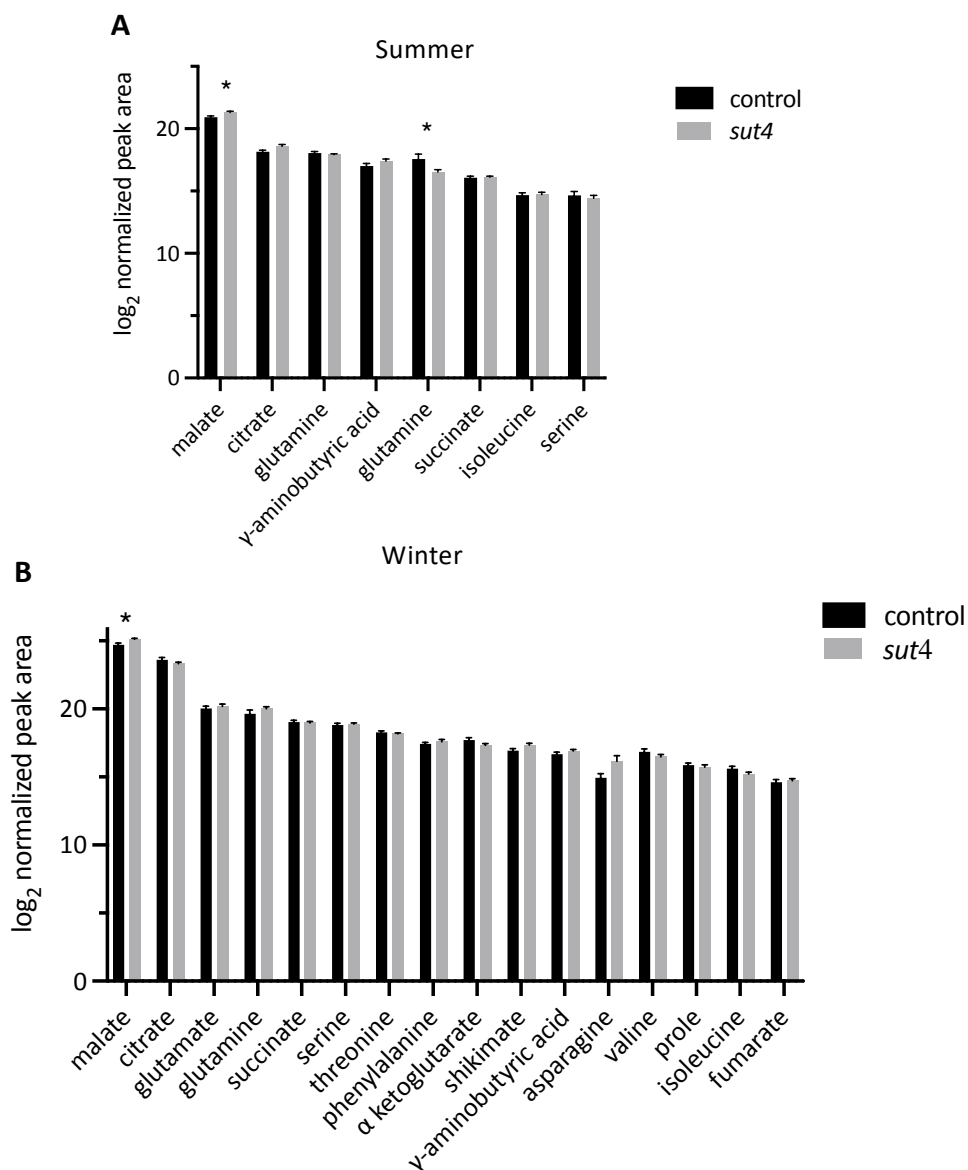
## XYLEM SAP

Summer		Winter
<b>1.40</b>	citrate	<b>0.78</b>
1.16	aconitate	0.59
0.21	α - ketoglutarate	<b>1.70</b>
0.77	succinate	<b>1.40</b>
<b>0.61</b>	fumurate	<b>2.12</b>
<b>0.78</b>	malate	<b>1.41</b>
<b>1.80</b>	arginine	0.58
<b>2.87</b>	asparagine	0.33
<b>0.85</b>	glutamate	<b>-0.89</b>
<b>1.95</b>	glutamine	<b>-1.09</b>
<b>0.76</b>	isoleucine	<b>-0.71</b>
<b>1.67</b>	lysine	<b>-0.69</b>
1.65	methionine	0.00
-0.49	phenylalanine	<b>-0.56</b>
1.40	serine	-0.32
0.65	threonine	-0.89
0.36	tyrosine	-0.62
0.68	valine	<b>-0.76</b>
-0.15	fructose	-0.51
0.61	galactitol	-0.42
-0.86	glucose	<b>-1.12</b>
<b>2.73</b>	mucic acid	0.53
-0.14	myoinositol	-0.17
<b>-2.06</b>	quinic acid	<b>-2.00</b>
	threitol	<b>1.21</b>



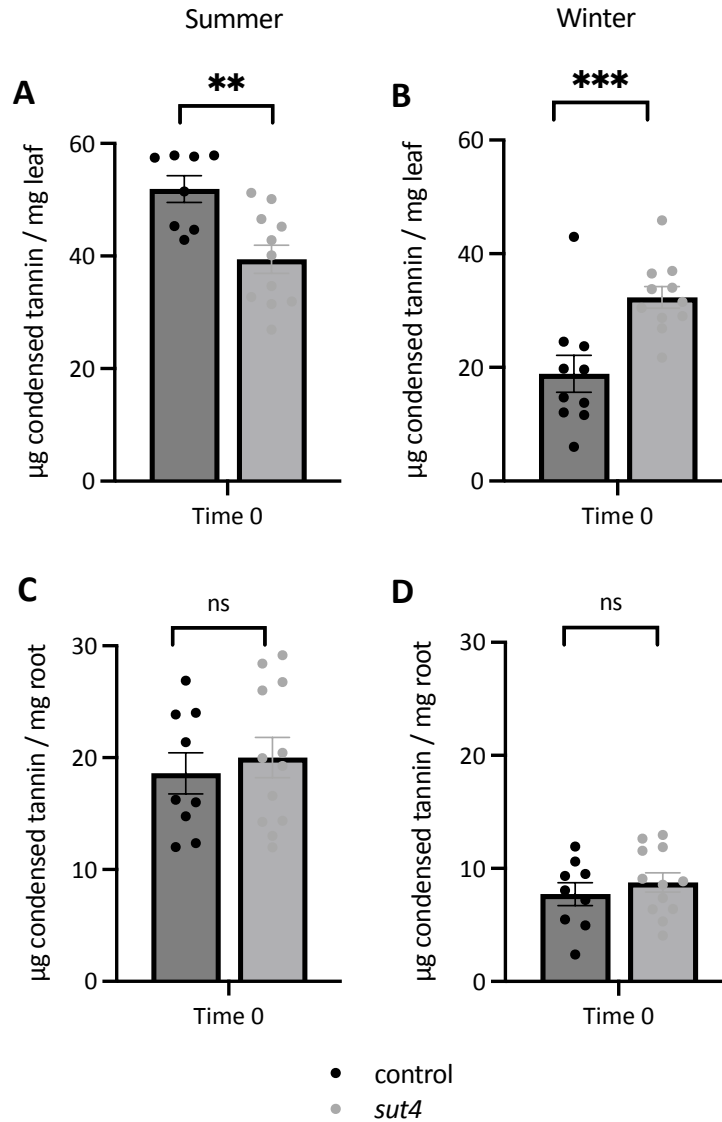
### SUPPLEMENTAL FIGURE 2.S5: Xylem sap metabolite relative abundance.

Metabolite averages ( $n = 10$  and  $12$  for control and *sut4*, respectively), were converted to response ratio (*sut4*/control) and log<sub>2</sub>-transformed for heat maps. Blue and red colors indicate decreased or increased metabolite abundance in mutants, while grey indicates no change. Significance between genotypes was obtained by the two-sample *t*-test and is indicated in bold, italic font ( $P < 0.05$ ).



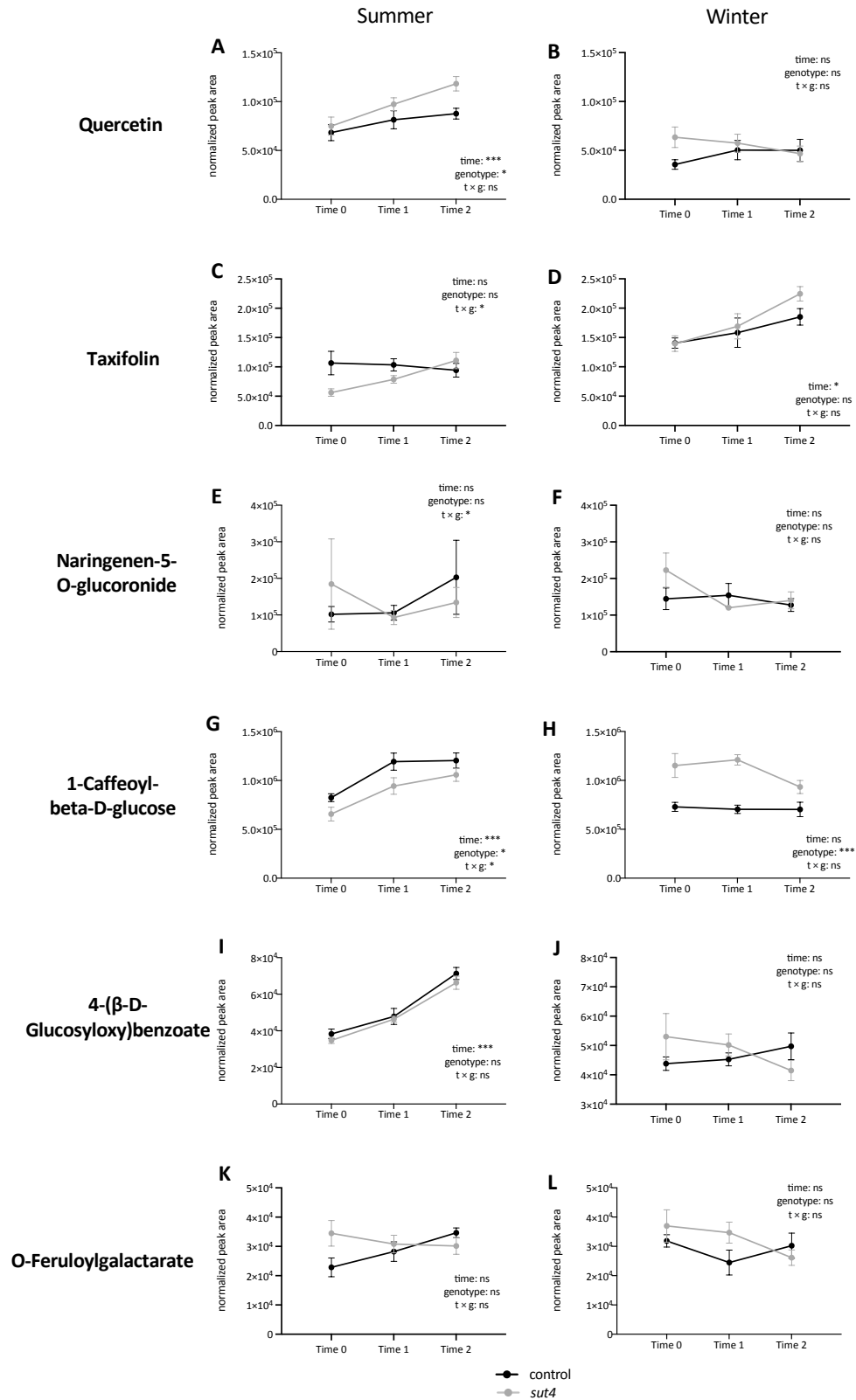
**SUPPLEMENTAL FIGURE 2.S6: Root metabolite relative abundance.**

Overall relative abundance of normalized, log<sub>2</sub>- transformed peak areas of steady state Krebs cycle intermediates and amino acids in control and *sut4* plants in Summer (A) and Winter (B). Data are presented as the mean  $\pm$  SE ( $n = 11-18$ ). Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).



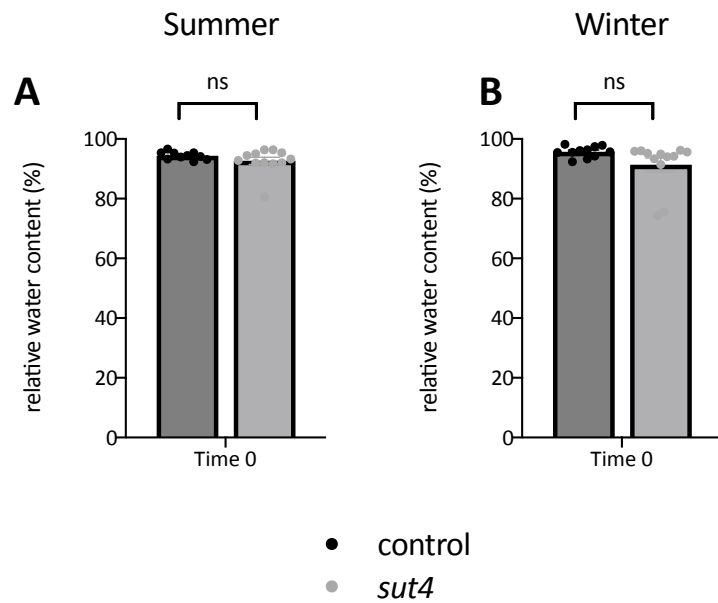
**SUPPLEMENTAL FIGURE 2.S7: Leaf and root condensed tannin abundance.**

CT content in mature leaf (i.e., LPI-15) immediately prior to Summer (A) and Winter (B) coppicing and in mature coarse roots prior to Summer (C) and Winter (D) coppicing. Data are mean  $\pm$  standard error from  $n = 9 - 12$  biological replicates for control and *sut4* lines. Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).



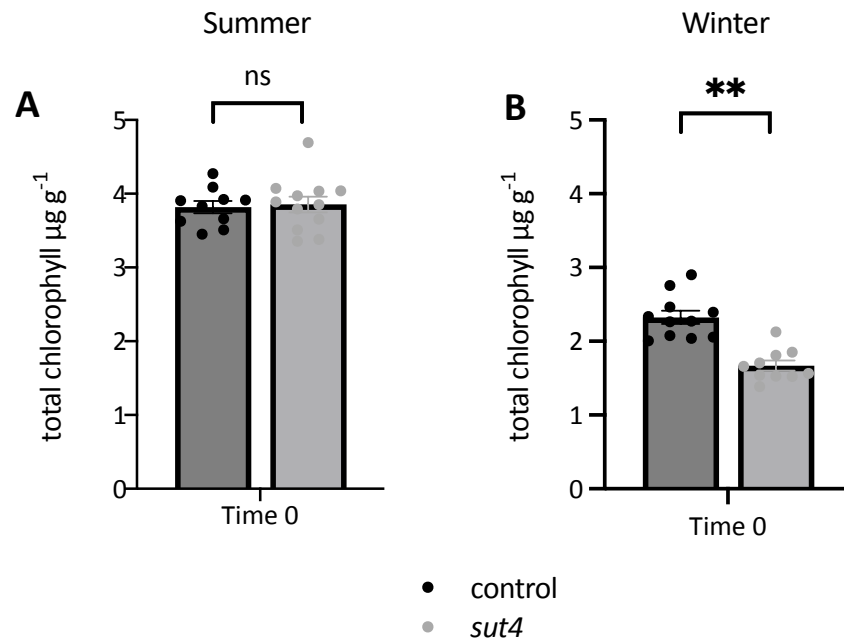
**SUPPLEMENTAL FIGURE 2.S8: Defense and phenylpropanoid metabolism response in bark of *sut4* coppiced poplar.**

(A-B), relative abundance of quercetin in Summer (A) and Winter (B); (C-D), relative abundance of taxifolin in Summer (C) and Winter (D); (E-F), relative abundance of naringenin-5-O-glucuronide in Summer (E) and Winter (F); (G-H), relative abundance of 1-Caffeoyl-beta-D-glucose in Summer (G) and Winter (H); (I-J), relative abundance of 4-( $\beta$ -D-Glucosyloxy)benzoate in Summer (I) and Winter (J); (K-L), relative abundance of O-Feruloylgalactarate in Summer (K) and Winter (L). Data are presented as the mean  $\pm$  SE ( $n = 6 - 8$ ). t, time; g, genotype; t x g, time x genotype interaction; ns, nonsignificant; \*,  $P \leq 0.05$ ; \*\*\*,  $P \leq 0.001$ .



**SUPPLEMENTAL FIGURE 2.S9: Leaf relative water content.**

Relative water content (RWC) in mature leaf (i.e., LPI-15) immediately prior to Summer (A) and Winter (B) coppicing. Data are mean  $\pm$  standard error from  $n = 10 - 12$  biological replicates for control and *sut4* lines. Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).



**SUPPLEMENTAL FIGURE 2.S10: Leaf chlorophyll content.**

Steady state total chlorophyll content in mature leaf (i.e., LPI-15) immediately prior to Summer (A) and Winter (B) coppicing. Data are mean  $\pm$  standard error from  $n = 10 - 12$  biological replicates for control and *sut4* lines. Statistical significance was determined by Student's *t* test between control and *sut4* plants ( $P < 0.05$ ).

**SUPPLEMENTAL TABLE 2.S1: LC-MS/QTOF metabolite identification information.**

<b>Metabolite name</b>	<b><i>m/z</i></b>	<b>RT</b>	<b>Formula</b>	<b>Summer prediction score</b>	<b>Winter prediction score</b>
Salicylic acid	137.0244	4.54	C7 H6 O3	85	87
Luteolin	285.0431	2.68	C15 H10 O6	84	78
4-(β-D-Glucosyloxy)benzoate	299.0771	1.07	C13 H16 O8	85	82
Salicylic acid glucoside	299.0783	2.50	C13 H16 O8	97.5	98
Quercetin	301.0347	5.33	C15 H10 O7	86	93
Taxifolin	303.0491	4.45	C15 H12 O7	86.5	97
1-Caffeoyl-beta-D-glucose	341.0862	2.65	C15 H18 O9	80	98.3
4-caffeoylquinic acid (CQA)	353.0859	3.34	C16 H18 O9	83.5	76
5-caffeoylquinic acid (CQA)	353.0877	2.02	C16 H18 O9	82	97
3-caffeoylquinic acid (CQA)	353.0879	2.75	C16 H18 O9	95.5	99
Salicin	365.0644	1.63	C13 H19 O10	68	72
O-Feruloylgalactarate	385.0775	2.32	C16 H18 O11	82.2	82.5
Salicortin	423.1271	4.55	C20 H24 O10	94.5	97.5
Naringenin 5-O-glucuronide	433.1138	4.43	C21 H22 O11	82.9	85
Naringenin 7-O-glucoside	447.0931	4.7	C21 H22 O10	83.2	77.5
Tremulacin	527.1568	5.67	C27 H28 O11	99.5	99.5
Rutin	609.1451	4.48	C27 H30 O16	97	90

Metabolites reported on in the main text including their *m/z*, retention time, formula and library match prediction score of 100.

CHAPTER 3  
CRISPR KNOCKOUT OF WINTER BIASED *SUTS* ALTERS PHENOLOGY,  
BIOMASS ACCRUAL, AND WOOD COMPOSITION OF FIELD GROWN HYBRID  
POPLAR <sup>2</sup>

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<sup>2</sup> Tuma, T.T., McInnes, H., Pham, H., Bewg, W.P., Nyamdari, B., Nambiar, D.M., Urbanowicz, B.R., Harding, S.A., & Tsai C.J. To be submitted to *Journal of Experimental Botany*

## ABSTRACT

Woody perennial trees transition between life as photoautotrophs and life as heterotrophs annually. As carbohydrate utilization patterns change to accommodate seasonal needs, so does the expression of genes that encode various sucrose-proton symporters (*SUTs*). The poplar genome contains five *SUT* gene family members with roles in intra-cellular and long-distance sucrose transport. The single-copy *SUT4* and the *SUT5/SUT6* genome duplicates exhibit winter-biased expression while the *SUT1/SUT3* paralogs display summer-biased expression. Here, we used CRISPR mutagenesis to investigate the importance of winter-biased *SUTs* to carbohydrate allocation, plant phenology, and biomass accrual in *Populus tremula* × *P. alba* under field conditions. During the first growing season, little change was observed between the mutants and control genotypes from date of out-planting to autumn in terms of growth. Fall leaf senescence developed earlier and spring bud flush the following year was delayed in *sut4* compared to the other lines. Subsequent changes in stem diameter growth were consistent with a *sut4* effect on phenology which penalized stem growth. The *sut4* mutants exhibited altered sugar partitioning and reductions in abundance of cold and desiccation tolerance associated oligosaccharides, raffinose and galactinol. *sut5/6* had essentially no impact on biomass or seasonal phenology of field-grown trees but did perturb wood cell wall composition. In light of earlier greenhouse work, the results of this study suggest that *SUT4* function may be more critical for daylength sensing and leaf area duration than for the provisioning of summer stem growth or biomass yield. These findings also highlight the importance of field trials for advancing basic research conducted in laboratory and greenhouse conditions to applied agricultural settings and for biotechnology efforts.

## INTRODUCTION

Woody trees annually cycle through periods of active growth, leaf senescence and abscission, and dormant bud quiescence in accordance with temperature and day length cues (Cooke et al., 2012; Lang et al., 1987; Rohde & Bhalerao, 2007). The timing of such environmental adjustments influences the process of plant phenology, which in turn dictates perennial growth in temperate climates with freezing winter temperatures (Charrier et al., 2018; Tixier et al., 2017). In sink organs that remain active after fall defoliation, reserves of nonstructural carbohydrates (NSC) are consumed to sustain winter survival (Kozłowski, 1992; Traversari et al., 2018). During the winter, NSC are utilized to regulate sucrose and oligosaccharide pools (e.g., galactinol, raffinose, stachyose) for metabolism, protein signaling, cellular maintenance, and protection against reactive oxygen species (Ameglio et al., 2001; Charrier et al., 2018; Guy et al., 2008; Regier et al., 2010; Tarkowski & Van den Ende, 2015; Thomashow, 1999). With the arrival of spring, NSC pools facilitate the emergence of new organs and tissues before resumption of photosynthesis (Barbaroux & Bréda, 2002; Loescher et al., 1990; Richardson et al., 2013; Tixier et al., 2019). Not surprisingly, seasonal variation in NSC dynamics is evolutionarily conserved across various phylogenetic groups (e.g., gymnosperms, angiosperms), life habits (e.g., evergreen, deciduous), and climate biomes (e.g., Boreal, Mediterranean, Tropical) (Barbaroux & Bréda, 2002; Furze et al., 2019; Martínez-Vilalta et al., 2016; Palacio et al., 2018). Consequently, sugars have multiple distinct and important roles for seasonal maintenance and in sustaining perennial tree growth.

Seasonal changes in the expression of carbohydrate-active genes which regulate NSC utilization have been reported for many tree taxa including Norway spruce (*Picea abies*) (Jokipii-Lukkari et al., 2018), oak (*Quercus robur*) (Dobbelstein et al., 2019) and eucalypts (*Eucalyptus dunnii*) (Dai et al., 2023). In poplar (*Populus trichocarpa*), genes encoding transporters for sucrose and monosaccharides, invertases and amylases for sucrose and starch hydrolysis, and synthases for raffinose, galactinol, and stachyose biosynthesis are more strongly expressed in stems during winter/dormancy than during summer/active growth (Ko et al., 2011). Many of these gene families contained distinct members that displayed opposite seasonal expression patterns. With specific regard to sucrose translocation, the *Populus* genome harbors five sucrose proton symporter (*SUT*) genes. Type I *SUT1* and *SUT3* are derived from Salicoid whole genome duplication and encode plasma membrane-localized proteins implicated in phloem loading and unloading (Payyavula et al., 2011). The poplar *SUT1* exhibits tissue-biased expression in the phloem and roots while *SUT3* is abundantly expressed in the phloem and xylem (Mahboubi et al., 2013; Payyavula et al., 2011; Xue et al., 2016). The transcripts of both *SUT1* and *SUT3* are more abundant during the summer than the winter (Ko et al., 2011). In contrast, transcripts encoding the Type III tonoplast localized sucrose proton symporter (*SUT4*) are detected at higher levels in the winter than the summer (Ko et al., 2011). *SUT4* is a single gene in *Populus*, predominantly expressed in many cell types (Payyavula et al., 2011; Harding et al., 2022) and its encoded protein mediates sucrose export from the vacuole (Eom et al., 2012; Schneider et al., 2012). The responsiveness of *SUT4* expression to various environmental cues as well as the impact of its silencing on starch use, cell turgor and root stress have been reported (Frost et al., 2012; Harding et al., 2020; Xu et al.,

2018; Xue et al., 2016). In addition, a role in light sensing has been proposed for the *SUT4* ortholog of potato (*Solanum tuberosum*) (Chincinska et al., 2008). The Type II members, *SUT5* and *SUT6*, are derived from Salicoid whole-genome duplication, encode plasma membrane sucrose symporters (Payyavula et al., 2011), and exhibit winter-biased expression (Ko et al., 2011). The physiological function of the Type II SUTs remains unspecified in any species, but the plantwide distribution of *PtaSUT5* and *PtaSUT6* transcripts in *P. tremula* × *P. alba* INRA 717-1B4 (hereafter 717) correlates more with that of *PtaSUT4* than of *PtaSUT1* or *PtaSUT3* (Payyavula et al., 2011; Xue et al., 2016). The contrasting expression amongst the *SUT* genes hints at the potential for seasonal specific roles amongst gene family members.

Sucrose transport is of particular interest in wood-forming perennial species, as sucrose serves as a source of energy for cell division and expansion and provides carbon skeleton for metabolism. While SUT relevance to phenology and perennial growth remains unexplored, manipulation of intracellular sucrose pools by heterologous overexpression of *Arabidopsis* sucrose phosphate synthase (*SPS*) led to elevated sucrose accrual, delayed leaf senescence, accelerated bud flush, and increased xylem fiber length in field grown hybrid poplar (*Populus alba* × *Populus grandidentata* Michx.) (Park et al., 2009). When grown under relatively stable and controlled glasshouse conditions, *SUT4* RNAi-knockdown 717 poplar lines exhibit relatively subtle growth differences compared to the wild type (WT) (Frost et al., 2012, Payyavula et al., 2011). In the present study, we sought to investigate the effects of single *SUT4*-knockout (KO) and double *SUT5/6*-KO on 717 hybrid poplar phenology and growth through a multi-year field trial. We present

data to show the greater importance than previously recognized of SUT4 function in tree response to environmental cues of daylength and temperature.

## METHODS

**Production of *sut* KO lines.** The generation of the *sut4* mutants and Cas9-only vector controls in the *Populus tremula* × *alba* 717 background were reported previously (Harding et al., 2022; Zhou et al., 2015). To generate the *sut5/6* double mutants, a single gRNA was designed to target all four alleles (AGCTCTCTCTCCTCAC) and expressed using the *Medicago truncatula* U6.6 promoter in the p201N-Cas9 vector, following the approach of Bewg et al. (2022). The dual knockout strategy was adopted because *PtaSUT5* and *PtaSUT6* are genome duplicates that share high levels of sequence identity (92% and 93% at the nucleotide and amino acid level, respectively) and exhibit similar tissue expression profiles (Payyavula et al., 2011). *Agrobacterium*-mediated transformation and plant regeneration was performed as describe (Bewg et al., 2022).

**Amplicon sequencing to determine mutation patterns.** Leaves from independent events of tissue cultured plants were collected for genomic DNA extraction and amplicon sequencing library preparation (Bewg et al. 2022) using consensus primers for *SUT5/6* (CCTACACGACGCTCTTCCGATCTRCCGATTCGGGTACCGT and GTTCAGACGTGTGCTCTTCCGATCACCGCAGAGCCAAATGAA). Samples were then barcoded with Illumina amplicon indexing primers, pooled, and sequenced on an Illumina MiSeq at the Georgia Genomics and Bioinformatics Core at the University of Georgia to obtain PE150 reads. Sequencing reads were processed and indel patterns identified using the Analysis of Genome Editing by Sequencing (AGEseq) program (Xue

& Tsai, 2015) with a mismatch allowance set at 1%, followed by manual curation. Tetra allelic mutations were confirmed in all lines (Supplemental Table 1).

**Plant propagation and field establishment.** Three independent lines each for *sut4* and *sut5/6* mutants—each with their own wild-type and Cas9 line controls—were selected for functional analysis. Clonal replicates were propagated from single-internode stem cuttings and acclimated in a mist chamber for 6 weeks. Cuttings were then transferred to 1-gallon pots containing commercial soil mixture (Fafard 3B) supplemented with Osmocote (15-9-12 NPK, 3-month slow release) and placed in a walk-in growth chamber for ~3 weeks. Plants were moved into an adjacent greenhouse for 2 weeks before transfer to an on-site lath house (open sided greenhouse) for an additional 2 weeks. For logistical reasons having to do with the timing of cutting establishment, *sut4* plants were slightly (~15%) shorter than control plants at the time of out-planting. After acclimation in the lath house, plants were transferred to 20-gallon pots containing a mix of Jolly Gardener premium soil (75% aged pine bark, 25% peat moss) and Fafard 3B with additional Osmocote (15-9-12 NPK, 3-month slow release) and planted at a fenced, 1-acre nursery at the University of Georgia’s Whitehall Forest (Athens, GA) in summer 2021. Genotypes were completely randomized throughout the site and spaced 1.5 meters apart from one another (Supplemental Figure 1A). The first planting occurred in early June 2021 for *sut4* mutants and their controls, and second planting occurred in early August 2021 for *sut5/6* double mutants and their controls.

Prior to release, the project received approval from the USDA APHIS Biotechnology Regulatory Services. Before out-planting occurred, a rhizome barrier of woven plastic was placed across the nursery site and a piece of heavy-duty plastic

sheeting was placed under each pot to aid in weed suppression and to prevent rooting into the soil. The field site was hand weeded and monitored for root suckers at least once monthly. Each independent tree was labeled with one metal tag and two plastic tree pot tags with a unique identifying number and the transgenic-event identifier. Plants were watered using an overhead irrigation system. The site was watered between 2-4 hours daily from early April to late October.

**Field growth, trophic interactions, and phenology.** The diameter of the main stem ~1m above the soil surface was measured every two months from August 2021 - April 2023. Plant height was measured from the base of the stem at soil level to shoot tip in April 2022 and 2023. Trophic interactions affecting leaves of the field grown trees were scored in July 2022 and April 2023. Leaves were assigned a score ranging from 1 – 3 for biotic (pathogen and herbivory) damage where, 1 = no damage, 2 = some to moderate levels of damage, or 3 = severe damage. On October 11<sup>th</sup>, 2022, leaf color was compared between genotypes as an indicator of leaf senescence. Trees were also monitored throughout the fall to compare onset and rate of leaf abscission between genotypes. In the spring, the appearance of bud flush on the dominant stem and flowering were monitored. No floral tissues were detected in the first growth season, but catkins were observed during spring of the second growing season (February 2023). The total number of trees that developed catkins was recorded prior to their removal from the field site. Further information regarding the growth cycles, phenotyping, and sampling are reported in the Supplemental Figures (Supplemental Figure 1B).

**Tissue sampling.** Leaf and stem tissues were collected multiple times during the field experiment (Supplemental Figure 1B). Approximately 12 – 17 months after out

planting, stem cores (10 mm in length and 2 mm in diameter) were collected from the main stem ~1 meter above soil level using a micro-coring device (Costruzioni Meccaniche Carabin C, San Vito di Cadore, Italy) according to Rossi and colleagues (2006). Stems were approximately 2–6 cm in diameter at the time of sampling. Increment cores were collected from the same stems during active growth in August 2022 (summer) and during dormancy in January (2023) (winter). Xylem and bark were separated from the cores in the field, snap-frozen in liquid nitrogen and before being transported back to laboratory facilities where they were stored at -80°C until sample processing occurred. Similar sized, mature source leaves (i.e., LPI-12) based on the leaf plastochron index (LPI) of Larson and Isebrands (1971) were sampled from the dominant stem in the summer (August 2022). Temperatures ranged from a night-time low of 22°C to a daytime high of 31°C (daily average 25°C) on the day of summer sampling, and from a low of 3°C to a high of 18°C (daily average 11°C) on the day of winter sampling. Catkins were observed in February 2023 after the second winter in the field. Catkins were collected on March 1, 2023, and divided into three developmental stages based on size (see Figure 4). All tissue sampling occurred under sunny conditions between 11AM – 2PM. Leaf and floral tissues were snap frozen, ground under liquid nitrogen with a mortar and pestle, and stored at -80°C.

**Metabolite profiling.** Bark, xylem, and leaf tissues were lyophilized for 48 hours (FreezeZone 2.5, Labconco), ground through a 40-mesh sieve using a Wiley Mill (Thomas Scientific), and further ball-milled to a fine powder in a S1600 Mini G Bead-beater (Spex SamplePrep; Metuchen, New Jersey) for metabolite profiling by Gas Chromatography-Mass Spectrometry (GC-MS). Tissue powders ( $10.0 \pm 0.5$  mg) were

extracted with 500  $\mu$ l methanol:chloroform (1:1, v/v), containing adonitol (Sigma-Aldrich) as a loading standard, sonicated in a pre-chilled water bath (4°C) for 15 minutes, before adding 200  $\mu$ l of water, followed by an additional 5-minute sonication. The mixture was centrifuged at 14,500 rpm for 5 minutes, vortexed, and then 10  $\mu$ l of the upper aqueous-methanol phase was transferred to a glass insert and evaporated to dryness in a centrifugal vacuum concentrator (Centrivap, Labconco). Carbonyl moieties were methoximated in 15  $\mu$ l of methoxyamine hydrochloride/pyridene (20 mg/ml) for 30 minutes at 30°C and silyated with 30  $\mu$ l of *N*-methyl-*N*-(trimethylsilyl)trifluoroacetamide (MSTFA; Sigma Aldrich) for 90 minutes at 60°C (Jeong et al., 2004).

Following sample randomization, 1  $\mu$ l of the derivatized extract was injected in splitless or split (25:1) mode and resolved with a DB-5MS column (30 m  $\times$  0.25 mm with a DuraGuard pre-column) in an Agilent 7890A oven and detected using an Agilent 5975C single quadrupole mass spectrometer (Agilent Technologies, Wilmington, DE). Flow rate and thermal ramping conditions were as described (Harding et al., 2014). Mass spectral (*m/z* 50-500) output was collected with Chemstation software (Agilent Technologies), and deconvoluted with AnalyzerPro (SpectralWorks, United Kingdom). Peak identities were assigned based on the NIST08, Fiehnlab (Agilent) plant metabolite national library and in-house spectral libraries from authentic standards (Bowsher et al., 2015; Frost et al., 2012; Jeong et al., 2004; Xue et al., 2013). A standard mix of succinic acid, sucrose, glutamic acid, fructose, glucose, and ascorbic acid was loaded at the beginning and end of each sample sequence to monitor derivatization and instrument performance. Peak intensities were normalized by the internal standard and reported on a

sample dry weight basis (normalized peak area). Sucrose and hexose abundance (sum of fructose and glucose) was reported as  $\mu\text{g}/\text{mg}$  dry weight.

**Starch.** Starch content was determined by hydrolyzing starch to glucose using enzymatic digestion with  $\alpha$ -amylase and amyloglucosidase (Chow & Landhausser, 2004). In brief, 10 mg of lyophilized, wiley- and ball-milled tissue (e.g., leaf, bark, root, wood) powder were extracted three times with 1 ml of methanol. The remaining tissue was solubilized in 0.5 ml of buffer (0.1 M sodium acetate, pH 5.0, with 5 mM  $\text{CaCl}_2$ ) containing 500 U of  $\alpha$ -amylase (Sigma A4551). Following a 2-hour incubation at  $65^\circ\text{C}$ , samples were cooled and 10  $\mu\text{l}$  of sodium acetate buffer (pH 5.0) containing 5 U amyloglucosidase (Sigma A1602) was added to each digest. Digests were then incubated at  $50^\circ\text{C}$  for 48 hours with continual, low-speed shaking. Following enzymatic digestion, samples were diluted with 500  $\mu\text{l}$  of  $\text{H}_2\text{O}$ , vortexed, and centrifuged. Twenty microliters of the supernatant were removed, dried, and derivatized for GC-MS as described above. Total starch content (expressed as  $\mu\text{g}$  starch per mg of dry tissue) was calculated based on a glucose standard curve. Chromatograms contained only glucose and adonitol loading standard peaks.

**Condensed tannins.** Freeze dried tissue powder (10 mg) was extracted in 600  $\mu\text{l}$  of methanol for 15 minutes in a sonicator bath to extract interfering chlorophyll. The depigmented pellet was dried in a Centrivap, and pellet-bound condensed tannin (CT) content estimated using the butanol-HCl method (Harding et al., 2005; Porter et al., 1985). Pellets were incubated and hydrolyzed at  $95^\circ\text{C}$  for 20 minutes in 1 ml of a butanol-5% hydrochloric acid solution containing ferric ammonium sulfate. CT

absorbance was read at  $A_{550}$  (SpectraMax M2; Molecular Devices) and quantified against aspen leaf CT standards (Harding et al., 2005).

**Stem water and wood density estimates.** Total and relative water content (RWC) were determined in March 2023 for wood and bark from a 2.5 cm stem section excised 1 m above soil level at mid-day. Bark was separated from the wood of a razor-trimmed stem length of 1 cm, and fresh weights were obtained in the field. Samples were placed in MilliQ-H<sub>2</sub>O for 48 hours, blotted dry, and weighed to obtain hydrated weight (HW). Samples were then oven dried for 72 hours at 104°C to obtain dry weights (DW). Relative water content (RWC %) of the bark and xylem were calculated using the following formula:  $(FW - DW) / (HW - DW) \times 100 = RWC$ . Wood moisture content ( $\alpha$ ), basic wood density ( $\text{kg m}^{-3}$ ), fiber saturation point ( $\alpha_f$  %) and the amount of free water available to support the hydraulic network ( $\alpha - \alpha_f$ ) (i.e., the water that is available for transport throughout the hydraulic network and not bound to cell walls) were determined following the published approach (Berry & Roderick, 2005; Traversari et al., 2018). Wood density was estimated after first placing a 2.5 cm stem segment in water on an analytical balance (weighing error of  $\pm 0.5$  mg) and submerging to determine the sample volume based on water displacement (water levels before and after wood immersion). Xylem samples were then oven dried and weighed for dry mass. Wood density was calculated on a dry mass to wet volume ratio. The fiber saturation point ( $\alpha_f$ ) was calculated using the following formula:

$$\alpha_f = \frac{0.22}{\sqrt{\frac{\text{basic density}}{\rho_w}}}$$

following the approach of Roderick & Berry (2005), where  $\rho_w$  is the density of liquid water ( $\text{kg m}^{-3}$ ). The amount of free water available to support the hydraulic network was calculated by determining the difference between  $\alpha - \alpha_f$  and can be used as an indicator of xylem integrity.

**Cell wall composition analyses.** Fifteen-cm long pieces of the main stem were destructively harvested following bud flush in March 2023 (Supplemental Figure 2). Stem segments were debarked, oven dried at  $55^\circ\text{C}$  for 24 hours, and ground to pass through a 40-mesh screen using a Wiley mill. Samples were then run through 99 cycles of hot ethanol extraction using a Soxhlet extraction unit (Buchi) and air dried. The residues were hydrolyzed in 2 M trifluoroacetic acid for 2 hours at  $120^\circ\text{C}$ . Released monosaccharides were analyzed as their alditol acetate derivatives by GC-MS using an Agilent 7890A GC interfaced to an Agilent 5975C mass selective detector, with a 30 m x 0.25 mm SP2330 capillary column at the University of Georgia Complex Carbohydrate Research Center.

**Statistics.** Repeated measures analysis of variance (ANOVA) was used to determine significant differences in growth over time, genotypic effects, and their interactions using *R* version 4.1.0 (R Core Team, 2016) in Rstudio (version 2022.12.353). A principal component analysis (PCA) of the catkin metabolite profiles was used to assess variation between control and *sut4* mutants of each developmental stage.

## RESULTS

### *Biomass yield was reduced in field-grown *sut4* poplar*

We established an outdoor trial in summer 2021 to test the extent to which CRISPR-KO targeting *SUT* genes with winter-biased expression (Supplemental Figure 3)

would alter phenology and/or seasonal growth (Supplemental Figure 1B). KO of *PtaSUT4*, but not of *PtaSUT5/6*, led to reduced stem growth under field conditions (Figure 1A). Diameter of the dominant stems did not change during fall through early spring of August, 2021 – April, 2022. However, control stem diameters increased more than *sut4* stem diameters between April, 2022 and June, 2022 shortly following spring flush. The diameter differential of June then remained constant through the subsequent fall, winter and spring measurements. Stem diameters did not differ between *sut5/6* mutants and their respective controls during the measuring period (Figure 1A). Tree height was slightly greater in the controls and *sut5/6* trees compared to the *sut4*'s at the end of the first growth season in one-year-old trees (Figure 1B). At the end of the experiment, tree height was ~ 25% greater in control and *sut5/6* than in *sut4* (Figure 1B). Overall, growth was comparatively reduced in the *sut4* trees but not the *sut5/6* lines (Figure 1C).

#### *Leaf area duration reduced in sut4*

Signs of leaf senescence were more evident in *sut4* than the other lines when leaves were compared in late October (Figure 2A). At this time, the *sut4* mutants, but not the control lines or *sut5/6* mutants, displayed leaf yellowing consistent with chlorophyll loss. By mid-November nearly 90% of *sut4* trees had lost all of their leaves while the majority of the controls and *sut5/6* mutants still retained the majority of their foliage (Figure 2B). In early December the majority of the trees had lost nearly all of their foliage (Figure 2C). Early indicators of leaf bud flush the following spring (March 2022) was delayed by an average of 7 days for the *sut4* trees compared to the controls and *sut5/6* mutants (Figure 3).

Hybrid poplar's develop flowers after 5-8 years of maturity (Mohamed et al., 2010). No floral structures (i.e., catkins) were observed in spring 2022. Surprisingly, catkins were observed on many of the trees in late February through early March 2023 (Figure 4A-B) and removed immediately to comply with APHIS regulations. Both *sut4*-KO and control trees developed their floral structures prior to leaf bud flush (Figure 4C) as is typical of temperate trees. In total, 55% of the *sut4* and 56% of their controls and 21% of the *sut5/6* and 23% of their controls started to flower in March 2023 prior to their third year of growth or after less than 3 years of growth in the field (Figure 4D). No significant differences were detected between genotypes.

#### *Altered sugar homeostasis*

We quantified levels of monosaccharide and oligosaccharide sugars in the bark, xylem, and mature source leaves of the field grown poplars under summer and winter seasons. Sucrose was more abundant in bark and xylem of *sut4* mutants than control or *sut5/6* mutants regardless of season (Figure 5A-B). Interestingly, xylem sucrose variance was greater in *sut4* than the other lines, both in summer and winter (Figure 5B). Source leaf sucrose content was highest overall in *sut4* (Figure 5C), consistent with earlier work on *SUT4*-RNAi and *sut4* mutant poplars (Harding et al., 2022; Payyavula et al., 2011) in the greenhouse. Leaf sucrose content did not differ between *sut5/6* plants and their controls (Figure 5C). As in the xylem, leaf sucrose exhibited greater variance in *sut4* than the other lines under field conditions.

While sucrose abundance decreased, hexose (fructose and glucose) levels increased sharply in bark and xylem of all lines between summer and winter (Figure 5D-E). Xylem hexose abundance varied more within *sut4* than within the other lines in both

summer and winter. The ratio of hexose to sucrose was much lower in bark of *sut4* than other lines during summer, but not during winter by which time sucrose levels had decreased (Figure 5A, D). Leaf hexose varied greatly within each genotype under field conditions and was higher in the leaves of the *sut4* lines but not the *sut5/6* trees (Figure 5F). Bark and xylem starch abundance differed little between genotypes in summer or winter and exhibited large declines of similar magnitude in all genotypes during the transition to winter growth (Figure 5G-H).

*Raffinose response to winter conditions was perturbed*

The sugar alcohol myo-inositol and oligosaccharides galactinol and raffinose are metabolically related, with glucose-phosphate-derived myo-inositol giving rise to galactinol, and eventually along with sucrose, to raffinose and other raffinose family oligosaccharides (Sengupta et al., 2015). These metabolites offer protection during cold or drought (ElSayed et al., 2014; Wang et al., 2012). Myo-inositol was more abundant in stem tissues of *sut4* than other lines in summer, but not in winter (Figure 6A-C). During the summer, stem galactinol and raffinose abundance were generally lower for all genotypes (Figure 6D-E, G-H). With the transition to winter, stem galactinol and raffinose levels increased less in *sut4* than in *sut5/6* or the respective control lines (Figure 6D-E, G-H). Summer leaf galactinol content was higher in the *sut4* trees and lower in the *sut5/6* trees compared to their controls (Figure 6F), while leaf raffinose content was more variable and did not differ between genotypes (Figure 6I).

*Tricarboxylic acid cycle homeostasis was reduced in *sut4* but not *sut5/6**

The tricarboxylic acid (TCA) cycle links carbohydrate inputs with respiration and numerous biosynthetic pathways and is central to cell metabolism (Cooke & Weih, 2005;

Fernie et al., 2004). Bark concentrations of the most abundant TCA cycle intermediates, malic and citric acids, were lower in *sut4* than controls in both summer and winter but were unchanged in *sut5/6* (Figure 7A-F). Succinic acid was detected at slightly higher levels in the bark and leaves of the *sut4* mutants during the summer but did not differ from the control lines during the winter (Figure 7G). A putative TCA-like compound identified as cis-fumaric acid (metabolite confidence level 93%) and fumaric acid exhibited notably steeper declines in *sut4* winter bark than in control bark (Figure 7J-K).  $\alpha$ -ketoglutarate abundance did not differ in the bark of either of the *sut* mutants during the winter. Overall, xylem TCA concentrations differed little between *sut4* and the other lines in summer or winter, neither did *sut5/6* stems (Figure 7H).

#### *Non-sucrose disaccharides*

Several disaccharide-like metabolites including putative melibiose (a disaccharide of glucose-galactose) and isomaltose were less abundant in bark of the *sut4* mutant than controls in the winter (Table 1). Interestingly, these along with putative sophorose and trehalose, both glucose-glucose disaccharides, were more abundant in *sut5/6* bark than their respective controls in the winter (Table 1). Levels of these putative non-sucrose disaccharides trended higher in the xylem of both *sut* mutants than their respective controls in the winter (Table 2).

#### *Secondary metabolism*

Phenylpropanoid secondary metabolites (e.g., flavonoids, anthocyanins, tannins, and salicinoids) derived from phenylalanine account for a significant proportion of photosynthetic carbon in leaves and stems of *Populus* (Lindroth & Hwang, 1996). The synthesis of such metabolites and their glycosylation are heavy carbon sinks, and their

maintenance may occur at the expense of growth. Salicinoids and flavonoid biosynthesis all begin with *p*-coumaric acid and hydroxycinnamate intermediates of the central phenylpropanoid pathway (Boerjan et al., 2003; Tsai et al., 2006; Weisshaar & Jenkins, 1998). Key hydroxycinnamates included *trans*-cinnamic acid, *p*-coumaric acid and caffeic acid, all of which were at substantially lower abundance in winter bark of *sut4* than controls (Table 1). Xylem content of hydroxybenzoic acid was higher in *sut4* relative to controls in both summer and winter (Table 2). Salicortin, a phenolic glycoside (Babst et al., 2010; Lindroth & Pajutee, 1987) was more abundant in *sut5/6* bark than respective controls in summer and winter (Table 2). Finally, levels of phenylpropanoid pathway end-product, condensed tannins, were higher in the leaves of both the *sut4* and *sut5/6* trees than the controls (Supplemental Figure 4A). Levels condensed tannins were higher in the bark of the *sut5/6* mutants in the summer and winter but did not differ significantly between the *sut4* trees and their controls (Supplemental Figure 4B).

#### *Stem water content dynamics & xylem hydraulic properties in sut mutants*

We examined the extent to which intracellular sucrose compartmentalization influenced hydration and solute concentrations by conducting water content analyses. Relative water content analyses of stem bark and wood revealed that the both the *sut4* and *sut5/6* mutants exhibited a different water use strategy than their respective controls (Table 3). The *sut4* mutants displayed a slightly increased RWC in the bark compared to the controls while the RWC was similar between the *sut5/6* and control lines. In the xylem, the RWC did not differ between the *sut4* mutants and their respective controls (Table 3). However, the RWC in the xylem of the *sut5/6* lines was reduced (by ~8%) relative to control trees.

The reduced water content in the xylem of the *sut5/6* mutants suggests that the *sut5/6* poplar detain less water in their xylem, which may reflect a decreased ability to retain water. Nevertheless, the basic wood density was similar between the *sut5/6* and control trees (Table 3). However, the *sut4* mutants exhibited a reduced wood density than the controls. The *sut4* mutants also exhibited a higher fiber saturation point ( $\alpha_f$ ), indicating that the *sut4* mutants had a greater amount of water bound to xylem cell wall than the controls (Table 3). In addition, the amount of free water available to support the hydraulic network ( $\alpha - \alpha_f$ ) was higher in the *sut4* mutants relative to the controls (Table 3).

#### *Wood chemical properties quantitatively changed in sut5/6 trees*

Extractive-free wood samples were subjected to cell wall composition analysis to probe the effects of *sut* perturbation on structural polysaccharide abundance.

Surprisingly, neutral sugar abundance did not differ between the *sut4* lines and their controls (Table 4). When compared to the controls, the *sut5/6* trees had reductions in rhamnose (~20%), fucose (~15%), mannose (~40%), and glucose (~40%) (Table 4).

#### *Metabolite profiling of developing catkins*

To assess whether *sut4* influenced catkin metabolism, metabolic profiling was carried out for three size classes of catkins (e.g., unopened floral bud, newly emerged catkin, elongating catkin) from *sut4* and control line plants (Figure 8A). Sufficient material for replicated profiling of all three size classes of catkins was not available for *sut5/6*. Principal component analysis (PCA) revealed that catkin size classes were metabolically distinguishable by their clustering along PC1, which explained 28.5% of profile variance (Figure 8B). Catkin metabolic profiles thus changed during expansion.

PC2 explained 18.7% of variance, and it appears from the separation of genotype clusters along the PC2 axis that there were genotype effects on the abundance of certain metabolites (Figure 8B). The loadings plot of individual metabolite influence on clustering was then carried out in conjunction with abundance heatmaps (Figures 8C-D). In the loadings analysis, maltose, myo-inositol, dehydroascorbic acid, fructose, and glucose contributed relatively strongly to clustering by catkin size (PC1 in Figure 8C). Relative abundance of those metabolites changed similarly in both genotypes during catkin expansion (Figure 8D). In contrast, catechol glucoside, raffinose, taxifolin, arabinitol, citric and arbutin exhibited relatively strong influences on PC2 (genotype) metabolic variance. In general, with the exception of arabinitol in the unopened floral buds, and galactinol and arbutin in the newly emerged to elongating catkins, metabolite abundance was lower in *sut4* than control line catkins (Figure 8D).

#### *Trophic interactions*

Although the female 717 clone is native in Europe (i.e., Pont du Gard, France), increased sucrose content caused by altered sucrose trafficking could attract herbivorous insects (e.g., aphids) to sugar rich or more highly nutritious tissues. In addition, altered sucrose content could also affect susceptibility to fungal pathogens or could interfere with the expression of genes and production of secondary metabolites or defense related enzymes. Modest insect and pathogen infection was observed on the hybrid trees, but this was not dependent on the genotype (Figure 9). These results suggest that perturbation of *SUTs* did not influence the biotic interactions with respect to herbivores, pathogens, or mutualistic organisms with this introduced poplar clone.

## DISCUSSION

Seasonal alternation between carbohydrate storage during photoautotrophic growth and remobilization during heterotrophic subsistence is a hallmark of the perennial lifestyle (Campoy et al., 2011; Rohde & Bhalerao, 2007; Tixier et al., 2019). However, disruptive effects of global climate change on the timing of perennial marker events such as fall leaf senescence and spring bud flush are becoming increasingly clear (Calinger & Curtis, 2023; Cook et al., 2012; Estiarte & Peñuelas, 2015). In the present study, we found evidence to suggest that tree responses to climate change will depend on specific aspects of sucrose trafficking. For example, stem diameter growth was affected by altered timing of phenological events in *sut4* but not *sut5/6* poplars. In addition to altered growth rates, we also found that the metabolic responses, water use strategies, and cell wall components were differentially perturbed between the two *sut* mutant groups.

This is one of the first field studies to utilize CRISPR gene knockouts to characterize physiological processes in forest trees under natural field conditions. We selected winter-biased *SUTs* to examine how altered sucrose trafficking influenced tree utilization of reserves, growth and phenology over the course of four seasons. The largest differences to biomass yield occurred in the *sut4* mutants (Figure 1B); yet this did not appear to result from a negative effect on sucrose provisioning towards stem growth during the summer. In considering this possibility, the radial growth differential between *sut4* and controls increased in late spring and the early summer but not during other seasons of the year (Figure 1A). Winter depletion of bark or xylem sugar or starch reserves was not impaired in *sut4* mutants (Figure 5). Therefore, spring stem growth, and thus overall growth of the *sut4* trees may have been compromised by factors other than

the availability of local carbohydrate reserves. Interestingly, such changes to tree growth were not found in the *sut5/6* mutant trees.

In addition to the role of sugars during drought response, nonstructural sugars may also act as osmoprotectants during periods of reduced water availability and low temperatures such as in the winter (Guy et al., 2008). For instance, raffinose and galactinol accumulate in response to low temperatures (Guy et al., 2008), and genes associated with their biosynthesis are up-regulated in the stems of *Populus trichocarpa* in the winter (Ko et al., 2011). Both sucrose and myo-inositol are precursors to the synthesis of galactinol. Galactinol acts as a precursor for raffinose biosynthesis by combining galactinol with sucrose to form raffinose, and thus acts as an important building block for raffinose biosynthesis (Sengupta et al., 2015). The winter increases of raffinose and its precursor galactinol were detected at comparatively lower levels in the stems of the *sut4* trees than the controls and *sut5/6* trees (Figure 6). Thus, the results of our study suggest that *sut4* perturbation caused a disproportionately greater seasonal effect on the accrual of oligosaccharide sugars associated with cold tolerance and perhaps the preparation for increased growth in the spring. Furthermore, because galactinol and raffinose serve as signaling molecules during the transition from dormancy to active growth (ElSayed et al., 2014; Falavigna et al., 2018), their reduced levels in the *sut4* stems compared to the controls could also explain the delay in bud break and resumption of growth observed in the spring.

Our results also suggest that the shorter leaf lifespan in *sut4* trees may have contributed to reduced stem growth in the spring. This growth transition may have occurred in conjunction with altered metabolic status in the stems during the winter

(Figures 6-7). The *sut4* plants exhibited advanced leaf senescence in the autumn (Figures 2 and 3), which was unanticipated given the elevated levels of antioxidants (e.g., condensed tannins, galactinol) found in the leaves during the summer and bark in both the summer and winter (Supplemental Figure 4). Given that leaf senescence is triggered by responses to reactive oxygen signaling (Petrov et al., 2015) and increased abundance of antioxidants can protect against oxidative stress, (Gourlay & Constabel, 2019) the accelerated onset of seasonal senescence in the *sut4* trees suggests a complex interplay between antioxidant activity, sucrose trafficking, and environmental changes. Abiotic stresses such as drought and temperature known to affect the timing of leaf senescence also affect *SUT4* gene expression in poplar (Harding et al., 2022; Xu et al., 2018). Interestingly, down-regulation of *StSUT4* in potato was found to alter light quality sensing (Chincinska et al., 2013; Chincinska et al., 2008). Drought can accelerate leaf senescence in deciduous species (Estiarte & Peñuelas, 2015) and delays in bud burst after prior season drought have been reported (Vander Mijnsbrugge et al., 2016). Warming temperatures can also advance leaf fall, negatively impact endodormancy, and delay bud-break in some species (Calinger & Curtis, 2023; Cook et al., 2012). An alternative explanation is that the nutrient (e.g., nitrogen, phosphorus, potassium, micronutrients) recapture from senescing leaves in the *sut4* mutants occurred at an earlier time point relative to the controls and as a result this delayed the spring bud flush (Figure 3). Because the timing of leaf senescence and spring bud flush is often coordinated to optimize tree allocation and growth throughout the perennial growth cycle (Cooke & Weih, 2005; May & Killingbeck, 1992), perturbed fall nutrient recapture may be one plausible explanation for the altered growth. It is also possible that these phenological

changes occurred as the result of altered hormonal (e.g., ethylene, abscisic acid) signaling or redox regulation corresponding to stress tolerance (Jibrán et al., 2013).

The poplar *SUT5* and *SUT6* paralogs exhibited preferential winter expression like *SUT4*, but have overall lower tissue expression than *SUT4*, with as-yet uncharacterized function in plasma membrane sucrose transport (Payyavula et al., 2011; Peng et al., 2014). We show that perturbation of *SUT5* and *SUT6* had modest effects on tree growth and seasonal phenology. However, the *sut5/6* mutants displayed altered cell wall polysaccharide compositions not seen in *sut4* mutants, supporting functional divergence of the *sut* gene family members. Furthermore, most of the phenotypic differences observed in the *sut5/6* trees were specific to the xylem or wood. For example, relative water content was reduced by approximately 8% (Table 3) which corresponded with altered cell wall composition in the form of reduced neutral sugars (Table 4). Yet, no growth anomaly was observed in the *sut5/6* mutants suggesting a condition role for *SUT5* and *SUT6* in secondary stem growth.

Drought and water deficit strategies in trees may be influenced by carbohydrate metabolism and osmotic balance (Sevanto et al., 2014). Water deficits may hinder the development of wood formation by decreasing turgor pressure in the cambium, which may hinder stem growth (Zweifel et al., 2016). Given that osmotic adjustments are influenced by nonstructural carbohydrate compounds, we anticipated that the large amount of soluble carbohydrates present in the stems of the *sut4* (Figure 6) had the potential to influence their water use strategies and responses within the cambial region/cell wall. The higher water content in the bark of the *sut4* mutants is consistent with an increased reserve of water or turgor from the impaired vacuolar sequestration of

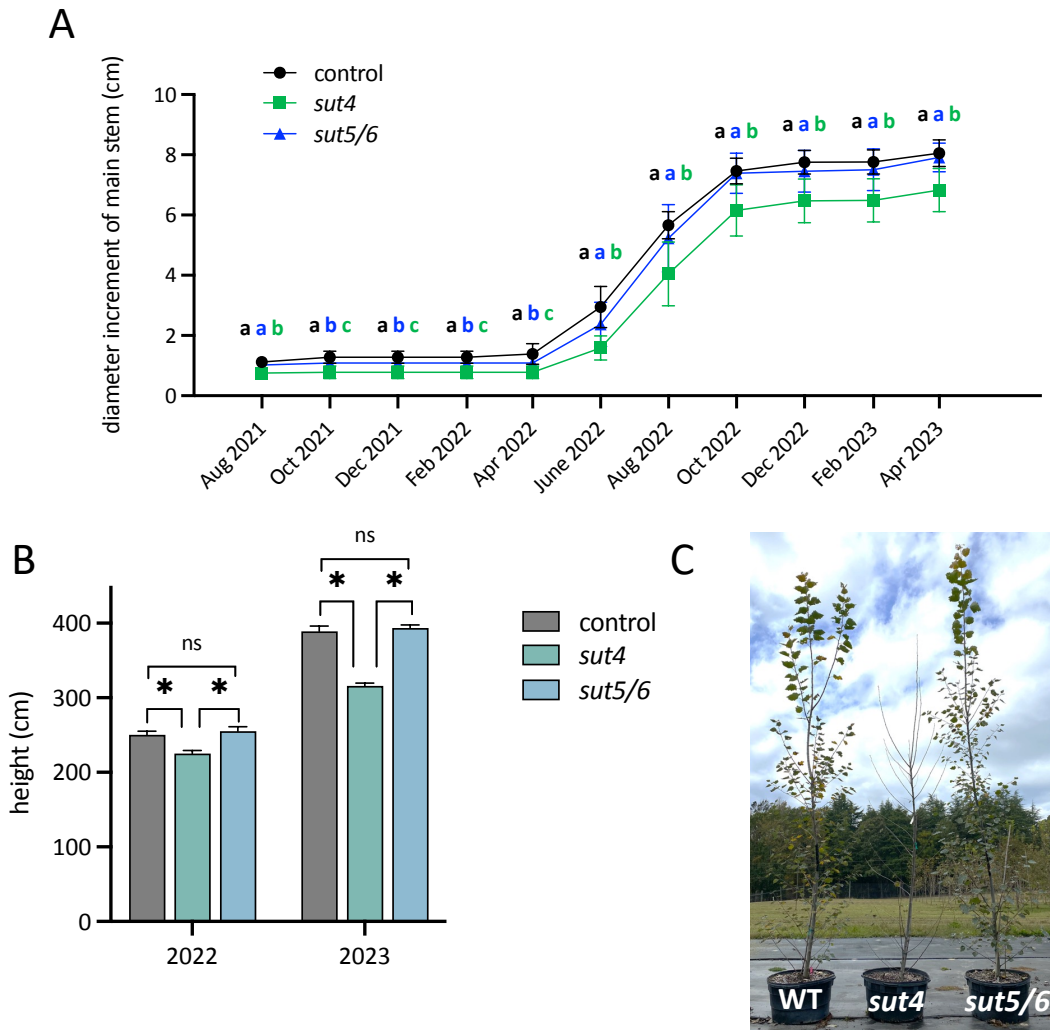
sucrose. As a consequence of this, it is possible that the increased sucrose abundance could have hindered mobilization of sucrose to the cell wall matrix, which could explain the reduced wood density in the *sut4* mutants. The reduced wood density has the potential to contribute to reduced resistance towards embolism and cell wall collapse, both of which are common in poplar (Sperry et al., 1991). The slightly higher amount of water bound to the cell wall ( $\alpha_f$ ) in the *sut4* mutants supports this idea further by suggesting that these poplar mutants could be more sensitive to embolism or drought tolerance. Yet, given the abundance of sucrose caused by *SUT4-KO*, the mutants retained overall a greater amount of free water available to support the hydraulic network ( $\alpha - \alpha_f$ ) when compared to the controls. Such alterations in water usage, although speculative, may have also contributed to the altered bud flush and biomass trends reported in the *sut4* mutants.

Environmental sensing mechanisms to light, temperature, and photoperiod can be influenced by the expression and activity of SUTs. For instance, sucrose can promote superoxide signaling and expression and alter circadian rhythm amplitude in the evening (Román et al., 2021). Leaf senescence may also be positively regulated by sugars, and sucrose in particular, together with other evidence for down-regulation of genes involved in sugar biosynthesis and their transport during senescence (Rolland et al., 2006), suggesting a complex signaling and sensing response to environmental cues. Sucrose partitioning is also coordinated directly with signaling pathways related to secondary metabolism (Roitsch & González, 2004; Wingler & Roitsch, 2008), highlighting how changes to sucrose and sugar abundance can influence the availability of carbon skeleton for either the induction or repression of metabolite biosynthesis. Consistent with a role for sucrose in stress response, *SUTs* exhibit transcriptional adjustments to various

environmental stimuli (Xu et al., 2018). In particular, *SUT4* expression shows dynamic and consistent responses to environmental stimuli (Xu et al., 2018). The present study further supports this notion by highlighting the participation of *PtaSUT4* in mediating the complex responses between resource allocation, environmental cues, productivity, and varying physiological demands.

In conclusion, our results suggest that amongst the *SUT* genes exhibiting winter-biased expression in poplar, *SUT4* may have larger roles than *SUT5/6* in protective metabolism in winter stems and in leaf responses to changes in daylength and abiotic stress.

## FIGURES, TABLES, AND LEGENDS

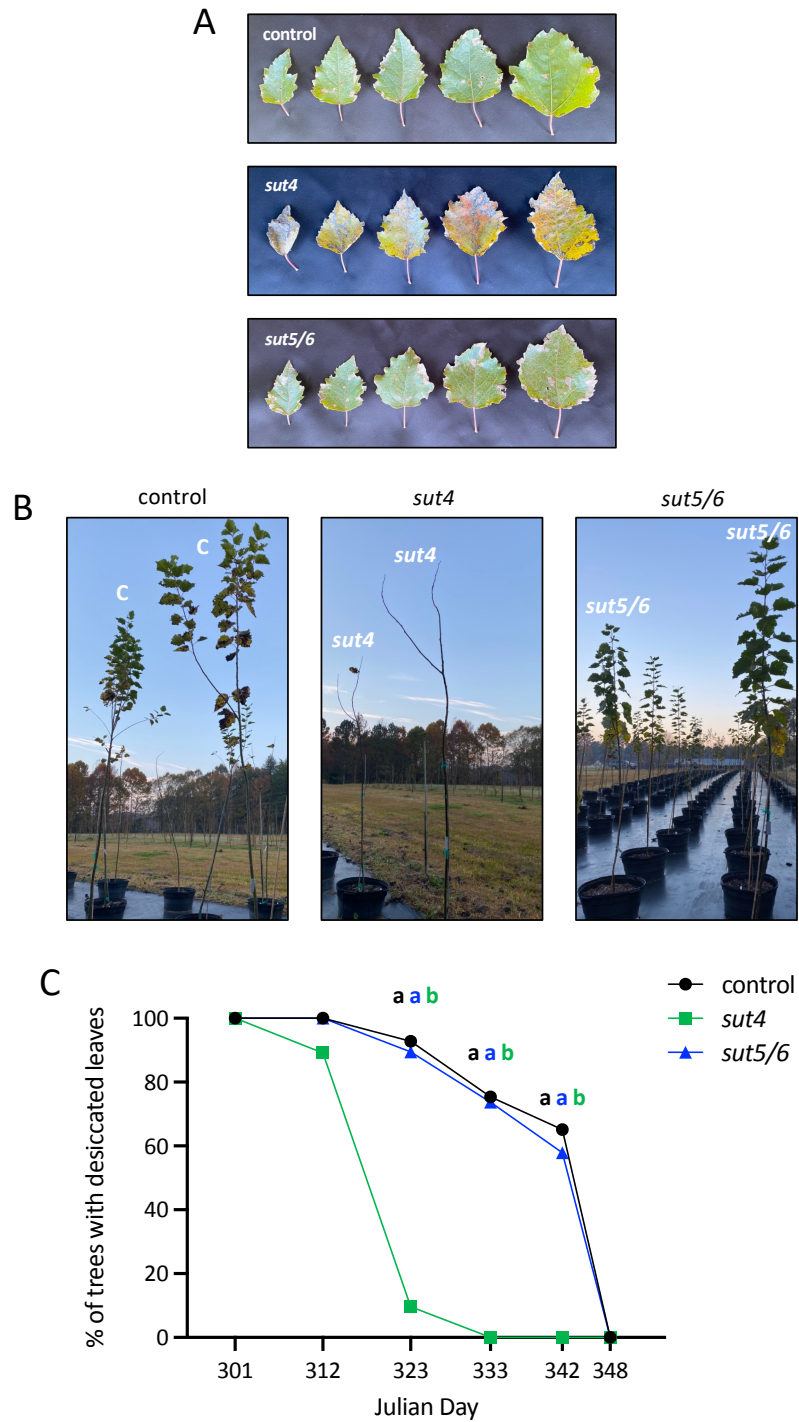


**FIGURE 3.1: Biomass yield and growth characteristics of *sut* and control field grown poplars.**

(A) Stem diameter of trees measured 40 inches above root collar bi-monthly. Data are mean  $\pm$  standard deviation from  $n = 17 - 49$  biological replicates for genotypes. The effects of genotype or time were assessed by a repeated measures two-way ANOVA, followed by Tukey's multiple comparison test with a 99% confidence interval. Genotypes with the same letter at a given date were not significantly different from each other based on post hoc multiple group testing.

(B) Height of dominant stem. The height was measured at the beginning of the growing season in 2022 and 2023. Data are mean  $\pm$  standard error and represents the independent biological replicates of trees per line ( $n = 15 - 22$  using pooled transgenic events and biological replicates). Significance was conducted using two-sample  $t$ -test (\*, \*\*, \*\*\* represent  $P < 0.05$ , 0.01, and 0.001, respectively).

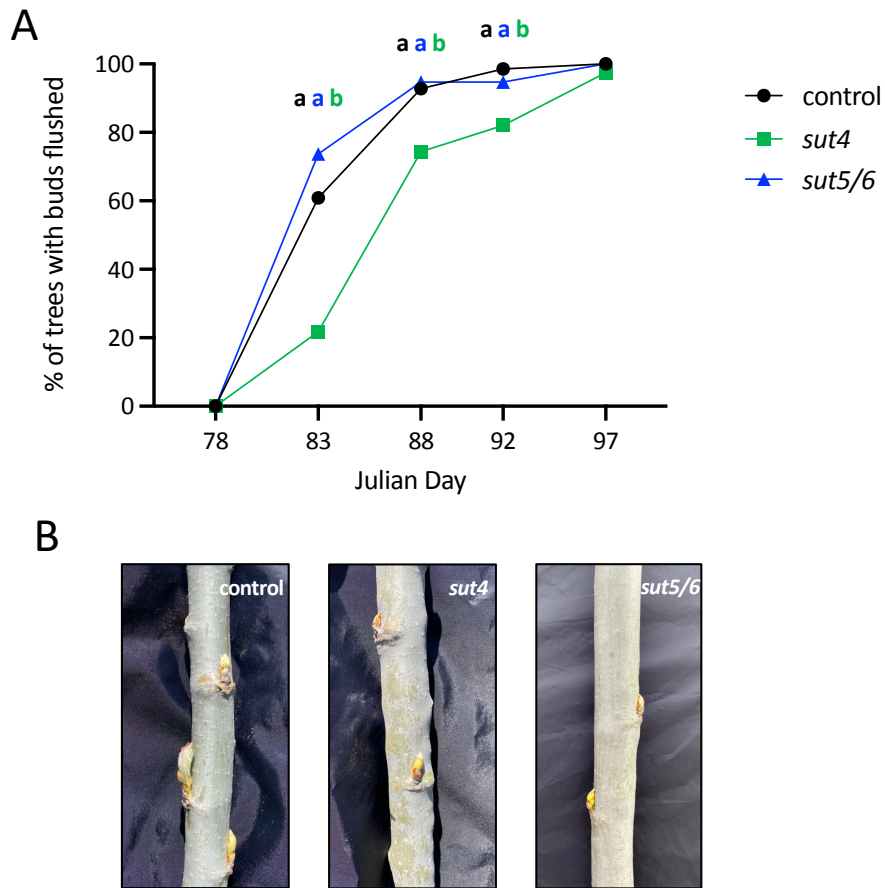
(C) Visualization of growth phenotypes in control, *sut4*, and *sut5/6* poplar fourteen months after field transplanting.



**FIGURE 3.2: Fall leaf senescence in field grown *sut* and control poplars.**  
 (A) Representative examples of adaxial view of leaf LPI-4 to LPI-10 prior to leaf abscission.

(B) Representative photos of field-grown trees taken in November 2021. Images of representative trees selected for images from the field site are labeled with their respective genotypes.

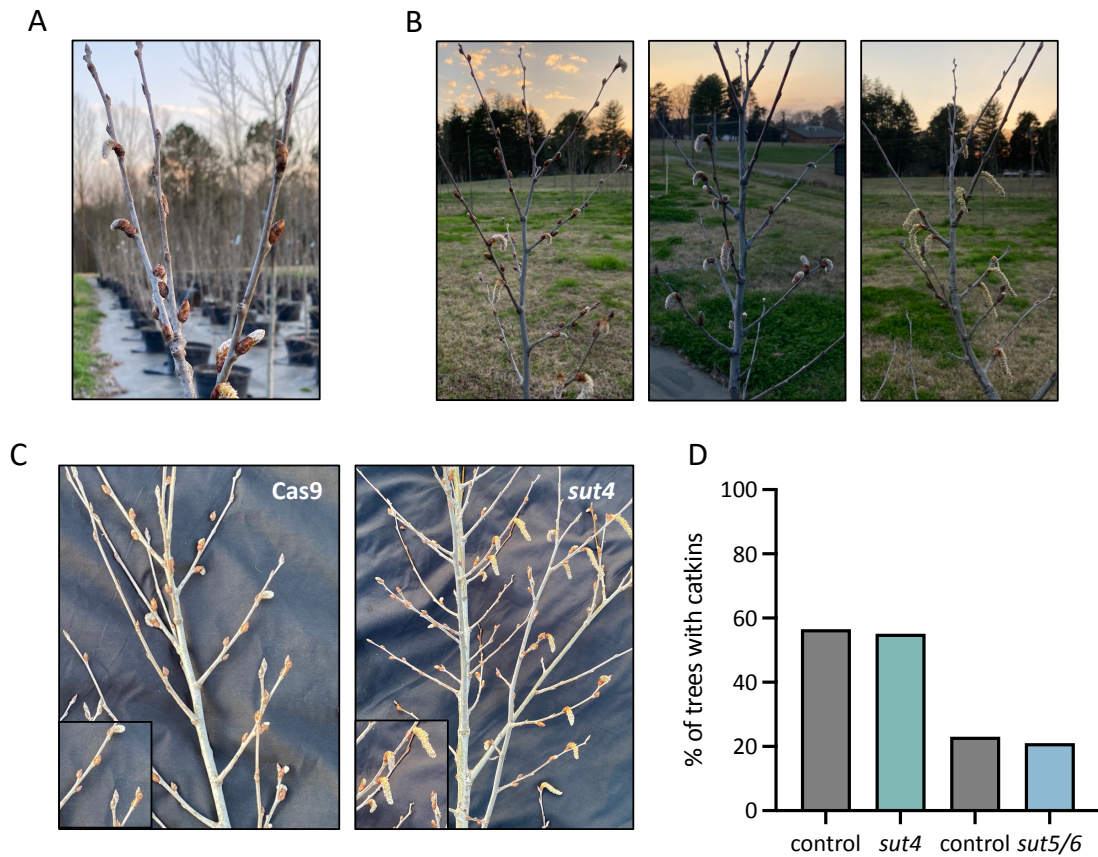
(C) Leaf senescence and abscission was evaluated in the fall when the trees had lost all of their leaves from the main dominant stem. Data represents the percentage of trees per line that had flushed buds ( $n = 19 - 78$  using pooled transgenic events and biological replicates). The effects of genotype or time were assessed by a repeated measures two-way ANOVA, followed by Tukey's multiple comparison test with a 99% confidence interval. Genotypes with the same letter at a given date were not significantly different from each other based on post hoc multiple group testing.



**FIGURE 3.3: Spring bud flush in field grown *sut* and control poplars.**

(A) Bud flush was evaluated in the spring when the trees were still small enough to observe the epicormic buds on the main stem. Data represents the percentage of trees per line that had flushed buds ( $n = 19 - 78$  using pooled transgenic events and biological replicates). The effects of genotype or time were assessed by a repeated measures two-way ANOVA, followed by Tukey's multiple comparison test with a 99% confidence interval. Genotypes with the same letter at a given date were not significantly different from each other based on post hoc multiple group testing.

(B) Representative photos of bud flush in field grown trees taken in early March 2022.



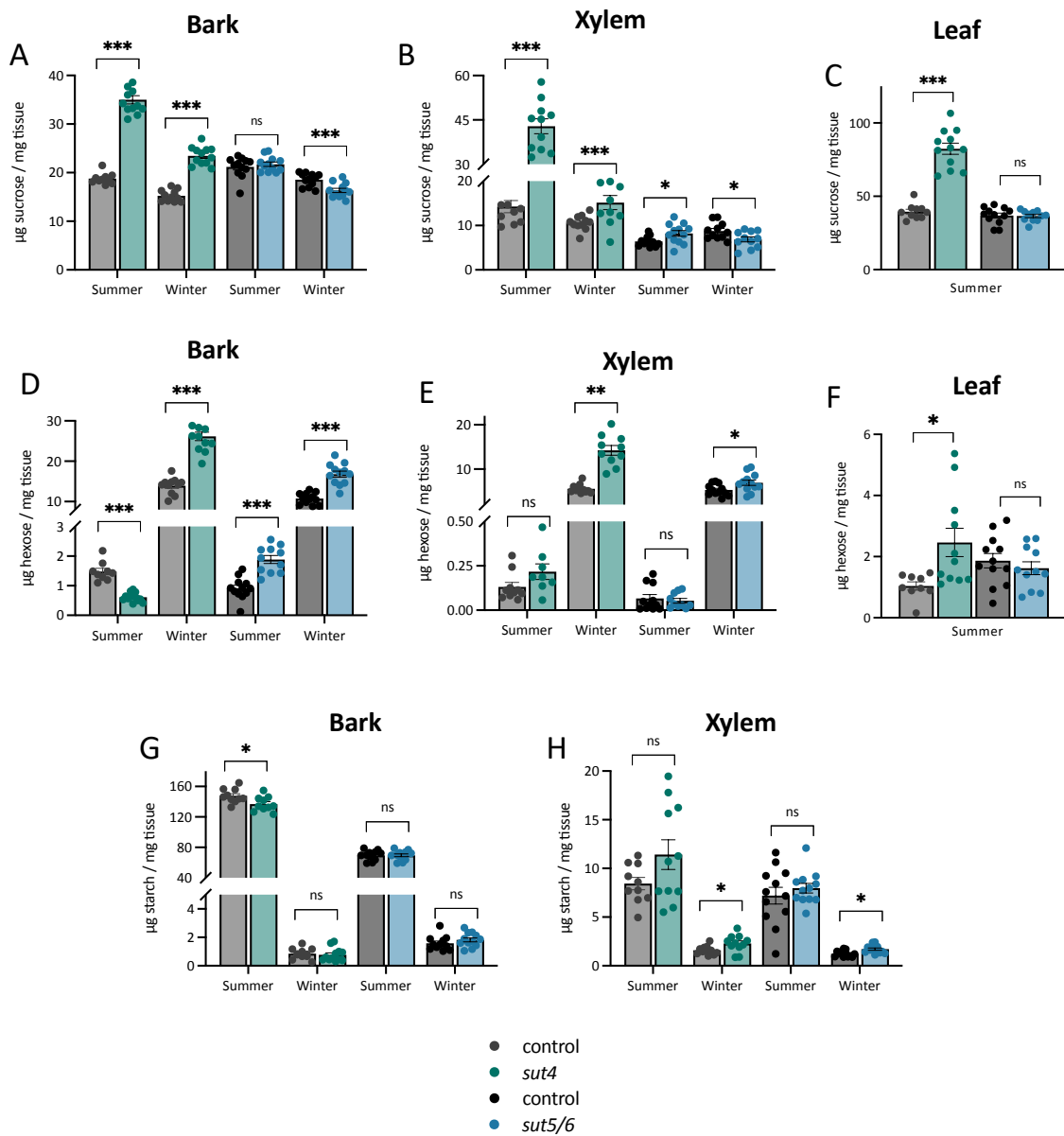
**FIGURE 3.4: Flowering phenotypes in *sut*-KO transgenics.**

(A) First sign of axillary inflorescence bud flushing on early spring 2023 in nursery grown hybrid poplar.

(B) Representative of catkins from multiple trees of various developmental stages on field grown poplar.

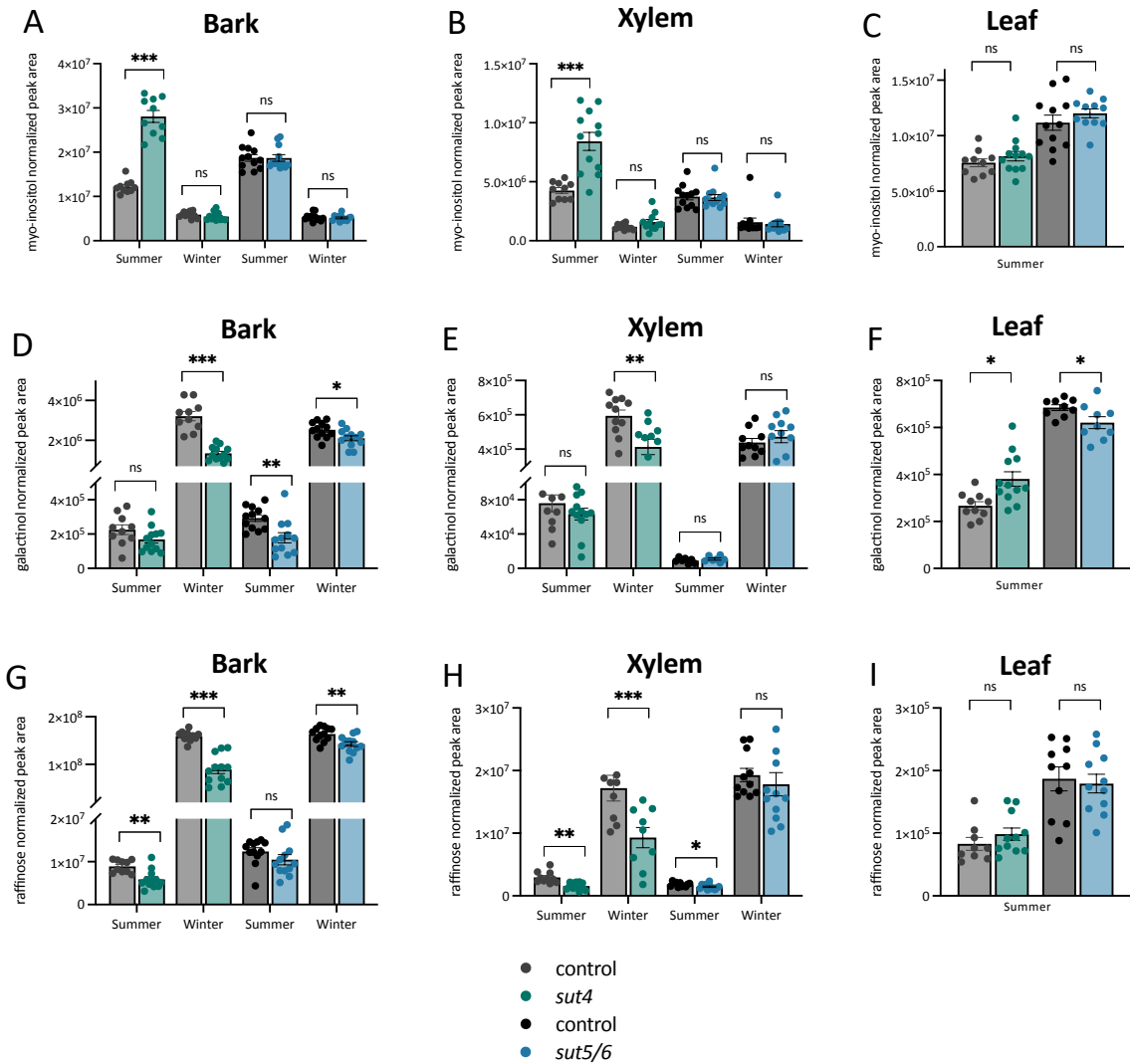
(C) Representative photos of *Cas9* and *sut4* catkins on field trees.

(D) Total % of trees per genotype that developed catkins during the spring of the 2023.



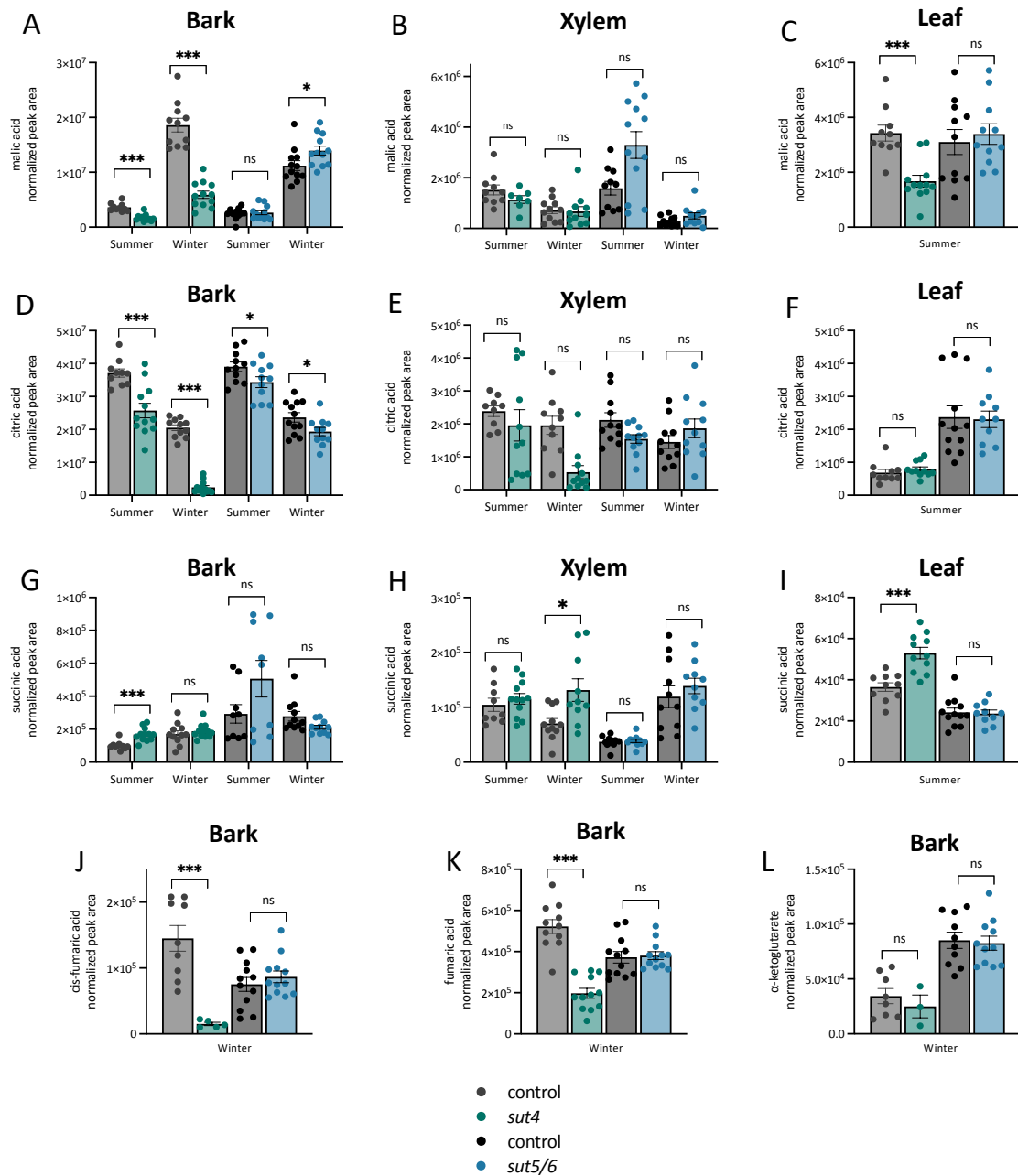
**FIGURE 3.5: Sugar homeostasis in response to *sut-KO*.**

(A-C) Sucrose, (D-F), Hexose (Fructose + Glucose), and (G-H) Starch contents in Bark (A, D, G), Xylem (B, E, H) and mature Leaf (C, F) organs in Summer and Winter. Data are mean  $\pm$  standard error from  $n = 8-12$  biological replicates for control and *sut* lines, respectively. Significance testing was conducted using two-sample *t*-test (\*, \*\*, \*\*\*) represent  $P < 0.05, 0.01, \text{ and } 0.001$ , respectively).

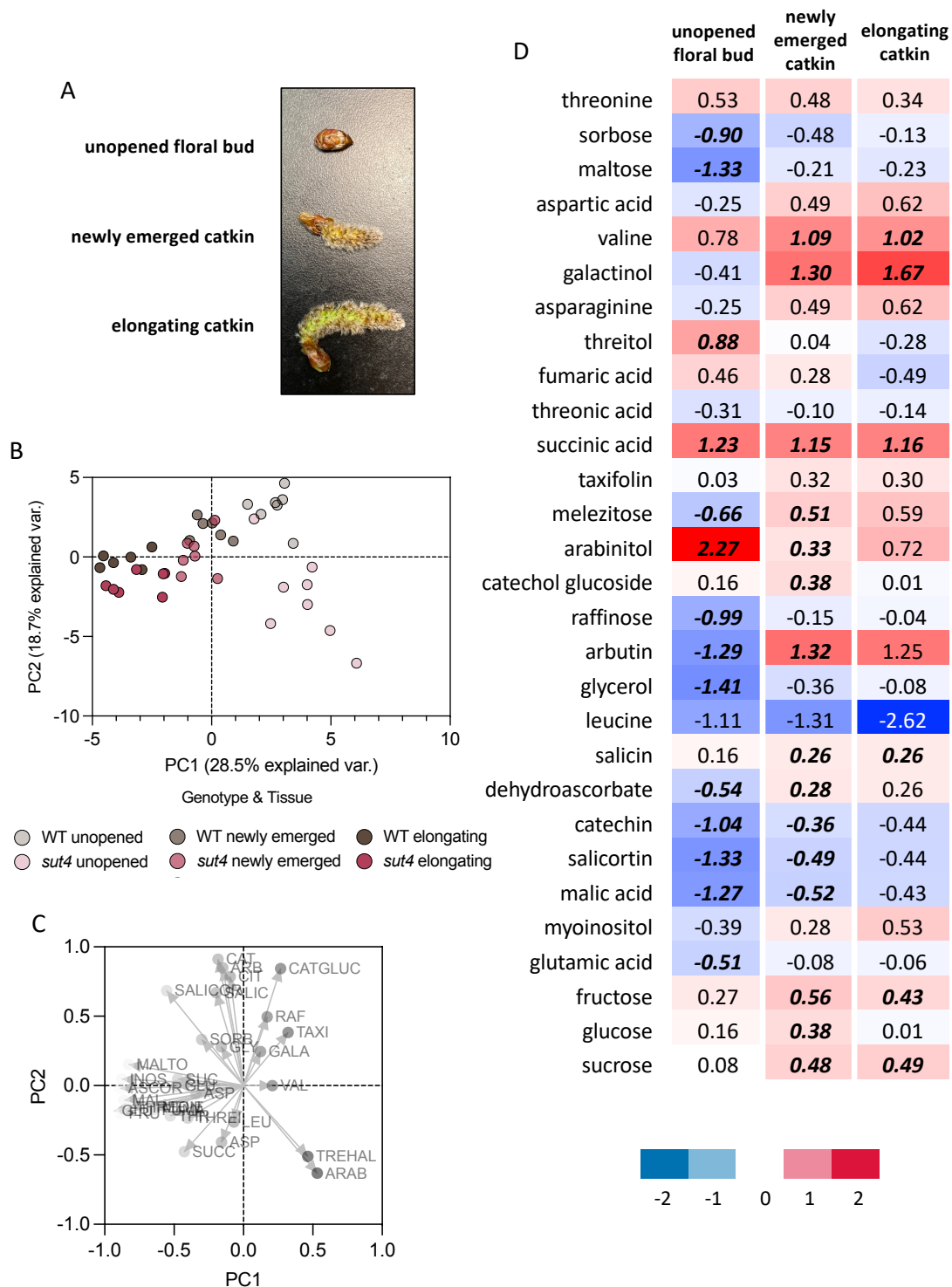


**FIGURE 3.6 Oligosaccharide homeostasis in response to *sut-KO*.**

(A-C) Myo-inositol, (D-F), Galactinol and (G-I) Raffinose contents in Bark (A, D, G), Xylem (B, E, H) and mature Leaf (C, F, I) organs in Summer and Winter. Data are mean  $\pm$  standard error from  $n = 8-12$  biological replicates for control and *sut* lines, respectively. Significance testing was conducted using two-sample *t*-test (\*, \*\*, \*\*\*) represent  $P < 0.05, 0.01, \text{ and } 0.001$ , respectively).



**FIGURE 3.7: Steady state tricarboxylic acid cycle metabolites response to *sut-KO*.** (A-C) Malic acid, (D-F), Citric acid (G-I) Succinic acid, (J) Cis-fumaric acid, (K) Fumaric acid, and (L)  $\alpha$  – ketoglutarate contents in Bark (A, D, G, J-L), Xylem (B, E, H) and mature Leaf (C, F, I) organs in Summer and Winter. Data are mean  $\pm$  standard error from  $n = 8-12$  biological replicates for control and *sut* lines, respectively. Significance testing was conducted using two-sample *t*-test (\*, \*\*, \*\*\* represent  $P < 0.05$ , 0.01, and 0.001, respectively).



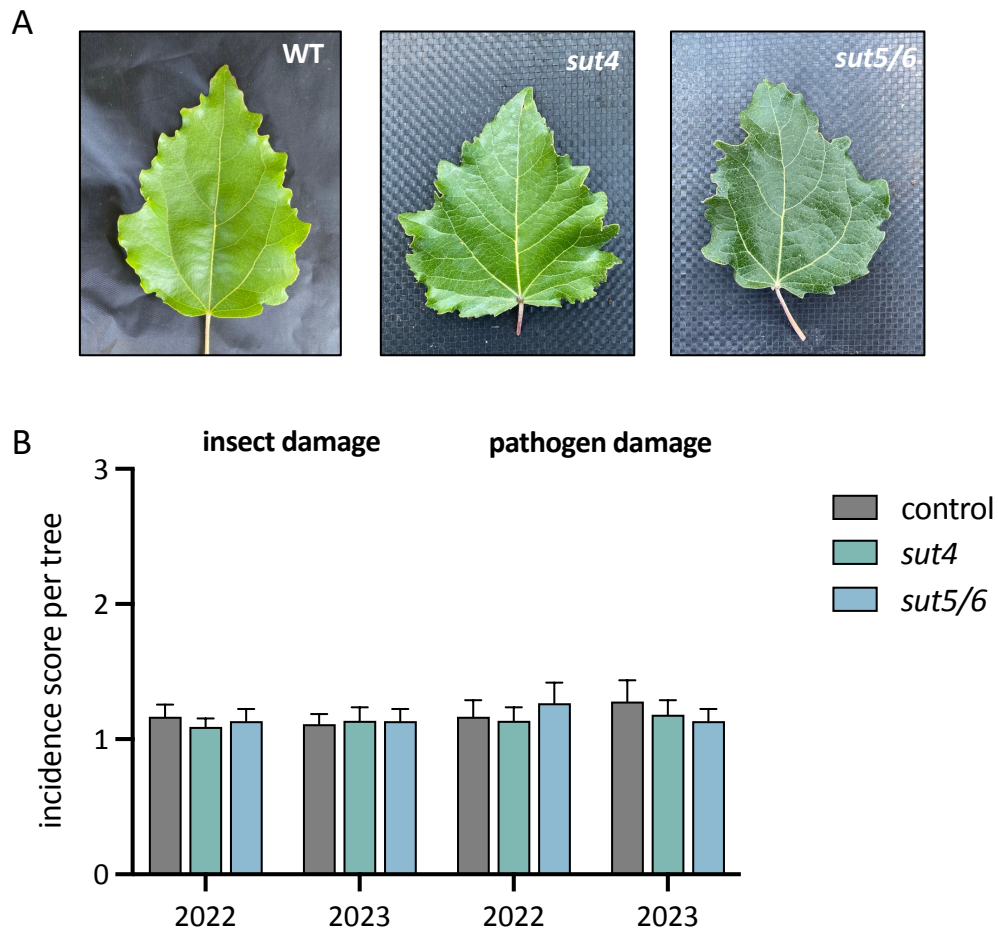
**FIGURE 3.8: Changes in sugar contents and metabolites during poplar catkin development.**

(A) Catkins across various developmental stages in female poplar. Tissues were collected to be representative of three distinct developmental stages (e.g., unopened floral bud, newly emerged catkin, elongating catkin).

(B) Principal component analysis (PCA) of metabolite abundance in the three stages of developed catkins (i.e., unopened, emerged, elongating) for control and *sut4* field grown poplars.

(C) PCA loadings of metabolites. Color gradient indicates loading values ranging from -1 (white) to +1 (black).

(D) Normalized metabolite levels of catkins across three developmental stages from  $n = 8-12$  biological replicates per developmental stage for control and *sut4*. Normalized peak areas were converted to response ratio (*sut4*/control) and log<sub>2</sub>-transformed to indicate abundance and displayed in a heat map. Blue and red colors indicate a lower or higher abundance of metabolites. Values in bold-face, italic indicate statistical significance ( $P < 0.05$ ).



**FIGURE 3.9: Biological interactions of field grown poplars.**

(A) Representative leaves documenting lack of biological interactions between genotypes field grown trees.

(B) Incidence scores represent the level of pathogen or insect damage on the total leaf surface of tree. Trees were scored twice in the second and third year of tree growth. The data represent mean  $\pm$  SD. No significant differences between genotypes were detected.

**TABLE 3.1: Bark disaccharide and phenylpropanoid metabolite abundance in *sut* mutant and control field grown poplar.**

	Summer		Winter		Summer		Winter	
	WT	<i>sut4</i>	WT	<i>sut4</i>	WT	<i>sut56</i>	WT	<i>sut56</i>
<b>Disaccharides</b>								
Melibiose	-	-	<b>7,095 ± 1,640</b>	<b>2,129 ± 737</b>	-	-	<b>6,374 ± 1,101</b>	<b>10,641 ± 2,261</b>
Isomaltose	-	-	<b>1,088 ± 257</b>	<b>303 ± 120</b>	-	-	<b>992 ± 160</b>	<b>1,639 ± 334</b>
Maltose	206 ± 49	192 ± 23	413 ± 59	396 ± 55	608 ± 168	579 ± 51	327 ± 42	309 ± 32
Sophorose	<b>127 ± 37</b>	<b>212 ± 38</b>	<b>106 ± 42</b>	<b>150 ± 50</b>	170 ± 26	254 ± 139	<b>56 ± 28</b>	<b>101 ± 39</b>
Trehalose	294 ± 77	296 ± 85	251 ± 69	272 ± 77	-	-	<b>275 ± 53</b>	<b>377 ± 106</b>
<b>Phenylpropanoids</b>								
<i>Trans</i> -cinnamic acid	1,373 ± 293	1,405 ± 248	<b>1,654 ± 171</b>	<b>1,148 ± 158</b>	1675 ± 653	1431 ± 280	1,147 ± 248	1,304 ± 196
<i>Para</i> -coumaric acid	<b>149 ± 67</b>	<b>66 ± 18</b>	<b>1,508 ± 337</b>	<b>637 ± 175</b>	<b>109 ± 41</b>	<b>182 ± 28</b>	<b>623 ± 197</b>	<b>932 ± 288</b>
Caffeic acid	-	-	<b>102 ± 18</b>	<b>46 ± 15</b>	-	-	60 ± 19	62 ± 23
Hydroxybenzoic acid	-	-	<b>59 ± 11</b>	<b>47 ± 14</b>	-	-	41 ± 9	47 ± 13
Salicortin	383 ± 102	404 ± 131	1,887 ± 1,139	1,697 ± 1,157	<b>888 ± 264</b>	<b>1,839 ± 504</b>	<b>5,096 ± 2,348</b>	<b>8,847 ± 2,435</b>
Salicin	4,311 ± 2160	4,682 ± 2376	<b>27,280 ± 4,152</b>	<b>20,254 ± 3,067</b>	11,534 ± 7,044	13,352 ± 7,220	30,065 ± 5,636	33,295 ± 7,384

Data represent mean ± SD of  $n = 6 - 12$  biological replicates. Statistical significance determined by two-sample Student's  $t$  test and indicated with bold-faced font. Normalized peak areas are divided by 1,000 to facilitate comparisons.

**TABLE 3.2: Xylem disaccharide and phenylpropanoid metabolite abundance in *sut* mutant and control field grown poplar.**

	Summer		Winter		Summer		Winter	
	WT	<i>sut4</i>	WT	<i>sut4</i>	WT	<i>sut56</i>	WT	<i>sut56</i>
<b>Disaccharides</b>								
Melibiose	-	-	-	-	-	-	1,217 ± 461	1,545 ± 711
Isomaltose	-	-	-	-	-	-	159 ± 64	220 ± 97
Maltose	-	-	229 ± 23	244 ± 29	-	-	-	-
Sophorose	33 ± 32	57 ± 27	592 ± 258	893 ± 217	40 ± 31	26 ± 19	668 ± 450	846 ± 447
Trehalose	<b>72 ± 39</b>	<b>189 ± 101</b>	2,390 ± 1,036	3,020 ± 1,295	60 ± 37	85 ± 81	2,955 ± 2,109	3,118 ± 1,795
<b>Phenylpropanoids</b>								
<i>Trans</i> -cinnamic acid	941 ± 211	1,133 ± 243	83 ± 9	75 ± 17	619 ± 110	593 ± 41	679 ± 123	654 ± 193
Hydroxybenzoic acid	<b>13 ± 4</b>	<b>35 ± 29</b>	<b>8 ± 1</b>	<b>23 ± 12</b>	-	-	10 ± 5	11 ± 2
Salicortin	187 ± 164	474 ± 510	692 ± 668	678 ± 507	45 ± 32	74 ± 55	853 ± 656	765 ± 426
Salicin	178 ± 121	266 ± 224	1,066 ± 1,023	1,864 ± 1,924	63 ± 49	54 ± 43	990 ± 785	1,261 ± 1,792

Data represent mean ± SD of  $n = 6 - 12$  biological replicates. Statistical significance determined by two-sample Student's *t* test and indicated with bold-faced font. Normalized peak areas are divided by 1,000 to facilitate comparisons.

**TABLE 3.3: Water content and xylem wood physical properties of *sut* mutant and control field grown poplar.**

Parameter	Control	<i>sut4</i>	Control	<i>sut56</i>
Bark RWC (%)	<b>81.9 ± 1.8</b>	<b>82.8 ± 1.5</b>	82.6 ± 1.8	81.1 ± 2.2
Wood RWC (%)	84.4 ± 4.5	83.5 ± 2.2	<b>85.2 ± 5.6</b>	<b>77.3 ± 4.0</b>
$\alpha_f$	<b>0.32 ± 0.01</b>	<b>0.34 ± 0.01</b>	0.33 ± 0.01	0.33 ± 0.02
$\alpha - \alpha_f$	<b>0.61 ± 0.04</b>	<b>0.84 ± 0.10</b>	0.55 ± 0.06	0.51 ± 0.09
Basic density (kg m <sup>-3</sup> )	<b>444.4 ± 21.9</b>	<b>402.1 ± 33.5</b>	440.6 ± 20.4	448.7 ± 49.7

$\alpha_f$ , fiber saturation point;  $\alpha - \alpha_f$ , free water available to support the hydraulic network. Data represent mean values ± SD of  $n = 5 - 6$  biological replicates per line. Significant differences ( $P < 0.05$ ) between *sut* mutant and their respective controls was determined based on Student's *t*-test and indicated with bold-faced font.

**TABLE 3.4: Cell wall material composition from wood of *sut* mutant and control field grown poplar.**

Structural sugar yields	Control	<i>sut4</i>	Control	<i>sut56</i>
Rhamnose	2.98 ± 0.25	2.90 ± 0.25	<b>3.01 ± 0.18</b>	<b>2.42 ± 0.32</b>
Fucose	0.47 ± 0.07	0.47 ± 0.03	<b>0.49 ± 0.03</b>	<b>0.42 ± 0.03</b>
Arabinose	4.75 ± 2.60	4.02 ± 1.44	4.12 ± 0.88	4.56 ± 0.91
Xylose	96.64 ± 15.32	87.50 ± 10.76	97.43 ± 0.06	95.88 ± 8.16
Mannose	7.09 ± 2.28	6.26 ± 1.64	<b>6.26 ± 0.48</b>	<b>3.58 ± 1.35</b>
Galactose	5.61 ± 0.70	5.27 ± 0.48	5.00 ± 0.46	4.80 ± 0.37
Glucose	18.97 ± 5.71	17.25 ± 5.13	<b>17.61 ± 2.79</b>	<b>11.37 ± 4.60</b>
Total sugars	136.54 ± 14.38	123.70 ± 12.94	133.94 ± 9.69	123.07 ± 7.48

Data represent mean values ± SD of  $n = 6$  biological replicates per line and are presented as ( $\mu\text{g}/\text{mg}$ ). Significant differences ( $P < 0.05$ ) between *sut* mutant and their respective controls was determined based on Student's *t*-test and indicated with bold-faced font. Cell wall composition analysis was performed by Deepti Nambiar & Breeanna Urbanowicz at the University of Georgia Complex Carbohydrate Research Center.

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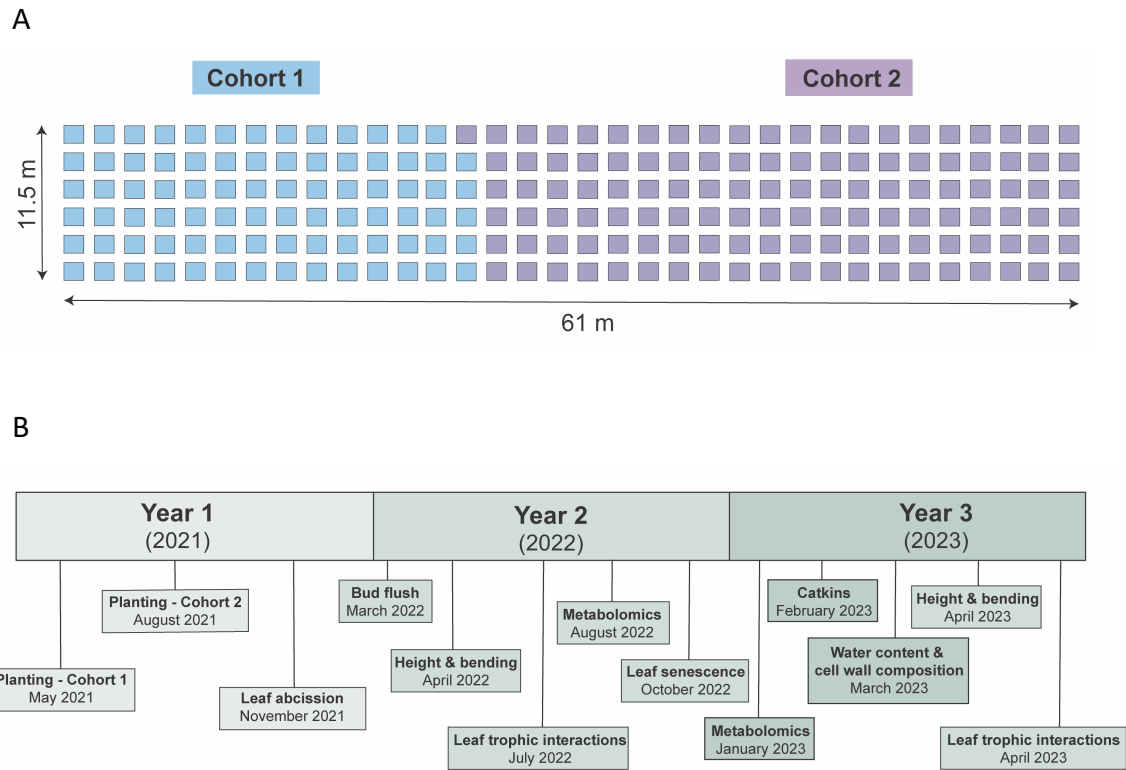
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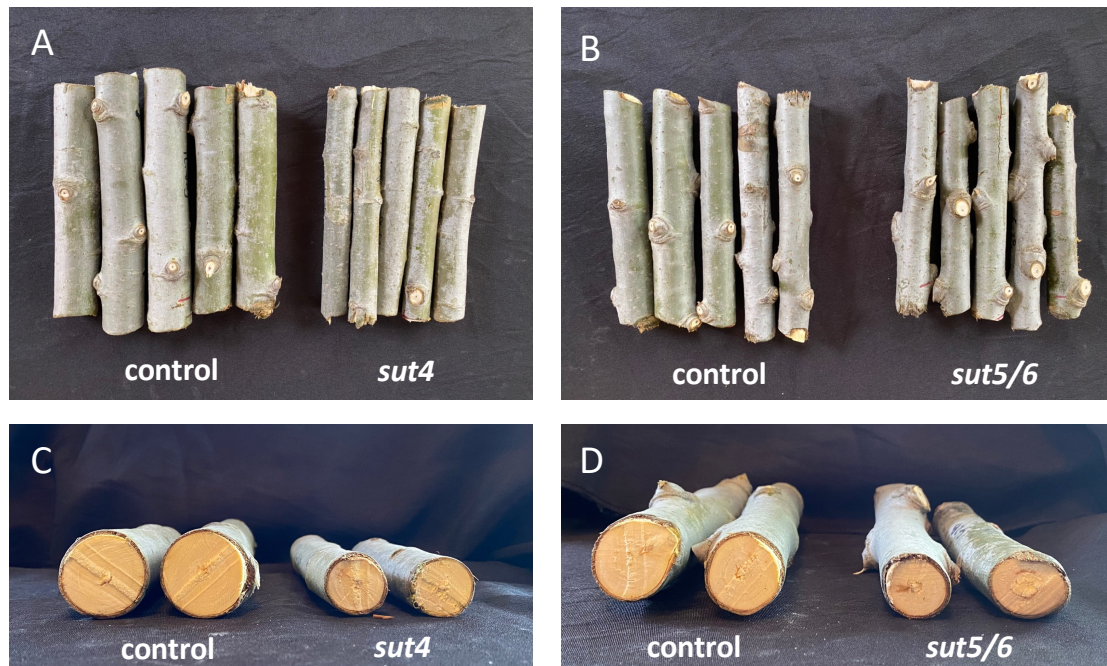
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**SUPPLEMENTAL FIGURE 3.S1: Field trial experimental design and sampling scheme.**

(A) Field trial design of plot with distances of two out-planting cohorts of hybrid poplar. Genotypes were completely randomized throughout the plot.

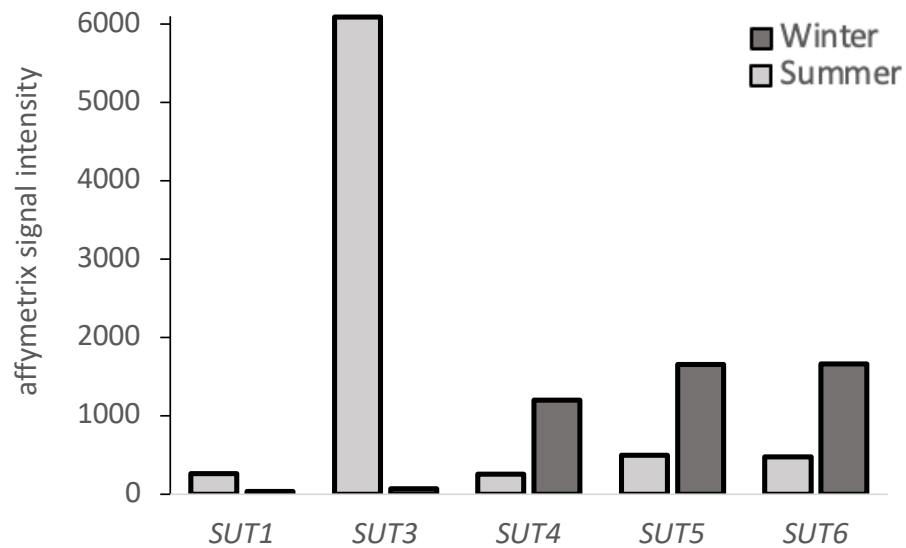
(B) Timeline and schematic of sampling dates. Trees were planted out in the field in June 2021 and harvested repeatedly until the conclusion of the trial in April 2023. Diameter measurements of main stem occurred bi-monthly throughout the course of the trial.



**SUPPLEMENTAL FIGURE 3.S2: Phenotypic growth differences between stems of control and *sut* field grown poplar following destructive sampling for wood chemistry analyses.**

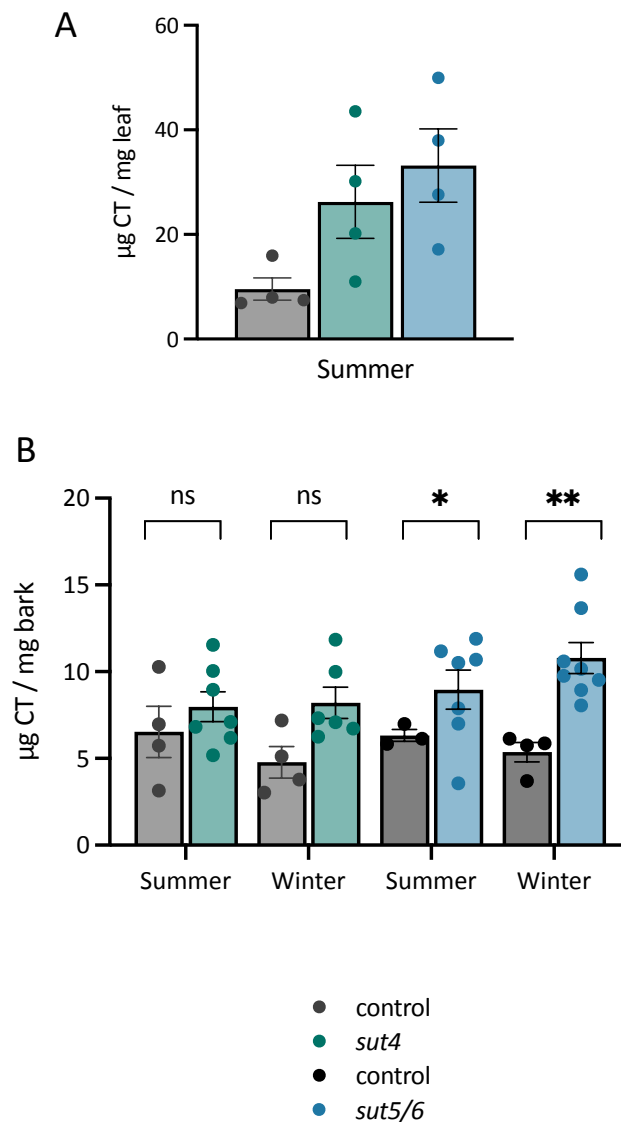
At harvesting in spring 2023, 2-year-old poplar trees were cut into 15cm sections for compositional analysis. Longitudinal photos of stem are shown for the *sut4* mutants and controls (A) and for the *sut5/6* mutants and controls (B). Photos of transverse cross - sections of stems are shown for the *sut4* mutants and controls (C) and for the *sut5/6* mutants and controls (D).

### Seasonal expression of *SUT* gene family



**SUPPLEMENTAL FIGURE 3.S3: Divergent seasonal expression of *SUT* gene family in poplar.**

Transcript abundance of *SUT* gene family in stems (bark and xylem) of *Populus trichocarpa* in Winter and Summer. Data was extracted from Ko et al., 2011 and reprinted here. The *SUT1* and *SUT3* paralogs display summer biased expression, while the single copy *SUT4* and the *SUT5* and *SUT6* paralogs exhibit winter biased expression.



**SUPPLEMENTAL FIGURE 3.S4: Condensed tannin abundance in leaves and bark.**

(A) CT abundance of mature leaf (i.e., LPI-12) in summer. Data are mean  $\pm$  standard error from 4 biological replicates for control and *sut* lines. No significant differences between genotypes were detected.

(B) CT abundance in bark in summer and winter. Data are mean  $\pm$  standard error from 3 - 8 biological replicates for control and *sut* lines. Statistical significance was determined by Student's *t* test between WT and *sut4* plants ( $P < 0.05$ ).

**SUPPLEMENTAL TABLE 3.S1: Mutation patterns of the SUT5/6-KO mutants.**

Line	Allele	Read #	Indel/WT %	Pattern
<b><i>SUT5/6-5-2A</i></b>	SUT5a	7	100	AAATTCGGGCTGGGGCC <u>TTGC</u> <b>.AGCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT5m	9	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.-GCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT6a	1	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGCCAATCCA</b>
	SUT6m	4	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGGCAACTCCA</b>
<b><i>SUT5/6-5-2B</i></b>	SUT5a	8	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT5m	8	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.-GCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT6a	7	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGCCAATCCA</b>
	SUT6m	3	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGGCAACTCCA</b>
<b><i>SUT5/6-6-1A</i></b>	SUT5a	12	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT5m	8	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT6a	10	100	AAATTC--- <u>TTGC</u> ----- <b>-----</b>
	SUT6m	4	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.A--TCCTCTCTCTCACCTCCCTATATTCAGGCAACTCCA</b>
<b><i>SUT5/6-5-1</i></b>	SUT5a	10	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.-GCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT5m	11	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.-GCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT6a	3	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGGCAACTCCA</b>
	SUT6m	1	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGGCAACTCCA</b>
<b><i>SUT5/6-5-2C</i></b>	SUT5a	18	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.A--TCCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT5m	17	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.-GCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT6a	5	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGGCAACTCCA</b>
	SUT6m	4	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGGCAACTCCA</b>
<b><i>SUT5/6-11-2A</i></b>	SUT5a	15	100	AAATTCGGTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT5m	25	96.15	AAATTCGGTGGGGCC <u>TTGC</u> <b>.A--TCCTCTCTCTCCTCACCTCCCTATATACAGGCAACTCCA</b>
	SUT6a	5	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.AAGCTCTCTCTCTCCTCACCTCCCTATATTCAGGCAACTCCA</b>
	SUT6m	100	100	AAATTCGGCTGGGGCC <u>TTGC</u> <b>.-----TCACTCCCTATATTCAGGCAACTCCA</b>

CRISPR mutagenesis editing patterns determined by amplicon sequencing. The gRNA is shown in bold font (PAM underlined) and indel mutations are indicated in red font. Subsequent lines used for phenotypic characterization are indicated with bold, italic font. The *SUT5/6* transgenic plants were generated by Holly McInnes, Hongduyen Pham, & Patrick Bewg.

## CHAPTER 4

### THE DARK SIDE OF DEVELOPMENT: A SYSTEMS CHARACTERIZATION OF THE NEGATIVE MENTORING EXPERIENCES OF DOCTORAL STUDENTS <sup>3</sup>

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<sup>3</sup> Tuma, T. T., Adams, J. D., Hultquist, B. C., & Dolan, E. L. (2021). The dark side of development: A systems characterization of the negative mentoring experiences of doctoral students. *CBE—Life Sciences Education*, 20(2), ar16.

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## ABSTRACT

Effective mentoring promotes the development and success of graduate students. Yet, mentoring, like other relationships, can have negative elements. Little knowledge exists about the problematic mentoring that graduate students experience despite its potentially detrimental impacts. To begin to address this gap, we conducted an exploratory, interview study to define and characterize negative mentoring experiences of 40 life science doctoral students. Students attributed their negative mentoring experiences to interacting factors at multiple levels –from interpersonal differences and poor relationship quality to research group, departmental, organizational, and discipline-level issues – all of which they perceived as harmful to their development. We found that doctoral students experienced forms of negative mentoring similar to those reported in workplace and undergraduate research settings, but they also experienced negative mentoring that was unique to academic research and their stage of development. Our results are useful to mentors for reflecting on ways their behaviors might be perceived, to mentees for avoiding situations that might be conducive to negative mentoring, and to programs and institutions for improving structures and processes to prevent negative mentoring. Our findings also serve as a foundation for future research on the prevalence and impacts of negative mentoring experiences in graduate education.

## INTRODUCTION

Graduate education in science, technology, engineering, and mathematics (STEM) fields in the United States prepares professionals who contribute substantively to the national and global economy, environment, security, and health. The U.S. higher education system consistently remains the largest destination in the world for students to pursue graduate education (National Academies of Sciences, Engineering, and Medicine [NASEM], 2018). Over the past decade STEM graduate education has received increased attention due to high rates of attrition and growing concern over deteriorating graduate student well-being (Levecque et al., 2017; Sowell et al., 2015). For example, attrition from STEM doctoral programs has remained alarmingly high, with over 50% of students leaving before completing their intended degree (Golde, 1998; Lovitts, 2002; Sowell et al., 2015). Equally concerning are recent findings that the majority of graduate students report significantly higher levels of stress, burnout, substance use, and mental health problems (e.g., anxiety, depression) than the general population (Allen et al., 2020; Evans et al., 2018; Hish et al., 2019; Hyun et al., 2006; Levecque et al., 2017; Nagy et al., 2019). As a result, there is a growing interest in identifying and addressing the factors that lead to these undesirable outcomes (NASEM, 2018).

In response, NASEM reports (2018) have called for systemic changes to STEM graduate education with a high priority aimed at improving mentoring relationships and practices. Mentorship has most recently been defined as a professional, working alliance in which a more experienced individual (the mentor) acts as a guide, role model, and sponsor to support the personal and professional growth, development, and success of a less experienced individual (the mentee) (NASEM, 2019). Mentors provide career

support (e.g., career guidance, sponsorship, advancement) and psychosocial support (e.g., counseling, encouragement, role modeling, acceptance) to mentees, which increases the quality of and satisfaction with the mentoring relationship and can improve the outcomes realized by both mentees and mentors (Eby et al., 2013; NASEM, 2019).

In most STEM fields, a principal investigator (PI) of a research group or a faculty advisor is responsible for guiding and supervising the work of a graduate student during their graduate research, with an implicit expectation that the faculty member is a mentor to the graduate student mentee. There is ongoing debate about whether the working relationship between a doctoral advisor and doctoral student is truly a “mentoring” relationship, since not all faculty are viewed as or rewarded for acting as mentors to their students. This distinction is significant because a mentor provides ongoing support and develops a deeper personal relationship, while an advisor provides practical guidance for completing degree requirements and improving content knowledge, in addition to acting as a role model (Eby & Dolan, 2015; NASEM 2018). The difference between an advisor or supervisor and a mentor has empirically been demonstrated to be distinct for employees in the workplace (Ragins et al., 2017; Sosik & Godshalk, 2000), suggesting that mentoring provides important forms of support that an advising relationship likely will not. While the role of faculty members during graduate education has remained contentious (e.g., supervisor, advisor, mentor), we elected to focus on the faculty-graduate student relationship as a mentoring relationship because of the importance of this relationship to graduate students’ training and the assumption that this relationship involves mentorship to some extent given the apprenticeship model characteristic of STEM graduate education.

Effective, high quality mentorship is characterized by the amount of career and psychosocial support provided to the mentee and the overall satisfaction, trust, effectiveness, and reciprocity of the mentoring relationship (Eby et al., 2013; Eby & Robertson, 2020). Such mentorship during graduate education is an essential element of graduate students' development, training, and success (NASEM, 2019). Multiple studies have shown the power of effective mentorship, demonstrating that mentoring is positively related to graduate students' persistence in academic research (McGee & Keller, 2007; Williams et al., 2016), scholarly productivity (Cronan-Hillix et al., 1986; Lunsford, 2012; Paglis et al., 2006; Steiner et al., 2002, 2004; Tenenbaum et al., 2001), research self-efficacy (Paglis et al., 2006; Tenenbaum et al., 2001), rate of degree completion (Lunsford, 2012), and program satisfaction (Lunsford, 2012; McAllister et al., 2009). In fact, some scholars have argued that a graduate student's relationship with their advisor is *the* most important influence on the doctoral student experience (Barnes & Austin, 2009; Lovitts, 2002; Sverdlik et al., 2018; Zhao et al., 2007). This may be particularly true for graduate students in STEM fields because their dissertation research is often directly related to the research agendas of their advisors (Golde, 1998, 2005; Welde & Laursen, 2008).

Despite its apparent importance, graduate mentorship in STEM is understudied compared to studies of mentoring in workplace settings (NASEM, 2019). Meta-analyses of mentoring in the workplace have found small to moderate effects of being mentored (Allen et al., 2004; Eby et al., 2013; Eby et al., 2008; Eby & Robertson, 2020). Furthermore, these studies revealed substantial heterogeneity in the size of the effects of mentorship, suggesting that simply being in a mentoring relationship will not always lead

to positive outcomes. Rather, these findings suggest certain mentoring practices are more effective than others, that the quality of mentorship can vary, and that not all mentoring relationships are beneficial (Eby et al., 2000; Ragins et al., 2000). Scholars collectively refer to the dysfunctional elements of mentoring relationships or less than favorable interactions with mentors as “negative mentoring experiences” (Eby et al., 2000; Limeri et al., 2019; Scandura, 1998; Simon & Eby, 2003). However, the occurrence of a negative experience does not necessarily indicate that the entire mentoring relationship is negative or harmful. Instead negative mentoring experiences can include problematic aspects of an otherwise positive or healthy relationship (Scandura, 1998; Simon & Eby, 2003). In fact, an extensive body of research on intense interpersonal relationships has shown that dysfunctional, unpleasant or problematic events are likely to occur in any prolonged relationship (Duck, 1994; Kram, 1983).

Eby and colleagues’ (2000) seminal work on the negative mentoring experiences of employees in the workplace revealed that over 50% of mentees reported a negative mentoring experience with their workplace mentor, suggesting that negative mentoring may be a widespread issue. Negative mentoring experiences can range from mild, unintentional shortcomings, such as lack of mentor expertise or availability, to more severe and intentional behaviors, such as sabotage and harassment (Eby et al., 2000; Eby & Allen, 2002). These dysfunctional mentoring experiences can lead to a range of negative professional and personal outcomes, such as increased turnover intentions and deteriorating mental health (Eby & Allen, 2002). Furthermore, negative mentoring experiences can have a disproportionately strong effect on mentee performance, productivity, retention, and emotional state compared to high-quality mentoring

experiences (Eby et al., 2010; Eby & Allen, 2002). In fact, negative mentoring in the workplace may be more detrimental than having no mentor at all (Eby et al., 2010; Eby & Allen, 2002). However, it remains unclear if these findings are transferable to STEM research settings and to graduate research in particular.

Johnson & Huwe (2002) hypothesized the potential dysfunctional mentoring experiences that graduate students could encounter with their research mentors in the form of a typology that included poor relationship match, mentor incompetence, neglect or abandonment, hostile or resentful behaviors, exploitation, coercion, and sexual attraction and exploitation. However, this framework has not been empirically tested. The handful of studies exploring less positive mentoring experiences of graduate students are limited to the field of psychology (Clark et al., 2000; Goodyear et al., 1992; Kalbfleisch, 1997). A recent report indicated that there are no empirical conceptualizations of the construct of negative mentoring in STEM graduate education (NASEM, 2019). The paucity of knowledge on this subject warrants attention given graduate students' dependence on their advisor for support and the significant role that advisors play during graduate students' education (Maher et al., 2017; Sverdlik et al., 2018; Zhao et al., 2007).

In the present study, we conducted an exploratory investigation to define and characterize the negative mentoring that graduate students experience in their research. We conducted semi-structured interviews with a sample of life science doctoral students in the U.S. ( $n = 40$ ) who represented diverse institutions, socio-demographics, and program timepoints, and who indicated that they had negative experiences with their research mentor. Participants not only reported issues specific to their mentor and mentoring relationship, but also spoke unprompted and candidly about research group,

departmental, and institutional issues, as well as issues they attributed to the nature of academic science research that they perceived were affecting the mentoring they experienced. In order to capture these experiences, we made the post-hoc decision to analyze and interpret our results using ecological systems theory (Bronfenbrenner, 1977; Chandler et al., 2011). Ecological systems theory allows for the investigation of the fundamental behaviors and processes of individuals and their relational aspects, as well as how these practices and norms are shaped by organizational and disciplinary cultures. By using this analytical framework, we gained insight into the contextual factors, including departmental, institutional, and discipline-level issues, which graduate students perceived as shaping and constraining their mentoring experiences (Chandler et al., 2011). Here we report the results of these analyses at each level of the graduate life science research mentoring ecosystem, ranging from interpersonal differences and poor relationship quality, to research group, departmental, organizational, and discipline-level issues, all of which doctoral students perceived as impacting their personal and professional development (Figure 1).

## **METHODS**

This study was reviewed and determined to be exempt by the University of Georgia Institutional Review Board (STUDY00006750).

**Participants.** We utilized a purposeful sampling strategy (Merriam, 1998) to recruit a diverse group of participants with respect to social identity (e.g., gender, race/ethnicity) and institution (e.g., private/public, location). We contacted potential participants by emailing listservs of life science professional society graduate student groups, asking administrators and graduate coordinators at U.S. research universities to

distribute study invitations to doctoral students, and emailing doctoral students directly at the email addresses publicly available on department websites from U.S. research institutions. Participants were also asked to share the study information with peers whom they believed met the study criteria (i.e., snowball sampling). Because we distributed emails to lists and departmental directories, we are unable to accurately estimate response rates.

We chose to focus on doctoral students in the life sciences because the life sciences represent the largest and most demographically diverse sub-field within STEM in the U.S. (National Science Foundation [NSF], National Center for Science and Engineering Statistics, 2019). We also expect the mentoring norms and practices, as well as the nature of graduate education, to differ across STEM disciplines; we sought to account for these differences to some extent by limiting our sample to the domain of life sciences. It is worth noting, however, that the life sciences span a wide range of research contexts and approaches (e.g., bench, fieldwork, computational). Thus, to some extent, the life sciences may serve as a microcosm of the range of mentorship that STEM graduate students experience. We minimized recruitment from our own institution given the proximity of participants to our research group and the sensitivity of the subject matter. Not surprisingly, the majority of doctoral students were reluctant to participate without being granted complete confidentiality due to the sensitive nature of the topic and fear of repercussions. Some of our participants reported they only participated in our study because they would be graduating prior to the dissemination of the study results, which they believed would minimize potential repercussions.

Participants were emailed the study information and a link to an online screening survey (see Supplemental Material) using the secure survey service Qualtrics, following a screening procedure similar to prior research on the negative mentoring experiences of undergraduate life science researchers (Limeri et al., 2019). In the screening survey, participants self-reported their eligibility, specifically that they: (1) were working or had worked as a graduate researcher for at least one academic year, (2) were pursuing or had earned a PhD in a life science discipline within the past year, and (3) had at least one experience that was perceived as negative with their research mentor, therefore having a direct experience with the phenomenon under study (Morse et al., 2002). Participants were asked to rate the quality of the mentoring relationship with their graduate advisor and the quality of their graduate education experience on two, seven-point Likert-scale items ranging from -3 to +3, and to explain the rationale for their rating. Finally, participants were asked to report demographic information (e.g., degree status, years of PhD completed, gender, race, and ethnicity).

We received 101 survey responses with varying degrees of completion. We strategically selected a sub-sample of these individuals for interviews who rated their relationship quality with their graduate advisor as negative or less than ideal (+1 to -3) and who represented a range of personal characteristics, program timepoints, and institutional affiliations and thus could report on a range of dysfunctional mentoring experiences (Patton, 1990). We also used the short answer section as confirmation that we were inviting doctoral students to participate who had indeed experienced a range of negative mentorship. We contacted 50 individuals and ultimately interviewed 40 individuals (10 did not respond to the interview invitation), representing 22 U.S.

institutions, including public and private institutions that were classified as high or higher research activity (Carnegie Classification of Institutions of Higher Education, accessed December 2019; see Table 1). We opted to stop additional data collection after interviewing these 40 individuals because we had reached saturation, meaning that participants began reporting ideas that had already been described by other participants (Guest et al., 2006). We elected not to ask participants to provide any information about their mentors (e.g., career stage, participation in mentoring professional development) because exploring the influence of these factors would require a different study design and methods, although some of this information was revealed organically during the interviews.

**Data Collection.** We collected data using semi-structured interviews over phone or video conference. Each interview lasted 40-60 minutes and was audio recorded. T.T.T. (a life science doctoral student) conducted all of the interviews to ensure consistency and because we believed that participants would be more forthcoming about their experiences with a peer. We designed the interview questions to gain an in-depth understanding of any negative or problematic aspects of the mentoring that doctoral students experienced during their research. Specifically, our questions probed into doctoral students' perceptions of their mentor's behaviors and traits and the quality of their relationship with their mentor, as well as any problematic events, situations, or negative elements of their mentoring experiences (see Supplemental Material). We did not ask participants about how their research group, department, institution, or disciplinary culture contributed to their negative mentoring experiences, but participants described these issues unprompted. When participants commented on these elements, we asked

spontaneous follow-up questions to understand how these components shaped their mentoring experience. Interview recordings were transcribed verbatim by Rev.com and checked by the researchers for accuracy. All identifying information that participants described in their interviews (e.g., names of individuals and institutions, research techniques, model organisms) were removed and replaced with pseudonyms to protect participant confidentiality. Participants were offered a \$25 Amazon gift card as compensation for participating in an interview.

**Data Analysis.** We conducted qualitative content analysis to define and characterize negative mentoring experiences in life science doctoral education. Because participants brought up contextual factors unprompted, we saw a need for additional theoretical framing to fully understand these mentoring experiences. Therefore, we used ecological systems theory to understand how multi-level influences shape negative mentoring outcomes. Ecological systems theory posits that phenomena are shaped by multiple environments (i.e., systems) that interact with and influence one another (Bronfenbrenner, 1977). We used this theory in our analysis to understand how negative mentoring experiences are shaped and effected by systems occurring at four distinct levels – individual mentor issues (ontogenic system), relationship issues (dyadic system), local environmental influences (micro system), and discipline-level influences (macro system) (Figure 1) (Chandler et al., 2011).

We began our analysis by importing the interview transcripts into MaxQDA (Verbi Software, 2019) for open coding to identify segments of the text (i.e., quotes) that described a distinct negative mentoring experience (Saldana, 2015). T.T.T. carefully read and identified distinct negative mentoring experiences, which were then categorized into

one of the four systems outlined in ecological systems theory. T.T.T. and E.L.D. independently indexed a subset of the quotes from each of the four levels individually using an *a priori* set of codes originating from prior studies examining the negative mentoring experiences of employees (Eby et al., 2000; Scandura, 1998) and undergraduate researchers (Limeri et al., 2019) to generate a preliminary codebook. We also incorporated themes from literature describing supervisory issues in the workplace (Cortina et al., 2001; Schyns & Schilling, 2013; Tepper et al., 2017). We expected that the integration of these themes would help us interpret and make meaning of the data. Our codes consisted of short phrases or sections of the text that contained a specific example of a negative mentoring experience, in addition to a definition to describe the experience.

We then tested our preliminary codebook with the entire dataset. At least two researchers (T.T.T, J.D.A, B.C.H) re-read each transcript in its entirety, looking for evidence of negative mentoring experiences, and coded the transcripts using our preliminary codebook in a very iterative process. We met after coding several interviews to discuss our codes until we reached consensus. When we came across a new phenomenon that was not represented in an existing code, we created a new code to capture this experience (Starks & Brown Trinidad, 2007). When we added, modified, or collapsed codes, we revisited our prior transcripts and looked for evidence of quotes that were aligned with the revised code (Saldana, 2015). Throughout this process we further refined the definitions of the codes to ensure that our codes accurately captured the participant experiences. For experiences on which we could not reach consensus, we consulted with an additional author until consensus could be reached. We also used axial

and pattern coding to identify and group together codes that represented similar themes in order to capture the common ways that doctoral students experienced negative mentoring (Saldana, 2015; Strauss & Corbin, 1998). For example, codes relating to problematic supervisory issues (e.g., abusive, micromanaging, hands-off) were all grouped into one theme termed “supervisory styles.”

We took additional methodological steps to ensure that our analysis accurately captured contextual variables that were related to participants’ negative mentoring experiences. We utilized process coding, which identifies actions or gerunds in the data in order to examine connections and processes between phenomena (Saldana, 2015). This approach allowed us to identify potential relationships between negative mentoring experiences across the system levels to determine how these phenomena related to themes in the ontogenic and dyadic systems. Specifically, we looked for instances of micro (local environmental influences) and macro (discipline-level influences) phenomena and attempted to trace these instances back to how doctoral students described them as influencing their mentor’s attitudes, behaviors, or characteristics (ontogenic) or their relationship with their mentor (dyadic). We included the experiences that we could trace back to ontogenic or dyadic phenomena and excluded the experiences that did not have a clear connection to a mentor or mentoring per se. For example, we included experiences where participants described how contextual variables shaped their mentors’ behaviors and mentoring relationship (e.g., promotion and tenure). Some participants recalled poor experiences with graduate school (e.g., dysfunctional departments or institutions, systematic inequalities) but they did not specify whether or how these experiences related to their mentoring experience, so these experiences were

not included. After we completed our analysis, we organized the emergent themes into a conceptual model to explain the manifestations of negative mentoring experiences within the academic life science research ecosystem.

We took several steps to ensure the trustworthiness of our findings. First, we repeatedly compared quotes within and across codes and across systems to ensure that our thinking remained stable over time (Kolb, 2012). Second, all researchers were fully immersed in the data for an extended period of time and read the transcripts multiple times during the analysis, which allowed us to critically and thoroughly analyze and interpret the data. Two or more researchers coded all of the data to consensus, which reduces potential variability among coders and minimizes the likelihood of omitting critical components of this complex construct (Belur et al., 2018). We also sought out external feedback from experienced qualitative researchers, life science graduate faculty, and members of the University of Georgia Biology Education Research Group, who provided an outside perspective on our data and interpretations to help ensure the credibility and dependability of our findings (Hsieh & Shannon, 2005; Lincoln & Guba, 1985).

**Researcher Characteristics.** Our experiences and perspectives as researchers are also relevant for interpreting the results. T.T.T. (doctoral student), J.D.A. and B.C.H. (undergraduate students), and E.L.D. (faculty member) are researchers in life science departments at a public, high research activity doctoral university and have science training in the life sciences. We were all familiar with prior research on negative mentoring experiences in the workplace and undergraduate research settings. Our familiarity with this literature helped us identify and ascribe meaning to various types of

negative mentoring experiences, while the open coding process helped to ensure that our analysis included the experiences unique to doctoral students. We have all participated in mentored research experiences in the life sciences, and we (T.T.T. & E.L.D.) have prior experience studying mentoring relationships in academic and research settings. Our complementary positionalities as a research group helped us balance potential biases and strengthened our holistic interpretation of the data (Miles et al., 2014). Specifically, E.L.D. is the PI of a research group with 15+ years' experience mentoring graduate students and is the doctoral advisor of T.T.T. Additionally, J.D.A. and B.C.H. are undergraduate researchers who brought an “outsider” perspective to the graduate mentoring relationship.

## RESULTS

Here we present the findings of our exploratory study to describe and characterize the negative mentoring experiences of life science doctoral students. Doctoral students in our sample attributed their negative mentoring experiences to multiple levels of the science research ecosystem: practices, values, and norms of science that influence mentorship (**macro system**); research group, departmental, or organizational factors that influence mentorship (**micro system**); relationship quality and functions between the mentor and mentee (**dyadic system**); and mentor behaviors and characteristics (**ontogenic system**). We present descriptive accounts of the ways doctoral students in our sample experienced negative mentoring, starting with the overarching themes at the macro level and concluding with the mentor specific traits at the ontogenic level (summarized in Table 2). We also indicate the number of participants who reported experiences related to each theme to give some sense of the commonality of the theme in

our sample. However, counts should not be interpreted as indicators of the prevalence of negative mentoring experiences in the national population of life science doctoral students because our study design and methods were not intended to measure frequency.

**Macro System.** The macro system refers to the practices, values, and norms of academia and life science research that influence mentorship practices and shape negative mentoring experiences. Doctoral students described four macro level phenomena that they perceived as influencing the mentorship they received: gatekeeping, lack of incentives for quality mentorship, power structures, and role tension (presented alphabetically).

**Gatekeeping.** Several participants (n=5) described the culture of graduate education and of science in general as a gauntlet where only the “best” survive. Participants felt that the culture of academic science research purported the view of science and graduate training as extremely difficult and that poor mentorship were a necessary part of training that would ultimately help them succeed or “weed out” those who would not be successful. In this sense, negative mentoring experiences were promoted as a gatekeeper to deter individuals who did not have the necessary talent or disposition. Participants described the culture of academic training as one where only those who were the strongest, smartest, and most passionate would survive and be able to pursue a career in science. The people who left science because of negative mentoring experiences were perceived as doing so because they lacked the characteristics or talent to prosper as a scientist, as Makayla recalled:

*“I did an internship at a large funding organization... I was talking with my supervisor one time... and they said ‘Well, we don’t care about the people who give up because they are badly mentored. We care about the people that are so great that they will become great scientists no matter what people do to them’...*

*That's the attitude that people have in science. The fact that it's not supposed to be a profession or a job, but that it's supposed to be a passion... Some sort of like tortured artist thing whereby you're so passionate about your art that they can't make you not do it... And that is such a toxic attitude... but people see being deterred by bad mentoring as lack of commitment to the art..."*

**Lack of incentives for quality mentorship.** Some doctoral students (n=6) in our sample described cultural beliefs, values, and norms within academic research that undermined the formation of high-quality mentoring relationships. In most cases, participants explained that their mentors were focused on advancing their own careers (e.g., achieving promotion and tenure), and that providing quality or effective mentorship would not help them achieve these goals. Specifically, participants explained that only research productivity (i.e., grant funding, publications) were weighed in how their mentor was evaluated and that there were no incentives, rewards, or expectations to provide quality mentorship. For instance, Kamala reasoned that the promotion and tenure process played a key role in shaping her marginal mentoring experience:

*"My mentor doesn't have tenure yet, so a lot of the things that she's done I felt have been because she's presumably under a lot of pressure to get tenure... She made me feel like my research didn't deserve as much attention as some others' in the lab... I wanted to apply to give a talk at a conference... and at this point I'm a sixth-year graduate student and I presented my first poster two months ago... I tried to talk to her about it because I would really like to present and get feedback on my work. She said 'Well, you're welcome to try to get an abstract but I want you to apply to conferences where no one will know me.' Because outside feedback from people in her field, that aren't at the same university is an important part of her tenure package and how she's evaluated... She's trying to establish herself in the field... and market the lab in a very specific way, and my sense is that my project didn't fit into that."*

**Power structures.** About a quarter of the participants (n=11) described that the power differentials and hierarchy between graduate students and PIs were pervasive elements of academic culture that contributed to their negative mentoring experiences. PIs were perceived as having the freedom to function as they pleased and were able to

exert power over their mentees without any checks and balances or accountability for their actions. For example, Su described that “the bad professors can do whatever they want and have to do something super, super bad in order to get punished.” Other participants felt their mentors were “untouchable,” even as assistant professors without tenure, although full and associate professors were believed to be even more powerful. For example, some mentors blatantly told their mentees that they were in the position of power, which allowed them to coerce or threaten their mentees (e.g., withholding a letter of recommendation). Participants felt that the power differential allowed dysfunctional mentor behaviors (ontogenic) and poor mentoring relationships (dyadic) to develop and persist. Because of mentors’ power and control, participants felt unable to defy their mentors or address issues with them. For example, Jada experienced mentoring issues at the ontogenic and dyadic levels that she attributed to her reliance on her mentor for professional endorsement:

*“This is not just a teacher or a professor that I’m taking a course with, this is my mentor, my PI. Any letters of recommendation that I really need would come from him because he’s known me...for an extended period of time. But I choose not to dwell on [my issues with him] or show negative feelings towards him, because I know that he still has to sign off on my degree. He still has to write a letter. I may need his connections... I need his approval at the end of the day.”*

Participants also described how the norms of science, especially the enactment of these norms in policy and practice, contributed to and enforced the power differential between doctoral students and faculty. For example, participants explained how graduate program policies and procedures ensured PIs held power because PIs had to sign off or approve mentees’ research in order for mentees to graduate. Other participants explained that it was a norm in the discipline for their PIs to serve as authors on their research publications, regardless of their contribution to the project, which reinforced PIs’ power

over doctoral students. Kara recalled her experience writing a paper and then submitting it to a journal in her PI's name to increase the likelihood of it being favorably reviewed because of her PI's reputation and connections (i.e., power), as opposed to the quality of the work.

*“We submitted the proposal for the editorial review board to consider and you can only submit it in one person's name. We know someone on the review board and they said we should definitely submit it in your advisor's name because they won't accept something by an unknown grad student. Just put down your advisor's name and they'll definitely look at it and consider it. It was sort of funny... I wrote the entire outline, the intro letter, and the entire application. She didn't really do anything with it, but then we submitted it in just her name.”*

**Role tension.** Several doctoral students (n=6) reported that there appeared to be a tension in academic research between graduate education as a developmental experience and graduate research as a job. Specifically, doctoral students felt that they were simultaneously playing two competing roles: a learner and an employee. Many doctoral students were funded from their PIs research grants, which set up the implicit expectation that they were employees. Participants described how their mentors treated them like employees whose sole responsibility was to produce research results and thus their relationship was more supervisory rather than developmental. Some participants indicated that they were expected to produce data constantly and that there was little room for career exploration or skill and interest development that did not directly relate to their research. For example, mentors were known to be reluctant about supporting mentees' pursuits or interests outside of academic research (e.g., internships, professional development courses) because this meant they were not working on the projects that their mentors viewed as valuable or productive. This disconnect about the purpose of graduate

education allowed for tension to form regarding the type of relationship and support the mentees desired and what their mentors were able to provide. Ash explained:

*“I definitely feel like a cog in a machine... me being viewed as like a disposable or interchangeable asset rather than a developing scientist or a human myself. Like I am an employee working for a salary, just churning out results, rather than a student or mentee that needs mentorship and might go onto bigger things one day.”*

Collectively, these macro system results indicate that graduate students in our sample attributed at least some of the negative mentoring they experienced to aspects of academic research and the nature of graduate education. These participants acknowledged that at least some of their poor experiences with mentors were attributed to the larger system rather than the ill intent of individual mentors.

**Micro System.** The micro system refers to factors in the local environment, including the research group, department, and institution, that contribute to or otherwise influence graduate students’ negative mentoring experiences. Participants described three micro level phenomena: collegial protections, insufficient structure, and social undermining.

**Collegial protections.** A fifth of our participants (n=8) described that faculty in their graduate programs were protected when doctoral students expressed concern over their mentoring relationships. The protections occurred for a variety of reasons that included academic freedom, seniority, and program or departmental needs. Doctoral students perceived that these protections allowed mentoring problems to go unchecked or unresolved because many faculty were hesitant to address or confront their colleagues. For example, doctoral students described that early-career, untenured faculty appeared unwilling to intervene to defend graduate students who experienced negative mentoring

behaviors from senior, tenured faculty. Doctoral students also perceived that faculty mentors who were known to be successful with grant funding or private donations were also allowed to mentor as they pleased. Some participants described that their mentors were “very likeable” in their department and had received awards or formal recognition for their research, teaching, or mentoring, making it difficult for doctoral students to gain credibility when they claimed they were experiencing dysfunction in their mentoring relationship. Other doctoral students explained how faculty took a laissez-faire attitude towards colleagues’ mentoring behaviors because interfering ran counter to the tenet of academic freedom. The prevailing belief in these local environments was that faculty were free to function as they pleased because of their position or status in the university, as Brock explains:

*“Everyone knew how poor my [mentoring relationship] was. People would stop me in the hallway and tell me like, ‘I’ve heard how poorly things are going with the [mentor].’ And I’m like, ‘yeah it sucks.’ And they’d be like, ‘I’m so sorry,’ and move on... All you did is make yourself feel better about making me understand that you know, but aren’t going to do anything... Step up, you are tenured. Tell that person to stop behaving this way... I completely understand, for someone that’s tenure track, I also would not put my career on the line. But if you’re tenured, I don’t understand why people wouldn’t just call it out and say, ‘That person is behaving poorly and abusing people.’ What’s the risk?”*

**Insufficient structure.** Nearly half of the participants in our study (n=18) expressed concern about a lack of policies or procedures aimed at providing structure or addressing issues that arose in mentoring relationships. Some of these students were in situations that were particularly unstructured, such as their mentors being on sabbatical or on personal leave for an extended period. Students in these situations noted that they did not receive any support or resources from their department or university to take the place of their inaccessible mentor. Other students focused on the lack of structure for reporting

mentoring issues. Several participants sought out help from their graduate coordinator or departmental and institutional leadership. Of these participants, some reported that their attempts were dismissed or that they were actively discouraged from reporting mentoring issues. Others reported not seeking support because they perceived that these attempts would be disregarded or not taken seriously, or that the individuals in these positions were inaccessible or unwilling to advocate on their behalf. Yet other participants described a competitive or hostile departmental culture that made them hesitant to show any signs of shortcomings, either of their own or their mentor. They were concerned that bringing attention to mentoring issues would be a sign of weakness for themselves or their mentor. Collectively, these students believed that there should be program-level supports in place to assist them when they were experiencing mentoring issues, as Laurel highlights:

*“At my university if two faculty members have conflict, then they go to HR [human resources]. If two graduate students have a conflict, I think they go to the chair of the department. But if a graduate student and a faculty member have a conflict, there is no course of action or procedure... So there’s really nowhere to go if you are having issues.”*

A number of doctoral students felt that dissertation committees were a natural structure to buffer against limited support from their mentors. However, several students described how their attempts to receive support from their committee members were unsuccessful. Participants recalled that it was common for their committee members to have constraints on their time, resources, and expertise that prevented them from providing effective mentoring support. For example, Olivia described how she relied on her committee members because her mentor was inaccessible, but struggled to receive adequate support:

*“I’ve been trying to reach out more and rely on [committee members] for resources. My committee hasn’t really been too great, but they also aren’t being*

*difficult... I feel like I'm not getting enough guidance from them... The one that I thought would be the bioinformatics person, I found out that they are not a bioinformatics person. He hasn't been helpful. Another is just very absent, he's like, 'get it done and get out of here.' The third, is really nice and I like her, but they are the furthest removed from my research... I feel like I'm not getting any real guidance on the direction of my research."*

**Social undermining.** Over half of the doctoral students in our sample (n=23) described instances where mentors acted in ways that undermined their standing in their research group, department, and institution (Duffy et al., 2002). Although these behaviors could fit within the ontogenic system, we categorized these experiences as part of the micro system because participants described these experiences as having micro-system level effects, such as harming their relationships and reputation with others in their local environments. Doctoral students described instances where mentors gossiped or spread rumors about them, created divisiveness between the mentee and others, or made insidious or belittling comments about them in front of dissertation committee members, research group members, or other influential people in the students' immediate environment. Doctoral students felt these damaging remarks seemed out of place or inappropriate, especially in the presence of others. They perceived these actions as harming their reputation and research-related success, as Isaac explained:

*"We would have a group class that she would teach. In the middle of lecture she'd start critiquing me in a way that was nothing to do with the lecture or anything... These sort of small little snippets in front of other students that I feel are really not helpful... plus I don't understand why a professor would demean a student in front of other students. I understand it being critique in a one-on-one meeting setting, but to critique someone actively and verbally in front of other students I was uncomfortable with."*

Participants also described how their mentors' interactions with other research group members promoted a working environment that was pernicious, aggressive, or

otherwise not conducive to their professional growth and productivity. These instances made it challenging for mentees to seek support from lab mates and strained their relationship with their mentor, especially if their mentor avoided or was unable to effectively address confrontations or disputes that occurred among lab members. Some doctoral students indicated that they were in research groups where their mentor's spouse was an employee in the group, and they described how this could contribute to negative mentoring experiences. These situations typically involved the student confiding in the spouse, who then reported the details of the conversation to the mentor. In other cases, a spouse's presence in the lab was perceived as a "spy" who then reported lab goings-on to the mentor. Doctoral students reported that these experiences led to a sense of discomfort and mistrust in the research group, which compromised the quality of the work environment. Maria recalled how her mentor's spouse made it difficult for her to form working relationships with others or to solicit support from her mentor:

*"It was always him and his wife, they always had to be together in everything for some reason... Our lab schedule was just so strict and we couldn't take a day off... If we were late or took a day off, his wife would come yelling at us in front of everyone in the lab and it was just so scary... the lifestyle of lab... we just didn't have any liberty at all. [The spouse] was always on top of us and [my mentor] always took her side. He never took any perspective other than hers."*

Considered together, these micro system results indicate that local environmental factors either created situations where negative mentoring could be experienced or failed to protect doctoral students when negative experiences occurred.

**Dyadic System.** The dyadic system is represented by the mentoring relationship, which encompasses its quality (e.g., level of trust, reciprocity, connectedness in the relationship) and functions (e.g., the level and forms of support the mentor offers the mentee). Experiences within the dyadic system were specific to individual mentee-

mentor relationships and could vary from one mentee to another, in contrast to the ontogenic system, which was attributable to the mentor and affected all mentees.

Doctoral students reported four forms of dyadic level negative mentoring: interpersonal mismatch, limited career support, limited psychosocial support, and poor relationship quality.

**Interpersonal mismatch.** Nearly half of the doctoral students in our sample (n=19) noted that they did not match with their mentors in terms of personality, workstyles, communication preferences, or values. Mentees perceived that, because they did not match well with their mentor, they missed many of the outcomes associated with successful mentoring relationships. Some students noted general mismatches between themselves and their mentor. For example, Addison explained:

*“He would give, I suppose, ‘suggestions’ and he wanted the students to guide the project ultimately, but I wanted a bit more of like, ‘Let’s talk through these things together and then have an agreement about whatever I’m going to do and then I’ll go do it.’ He was more of an ideas person and he was not a pragmatist, where I was always much more realistic.”*

Other participants commented on specific mismatches in terms of career goals that resulted in lower quality relationships with their mentors. Adrianna explained how she and her mentor had different viewpoints and values on the goals of graduate school:

*“It got to a point where she was having a really hard time understanding why I cared for other things that weren’t related to academia. She’s like, ‘I think it’s great that people out there in the world are doing things to make the world a better place.’ But she also just had a hard time understanding why I cared, when [she thought] my priority, and not only my priority, but the main thing in my life should only be grad school. That was very hard for me, because that’s something very core of who I am... improving the community.”*

**Limited career support.** Almost all of the graduate students in our sample (n=38) expressed concerns that they did not receive sufficient career advice or scientific

guidance from their mentors. Several graduate students described instances where their mentors prevented or discouraged them from presenting their research at or attending conferences. For example, Aaron described how his mentor did not allow graduate students with incomplete work to attend conferences, saying that,

*“[My mentor] doesn’t allow his students to go to conferences unless their project is finished, because he has been scooped before and is fearful of that happening again.”*

Other participants described situations where their mentors did not provide them with guidance or feedback with writing proposals, job applications, or manuscripts. Evan described his experience of attempting to secure funding for his research with little to no help from his mentor:

*“I wasn’t funded when I came to the lab... I am constantly applying for grants. I know that is your job as a grad student, but at some point, you’re sort of expected to have a PI write for some money... I just got an email from him and it says “Hi Evan. I just ran across this page of various grants. Cheers, Mentor.” That’s it. It’s a link. A link to a website with 20 different hyperlinks. So, it’s like yes, I know how to use Google... Can you say the ones that you’ve applied to in the past that have been successful? Or that your colleagues applied to? I mean, I guess I need to take some responsibility. I’m a smart dude or I wouldn’t be in grad school, but it’s just overwhelming. I’m supposed to be teaching, taking classes, and I’m swamped with research and it’s just like do all that while finding your [own] funding.”*

In other instances, participants wished that their mentors would have advocated on their behalf in committee meetings or assisted them with networking at conferences. Addison described her experience of writing her dissertation and trying to defend her thesis while her mentor was not engaged:

*“I had met my end of the bargain and got [my mentor] the dissertation. He read the first two chapters of my dissertation and gave me edits, and skimmed the remaining three. Two of which were ones with data we had never really talked over... so the lack of comments was especially not helpful... He also wasn’t advocating for me on behalf of my committee, he wasn’t making time, he wasn’t guiding any of the process. He would write, at least in two emails, ‘Just do*

*whatever you need to do to make them like your dissertation. Just make it work.’ I would get some edits back from the committee and want to talk them over with him, and he would say ‘Just do it.’ I would and he would come back with, ‘Oh well now I need to edit this. I want more say in this.’ I was like, look, you can’t give me full responsibility in doing it the way it needs to be done and then try to take it back and put your hands back in. Either you are in this and helping me or you let me do whatever I need to do to finish and you just sign it off.”*

**Limited psychosocial support.** The majority of doctoral students in our sample (n=28) also expressed concerns about not receiving validation or appreciation from their mentor. Mentees wished that they would receive more verbal encouragement, counseling, or emotional support, particularly during challenging or stressful events in graduate school. For example, Thea commented on how her mentor’s lack of praise undermined her development:

*“I wanted a lot more attention than he was giving me. I think a lot of that was because I was really insecure about research... I just wanted someone to tell me that I was doing a good job or that I was in the right direction. I don’t think I heard a ‘good job’ from my mentor until I defended my dissertation.”*

Other doctoral students described instances where their mentors made comments that undermined their confidence. For instance, Rosalie described how her mentor frequently made comments that made her feel invalidated and unappreciated, explaining that:

*“by the end... I definitely wasn’t happy, which I think is pretty normal... I just didn’t want to deal with the confrontation and always being told that I’m wrong without any explanation. It was just very discouraging.”*

In other situations, mentors appeared to question the students’ commitment to the program and to their degree. Laurel described how her mentor’s comments made her feel unmotivated and discouraged her from viewing herself as an academic:

*“He told me that he thought I wasn’t going to graduate and that he thought that he wanted my PhD more than I want my own PhD, which I think is one of the worst insults that I’ve ever heard. Coming off of the fact that I had been*

*struggling so hard to pass my qualifying exam, to hear that I'm not going to graduate was a really hard thing and exactly the opposite of what motivates me. I am not motivated by fear or by stress, I'm motivated by opportunity. Him telling me that I'm not going to graduate made me want to work less hard."*

**Poor relationship quality.** Nearly half of the doctoral students in our sample (n=19) felt that their mentoring relationships were generally of poor quality, lacked positive relational elements (e.g., empathy, reciprocity, respect), or that they did not have a strong personal attachment or connection with their mentor. Some mentees reported that their relationship with their mentor was practically non-existent, while others noted a lack of closeness or trust. For instance, Thea recalled that her relationship with her mentor felt insubstantial, explaining that:

*"Compared to a lot of people I wouldn't call it bad. It wasn't terrible, it just wasn't great. It just, it was almost like he wasn't a mentor to me at all."*

Often mentees indicated that their mentoring relationship felt compulsory or lacked depth beyond a supervisory or formally assigned relationship. Ash described:

*"I just get the feeling sometimes like that she couldn't care less about what I'm really doing in the lab as long as it produces results. This lab is pretty well funded and there are a lot of students that would like to get into it... Sometimes I feel easily replaceable and that she really couldn't care less... If I told her tomorrow that I was leaving the lab, she probably wouldn't bat an eye, at least to my face."*

Some participants felt that their mentors tried to resolve their relational issues, but that their attempts were not successful and contributed to future issues. For example, Lily likened her relationship with her mentor to that of an abusive romantic relationship:

*"Whenever we had big fights... she would say 'Let's go out for dinner.' She would always be nice to me right after a fight... She'd listen and apologize but then she'd do the same thing again. Looking back on it is ridiculous... It was like how you bring flowers to your girlfriend after you beat them up. Not joking, that's really what it was like. But then she'd do the same thing again and again."*

Other doctoral students felt that their mentor was not sincere or believable, which undermined trust in the relationship. Lee described how his mentoring relationship was characterized by distrust:

*“If I ask [my mentor] a question and he tells me an answer, and then the next day he completely forgets the way he worded things. Now I’ve learned to write things down, repeat it to him, and he says ‘yes.’ One day he told me straight up that I am lying, that I had made it up, and I was like ‘I literally wrote down word for word what you told me to do.’ ... So I distrust him about certain things.”*

Collectively, the dyadic system results indicate that all of doctoral students in our sample experienced one or more problems with the quality of their mentoring relationship and the support they received from their mentors.

**Ontogenic System.** The ontogenic system is characterized by individual-level characteristics and behaviors of the mentor as perceived by the mentee. We observed six main forms of ontogenic-level negative mentoring experiences: deceit, inaccessibility, limited expertise, limited interpersonal abilities, problematic supervisory styles, and unequal treatment.

**Deceit.** About a quarter of participants in our sample (n=12) described instances where their mentor behaved or acted in ways that misrepresented or “hid” information about research obligations, expectations, lab or work norms, and career motivations from their mentees. Doctoral students recognized that these actions had occurred after they discovered information that contradicted their mentors’ justifications or explanations. In many situations, participants felt that these actions were related to the mentor’s own career motivations or outcomes (e.g., tenure, sabbatical, professional moves, retirement, authorship decisions). These behaviors often led to strained relationships because mentees felt that they were not trusted by or able to trust their mentors. Ash described

how his mentor moved their laboratory to a more prestigious institution, providing no information about the move until the plans had already been solidified:

*“A week before lab meeting, [my mentor] said, ‘I have some lab business to discuss after lab meeting next week, so please make sure to attend.’ I didn't think much of it... but the rumor mill got churning and some people figured it out that somehow she was moving to another campus, a more prestigious campus. I heard those rumors and thought, ‘There's no way. That would be crazy,’ but that's what it ended up being. This must have been all but certain for a matter of months and she didn't share anything about the process or the possibility of it with those of us in the lab who it really impacts... It was really a bummer to feel that way... like this important information had been hidden from us because it wasn't necessary to our productivity I guess, but it is necessary for our future planning and especially for me.”*

**Inaccessibility.** Almost all of the doctoral students (n=38) in our sample reported that they did not receive sufficient attention from their mentor, primarily because they perceived their mentor was too busy with other professional obligations, their mentor had personal issues that demanded their attention, or that their mentor was emotionally unavailable. Graduate students felt that their mentor's busyness or personal issues compromised the quality of their relationship and their mentor's capacity to provide support. Some participants reported that their mentors had professional obligations or competing demands that severely constrained the amount of time they were able to devote to the mentee. Others noted that their mentors had administrative responsibilities (e.g., department head, graduate coordinator) that made them “*extremely busy.*” Some described how their mentors were chronically inaccessible due to conference travel, field work, and other responsibilities of their position (e.g., grant writing, teaching). Addison remarked:

*“He had a lot of administrative duties. We would see him in the lab maybe like three times a year... His presence in the lab itself was minimal, and I started seeing him one-on-one a lot less because he was physically out of the country. He'd be giving talks and he would just have these other responsibilities.”*

Mentees also attributed their mentors' inaccessibility to personal demands such as family issues, emotional difficulties, and life-changing situations (e.g., marital problems, mental health issues, moving), which impacted their ability to mentor effectively. Doctoral students recognized that these issues were often outside of their mentor's control, but they also expressed frustration that these personal experiences negatively impacted their mentor's work performance and accessibility. Some participants felt that their mentors were *"just too overwhelmed to be a proper mentor,"* or were known to *"fall asleep [during lab meetings] because [they were] so exhausted from everything."* Heather described how her mentor's role as the director of a graduate program impacted her ability to provide effective mentoring support:

*"She was just super removed from lab, as far as her [office] location and that her focus was on the master's program and not her PhD students... Each time it was just a different excuse. First, it was the master's program. Then it was health issues with her parents. And then it was other stuff with her husband and her kids. And now it's like her and her health, so she wants to retire so she can focus on her health. So it's always something outside of the lab that has the priority..."*

Several participants also described instances where they felt neglected or abandoned when their mentor went on sabbatical. Doctoral students recognized that were expected to be operating predominantly independently during their graduate education, but they also desired periodic guidance and support from their mentor to alleviate feelings of neglect or abandonment. Evan recalled the experience of needing and failing to receive support from his mentor:

*"He got tenure right at the end of my first year here. He and his wife both did... and then they both went on a one year long sabbatical... So that's been difficult. He's been even less responsive. He's been you know, dealing with his own stuff. He's been homeschooling his children the first semester he was over on sabbatical in Europe, so that was taking up a ton of this time. He's collaborating with other universities..."*

In addition to being physically inaccessible, the majority of our participants perceived that their mentors were emotionally unavailable or inaccessible. Specifically, doctoral students felt that when they confided in or revealed something emotionally sensitive to their mentor (e.g., personal stressors, concerns over qualifying examinations), their mentor appeared to lack empathy or seemed inattentive or disinterested. When some doctoral students confided their concerns with their mentor, they felt they received an emotionally inappropriate or invalidating response. They expressed disappointment in not being able to rely on their mentor for support, as Makayla remarked:

*“I got divorced and it was a terrible, terrible time... I wanted to take a bit of a break. [My mentor] took me to coffee saying that she’d gotten divorced as well when she was younger and she wanted to talk about it. I kind of thought, because I am an idiot, ‘Oh look a human side. This is great.’ But no, the coffee was to explain to me how this was the wrong time to take time off because I really had to hunker down and work... bury myself in work to make myself feel better. That was her advice. It did not make me feel any better... Apparently, she was relating to me by saying, ‘I’ve been in the same situation as you and this is how you fix it – by working 12-hour days until I tell you to stop.’ That’s not good advice. I felt that she was in a position of power and a position to help me, and she chose not to.”*

**Limited expertise.** Over half of the doctoral students in our sample (n=23) noted that their mentor did not have sufficient knowledge, skills, or abilities to provide effective guidance. Some participants described situations in which their mentor was not familiar with an experimental technique, methodology, or the relevant literature necessary for their research. Others spoke more generally, noting that their mentor appeared to not have sufficient knowledge to provide substantive guidance about the research, as Anny explained:

*“[My mentor] had many projects in the lab, like most PIs do. He put me on the one that he cares the least about and knows the least about. I think that was a mistake. Usually PIs know at least a little bit about each project. Looking back, I don’t know why he even has that project going on because he knows nothing*

*about it... He didn't know any of the relevant literature. I would be stuck on something and try to figure it out and I'd tell him and he would just not know. And he would never admit [that he didn't know] it either."*

Other doctoral students felt that their mentors had minimal expertise in the practice of mentoring, which limited their ability to effectively support graduate students. Some students attributed this to the fact that their mentors were new faculty members and that they were the first graduate student to join their research group. Others felt that their mentor generally had little knowledge or had not received training or professional development on how to mentor graduate students. For example, Laurel described how her mentor's inexperience contributed to a marginal mentoring experience:

*"I think his poor mentorship is not because he's a bad person or a bad guy, I think he's just so new that he couldn't even fathom that people approach problems in a different way than him... He's actually commented and [said that] it's actually taken him a long time to realize that each student needs their own things and to be mentored in their own ways. I think a lot of our conflict was driven by his lack of mentor experience. He's even admitted that he had received no training in how to be a mentor. His post-doc mentor matched the style that he needed, so he's never thought about other mentorship styles."*

**Limited interpersonal abilities.** The majority of participants in our sample (n=34) felt that their mentors were interpersonally maladroit or ineffective in interacting, communicating, or working with others as a result of limited social skills. Some instances involved mentors engaging in behaviors inappropriate for the workplace, such as discussing romantic interests or over-sharing details from their personal life. For example, Gabriela explained how her mentor confided confidential information about his personal life with her:

*"[My mentor] just kept telling me about all this stuff that he was going through. Some of which was very inappropriate. Like 'I don't know if I love my wife anymore'... I should have had the nerve to stop him and tell him like, 'Hey this is uncomfortable, I don't want to know this.'"*

Gabriela's mentor continued to overstep professional boundaries by providing unsolicited advice on her personal life, saying,

*“You should date this guy,’ and, ‘You should see this other person.’ And, [my mentor] said ‘Oh I’m going to try to date this grad student.’ Telling me all these things. And I was like, ‘Stop, please.’”*

Other participants described how their mentors made inappropriate jokes and comments, swore, or used repugnant language. For example, doctoral students recalled how their mentors were known to explicitly promote their personal opinions and make statements that were perceived to be uncalled for in the workplace, such as *“you shouldn’t have kids while in graduate school,”* or that *“anyone who works in industry is basically a blood-sucking leech.”* In a particularly extreme situation, a doctoral student recalled how her mentor made an extremely vulgar remark and referred to her as *“a sexual assault magnet.”*

Other instances of interpersonal incompetence occurred when doctoral students felt that their mentors had personality traits, attitudes, or behaviors that undermined their relationship. For example, participants described their mentors as condescending, defensive, dismissive, hot-tempered, narcissistic, or rude. In other cases, doctoral students believed that their mentors had underdeveloped “soft skills” or were just generally difficult to work with. Some participants described that these traits were persistent throughout their mentoring relationship, while others felt that their mentor’s behavior had progressively deteriorated or changed since when they had initially joined the lab. Other participants expressed frustration because their mentors appeared to have multiple, oscillating personalities that were unpredictable. For example, Steven recalled how his

mentor's behavior appeared to be influenced by interpersonal or environmental stresses which made it difficult for him to ask her for support:

*“She runs very hot and cold... Some days she would come in and she'd be just a lovely person. She'd be fine to work with. But then, the next day, it'd be the complete opposite person. It was this ticking time bomb of anger and frustration that we would try to work around. I would dread coming into the office, thinking, is today going to be the day she's going to blow up on me for something? There was that constant fear and level of anxiety coming into the office every day and potentially dealing with that.”*

Doctoral students also described how their mentors behaved in passive aggressive ways or were known to make indirect or subtle disparaging remarks (i.e., microaggressions). These situations made it challenging for mentees to engage or interact with their mentors. Adrianna, an international student, described one situation where she had wanted to return to her home country for holiday break and her mentor initially agreed. However, when Adrianna returned, she explained how her mentor appeared to be irritated that she had spent time out of lab:

*“After I came back, she was very annoyed. Really openly annoyed at me for quite some time. It was definitely a stressful period for me. She's my advisor, and of course I needed to talk to her, but the conversations were always very tense. It's not like she ever openly told me how annoyed she was, but everyone in the lab could tell.”*

**Problematic supervisory styles.** Almost all of the doctoral students in our sample (n=34) described problematic supervisory styles, which included abusive supervision, hands-off supervision, and micromanagement. All three styles were perceived as ineffective or detrimental, undermining the formation of a healthy and productive working relationship. Over half of the doctoral students in our study reported forms of abusive supervision (Tepper et al., 2017), such as yelling, name calling, credit taking, punishment, intimidation, and coercion, as well as making explicit or implicit

threats and encouraging competition between lab members. Makayla explained how her mentor would engage in abusive behaviors such as yelling, aggressive outbursts, and accusations:

*“She'd call you incompetent all the time, at least on a weekly basis... She would explode, with this sort of tirade where she'd call you stupid or incompetent... She'd occasionally accuse you of making things up when they weren't working, which makes no sense because if you were going to make it up, surely, you'd make it up that it was working!... She also called me an idiot a couple of times... sometimes I am an idiot, but I sort of had this notion that you can't call people idiots when you're working, but clearly that was not the case. She'd also call you stupid. She'd call you a failure.”*

Other doctoral students reported that their mentor was “hands-off,” providing too little guidance or supervision on their research. These mentees expressed the need for more management to help them stay on track and make progress in their research. Although they appreciated the opportunity to function autonomously, they also felt that their mentor did not care about them or their work. For example, Evan wished that his mentor was more involved:

*“I think that one of the main things that was damaging to me and also to other graduate students is that he's been so hands-off. I am not saying that I need a babysitter and that I need a super hard deadline for me to have this paragraph of my manuscript [written] and this section of my manuscript to be done by. I don't need to be micromanaged, but I need to be paid attention to.”*

Yet other doctoral students expressed that their mentors engaged in “micromanagement” – being too involved in the day-to-day operations or too controlling of even straightforward tasks. Some doctoral students described how their mentors' curiosity and excitement over new findings, which was likely well intentioned, was perceived to be intrusive and added unnecessary stress for the student. Aaron explained:

*“As I'm developing the westerns, he's standing... looking over my shoulder and watching them develop. So I have to process this mentally for myself but also try to explain to him what we're looking at in real time. Even before I have a chance*

*to look and think about the data, I have to be able to interpret it and explain it and prove it to him.”*

**Unequal treatment.** Over a quarter of participants (n=14) described that their mentors treated individuals either more or less favorably on the basis of their personal characteristics, resulting in differential treatment. Doctoral students explained that their mentors appeared to treat certain individuals less favorably because of their race, gender, or other personal characteristics, or because of their professional interests or aspirations (e.g., teaching interests, non-academic careers). We distinguished these experiences from macro level phenomena (e.g., gatekeeping, role tension) because doctoral students described that these experiences occurred because of the direct actions of their mentors, rather than explicit departmental or cultural norms and practices that resulted in unequal treatment. Some participants described how their mentors made blatant, prejudicial statements such as, “[*You’re*] a Latino, you’ll have to work twice as hard to prove yourself.” Other mentors appeared to pass judgement on their mentee’s lifestyle choices, such as having children or getting married while in graduate school. For example, Clove explained, “*When we talked about my son, he’d always be like, ‘It’s unfortunate that you have this burden that makes it so that you can’t get work done.’ He thought I was not as effective as a researcher because I had a child.*”

Other doctoral students described how their male mentors appeared to have a closer, more casual relationship with their male mentees compared to their female mentees. Thea recognized that her mentor was likely trying to behave appropriately, but she expressed how these attempts resulted in differential treatment.

*“[Male graduate student] would house sit for [my mentor] while he was gone. They would go on trips to meet collaborators and conferences together... When they were at conferences, they would go out to get a beer together... My mentor*

*and [graduate student] would always have hang out time with the bros and I never saw my mentor interact that way with one of his female students... I think he was so afraid of being sexist that he ended up actually being sexist. He was so afraid of crossing a line that shouldn't be crossed that he instituted a barrier for his female students that he didn't institute for his male students. I think it's because he was trying to do the right thing... But there was a wall I hit as a female student... I know he's coming from what he thinks is best. He really thinks that putting up these barriers between himself and his female graduate students is good. But he doesn't realize that it's bad when you're not doing it with all of your students."*

Some doctoral students described that their mentors appeared to have preferences or played favorites amongst individuals. Participants identified these instances of favoritism because their mentors gave special or preferential treatment to others for no apparent reason. For example, Anny recounted how students in her lab were viewed and valued based on their position, "*My mentor thought that MD students were smarter than PhD students... none of the MDs in the lab had lab duties – the lab chores would be assigned to PhD students and postdocs but not to anyone who was a MD.*" Some doctoral students described how their mentors had more stringent expectations for them, but other members of the lab were allowed to perform or operate below these expectations. For example, Britney described:

*"My mentor always had a favorite... being the favorite meant that [other graduate student] could get away with anything. She could do whatever she wanted. She could just not show up and she wouldn't get in trouble... Anything [other graduate student] did, even if it was small, was wonderful and worth praise while everyone else in the lab got ignored."*

Altogether, the ontogenic-level results indicate that mentees suffer from a range of mentor behaviors, even behaviors that may be well intentioned.

## **DISCUSSION**

Here we identify and describe the negative mentoring that life science doctoral students experience with their research mentors. We found that mentoring relationships

during graduate education, like all interpersonal relationships (Duck, 1994; Scandura, 1998), can become dysfunctional or have problematic elements. Prior research has dichotomized negative mentoring experiences in terms of the effects on mentees' career or psychosocial outcomes (Scandura, 1998). However, doctoral students in our sample described how their negative experiences had *both* detrimental career *and* psychosocial effects, rather than one or the other. For example, doctoral students whose mentors prevented them from presenting their research at academic conferences indicated that they missed opportunities for career development and networking (i.e., career effects) and that this undermined their confidence and identity as a scientist (i.e., psychosocial effect). It is possible that doctoral students experience both career and psychosocial effects of negative mentoring because of their unique position as students and employees. Because they are students, doctoral students may need more space to learn, make mistakes, and get feedback and reassurance than employees. Yet, they also need support related to their career advancement like employees.

Prior research has also dichotomized negative mentoring experiences in terms of mentee perceptions of mentors' good or bad intent (Scandura, 1998). However, doctoral students in our sample typically did not focus on mentor intent. In fact, doctoral students attributed at least some mentor behaviors and relationship shortcomings to factors at the level of research groups, departments, organizations, and academic research (Figure 1), even though they were not prompted to do so. For instance, doctoral students perceived there was little if any incentive to provide quality mentoring (macro), which meant there was no expectation for their mentor to be accessible (ontogenic). Their mentor's inaccessibility led to lack of career and psychosocial support (dyadic) that continued

because insufficient structure was in place at the program level (micro) to provide other forms of support to the student or accountability from the mentor. These results draw attention to the fact that, even though destructive behaviors of mentors are not excusable, a faculty member is just one individual within a larger ecosystem and doctoral students are observing this during their research training. Other findings from our study suggest that there are unique constraints mentors face in academic settings that may hinder their abilities to engage in high-quality mentoring relationships. For example, many doctoral students described that their mentors had little mentoring competence or training (ontogenic). This contributed to poor attempts at mentor responsiveness to mentee needs, limited overall relationship quality (dyadic), and continuing conflicts within research groups (micro). Furthermore, these situations led to tension regarding the purpose of graduate education if mentees expressed interest in non-research related areas (macro). This is concerning because doctoral students may be more hesitant to report and address mentoring issues if they perceive these experiences are integral elements of a larger system that is beyond their control to change.

**Implications for Mentors, Programs, & Institutions.** Our results provide some evidence that macro and micro level actions are needed to achieve ontogenic and dyadic level improvements. For instance, graduate programs could equip mentors and mentees with mentoring maps that make explicit the variety of mentoring functions doctoral students need and provide a structure for identifying a collection of individuals who can provide mentoring support (Montgomery, 2017; NASEM, 2019). Mentoring maps may also help mentors recognize and make transparent to their mentees that they have the latitude to find other mentors who are able to give them support, professional assistance,

consultation, or guidance that they themselves are not able to provide. For example, a mentor who is not familiar with a technique or method (i.e., limited expertise) could connect a mentee with an individual with suitable expertise. It is important to note that the research advisor is still fulfilling the networking function of mentoring, by helping the mentee recognize the gap and find a suitable mentor to address it. Several studies have shown that having a “constellation of mentors” who fulfill different needs can lead to more positive overall mentoring experiences and mentee outcomes (Baugh & Scandura, 1999; Blaney, et al., 2020; de Janasz & Sullivan, 2004; Feldon et al., 2019).

Some of the forms of negative mentoring reported here could be addressed by widespread participation in mentoring professional development, such as *Entering Mentoring* (CIMER Project [www.projectcimer.org](http://www.projectcimer.org); Pfund, 2006; Pfund et al., 2014). For instance, issues at the ontogenic and micro levels, such as deceit and social undermining, relate to the component of *Entering Mentoring* on communicating effectively. Issues related to mentor accessibility, hands-off supervision, micromanagement, and career and psychosocial support are addressed in the component of *Entering Mentoring* on setting expectations. These curricular materials provide real-life scenarios that help mentors recognize problematic mentoring dynamics and develop strategies for addressing them or avoiding them all together, such as by using mentoring compacts and expectation-setting tools. Furthermore, *Entering Mentoring* is designed to equip mentors with tools and approaches to negotiate situations with mentees, rather than stipulating any single way of working with all mentees, who will come to a mentoring relationship and their graduate education with different needs, interests, expectations, and priorities. For instance, some mentees might desire more input and oversight while others might want more

independence. *Entering Mentoring* addresses how to align one's supervisory styles to meet particular mentee needs and desires (more or less supervision), including using Individual Development Plans (IDPs) to make mutual expectations for graduate student progress and developing clear and shifting supervisory style over the course of a doctoral student's education (from more to less supervision) (Clifford et al., 2013; Vanderford et al., 2018). Although there is some evidence of the effectiveness of *Entering Mentoring* (Pfund et al., 2014), future research is needed to determine whether participating in mentoring professional development mitigates or prevents negative mentoring experiences.

Some forms of negative mentoring reported here may not be alleviated with time-limited professional development. Resources, support, and interventions over time will likely be necessary to address deeper seated issues that have the potential to cause greater harm. For example, doctoral students in our sample reported unprofessional mentor behaviors that may require intercession at multiple levels over time (e.g., limited interpersonal abilities, abusive supervision). Educational interventions that equip individuals in positions of power (e.g., graduate coordinators, program directors, department heads) with skills to identify poor behaviors and engage in difficult conversations to mitigate it have effectively reduced workplace incivility (Howard & Embree, 2020; Stoddard, 2017). Such interventions could be adapted and deployed in academic research settings and tested for their effectiveness in reducing graduate negative mentoring experiences. Although such interventions may seem costly, they may ultimately reduce the cost of bad behavior (Porath & Pearson, 2010), especially the loss of graduate talent from the STEM workforce. In addition, some of the behaviors reported

here may qualify as human resources violations (e.g., workplace harassment) or violations of non-discrimination and anti-harassment policies (e.g., unfair treatment). Institutions should put structures in place to ensure graduate students are informed about what constitutes such violations and have access to support and protection for reporting potential violations.

Other negative mentoring experiences reported here indicate that students may expect their research advisor to provide all of the support they need to be successful in their research and their graduate programs. For instance, over half of the doctoral students in our study noted that their mentors' expertise was insufficient to provide guidance on their doctoral research. This experience may be due to a mismatch in expectations. For instance, students may expect their advisor to be able to answer all of their questions, dictate or approve all steps of their research, and provide emotional support when research is not progressing as planned. In contrast, advisors may see their role as a coach who provides advice on *how* to find answers and think through possible next steps of the research, but not as the source of all technical expertise or emotional support. Indeed, given that high-quality mentoring involves the provision of a wide-range of support (e.g., task assistance, exposure, protection, confirmation, counseling) (Eby et al., 2013), it is unreasonable to ask one faculty to operate as a sole mentor to a doctoral student. Again, mentoring maps may be helpful for addressing this by making various mentoring needs transparent for mentors and mentees and providing a structure for mentoring support that is not limited to the dyad. Expectations setting tools are also likely to be helpful for communicating and coming to consensus about expectations (Moses, 1985).

Different mentorship structures (e.g., co-mentoring, more empowered dissertation committees) and more diffuse funding models (e.g., training grants, departmental fellowships) should be explored for their potential to avoid graduate student reliance on a single faculty mentor. These ideas align with the National Academies' recommendation for improving STEM graduate education by evolving micro-level practices to improve mentorship for doctoral students (NASEM, 2018). These approaches offer the potential to reduce the adverse, macro-level phenomena such as the role tension experienced by graduate students in our sample. Our results also support the recommendation to add micro-level structures that enable meaningful evaluation of mentorship quality and competence in hiring, in annual performance reviews, and for promotion and tenure. Shifts in micro and macro level culture regarding the value of effective mentoring will likely be necessary to achieve widespread reduction or prevention of negative mentoring experiences. Lessons learned from efforts to promote undergraduate education reform, including evaluating, incentivizing, and rewarding teaching quality, may offer useful insights for accomplishing this (Corbo et al., 2016; Kezar, 2014).

**Implications for Mentees.** These findings should be reassuring to mentees that they are not alone in experiencing negative mentoring. Furthermore, there are tools and strategies that mentees can use to “mentor up,” taking a more active role in maximizing and cultivating the quality of their mentoring relationships (Lee et al., 2015). Mentees can mentor up even before they start their doctoral degrees and throughout their programs. For example, doctoral program applicants can use the results reported here to guide their explorations of their programs of interest. They may want to inquire about whether:

- Faculty participate in mentoring professional development or use mentoring tools such as mentoring compacts, expectations scales, and maps;

- Programs provide mentoring professional development and/or require faculty to complete it; and
- Programs have structures in place that enable mentees to report negative mentoring experiences, support mentors and mentees in conflict resolution, and enable mentees to safely transition to more positive mentoring situations if and when it is needed.

Mentees can also use the results reported here to guide their exploration of

mentors and research groups, especially in life science disciplines that include research rotations in the first year. Again, they can ask whether mentors have participated in mentoring professional development or use tools that support high quality mentoring (Clifford et al., 2013; Huskins et al., 2011; Masters & Kreeger, 2017; Montgomery, 2017; NASEM, 2019). They can ask research group members about the mentors' supervisory styles and *whether and how* mentors go about providing support that is responsive to individual mentee needs over time. The overarching goal of mentee exploration should not be on finding a single right answer, but rather on finding a fit with what they are seeking from a research advisor as a main, but not only, mentor. Mentees can also learn how to effectively solicit the desired support from their mentors, which can help them maximize the outcomes of their mentoring relationship and may prompt their mentor to provide additional support.

**Limitations & Future Research.** Our study has several limitations that should be considered when interpreting the results. Our sample was voluntary and limited in size (40 participants), degree type (doctoral), and discipline (life sciences). We collected data until we reached saturation, but it may be that students who did not volunteer had substantively different experiences that were not reported (e.g., harassment, discrimination, unwanted sexual attention). Another possibility is that some doctoral students expect negative mentoring experiences to be “normal” or anticipated elements of

STEM graduate training, and thus not worth reporting on. Future research needs to examine negative mentoring experienced by a larger sample of doctoral students from a broader range of disciplines, institution types, citizenship status (i.e., international), degree types (e.g., MS, MD/PhD), and programs (e.g., rotations, direct admit) to determine whether graduate students experience other forms of negative mentoring not observed here.

Our participants were reflective of the national demographics of individuals pursuing life science doctoral degrees, yet only 12 students (~30%) who identified as Black, Latinx, or Native American / Native Alaskan participated in our study and none of our participants identified as gender nonbinary. Current reform efforts aimed at broadening participation advocate for mentoring as strategy for improving access to and equity of STEM education. Indeed, a growing body of research has shown that quality mentorship during research experiences is important for women and individuals from racial and ethnic backgrounds that have been excluded from STEM (Aikens et al., 2017; Asai, 2020; Byars-Winston et al., 2015; Estrada et al., 2018; Griffin et al., 2018; Griffin et al., 2010; Hernandez et al., 2017; Hurtado et al., 2009; Lee et al., 2015; Lewis et al., 2016; McGee, 2020; Wilson et al., 2011). Consequentially, negative mentoring experiences could be disproportionately harming marginalized students. Future research should examine the specific forms of negative mentoring experienced by students from particular racial and ethnic backgrounds and gender identities, including experiences at the intersection of identities. Such investigations could provide additional insights on factors contributing to the continued underrepresentation of marginalized individuals in STEM fields.

Our study was cross-sectional and retrospective in nature, relying on doctoral students' recollections of their experiences and outcomes. Thus, the results may be subject to recall bias or conjecture about potential causes of negative experiences. Furthermore, studies from workplace settings have demonstrated that negative mentoring experiences are predictive of mentee turnover intentions (Eby & Allen, 2002). It is possible that doctoral students who left their graduate programs prematurely because of negative mentoring may have experienced considerably different forms of negative mentoring that were not captured in our study. Future research should make use of longitudinal study designs and methods, as well as established measures of graduate student outcomes in order to track negative mentoring experiences over time, identify other potential forms of negative mentoring, and determine their effects. Results from this research would be helpful for identifying key points during graduate education when students might need more or less support and for tailoring program resources accordingly.

We elected to study mentees' perspectives and opted not to collect data from mentors because prior research has found that mentee perceptions are predictive of their outcomes, regardless of mentor intentions or perspectives (Eby et al., 2008; Eby et al., 2010; Eby & Allen, 2002; Limeri et al., 2019; Scandura, 1998). It is important to note that mentoring is an interpersonal relationship involving two parties. Studies from workplace settings have found that mentors also experience "negative mentoring" from mentees (Eby & McManus, 2004). Future studies should examine negative mentoring experiences from the mentor perspective to understand how mentors might experience and be affected by negative mentoring.

We made the post-hoc decision to use ecological systems theory to interpret our data rather than collecting these data from all mentees or from programs and institutions directly. Future research should examine micro and macro level phenomena more systematically and directly to understand their influence on the occurrence and impacts of doctoral students' negative mentoring experiences. Results of this work could yield further insight into micro and macro level levers for change.

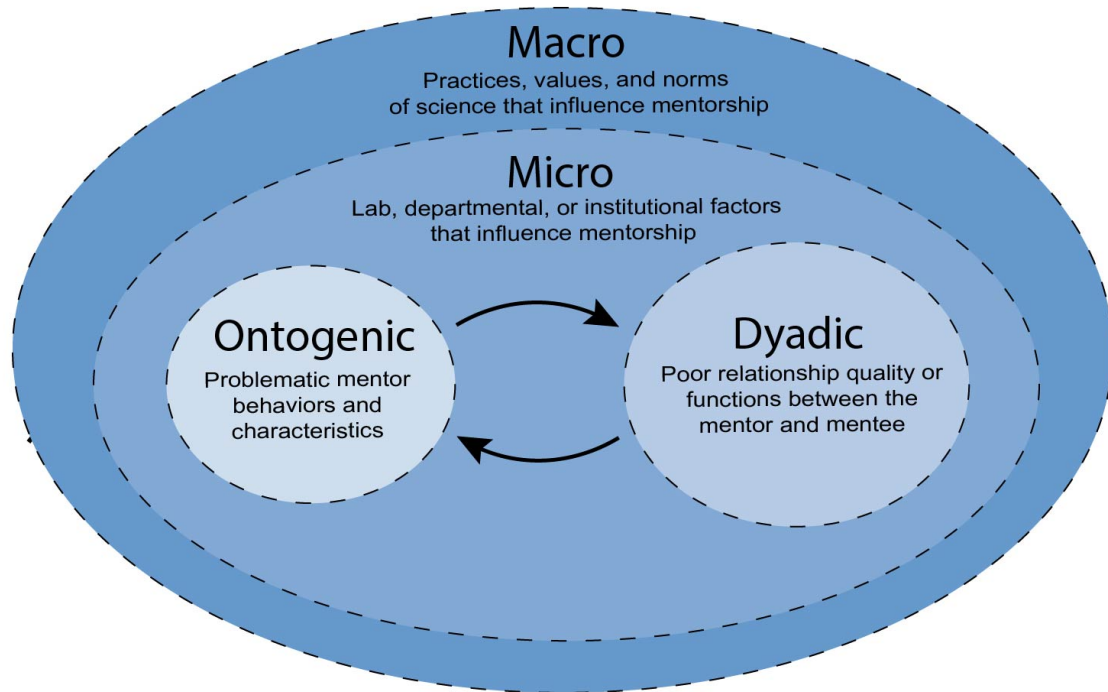
Finally, additional research is necessary in order to determine the prevalence of negative mentoring experiences and to characterize their causes and effects for doctoral students in STEM fields. A psychometrically sound, quantitative measure of graduate negative mentoring is needed to collect data from a sufficiently large and representative sample to determine the generalizability of our findings. The results presented here should be sufficient for identifying and defining the content domain of the construct of graduate negative mentoring experiences as a first step toward developing a quantitative measure (AERA, APA, NCME, JCSEPT, 2014; Bandalos, 2018). Once developed, the measure could be used to examine the base rates of negative mentoring at the program and institution level and to identify the impacts of negative mentoring, including whether and how mentees from different socio-demographic backgrounds experience negative mentoring differently. The proposed measure could be used to determine antecedents and correlates of negative mentoring experiences, and to characterize how these experiences manifest and change over the course of doctoral mentoring relationships. Such a measure could also be used to test the effects of the interventions, such as mentee and mentor professional development as well as changes in program and institutional structures intended to improve mentorship.

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## FIGURES, TABLES, AND LEGENDS

**FIGURE 4.1: Ecological systems conceptual model of variables influencing the negative mentoring experiences of life science doctoral students.**



We utilized ecological systems theory to interpret our results and gain insight into how various individual, relational, and environmental variables influence graduate students' negative mentoring experiences. We found evidence that doctoral students' negative mentoring experiences are not only shaped by problematic mentor behaviors and characteristics (ontogenic) and poor relationship quality and functions (dyadic), but also by research group, department, and institutional factors (micro) as well as the culture of science and academic research (macro). Doctoral students perceived that factors at the micro and macro levels had dynamic, reciprocal effects at the dyadic and ontogenic levels.

**TABLE 4.1: Study sample demographics ( $n = 40$ )**

<b>Description</b>	<b><math>n</math> (%)</b>	<b>Description</b>	<b><math>n</math> (%)</b>
<b>Gender<sup>1</sup></b>		<b>Research Context<sup>4</sup></b>	
Female	25 (62)	Bench	33 (82)
Male	15 (38)	Computational	15 (37)
<b>Race</b>		Fieldwork	8 (20)
American Indian or Alaskan Native	1 (3)	Theoretical	2 (5)
Asian <sup>2</sup>	7 (17)	<b>Years Completed</b>	
Black <sup>3</sup> or African American	3 (8)	1	8 (20)
North African & Middle Eastern	1 (3)	2	3 (8)
White	27 (66)	3	5 (12)
Prefer not to respond	1 (3)	4	12 (30)
<b>Ethnicity</b>		5	10 (25)
Hispanic or Latina/Latino	8 (20)	6	2 (5)
Not Hispanic	30 (75)	<b>Carnegie Classification</b>	
Prefer not to respond	2 (5)	High Research Activity (R1)	39 (97)
<b>Degree Status</b>		Higher or Moderate Research Activity (R2)	1 (3)
Pre-Candidacy	13 (32)	<b>Institution Type</b>	
Post-Candidacy	24 (60)	Public	30 (75)
Currently Post-Doctoral	3 (8)	Private	10 (25)

<sup>1</sup> We recognize that gender is a spectrum and acknowledge the limitations associated with collecting this demographic variable in the current form (Garvey et al., 2019).

<sup>2</sup> We recognize that participants who identify as Asian have a broad range of cultural and national identities, but we grouped our participants into a broad category termed “Asian”.

<sup>3</sup> Black refers to the heterogeneity of people within the US who identify as African, Afro-Caribbean, or African American.

<sup>4</sup> Counts do not sum up to 100% because some participant’s research integrated multiple research contexts.

**TABLE 4.2: Negative mentoring experiences reported by doctoral students.** Here, we present the main forms of negative mentoring experienced by level of the doctoral research mentoring ecosystem, including their conceptual definitions (left) and the operational manifestations (right).

<b>Conceptual Definitions</b>	<b>Operational Manifestations</b>
<b>Macro System:</b> Practices, values, and norms of STEM and academic research that influence mentorship	
<p style="text-align: center;"><b>Gatekeeping (n=5)</b></p> <p>Negative mentoring experiences are viewed as necessary or useful for eliminating individuals who do not have the disposition to succeed in science</p>	<ul style="list-style-type: none"> <li>- Negative mentoring experiences believed to be a necessary or embedded component of science graduate training</li> <li>- Experiencing negative mentoring is commonplace</li> </ul>
<p style="text-align: center;"><b>Lack of incentives for quality mentorship (n=6)</b></p> <p>Disciplinary beliefs, values, or norms that fail to incentivize or reward effective mentoring relationships</p>	<ul style="list-style-type: none"> <li>- Promotion and tenure influence mentor’s behavior and mentoring support</li> <li>- Evidence of effective mentorship practices are not considered in promotion decisions or rewarded</li> </ul>
<p style="text-align: center;"><b>Power structures (n=11)</b></p> <p>Mentors have power over mentees due to their position or other power-related beliefs, values, or academic norms</p>	<ul style="list-style-type: none"> <li>- Mentors are perceived to have power while mentees do not</li> <li>- Mentors have hierarchical control over mentees</li> <li>- Doctoral students perceive that they have no power in their mentoring relationship</li> </ul>
<p style="text-align: center;"><b>Role tension (n=6)</b></p> <p>The norms of academic research cause faculty to be reliant on graduate students to produce research even though the goals of graduate education may not always align with research productivity</p>	<ul style="list-style-type: none"> <li>- Funding model relies on research productivity and is believed to be in tension with doctoral student development and education</li> <li>- Tension over misaligned expectations for a learner versus an employee</li> </ul>

Table 4.2, continued.

Conceptual Definitions	Operational Manifestations
<b>Micro System:</b> Lab, departmental, or institutional factors in the local environment that contribute to and influence mentorship	
<p><b>Collegial protections (n=8)</b>  Mentee perceives that mentors in their department are safe from repercussions because of their seniority, department/program needs, or academic freedom</p>	<ul style="list-style-type: none"> <li>- Untenured mentors appear reluctant to stand up against senior, tenured faculty</li> <li>- Programs or departments continue to allow mentors to mentor even when they are known to engage in detrimental mentoring behaviors</li> <li>- Faculty justify or support mentors' actions, even if they are viewed as being harmful</li> <li>- Faculty have academic freedom that allows them to mentor as they see fit</li> </ul>
<p><b>Insufficient structure (n=18)</b>  Mentee believes that there is a lack of policies, procedures, or supports to assist them when experiencing dysfunction in their mentoring relationship</p>	<ul style="list-style-type: none"> <li>- Departmental or institutional leaders do not provide support or intervene to provide mentee with mentoring support</li> <li>- Omission of policies or plans in place to mitigate negative mentoring experiences</li> <li>- Departmental or institutional culture is perceived as not being conducive for fostering healthy mentoring relationships</li> </ul>
<p><b>Social undermining (n=23)</b>  Mentee believes that the mentor engages in actions that damage and undermine the mentee's ability to establish and maintain healthy working relationships in their local environment</p>	<ul style="list-style-type: none"> <li>- Gossips, spreads rumors</li> <li>- Belittles or gives contradictory advice during dissertation committee meetings</li> <li>- Talks down to mentee in front of others</li> <li>- Engages in actions that damage mentee's work-related success</li> <li>- Fosters a poor or hostile working environment</li> <li>- Spousal presence negatively influences research group</li> </ul>

Table 4.2, continued.

<b>Conceptual Definitions</b>	<b>Operational Manifestations</b>
<b>Dyadic System:</b> Poor relationship functions or forms of support between the mentor and the mentee	
<p><b>Interpersonal mismatch (n=19)</b> Mentee and mentor and have dissimilar values, personalities, workstyles, or communication preferences</p>	<ul style="list-style-type: none"> <li>- Mismatched personalities</li> <li>- Dissimilar career goals and outcomes</li> <li>- Dissimilar research interests</li> <li>- Different life priorities or values</li> </ul>
<p><b>Limited career support (n=38)</b> Mentee reports not receiving sponsorship, coaching, networking and exposure, or advice related to their career goals from the mentor</p>	<ul style="list-style-type: none"> <li>- Lack of engagement or interest in mentee's research or career development</li> <li>- Insufficient safety training</li> <li>- Lack of technical guidance</li> <li>- Limited or no feedback or advice on networking, career options, publishing, grant writing</li> <li>- Insufficient provision of networking or development opportunities</li> </ul>
<p><b>Limited psychosocial support (n=28)</b> Mentee feels that they did not receive counseling, affirmation, emotional support, acceptance, or confirmation from the mentor</p>	<ul style="list-style-type: none"> <li>- Passing judgement on mentee's career achievements or goals</li> <li>- Insufficient encouragement or validation</li> <li>- Lack of investment in mentoring relationship</li> </ul>
<p><b>Poor relationship quality (n=19)</b> Mentee has poor feelings about the mentoring quality or is generally unsatisfied with the mentoring relationship</p>	<ul style="list-style-type: none"> <li>- Little emotional connectivity or disclosure in the relationship</li> <li>- Mentee is dissatisfied with mentor</li> <li>- Mentee and mentor generally dislike or distrust each other</li> <li>- Mentor does not engage in social / relationship building activities with mentee</li> </ul>

Table 4.2, continued.

<b>Conceptual Definitions</b>	<b>Operational Manifestations</b>
<b>Ontogenic System: Problematic mentor behaviors and characteristics</b>	
<p style="text-align: center;"><b>Deceit (n=12)</b></p> <p>Mentor misrepresents or omits information from the mentee</p>	<ul style="list-style-type: none"> <li>- Lies to mentees about how their ideas or research will be used</li> <li>- Tells the mentee one thing and then does something different</li> <li>- Keeps mentee “out of the loop” on important issues</li> </ul>
<p style="text-align: center;"><b>Inaccessibility (n=38)</b></p> <p>Mentor has too many professional obligations or events in their personal life that excessively limit the amount of time the mentor can commit to the mentee</p>	<ul style="list-style-type: none"> <li>- Absent due to excessive traveling for conferences, field work, or other commitments</li> <li>- Absent due to too many leadership obligations</li> <li>- Does not spend time with mentee in favor of spending time writing grants, carrying out service responsibilities, or working on other research projects</li> <li>- Mental and/or physical health issues of the mentor or mentor’s family</li> <li>- Moves, relocates</li> <li>- Experiences marital troubles/divorce</li> </ul>
<p style="text-align: center;"><b>Limited expertise (n=23)</b></p> <p>Mentor appears to not have the knowledge, skills, or abilities to effectively guide the mentee</p>	<ul style="list-style-type: none"> <li>- Not current on ideas, theories, methods, or findings related to mentee’s research</li> <li>- Unable to give technical advice or guidance</li> <li>- Unable to effectively guide research or effectively supervise or mentor others</li> </ul>
<p style="text-align: center;"><b>Limited interpersonal abilities (n=34)</b></p> <p>Mentor has persisting traits, attitudes, and personality traits that limit their ability to communicate or interact with the mentee effectively</p>	<ul style="list-style-type: none"> <li>- Has a bad attitude, is rude, condescending, dismissive, defensive, narcissistic, conceited</li> <li>- Has oscillating mood or personality changes, is passive aggressive or behaves impulsively</li> <li>- Discusses romantic interests or intimate details, makes inappropriate jokes or comments, overshares personal information</li> <li>- Gives unsolicited personal advice</li> </ul>
<p style="text-align: center;"><b>Supervisory styles (n=34)</b></p> <p>Mentors approach to managing and directing does not match the mentee’s needs</p>	<ul style="list-style-type: none"> <li>- Takes credit</li> <li>- Punishes, intimidates, threatens, coerces, calls names, swears, yells</li> <li>- Encourages competition among lab members</li> <li>- Is detached from mentee’s day-to-day needs</li> <li>- Has a philosophy of little to no collaboration on research, of minimal communication or feedback</li> <li>- Meticulously oversees or is involved in research tasks</li> <li>- Attempts to control how mentee conducts research, allows mentee little autonomy or ability to make decisions about research</li> </ul>
<p style="text-align: center;"><b>Unequal treatment (n=14)</b></p> <p>Mentor treats mentee differently based on personal characteristics or mentor preferences</p>	<ul style="list-style-type: none"> <li>- Discrimination</li> <li>- Favoritism</li> </ul>

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### Supplemental File 4.1 Screening Survey Questions

1. We are interested in the quality of mentoring that graduate students experience as they do research. How would you rate the overall quality of your mentoring relationship with your graduate advisor? A rating of -3 is extremely negative or unfavorable, 0 is neutral, and +3 is extremely positive or favorable. (*Likert Scale*)

	-3	-2	-1	0	1	2	3
Relationship with Advisor	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

2. As a whole, how would you rate the quality of your graduate studies? A rating of -3 is extremely negative or unfavorable, 0 is neutral, and +3 is extremely positive or favorable. (*Likert Scale*)

	-3	-2	-1	0	1	2	3
Graduate Studies	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

3. Please describe your ratings. What factors or experiences prompted you to select these ratings? (*Text Entry*)

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The following questions are about your personal characteristics and will help the researchers ensure they have received input from students who represent a broad range of personal characteristics.

1. What best describes your degree status?
  - PhD Student
  - PhD Candidate
  - Postdoctoral researcher
  - Prefer not to respond
2. How many years of your PhD have you completed?
  - 1 years
  - 2 years

- 3 years
  - 4 years
  - 5 years
  - 6 years
  - 7 years
  - 7+ years
  - Prefer not to respond
3. What gender do you most closely identify with?
- Female
  - Male
  - Trans
  - Non-binary
  - Prefer not to respond
4. With which ethnicity do you most closely identify?
- Hispanic or Latino/Latina
  - Not Hispanic or Latino/Latina
  - Prefer not to respond
5. With which race(s) do you most closely identify? Please choose all that apply.
- American Indian or Alaskan Native
  - Asian
  - Black or African American
  - Native Hawaiian or other Pacific Islander
  - North African or Middle Eastern
  - White
  - Prefer not to respond

- 
6. We may want to contact you for an interview to better understand your experience. You would receive a \$25 Amazon gift card for participating in an interview. If you are willing, please enter your name and address below. **Please note that we will keep your information confidential but we need your name and contact information in order to schedule an interview.** *(Text Entry)*

First and last name:

Email Address:

## **Supplemental File 4.2 Interview Protocol & Questions**

### *Introductory comments & verbal consent*

Thanks for responding to our survey about your research experience and the mentoring you experienced during your graduate education. You agreed to participate in this study when you responded to the survey, but I want to check in and see if you have any questions before we proceed with the interview portion. I'd like to make an audio-recording of our conversation so I can be sure we capture your comments accurately and completely. We will transcribe your comments and replace any identifying information with pseudonyms. We will only use the transcript in our study, so no one else will hear your voice or know that you participated in the study or made specific comments about your research and mentoring experiences. Do you have any questions for me at this point?

And are you comfortable with my making a recording of our conversation?

- If yes, start recorder
- If no, then explain that we will be taking notes to make sure we capture their comments as well as possible

### *Interview Questions*

1. Let's start with you telling me a bit about your graduate experience. What institution are you at and what department are you housed in? What is your graduate research about? Is your research largely benchwork, computational, or fieldwork?
2. We are especially interested in problematic or negative mentoring experiences students have during their graduate education because the positive aspects are well documented. You rated the mentoring you experienced as [less than ideal]. Was there a particular person you had in mind or were you thinking about the mentoring you received in general? Was this your thesis advisor?
3. What made your relationship with this individual / the mentoring you experienced negative or problematic?
4. What qualities, characteristics, and/or attitudes of the individual / the mentoring that made the situation negative or problematic?
5. Were there any specific situations that made your relationship with the individual negative or problematic?
6. Did you or the individual try to address these issues? If so, how? And how successful was that? If not, why not?
7. How did these negative or problematic aspects of the mentoring you experienced affect you personally on a day to day basis? And for thinking about your future?

8. Is there anything else that you would like to share about your experience?
9. Do you have any questions for me?

## CHAPTER 5

# MEASURING NEGATIVE MENTORING EXPERIENCES: DEVELOPMENT AND NOMOLOGICAL VALIDATION OF THE MENTORING EXPERIENCES IN RESEARCH & GRADUATE EDUCATION (MERGE) SCALE <sup>4</sup>

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<sup>4</sup> Tuma, T.T., Adams, J.D., Choi, S., & Dolan, E.L. Measuring Negative Mentoring Experiences: Development & Nomological Validation of the Mentoring Experiences in Research & Graduate Education (MERGE) Scale. To be submitted to *Journal of Applied Psychology*

## ABSTRACT

Effective, high-quality mentorship has been linked to several positive outcomes for graduate students in Science, Technology, Engineering, and Mathematics (STEM) fields. While mentoring is often studied with a positive framing, a developing body of research indicates that not all mentoring relationships are fulfilling. Yet, there has been only modest research aimed at understanding the negative experiences graduate students can have with their research mentors and how these destructive experiences can influence their career and psychosocial outcomes. We conducted two sequential, mixed-methods studies to (1) develop a robust, theory-informed measure of graduate students' negative mentoring experiences, and (2) evaluate the casual relationships between negative mentoring experiences and their influence on the career and psychosocial outcomes of graduate students. In Study 1, we developed items for the measure based on prior research defining the construct of negative mentoring, established response process validity by gathering feedback on the items through cognitive interviews, and obtained evidence of content-related validity based on sorting task and feedback from subject experts. In Study 2, we refined the items and then collected and analyzed responses from a national sample of life science doctoral students to assess the internal structure as well as the convergent and divergent validity of the measure. In Study 2, we also begin to assess the predictive validity of the scale. We end by discussing implications for the use of the newly developed scale in STEM graduate education, both in terms of theory and applied practice.

## INTRODUCTION

Mentorship is considered be critical for developing talent and training the next generation of scientists in Science, Technology, Engineering, and Mathematics (STEM) fields. Quality mentorship from a faculty member during graduate education fosters the integration and socialization of students into the scientific community. Multiple quantitative and qualitative studies have shown that individuals with mentors experience greater personal and professional outcomes than those without mentors (Allen et al., 2004; Eby et al., 2008; Eby et al., 2013; Lunsford, 2012; Paglis et al., 2006; Tenenbaum et al., 2001; Zhao et al., 2007). Consequentially, mentorship, a close, developmental relationship in which a more experienced individual (the mentor) and a less experienced individual (the mentee) work together to support the personal and professional growth, development, and success of both relational partners, is thought to serve a critical role in developing STEM professionals (National Academies of Sciences, Engineering, and Medicine., 2019). In most STEM graduate education programs, mentorship occurs between a graduate student and a principal investigator (PI) of a research group or a faculty advisor.

Mentoring is generally perceived as a positive experience that is associated with many desirable attitudinal, behavioral, career, and health related outcomes for both the mentee and the mentor (Allen et al., 2004; Eby et al., 2013; NASEM, 2019). However, meta-analyses of mentoring have found small to moderate positive effects for both mentees and mentors, with effect sizes displaying substantial heterogeneity (Allen et al., 2004; Eby et al., 2008; Eby et al., 2013; Kammeyer-Mueller & Judge, 2008). Furthermore, the quality of mentorship reported during graduate education can vary

widely and mentees' experiences differ, even within the same institution, program, and lab (Griffin et al., 2022; Kumar & Blake-Beard, 2012; Maher et al., 2017; Ruud et al., 2018; Tuma et al., 2021). Consequentially, the quality of mentorship can vary, mentoring is dynamic and the relationship can experience fluctuations in quality and effectiveness, and not all mentoring relationships are satisfying or of high-quality (Eby et al., 2000; Eby & Robertson, 2020; Ragins et al., 2000). These findings highlight the need for a more nuanced understanding of the extent to which dysfunctional or non-fulfilling mentoring relationships occur and their potential outcomes.

Theoretical work recognizes that mentoring relationships, like any relationship, can be unfavorable or even dysfunctional (Kram, 1985; Scandura, 1998). For example, Scandura (1998) proposed that potential relational problems could be distinguished in terms of the intent of the mentor behavior (i.e., good or bad) and their career or psychosocial related effects. Empirical studies lend support for this theoretical work by showing that mentees can experience marginal, or even destructive, mentoring relationships (Eby et al., 2004; Eby et al., 2000; Limeri et al., 2019; Tuma et al., 2021). Studies from workplace settings have shown that both mentees (Eby et al., 2000, 2004, 2010; Scandura, 1998) and mentors (Eby et al., 2008; Eby & McManus, 2004) experience negative or destructive events in their mentoring relationships. These relational experiences, collectively referred to as negative mentoring experiences, can range from seemingly mild phenomena such as mismatches of values, personality, or workstyles, neglect, and lack of mentoring support to more intense phenomena, such as deception, manipulation, and undermining (Eby et al., 2000; Eby & Allen, 2002). These dysfunctional mentoring experiences are associated with a range of negative personal and

professional outcomes for the mentee, including reduced job satisfaction, greater intent to leave job, and increased stress (Eby et al., 2000; Eby & Allen, 2002; Eby & McManus, 2004). In fact, some evidence suggests that negative mentoring experience may have a stronger impact than a having no mentoring at all (Eby et al., 2010; Ragins et al., 2000). Furthermore, these negative experiences may also have costly and far-reaching impacts for both the mentor (Eby et al., 2008; Eby & McManus, 2004) and the organization (Scandura, 1998). However, it remains unclear if these findings are transferable to STEM research settings and to graduate research in particular.

Considerable attention has focused on relational problems within organizational and clinical supervisory mentoring relationships, but existing research on relational problems within academic and student-faculty mentoring remains relatively nascent (Allen & Eby, 2007; NASEM, 2019). Some studies of academic mentoring have acknowledged variation in the quality of mentorship experienced by mentees (Barnes et al., 2010; Bernier et al., 2005.; Burt et al., 2019; Clark et al., 2000; Dolan & Johnson, 2010; Goodyear et al., 1992; Thiry & Laursen, 2011) and anecdotes of negative mentoring have been reported by graduate students (NASEM, 2019). Scholars have proposed that graduate students can experience mismatches with their faculty mentor (e.g., communication style, personality, career interest, etc.) or experience more damaging behaviors such as neglect, mentor incompetence, interpersonal conflict, hostile or resentful behaviors, or boundary violations (e.g., disclosure of personal details, too much intimacy) that could hinder the development of a high-quality relationship (Johnson & Huwe, 2002). Some empirical research has acknowledge that faculty mentors can engage in sabotage, emotional abuse, harassment, manipulation, credit-taking, and

neglect towards their student mentees (Castelló et al., 2017; Clark et al., 2000; Johnson, 2003; Kalbfleisch, 1997; Kumar & Blake-Beard, 2012). Comparatively less work has attempted to determine the occurrences and outcomes of poor mentoring experiences. Prior suggests that 25-50% of mentees report some form of relationship dysfunction or conflict with their mentor (Clark et al., 2000; Eby et al., 2000; Goodyear et al., 1992). Therefore, negative mentoring may be a widespread issue. Furthermore, such destructive experiences can have longstanding effects on mentees career success (e.g., reduced work productivity, work disengagement) and their health and well-being (Eby & Allen, 2002; Kumar & Blake-Beard, 2012). Yet, to date, very little research has systematically and rigorously determined the antecedents, correlates, and outcomes of negative mentoring experiences within the context of student-faculty mentoring relationships (NASEM, 2019).

The National Academies of Sciences, Engineering, and Medicine indicated an urgent need for investigations aimed at defining and characterizing negative mentoring experiences and to investigate their prevalence and potential to have detrimental impacts in STEMM fields (NASEM, 2019). Moreover, negative mentoring experiences have the potential to cause disproportionately greater harm on historically minoritized individuals' integration into STEM fields. As a result, negative mentoring experiences may be further magnifying disparities in graduate education, driving talent out of the scientific workforce, and compromising the nature and quality of science itself. Furthermore, training a STEM PhD student is costly – both in terms of the time, money, and the effort invested by the doctoral student, faculty mentor, and university – and the return on these investments is reduced when doctoral students exit their program before finishing or

complete their program but pursue careers unrelated to their field of study. Employees who experience hostility and bad behavior from their supervisors in the workplace report decreased effort, time, and quality in their work, reduced commitment to the organization, and are more likely to take out their frustrations on their peers, withdraw from their work, and leave their job (Porath & Pearson, 2010). Destructive behavior can also lead to reductions in employees' cognitive performance, creativity, and willingness to help their peers (Harris et al., 2007; Porath & Erez, 2009; Zellars et al., 2002). These effects are alarming given that negative mentoring experiences in STEM fields have the potential to function in a similar manner. While the monetary costs associated with poor behavior during STEM doctoral training is currently incalculable, extant research from workplace settings suggests that negative experiences likely have far reaching costs for multiple stakeholders (i.e., students, faculty, universities, the scientific enterprise). With such high investments from university stakeholders and the general public (in the form of taxes), understanding the professional and personal costs associated with the negative mentoring experiences of graduate students is urgently warranted.

To date, there are no relevant measurement instruments that can be used to generate valid and reliable ratings of negative mentoring during graduate education and advance our understanding of the influence of negative mentoring on graduate student outcomes (NASEM, 2019). To address this need, we aimed to develop and collect validity evidence for a new, theory-informed measure of graduate students negative mentoring experiences, which we term the Mentoring Experiences in Research and Graduate Education (MERGE). The development of this scale will allow for research on the antecedents and correlates associated with negative mentoring experiences and how

these experiences influence relational processes and subsequent outcomes. Furthermore, this scale will be useful for practitioners such as graduate programs and university leaders who are aiming to improve the mentoring experiences of doctoral students during their graduate education. The development of a robust scale will also for evaluation of mentor's effectiveness and competence, which could be used to identify and inform decision making regarding faculty performance on annual evaluations or for promotion. Finally, the scale may also be beneficial for understanding the characteristics of both the mentor and the mentee that may predict and uniquely contribute to negative mentoring experiences, therefore providing useful on individual, dyadic, and program level factors that may predict negative mentoring experiences.

**Conceptual framework of negative mentoring experiences.** Drawing from existing research on negative mentoring, (Eby et al., 2000; Limeri et al., 2019; Scandura, 1998), Tuma and colleagues (2021) characterized and defined the construct of negative mentoring experienced by STEM graduate students by conducting an exploratory, interview based study. To define the content domain of the construct, Tuma et al. (2021) interviewed 40 life science doctoral students from 22 U.S. research institutions who reported at least one negative experience with their mentor. Using qualitative content analysis, they delineated the conceptual definitions and operational manifestations of negative mentoring experiences within STEM graduate education. Consistent with research on negative mentoring in organizational and clinical supervisory mentoring relationships, they found that mentees reported experiencing negative mentoring that hindered their career and psychosocial outcomes (Tuma et al., 2021). Specifically, they found that doctoral students experienced mentor inaccessibility, mentee-mentor

mismatches, abusive supervision, limited mentor expertise, and a lack of mentoring support and poor relationship quality (Tuma et al., 2021). In contrast to prior research, they found that doctoral students did not dichotomize negative mentoring in terms of an absence of positive behaviors (e.g., limited support) versus actively harmful behaviors (e.g., manipulation). Instead, doctoral students were unique in reporting the role of research groups, departments, and disciplinary culture of STEM in contributing to detrimental mentoring outcomes. Results from this study and existing research on negative mentoring experiences, suggest that mentees can experience negative mentor that ranges in form and severity and that influences their personal and professional outcomes (Eby et al., 2000; Limeri et al., 2019; Tuma et al., 2021).

Prior research has attempted to empirically distinguish the dimensions of negative mentoring experiences in workplace mentoring relationships. Eby and colleagues (2000) proposed a taxonomy consisting of five broad meta-themes of negative mentoring experiences (general dysfunctionality, lack of mentor expertise, manipulative behavior, distancing behavior, and mismatch within the dyad), which encompass three larger dimensions (mentor incompetence, poor mentor behavior, and general mismatch). Further research indicated that the five-factor structure of negative mentoring experiences from Eby et al., 2000, could be meaningfully clustered more parsimoniously in to two broader categories (Eby & Allen, 2002). These findings suggest that the two higher-order factors, which are distinguished by neutral and ill intent of the mentor, are also plausible for describing the dimensions of negative mentoring experiences (Eby & Allen, 2002). In addition to the two broad dimensions comprised of mentor intent and effects on career or psychosocial outcomes (Scandura, 1998), Simon & Eby (2003) found support for a third

category that is based on the specific of the mentor actions that could be distinguished in to targeted and diffuse behaviors. However, the most recent evidence comes from a scale development study with robust content, construct, and criterion-related validity evidence, which provided the strongest support for a five factor model of negative mentoring experiences (Eby et al., 2004). Yet, there may be conceptual overlap between the different dimensions of negative mentoring remains and the dimensions may be better distinguished by a higher-order factor structure. Furthermore, narrative accounts from doctoral students indicate that negative experiences have both detrimental career and psychosocial outcomes, rather than one or the other as previously conceptualized (Scandura, 1998; Tuma et al., 2021). It is plausible that such negative mentoring experiences are not empirically discriminable in academic settings and further investigation within the context of academic mentoring relationships may allow for additional advances for measuring and understanding the construct. Thus, clarity surrounding the dimensionality of negative mentoring experiences and their relative conceptual overlap is necessary for understanding how dysfunctional mentoring experiences may function in student-faculty mentoring relationships.

**Measurement conceptual framework.** Mentoring scholars have predominantly approached the measurement of mentoring processes (e.g., cultural diversity awareness, career and psychosocial support received, interpersonal comfort) from the mentee's perspective. In general, the reliability and validity evidence for the majority of measures for mentoring variables in STEMM fields is limited (Hernandez, 2019). Moreover, there is currently no validation evidence for measures aimed at assessing negative mentoring in STEMM contexts (Hernandez, 2019). In order to advance our understanding of the

challenges associated with negative mentoring, we aimed to define and operationalize construct of negative mentoring, develop a scale to measure these unique relational experiences, and examine relationships with variables we hypothesized to be associated with negative mentoring experience (i.e., nomological network).

Guided by the *Standards for Educational and Psychological Testing* (AERA et al., 2014), we sought to accomplish this by gathering validity (i.e., the degree to which evidence and theory support the interpretations of test scores for the proposed use of tests) and reliability (i.e., the consistency and precision of scores across replications of a testing procedure) evidence for the MERGE. In this study, the proposed interpretation of the test scores suggests that responses to the items on the MERGE capture and are representative of graduate students' negative mentoring experiences, with higher scores indicating greater negative mentoring experienced. To guide the development and validation process, we adopted a construct validity framework to identify and provide evidence in alignment with several separate but interrelated categories of validity (AERA, et al., 2014; Messick, 1995). Using this measurement framework, establishing construct validity relies on generating various sources of validity based on (i) test content (i.e., alignment between the content of a test and the construct it is intended to measure); (ii) response processes (i.e., alignment between the construct and the response engaged in by test takers); (iii) internal structure (i.e., inter-item relationships and the extent to which they represent the construct they are intended to measure); (iv) evidence based on relations to other variables (i.e., degree to which a variable external to a measure relates in a theorized manner); and (vi) potential consequences of testing (i.e., test scores

realized are interpreted and used as intended) (AERA et al., 2014). This study aims to provide these forms of evidence for the MERGE.

To generate rigorous validity and reliability evidence, we conducted two sequential, mixed-method studies. In Study 1, we developed items based on prior research defining the construct of negative mentoring, established response process validity by gathering feedback on the items through cognitive interviews, and obtained content-related validity based on sorting task and feedback from subject experts. In Study 2, we refined the items and then collected and analyzed responses from a national sample of life science doctoral students to collect validity evidence based on the internal structure and the convergent and divergent validity of the measure. In these studies, we sought to address three research questions. Specifically, we ask:

1. Is the MERGE productive and useful for generating accurate scores of negative mentoring experiences in STEM graduate education?
2. Are the MERGE scores related as theoretically expected with measures of similar and dissimilar constructs?
3. Does the MERGE allow for causal explanations between negative mentoring experiences and their influence on the career and psychosocial outcomes of graduate students?

## **METHODS**

This study received limited review by the University of Georgia Institutional Review Board and was determined to be exempt (PROJECT00003604).

**Study 1 Overview.** The purpose of Study 1 was to generate the test content of the scale of mentees' perceptions of negative mentoring experiences. Items were developed

following an exploratory study of doctoral students' negative mentoring experiences (Tuma et al., 2021). During this study we also obtained evidence of content-related validity and response process validity.

**Study 1 Methods.** We began by reviewing the original transcripts, conceptual definitions, and operational manifestations based on the narrative accounts of doctoral students' negative mentoring experiences (Tuma et al., 2021). Two subject matter experts (TTT & ELD) independently developed items based on these experiences (Tuma et al., 2021). We also adapted items from existing measures of workplace stressors such as sexual harassment (Fitzgerald et al., 1999), abusive supervision (Tepper, 2007), and illegitimate tasks (Semmer et al., 2010). After the initial development, we reviewed the items and deleted redundant items, which resulted in a final pool of over 210 items.

We next aimed to determine that the items were interpreted as intended (i.e., evidence based on response processes). Specifically, we aimed to ensure that respondents were engaging in cognitive thought processes that allowed for alignment between their understanding of the item and the item's intended meaning and that they were able to accurately report their agreement with the item's content. We conducted semi-structured cognitive interviews with life science doctoral students to uncover potential response process problems. Specifically, we used concurrent cognitive interviews, where participants were asked to verbalize their thinking and rationale for responding as they worked through the test items. Specifically, participants were asked to read and respond to the item, actively explain their interpretation of the item, and verbalize and describe the reasoning for their response. The concurrent nature of the interviews allowed us insight into the cognitive processes that occurred while participants responded to the test

content. Participants were compensated with a \$25 gift card to either Amazon or Starbucks. Given the large initial set of items, each participant reviewed only a subset of the total items (5 total dimensions equaling 40 items each), so that each item was reviewed by at least four individuals.

To provide further evidence of test content validity, we conducted a Q-sort activity (Nahm et al., 2002). We identified ten scholars with expertise in mentoring, career development, organizational psychology, and instrument development in the affective domain to provide their expert evaluation of the relevance and utility of the survey items. Experts were provided with the conceptual definitions of the dimensions of the construct, the instructions given to participants for completing the scale, and a randomized list of items being considered for inclusion in the scale. Experts were asked to provide three ratings for each item: (1) assignment of the item to the dimension of negative mentoring the item is intended to represent (i.e., construct rating), (2) their certainty that the statement fits the dimensions selected (i.e., confidence rating), and (3) the relevance and appropriateness of the item for each dimension (i.e., relevance rating). Experts were also asked if they felt the items covered the full range of content within each dimension and if they had any recommendations for improving the content coverage (i.e., construct underrepresentation and overrepresentation). Finally, experts were also asked to identify problematic and potentially ambiguous items.

**Study 1 Results.** In total, we interviewed 20 students who represented a range of socio-demographic backgrounds, English-language abilities, institution types from across the United States, and reported a range of mentorship quality, from mostly positive to mostly negative. The participant sample was stratified by mentoring experience, such that

~33% of sample was each comprised of self-reported mentoring experiences that were overall, positive, neutral, or negative. Participants represented 13 institutions and varied in terms of gender (14 women, 6 men), ethnicity (5 Latine, 15 not Latine), race (6 Asian, 3 Black, 10 White, 1 prefer not to respond), English language learner (14 native English speaker, 6 English language learners) and program time points (7 pre-candidacy, 13 post candidacy). Interviews lasted 50 minutes on average.

Using the results of our cognitive interviews, we revised or removed items that participants identified as having ambiguous wording, unclear intent, incorrect interpretations, or otherwise problematic. For example, participants have difficulty consistently understanding colloquial terms (e.g., passive aggressive, “keeps me out of the loop”, “stretch the truth”). Participants also reporting difficult responding to certain items that were intentionally written to be broad or applicable to many situations or contexts. To improve the clarity and interpretability of the items, the first author made changes and revised the item content to address the concerns raised in the cognitive interviews.

Based on the data collected from our expert feedback via the Q-sort activity, we further modified, added, or removed scale items in order to form a modified instrument. To accomplish this, item scores from experts was collated and items that received more than 70% agreement in terms of accurate placement were included for the next study. Seventy-four items (i.e., 60%) passed this criterion. The remaining 51 items (i.e., 40%) were reviewed, edited, or cut based on reaching consensus between the first and senior author. The remaining 89 items were retained and further scrutinized in Study 2 for potential inclusion in the MERGE.

**Study 2 Overview.** The purpose of Study 2 was to further refine the items and examine their psychometric properties. To accomplish this, we collected and analyzed responses from a national sample of life science doctoral students to determine the internal structure of the measure. In addition, we also began preliminary analyses to establish the nomological network of variables that are related (i.e., convergent validity) and distinct from other theoretically related (i.e., discriminant validity) constructs.

*Introduction.* Evidence for criterion-related validity is provided by examining the associations between the construct of interest (i.e., negative mentoring) and theoretically relevant outcomes. We expected that negative mentoring is a multidimensional construct (i.e., limited career and psychosocial support and interpersonal mismatch are conceptually similar but empirically distinct components of negative mentoring). However before examining these associations, it is a prudent step in instrument development to examine multiple measurement models in order to determine if there are other theoretically defensible factor solutions that explain the variance amongst the items in order to determine the most parsimonious model for the instrument (Bandalos, 2018). We expected that:

*Hypothesis 1:* Negative mentoring experiences comprise a multidimensional construct consisting of at least five distinct factors (Eby et al., 2004).

**Convergent and Discriminant Validity.** An additional type of validity evidence involves demonstrating that a construct is related to theoretically related constructs (i.e., convergent validity) but is distinct from other constructs (i.e., discriminant validity). The scores from the MERGE should be related to theoretically similar constructs, each of which is explained below.

*Cultural aware mentoring.* Culturally aware mentorship refers to mentorship that recognizes and is responsive to potential differences in cultural backgrounds, values, beliefs, and experiences. Through effective culturally aware mentorship, mentors demonstrate interest in and value students' cultural knowledge, frames of reference, and identities (e.g., race/ethnicity, sexual orientation, religion, cultural identity (Byars-Winston et al., 2018)). Research indicates that culturally aware mentorship can lead to a range of desirable outcomes for all individuals, but in particular for individuals from historically or currently marginalized backgrounds. For instance, culturally aware mentoring has been positively associated with science identity (Camacho et al., 2021; Haeger & Fresquez, 2016), satisfaction with research (Haeger & Fresquez, 2016), and perceived mentoring effectiveness (Black et al., 2022; Byars-Winston et al., 2023; Pfund et al., 2022). We hypothesized that mentors who have reduced understanding, appreciation, and respect for diverse backgrounds and who are unable or unwilling to recognize potential biases or stereotypes (i.e., those who are less culturally aware), will be negatively related to more high-quality and enriching mentoring relationships.

*Mentorship quality & effectiveness.* The extent to which the mentoring relationship is effective and high-quality is likely to influence the benefits realized from participating in the mentoring relationship. Mentoring effectiveness refers to the degree to which a mentoring relationship meets the needs of the individuals involved and is characterized by communication, trust, interpersonal comfort, support, and mutual understanding (Allen & Eby, 2003). We anticipate that mentoring relationships that do not meet the goals of the individuals or that are not of high-quality will hinder the development of an effective and beneficial mentoring relationship.

*Deep-level similarity.* A considerable volume of research has found that mentees who perceive themselves as more similar to their mentor report higher quality and more beneficial mentoring relationship than those who are less similar (Eby et al., 2013; Ghosh, 2014; Hernandez et al., 2017; Mitchell et al., 2015; Pedersen et al., 2022). Mentees can be similar to their mentors in many ways. By far, mentee perceptions of deep-level similarity (i.e., shared attitudes, perspectives, beliefs, values, and interests) have the largest effect on mentee perceptions of quality mentorship (Eby et al., 2013). Mentees who do not see themselves as highly similar or who do not identify with their mentors may feel as though they have less connection or rapport with their mentor. If the mentoring dyad is less similar, it is also possible that the mentee and the mentor may have different approaches to problem solving, ways of thinking, and approaches for addressing challenges, which may lead to a less fulfilling relationship.

*Perceived organizational support.* In the workplace, employees who perceive that their employer treats them fairly, values their well-being, and contributions, and who are supportive of their development (i.e., perceived organizational support), feel more obligated and committed to their organization (Dawley et al., 2008). An employee's perceptions of organizational support develop through their interactions with the organization and the organizational agents (e.g., supervisors, mentors). Through these interactions, employees learn the extent to which the organization values them, which then influences their job performance, commitment to the organization, and turnover intentions (Eisenberger et al., 2002; Erdogan & Enders, 2007; Loi et al., 2006). When applied to the arena of student-faculty mentoring, negative mentoring experiences may

influence graduate students' perceptions of the extent to which they feel their graduate program and university cares about them (i.e., perceived organizational support). Mentees who experience negative mentoring may feel unsupported or undervalued and these feelings may be exacerbated when they bring these issues to university leaders but these concerns are not acted upon (Tuma et al., 2021). Consequently, those who experience negative mentoring may feel as though their graduate program or university does not have their best interests in mind or is apathetic about their well-being. An alternative possibility is that perceived organizational support may mediate the relationship between negative mentoring experiences and mentee outcomes. For example, mentees who feel they receive greater support from their graduate program or university may be buffered from the impacts of negative mentoring, which mitigate their potential effects. Thus, the extent to which doctoral students feel supported by their graduate program and university can impact how they are impacted by negative mentoring experiences.

With respect to convergent validity, this leads us to propose the following hypotheses:

*Hypothesis 2:* Mentee perceptions of negative mentoring experiences will be negatively related to mentors' culturally aware mentoring behaviors.

*Hypothesis 3:* Mentee perceptions of negative mentoring experiences will be negatively related to their own perceptions of the mentoring relationship quality and effectiveness.

*Hypothesis 4:* Mentee perceptions of negative mentoring experiences will be negatively related to perceived deep-level or psychological similarity with their mentor.

*Hypothesis 5:* Mentee perceptions of negative mentoring experiences will be negatively related to their own perceptions of their graduate program's organizational support, such that the occurrence of negative mentoring experiences will relate to a negative affective view from the graduate program.

*Affective response towards graduate research.* Negative mentoring experiences should be a distinct construct from mentee reports of poor job satisfaction or their emotional response to their graduate research. Furthermore, we aim to rule out the possibility that perceptions of negative mentoring experiences only reflect general personal tendencies to view the work environment with a positive or negative lens. For example, it is possible that doctoral students with high positive affect towards their graduate research may be less likely to perceive negative mentoring or experience its potential effects differently while doctoral students with high negative affect towards their graduate research may be more likely to report it. As a result, testing for multicollinearity between negative mentoring experiences and emotional responses towards graduate research is critical for ensuring that mentee individual level differences are not biasing reports of negative mentoring experiences.

*Hypothesis 6:* Mentee perceptions of negative mentoring experiences will be distinct from affect towards graduate research/work.

*Personality.* Individual personality traits describe regularly stable patterns of thoughts, emotions, motivation, and behavior. Personality traits can be robust predictors

of students' educational experiences and academic outcomes (Komarraju et al., 2011). Consequentially, individual differences, such as personality traits, have the potential to influence mentorship effectiveness and the nature of negative mentoring experiences. The Five Factor Model or Big Five Model consists of five key dimensions: openness, conscientiousness, extraversion, agreeableness, and neuroticism (John & Srivastava, 1999). Openness includes qualities such as creativity, unconventionality, artistic sensitivity, and broad mindedness. Conscientiousness encompasses dependability, achievement, industriousness, planfulness, and goal-directness. Extraversion is associated with enthusiasm, sociability, ambition, positive emotionality, and assertiveness. Agreeableness includes cooperation, compassion, politeness, trustfulness, and empathy. Neuroticism refers to the likelihood of negative feelings, such as anxiety, hostility, personality insecurity, reduced self-esteem and depressive tendencies. Empirical evidence indicates that conscientiousness and neuroticism are associated with work motivation and performance (Barrick et al., 2001), yet there has been little investigation on the influence of personality within the context of mentoring relationships.

Personality traits may influence the perceptions of negative mentoring experiences for a number of reasons. For instance, mentees who are high in conscientiousness may be more sensitive to a lack of appreciation or encouragement for their hard work from their mentor. Mentees high in agreeableness may also feel more overwhelmed or stressed when receiving demanding or critical feedback from their mentor. Mentees who are high in openness and value freedom, creativity, and autonomy, may be more constrained by a mentor who is controlling or more attentive to the details of their work. Furthermore, it is also possible that mentees low in extraversion may be

less likely to participate in social interactions or relationship building activities, which may result in them perceiving less support from their mentor. Finally, it is plausible that mentees high in neuroticism may have a stronger emotional response to conflict or unpleasant experiences in their mentoring relationship. Thus, for a variety of reasons, individual-level personality traits may influence perceptions or endorsement of negative mentoring experiences. To rule out the possibility that negative mentoring reflects general personality traits rather than a distinct workplace stressor, we examined associations between the Big Five Model of personality traits and perceptions of negative mentoring experiences.

*Hypothesis 7:* Mentee perceptions of negative mentoring experiences will be distinct from personality and, in particular, openness, conscientiousness, and extraversion. In addition, neuroticism will demonstrate weak, positive correlations with negative mentoring experiences and agreeableness will demonstrate moderate, negative correlations with negative mentoring experiences.

### ***Study 2 Methods***

**Participants.** Participants were U.S. doctoral students currently conducting or who had done research as a graduate student for at least one year within the past year and were pursuing or had earned a PhD in a life science discipline from a doctorate-granting university. We recruited doctoral students directly to minimize potential biases from graduate coordinators or programs choosing to share the study information with individuals who had exclusively favorable mentoring relationships. We contacted participants by emailing doctoral students directly at their university affiliated email addresses that were listed publicly on departmental websites and directories from May to

July 2021. All participants received a recruitment email and invitation with a link to an online survey on the secure survey service, Qualtrics. Potential participants were told that the present study was designed to learn more about the quality of mentorship that graduate students receive and that all individuals with good, neutral, or bad mentorship quality were encouraged to participate.

In order to ensure the sample was reflective of the diversity of the life science doctoral talent pool, we purposefully recruited from Hispanic-Servicing Institutions (HSIs), Historically Black Colleges and Universities (HBCUs), and from graduate fellowship programs aimed at advancing diversity and inclusion in STEM fields (e.g., Howard Hughes Medical Institute Gilliam Fellows, The National Academies of Sciences Ford Foundation Fellows). To incentive study participation, eligible doctoral students who completely and accurately completed the survey were offered a \$15 gift card to Amazon, Chipotle, REI, or Starbucks. In addition, we utilized a modified tailored panel management recruitment approach (Estrada et al., 2014) that included compensation (i.e., gift card to participant's choice of selected vendors), personalized emails, and study branding.

We received a total of 601 responses with varying degrees of completion. Sixteen of these respondents completed <25% of the items and were removed due to their incomplete responses. 15 other doctoral students failed to pass attention checks and these careless and noncompliant responses were also removed. Our final analytic sample consisted of 565 doctoral students who represented 70 public and private institutions, and 38 states from varied geographic regions across the United States. An average of 8 participants ( $SD=6.5$ , range = 1-39) responded from each institution. Participants

represented predominantly R1 (highest research activity; 89.7%) institutions with comparably fewer from R2 (higher research activity; 10.3%) institutions according to the Carnegie Classification of Institutions of Higher Education. Approximately 69% of participants represented public universities, 31% private institutions, and 10% were from institutions serving Racially Minoritized student populations.

Additional demographic information for doctoral students and their mentors included in the analyses are summarized in Table 1 and Table 2, respectively. Doctoral students were also asked to report on their mentor socio-demographics (e.g., gender, race/ethnicity) and career stage (e.g., assistant-, associate-, or full- professor). Separate items were used to measure race and ethnicity on the survey. Participants could identify with multiples races: American Indian or Alaskan Native, Asian, Black or African American, Hawaiian or Native Pacific Islander, North African or Middle Eastern, or White.

**Measures.** Individuals who consented to participate were told that the study would ask them a series of questions about their dissertation advisor and the extent to which they acted as a mentor during their graduate research. Participants were explicitly instructed to think of their dissertation advisor and respond to the survey items with this individual in mind. Doctoral students who were co-advised or had multiple dissertation advisors were asked to identify one individual to respond about. Perceived negative mentoring experiences were measured in the survey using the 89-item instrument developed in Study 1. Additional details about the additional measures used in Study 2 are described below. A complete list of the measures and items are included in the Supplemental materials. Unless otherwise noted, variables were measured using five-

point Likert scales (i.e., 1 = “strongly disagree”; 5 = “strongly agree”) and items were coded so that higher values represent greater amounts of the construct.

### **Convergent Validity:**

*Cultural aware mentoring.* Cultural diversity awareness behaviors were measured using Byars-Winston & Butz's (2021) five-item scale (e.g., “*My mentor was willing to discuss race and ethnicity, even if it may have been uncomfortable for them.*”). We modified the response format of this scale from a five-point frequency response (i.e., 1 = “never”; 5 = “all of time”) to an agreeability response (i.e., 1 = “strongly disagree”; 5 = “strongly agree”) format.

*Mentorship quality & effectiveness.* Mentoring relationship quality was measured by Allen & Eby's (2003) five-item scale (e.g., “*I am very satisfied with the mentoring relationship my mentor and I have developed.*”)

*Deep-level similarity.* Deep-level similarity was measured using Ensher and colleagues (2002) eight-item scale (e.g., “*My mentor and I see things in the same way.*”)

*Perceived organizational support.* Perceived organizational support was measured using Eisenberger and colleagues (1997) eight-item scale (“*Help is available from my graduate program when I have a problem*”). The items were reworded by replacing ‘my organization’ with ‘my graduate program’.

### **Discriminant Validity:**

*Affective response towards graduate research.* Negative and positive affect towards graduate research were measured using Watson and colleagues (1988) ten-item scale. Participants were asked to think about their graduate research in general and not their mentor as they responded to the items. Participants responded to both positive (e.g.,

inspired) and negative (e.g., ashamed) affective, adjective markers about how their graduate research generally makes them feel on a day-to-day basis.

*Personality.* Personality traits were measured using the 20-item Mini-International Personality Item Pool (mini-IPIP) scale (Donnellan et al., 2006) to assess the dominant model of personality structure in trait psychology (e.g., agreeableness, conscientiousness, extraversion, intellect/imagination, and neuroticism). Participants were asked to think how well the statements described themselves and their personality in general, not as they desired to be in the future. Sample items include “*I feel others’ emotions*” (agreeableness), “*I get chores done right away*” (conscientiousness), “*I talk to a lot of different people at parties*” (extraversion), “*I have a vivid imagination*” (intellect/imagination), and “*I have frequent mood swings*” (neuroticism).

## **Study 2 Results**

*Evaluation of the Internal Structure of the MERGE.* We utilized an iterative confirmatory factor analytic (CFA) process to assess the internal structure of the scale and determine which model best explained the covariance matrix. Specifically, we evaluated whether more abstract or specific factor structures fit the data in a more parsimonious manner by testing a series of CFAs. A series of confirmatory factors models were conducted in R version 4.1.0 (R Core Team, 2016) and the statistical analyses for Study 2 were conducted using the lavaan (Rosseel, 2012), psych (Revelle, 2011) and mirt (Chalmers, 2012) packages. We used the robust maximum likelihood estimation to correct for any nonnormality in the data and to obtain the parameters. We then examined multiple absolute and relative fit indices to evaluate the adequacy of our hypothesized and alternative measurement models. Specifically, we evaluated the model fit holistically

by considering the Comparative Fit Index (CFI) and Tucker-Lewis Index (TLI) as relative indicators of model fit and the Root Mean Square of Approximation (RMSEA), Standardized Root Mean Square Residual (SRMR), and Chi-Square Test ( $\chi^2$ ) as absolute indicators of model fit. Following standard practices, we report Chi-Square but it is important to note that the Chi-Square test has a very high type II error rate with large sample sizes. As a result, it is likely that the Chi-Square will be significant even for parsimonious and well-fitting models.

We included a scale of sexual harassment to determine the extent to which negative mentoring experiences and sexual harassment represent conceptually similar or distinct constructs. To empirically test this, we adapted 5 items from the Sexual Experiences Questionnaire (Fitzgerald et al., 1995, 1999) to measure three dimensions (i.e., sexual coercion, unwanted sexual attention, and gender harassment) of sexual harassment. We observed low variance in the responses to these items, suggesting that most of the participants in our sample did not report experiencing sexual harassment from their mentor. We opted to dichotomize the sexual harassment items so that 0 reflected participants had never experienced sexual harassment and 1 reflected some degree of sexual harassment to decrease the skewedness of these items. In general, we found that sexual harassment displayed weak but positive correlations with the various dimensions of negative mentoring:  $r = 0.14$  with *neglect*,  $r = 0.23$  with *limited expertise*,  $r = 0.27$  with *deceit*,  $r = 0.27$  with *limited interpersonal abilities*,  $r = 0.26$  with *micromanagement*,  $r = 0.19$  with *limited career support*,  $r = 0.24$  with *poor relationship quality*,  $r = 0.28$  with *interpersonal mismatch*,  $r = 0.20$  with *limited psychosocial support*, and  $r = 0.13$  with *unequal treatment*. Sexual harassment was moderately positively

correlated with *abusive supervision* ( $r = 0.36$ ); however, this is not surprising, as they are likely both tapping into the same inappropriate supervisory construct. However, sexual harassment appears to be a unique construct that is distinct from negative mentoring experiences and was not included subsequent measurement model testing.

We first tested a model that examined the degree to which there is conceptual overlap between all dimensions of negative mentoring experiences (i.e., negative mentoring experiences is a unidimensional construct). We specified a one-factor model where all 66 items loaded on to the same factor. This model exhibited poor fit based on the global fit metrics (Table 3), suggesting that negative mentoring experiences are empirically distinguishable from each other.

The empirical characterization of ontogenic and dyadic negative mentoring experiences defined by Tuma and colleagues (2021) comprises 11 distinct negative experiences. Therefore, our second model tested the hypothesis that all dimensions of negative mentoring experiences are conceptually distinct (i.e., a 11-factor measurement model). The parameter estimates for the 11-factor model were within acceptable range and all of the factor loadings had acceptable values ( $>.40$ ; Bandalos, 2018) except for one item. The item, “*My mentor treats me the same as other mentees even though I have different needs,*” had a low factor loading of  $-0.04$  on the inaccessibility factor. The low loading value is substantially below the recommended cut off values, and we therefore opted to remove this item from the final measurement model. The 11-factor measurement model fit the data well (CFI = 0.884, TLI = 0.877, RMSEA = 0.055, SRMR = 0.062,  $\chi^2$  (2024) = 4,903,  $p < .0001$ ) (Table 3), no standardized factor loadings exceeded 1.0 (i.e., an ultra-Heywood case), and, in general, demonstrated acceptable inter-factor

correlations. However, inaccessibility and hands-off supervision demonstrated a very high factor correlation ( $r = .99$ ). This suggests that although inaccessibility and hands-off supervision may theoretically be distinctive forms of negative mentoring, our measure is not able to distinguish them empirically. Thus, we elected to combine the items comprising inaccessibility and hands-off supervision in to one single factor, which we termed “neglect”.

We then specified a 10-factor measurement model, which only differed slightly from our initially hypothesized 11-factor model. The 10-factor model was the best fit to the data when compared to the alternative factor models and fit the data nearly equivalently to the original 11 factor model (Table 3). Specifically, the 10-factor model fit the data well according to absolute fit metrics (RMSEA = 0.05, SRMR = 0.062,  $\chi^2$  (2034) = 4,927  $p < .0001$ ) but the relative fit indices were less than their recommended cut off values of  $\geq .90$  (CFI = 0.884, TLI = 0.877), suggesting poor model fit (Table 3). However, we caution readers from overinterpreting the values of the incremental fit indices. We examined the RMSEA of our null model to determine if the null model fits the data too well, thereby resulting in a low CFI value regardless of the fit of our models given the data. The RMSEA of our null model was 0.159, which suggests that our incremental fit indices (e.g., CFI, TLI) are unreliable due to the null model’s better than expected fit (Kenny, Kaniskan, & McCoach, 2014). As a result, we place more weight on the absolute fit indices (e.g., RMSEA, SRMR,  $\chi^2$ ) to examine model fit which indicate acceptable data-model fit (Table 3). The standardized factor loadings for each item ranged from 0.47 to 0.94 and are reported for each item in Table 4.

To simplify the final measurement model, we attempted to prune the 10-factor model by testing models that specified conceptually similar dimensions together (i.e., combining abusive supervision and limited interpersonal abilities, limited career support and limited psychosocial support) and testing various competing combinations. To accomplish this, we fit a series of 6, 7, 8, and 9 factor alternative confirmatory factor models to test for potential empirical overlap between the dimensions. The model fit statistics for these alternative models were not superior to the 10-factor model (Table 3).

Finally, we examined several nested alternative CFA models. Specifically, we tested the possibility that although there appear to be ten distinct underlying dimensions of negative mentoring experiences, they may be better represented by two higher level constructs (Eby & Allen, 2002, Scandura, 1998). To address this assumption, we fit a second-order CFA to the responses with two-higher order factors (i.e., neutral vs. bad mentor intent) and 10 first-order factors which were specified to load on to their respective first-level factors. We fit a 2 factor higher order factor model, where interpersonal mismatch, poor relationship quality, limited career support, limited psychosocial support, and neglect loaded on a second order latent factor (neutral mentor intent) and deceit, abusive supervision, micromanagement, limited interpersonal abilities, and limited expertise loaded on a second order latent factor (poor mentor intent). We also specified one final model to determine if negative mentoring experiences could be grouped in to three higher level constructs consisting of relationship issues, destructive mentor behavior, and lack of mentoring support. For this alternative CFA model we specified 10 lower order factors on to a 3 higher-order factor model where interpersonal mismatch and poor relationship quality loaded on to a higher-order factor (relationship

issues), deceit, limited interpersonal abilities, abusive supervision, and micromanagement loaded on to a higher-order factor (destructive mentor behavior), and limited expertise, neglect, limited career support, and limited psychosocial support loaded on to a final higher-order factor (lack of mentoring support). The results of these nested, higher-order models showed marginally acceptable fit to the data (Table 3), but neither of these higher-order CFA models were superior to the 10 lower-order factor model. Therefore, we conclude that the items used here to measure negative mentoring experiences are best supported by a 10 lower-order factor model. Furthermore, our results also indicate that negative mentoring experiences are related, but empirically distinct and discriminable constructs.

*Measurement Refinement Using IRT.* We then conducted further item-level analyses to examine the psychometric properties and functioning of each item to reduce the conceptual redundancy and cognitive load of the scale. By reducing the item number in the scale, we also aimed to reduce the fit of the null model to increase the utility of the relative fit metrics. To guide these decisions, we estimated a series of Item Response Theory models to inform decisions about the retainment and removal of items. We estimated a series of Generalized Partial Credit Models (GPCM) for each factor using the `gpcm()` function in the `mirt` package (Chalmers, 2012). We used the GPCM to examine item quality and functioning for each item by inspecting the alpha and beta parameters in concordance with the item information curves. Each GPCM has two types of item parameters: the alpha and beta parameter. The alpha parameter (i.e., discrimination parameter) represents the suitability of the item for discriminating respondents at different levels of the latent trait, with higher alpha values indicating greater

discrimination ability. The beta parameter (i.e., the location parameter) represents the location of the latent trait at which the item best discriminates among respondents, with a range of beta values spanning across response options providing the greatest information. The four beta parameters represent the borders between each of the five response options (e.g., strongly disagree, disagree, undecided, agree, strongly agree). The item curves display the ability ( $\theta$ ) on the x axis and the discrimination probability  $l(\theta)$  on the y axis and reveal the amount of “information” an item provides along the continuum of the latent trait. The item curves are the highest at the location where the item has the highest ability to discriminate.

To select a small subset of items to retain in the final measurement model, we fit a series of GPCMs for each dimension of the construct of negative mentoring experiences. We used the alpha and beta parameters and item test curve as analytic indicators to inform the scale development and refinement process. The alpha and beta parameters are presented in Table 5 and the complete set of item fit graphs are reported in the Supplemental Materials. We used our expert understanding of the latent variable and the degree to which the items were conceptually redundant to balance and inform these decisions. Using the results of the IRT models to guide our decisions, we elected to cut 2 items from *neglect*, 1 item from *limited expertise*, 2 items from *deceit*, 3 items from *limited interpersonal abilities*, 1 item from *abusive supervision*, 1 item from *micromanagement*, 3 items from *limited career support*, 0 items from *poor relationship quality*, 2 items from *interpersonal mismatch*, and 2 items from *limited psychosocial support*. This reduced the total number of items in the MERGE from 66 to 49. We then fit a new CFA model with the refined item set and found acceptable fit of the new model

(CFI = 0.91, TLI = 0.90, RMSEA = 0.052 (90% CI, 0.049 – 0.054), SRMR = 0.062,  $\chi^2$  (1082) = 2709.86,  $p < .0001$ ). We further assessed the goodness of our final measurement model's fit with equivalence testing (Marcoulides & Yuan, 2017; Peugh & Feldon, 2020). In contrast to null hypothesis testing, equivalence testing uses “T-Size” fit statistics to compare the amount of misspecification in a null model to a tolerable size of specification with adjusted cutoffs. The  $CFI_T$  was 0.893 which demonstrated mediocre fit and the  $RMSEA_T$  was 0.054 which demonstrated close fit.<sup>5</sup> Finally, we calculated coefficient omega ( $\omega$ ) values as measure of the scale's internal consistency (Table 8) (Dunn et al., 2014) and all values were within the acceptable range ( $> 0.70$ ). The final factor for the MERGE scale is presented in Figure 1 and the final set of items retained in the scale are reported in Table 8.

*Testing for Measurement Equity.* We also conducted measurement invariance analyses to examine the extent to which the scores from the MERGE functioned equivalently across various sociodemographic backgrounds (e.g., gender, race/ethnicity, socioeconomic status, degree status, international status, and program timepoint). Using a factor analytic framework in concordance with an omnibus approach (Putnick & Bornstein, 2016; Vanderford et al., 2018), we conducted measurement invariance tests. Specifically, we estimated a multiple-groups CFA model, in which the model estimated all parameters separately for each demographic group (i.e., a model where demographic groups can take on different parameter values) and compared the fit of this model to the null model (i.e., a single parameter estimated based on the entire dataset). If the two

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<sup>5</sup> The rescaled fit statistic values for the measurement model indicated for  $CFI_T$ : “poor”  $\leq 0.887$ , “mediocre” = 0.887 – 0.908, “fair” = 0.908 – 0.940, “close” = 0.940 – 0.983, and “excellent” are  $\geq 0.983$  and for  $RMSEA_T$ : “poor”  $\geq 0.116$ , “mediocre” = 0.093 – 0.116, “fair” = 0.057 – 0.093, “close” = 0.016 – 0.057, and “excellent” are  $\leq 0.016$ .

models demonstrate similar item parameters, then this can be used as an indicator that the items are measuring the construct in a similar manner between the two groups. Thus, similar model fit indices between the null model and the estimated group model provide evidence that the scores are not influenced by sociodemographic group membership.

We estimated models to test for measurement invariance for six sociodemographic variables: gender (man and woman), race and ethnicity (White, Asian, and Racially Minoritized), candidacy (pre-candidacy and post-candidacy), English language status (native English speaker and English language learner), international status (international and United States student), and economic status (low, mid, and upper class). Goodness of fit indices (e.g., CFI, TLI, RMSEA, SRMR,  $\chi^2$ ) for the measurement invariance tests are reported in Table 6. Our results suggest that the measurement invariance holds between groups across levels of measurement invariance given that the null model was equivalent or better fitting than the multi-groups model (Table 6). Thus, the scores from the MERGE function similarly across the sociodemographic groups tested.

*Criterion-Related Validity.* Evidence of convergent and discriminant validity are presented in Table 7. With respect to convergent validity, Hypotheses 2-5 were all supported. Culturally aware mentoring behaviors demonstrated moderate and negative correlations with all dimensions of negative mentoring experiences ( $r$  ranging from -0.34 to -0.62). Mentorship quality and perceived effectiveness demonstrated moderate to strong and negative correlations with all dimensions of negative mentoring experiences ( $r$  ranging from -0.42 to -0.87). The correlations between deep-level similarity and all dimensions of negative mentoring experiences were also moderate and negative ( $r$

ranging from -0.48 to -0.81). Finally, correlations between perceived organizational support and the dimensions of negative mentoring experiences were small to medium in magnitude ( $r$  ranging from -0.16 to -0.32).

With respect to discriminant validity, we examined associations between emotional responses to research and negative mentoring (Table 7). In contrast to our hypotheses, we found that mentee reports of negative affect towards their graduate research were moderately and positively correlated with all dimensions of negative mentoring ( $r$  ranging from 0.20 to 0.29). Furthermore, doctoral students' perceptions of negative mentoring experiences were negatively correlated with positive affect towards their graduate research ( $r$  ranging from -0.14 to -0.33). In summary, we found little support for Hypothesis 6. These results indicate that doctoral students' emotions towards their graduate research are correlated, and thus related, but distinct from their perceptions of negative mentoring. Instead, it is possible that emotions associated with negative mentoring may be an outcome of negative mentoring experiences.

We next examined correlations between the Big Five personality traits and the dimensions of negative mentoring to determine the extent to which perceptions of negative mentoring were influenced by personality traits (Table 7). We found that extraversion, agreeableness, and intellect did not correlate with negative mentoring experiences. Conscientiousness demonstrated a small negative correlation with interpersonal mismatch ( $r = -0.08, p = 0.04$ ) but was otherwise not related to negative mentoring experiences. Neuroticism exhibited small, positive correlations with deceit ( $r = 0.08, p = 0.04$ ), abusive supervision ( $r = 0.10, p = 0.02$ ), micromanagement ( $r = 0.13, p < 0.01$ ), limited career support ( $r = 0.11, p = 0.01$ ), poor relationship quality ( $r = 0.08, p =$

0.04), interpersonal mismatch ( $r = 0.11, p < 0.01$ ), and unequal treatment ( $r = 0.09, p = 0.03$ ). Thus, Hypothesis 7 was supported. These results suggest that, for the most part, doctoral student's perceptions of their negative mentoring experiences are not a function of their personality traits. However, our results also suggest that neuroticism may be broadly related to greater reports of negative mentoring and future studies are warranted in controlling for baseline levels of neuroticism.

## DISCUSSION

The purpose of this research was to develop a psychometrically sound instrument that can be utilized to measure graduate student mentees' negative mentoring experiences with their graduate research mentors in STEM graduate education. Guided by the pillars for establishing the validity and reliability of new psychological measures (AERA, APA, NCME, JCSEPT, 2014), the results of this study provide ample content-, construct-, and criterion-validity for measuring negative mentoring experiences. The development and validation of the MERGE will serve as the foundation for robust empirical studies investigating the antecedents, correlates, and outcomes associated with negative mentoring experiences.

One of the aims of the current work was to determine the conceptual overlap between the various dimensions of negative mentoring and the extent to which each dimension contributes to explaining mentee career and psychosocial outcomes. Our results suggest that mentees' perceptions of negative mentoring experiences are multidimensional. Furthermore, our findings also suggest that there are at least ten forms (i.e., neglect, lack of expertise, deceit, limited interpersonal abilities, abusive supervision, micromanagement, limited career support, poor relationship quality, interpersonal

mismatch, and limited psychosocial support) of negative mentoring experienced by mentees and that these forms are conceptually distinct and empirically discriminable. Although it may seem that there is considerable overlap between the dimensions and that they may be best represented by two broader categories of mentor intent (good vs. bad), our CFA results suggest these experiences are distinct (Table 3). These results are consistent with prior research suggesting that the construct of negative mentoring experiences is multidimensional and comprised of at least five distinct dimensions (Eby et al., 2004). Therefore, examining the full spectrum of negative mentoring experiences should be useful for understanding how such mentoring experiences hinder graduate students' personal and professional growth during their graduate training.

*Directions for Future Research.* The results of this research indicate multiple directions for future research. Scholars could investigate how experiencing negative mentoring affects students' wellbeing, self-efficacy, scholarly productivity, and career intentions. Future research should also examine whether students from particular social identities (e.g., gender, race/ethnicity) experience negative mentoring differently, such as whether they are more likely to experience negative mentoring and whether negative mentoring affects them in different ways. Experimental and intervention-based studies could also utilize the MERGE to determine whether or not the proposed intervention mitigates or reduces the likelihood of mentees' reports of negative mentoring. Finally, additional research aimed at understanding potential individual, relational, or organizational level antecedent variables that predict the likelihood of experiencing negative mentoring is critical for preventing these experiences from occurring in the first place. For instance, future research could measure individual departmental culture and

support for inclusive and effective mentorship and determine if negative mentoring experiences are less likely to be experienced where the culture and support for effective mentorship is valued, rewarded, or incentivized.

*Implications for Practice.* The MERGE can be used in several ways to promote effective mentorship. Graduate programs and university leaders can use the MERGE to identify instances of negative mentoring experiences and inform their decision making, which is a critical first step towards preventing negative mentoring experiences and mitigating its effects. The results of work could also be utilized to inform interventions, training professional development programs, or policy changes to address negative mentoring and reduce the likelihood of its occurrence. The MERGE scale could also be used to design and inform professional development for graduate students to “mentor up,” taking a more active role in their mentoring relationships. The regular administration of the MERGE at regularly scheduled intervals (e.g., once yearly) would also allow for mentors and institutions to determine their progress in improving mentoring competence and reducing negative mentoring experiences.

Mentorship is considered by many to be critical for developing the next generation of scientists, yet our research adds to the growing body of research highlighting that not all mentoring relationships are effective or high-quality. In fact, some may even be destructive or debilitating. As a result, mentoring may not yield all of the desirable outcomes that are commonly assumed to occur as a result of participating in a mentoring relationship. Mentees, mentors, and organizations should consider this when advocating mentoring as a potential solution to solve some of the grand challenges facing the STEM enterprise. Programs should consider how to pair and support mentees and

mentors to form high-quality relationships and determine what structures and supports are needed to sustain their effectiveness throughout the course of the relationship and graduate study. Finally, given that our results indicate that dysfunction in mentoring relationships appears quite likely, mentees and mentors should be more prepared for the likelihood that conflict and tension may occur in their mentoring relationship(s) and determine potential ways by which such conflict could be addressed before the relationship becomes damaging or dissolves altogether.

*Limitations.* There are several limitations associated with the current study. First, the data for the present study were collected from life science doctoral students, which limits the transferability of measure to other STEM disciplines. Given that the nature of mentoring relationships and graduate education differ by discipline, validity evidence should be collected before using the MERGE to measure negative mentoring experiences in other STEM fields. Second, the data were collected using a cross-sectional design which limits our ability to make claims about causality. Reverse causality and bidirectional effects are possible for some of the relationships examined, although it is unlikely that such bidirectional associations comprise the majority of the relationships. For example, it is plausible that doctoral student mentees who are struggling to balance the demands and workload of graduate education may fail to meet project deadlines or important milestones or they may gradually display a lack of motivation towards their research over time. Because of this, a mentor may invest less time and effort in providing mentoring support to the student which may result in the mentee feeling unsupported and thus more likely to report experience negative mentoring. In addition to determining the

potential for reverse causality, greater investigation into the sequence of events that contribute to negative mentoring experiences is warranted.

Importantly, our study lacks evidence for the validity and potential consequences of testing for negative mentoring experiences with the MERGE scale. Practitioners and university leaders may be keen to use the MERGE to identify mentors who are engaging in problematic behaviors and use the scores to guide decisions about possible administrative interventions or if certain faculty mentors should have reduced mentoring expectations. Yet, in this study, we did not collect any evidence to determine if the test scores can be used for this purpose or if particular cut scores should be utilized to inform such decisions (i.e., what evidence is necessary to establish problematic mentoring and subsequent intervention?). For instance, it remains unclear how much negative mentoring should be tolerated or when any administrative involvement should be pursued, if at all. Furthermore, we did not determine additional consequences that could result from the utilization of the MERGE. For instance, if the MERGE is used at the programmatic level to identify mentors who are engaging in problematic behaviors, mentors may be less motivated or likely to take on mentees that require greater support because they may be concerned about being identified as a poor mentor. Alternatively, mentees who report poor mentor behavior may face consequences and even retaliation for bringing attention to such issues.

Finally, the data collected in this study come from a single source (i.e., the mentee) and are self-reported. Such data subject to recall bias and possible conjecture regarding the causes of negative mentoring experiences. These potential biases are important to consider given that mentee and mentor reports of the same experiences are

not highly correlated (Fagenson-Eland et al., 2005; Welsh & Diehn, 2018), suggesting that there may be considerable disagreement within the dyad over the quality or dynamics of the mentoring relationship and the extent to which adequate mentoring support was provided.

*Summary.* This research addresses national calls to define and measure negative mentoring experiences and investigate their prevalence and potential to have detrimental impacts in STEMM fields. Our results indicate that graduate students report negative mentoring experiences that are conceptually similar but distinct and empirically discriminable and that influence their career and psychosocial outcomes. This study provides rigorous validity evidence for the Mentoring Experiences in Research & Graduate Education (MERGE) scale which will allow for robust future investigations aimed at understanding the consequences of negative mentoring experiences for mentees, mentors, departments, and universities.

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**FIGURES, TABLES, AND LEGENDS**

**TABLE 5.1: Demographic characteristics of doctoral students (*n* = 565)**

<b>Description</b>	<b><i>n</i> (%)</b>
<b>Gender</b>	
Woman	325 (58%)
Man	225 (40%)
Non-binary	13 (2%)
Prefer not to respond	2 (<1%)
<b>Race</b>	
American Indian or Alaskan Native	10 (2%)
Asian	131 (23%)
Black or African American	49 (8.5%)
Hawaiian or Native Pacific Islander	3 (<1%)
Middle Eastern	14 (2.5%)
White	319 (56%)
Prefer to self-describe	21 (3.7%)
Prefer not to respond	22 (3.8%)
<b>Ethnicity</b>	
Hispanic or Latinx/Latine	86 (15%)
Not Hispanic	465 (82%)
Prefer not to respond	14 (3%)
<b>Degree status</b>	
Pre-Candidacy	208 (37%)
Post-Candidacy	314 (55%)
Currently Post-Doctoral	40 (7%)
Prefer not to respond	3 (0.5%)
<b>International status</b>	
Yes	121 (21%)
No	443 (78%)
Prefer not to respond	1 (<1%)
<b>English First-Language</b>	
No	472 (84%)
Yes	89 (16%)
Prefer not to respond	4 (<1%)

**Table 5.1, continued.**

<b>Description</b>	<b><i>n</i> (%)</b>
<b>Research context<sup>1</sup></b>	
Bench	425 (75%)
Computational	277 (49%)
Fieldwork	167 (30%)
Theoretical	55 (10%)
Prefer not to respond	1 (<1%)
<b>Years completed</b>	
1	96 (17%)
2	110 (19%)
3	125 (22%)
4	89 (16%)
5	85 (15%)
6	43 (7%)
7+	13 (2%)
Prefer not to respond	4 (<1%)
<b>Relationship initiation</b>	
Direct admission	235 (42%)
Following laboratory rotations	304 (52%)
Other scenario	26 (5%)
<b>Subjective socioeconomic status</b>	
1 (bottom, worst off)	2 (<1%)
2	10 (2%)
3	32 (6%)
4	77 (14%)
5	91 (16%)
6	109 (19%)
7	147 (26%)
8	70 (12%)
9	18 (3%)
10 (top, best off)	2 (<1%)

<sup>1</sup> Counts do not sum up to 100% because some participant's research integrated multiple research contexts.

**TABLE 5.2: Demographic characteristics of doctoral student mentors ( $n = 565$ )**

<b>Description</b>	<b><i>n</i> (%)</b>
<b>Gender</b>	
Woman	196 (35%)
Man	364 (64%)
Prefer not to respond	5 (<1%)
<b>Race</b>	
American Indian or Alaskan Native	3 (<1%)
Asian	72 (13%)
Black or African American	12 (2%)
Hawaiian or Native Pacific Islander	1 (<1%)
Middle Eastern	12 (2%)
White	427 (76%)
Prefer to self-describe	10 (2%)
Prefer not to respond	31 (5%)
<b>Ethnicity</b>	
Hispanic or Latinx/Latine	28 (5%)
Not Hispanic	517 (92%)
Prefer not to respond	20 (3%)
<b>Rank</b>	
Assistant Professor	114 (20%)
Associate Professor	138 (24%)
Full Professor	292 (52%)
Other	14 (2%)
Prefer not to respond	7 (1%)

**TABLE 5.3: Results of Confirmatory Factor Analysis - Study 2**

Model	CFI	TLI	RMSEA	RMSEA 90% CI	SRMR	$\chi^2$	df	$\Delta\chi^2$	$\Delta df$
11 Factor	0.884	0.877	0.055	0.053 – 0.057	0.062	4903	2024		
10 Factor	0.884	0.877	0.055	0.053 – 0.057	0.062	4927	2034	24	10
9 Factor	0.879	0.873	0.056	0.054 – 0.058	0.063	5043	2043	140	19
8 Factor	0.875	0.869	0.057	0.055 – 0.059	0.061	5146	2051	243	27
7 Factor	0.865	0.859	0.059	0.057 – 0.061	0.062	5397	2058	494	34
6 Factor	0.848	0.842	0.063	0.061 – 0.065	0.063	5813	2064	910	40
1 Factor	0.726	0.714	0.099	0.097 – 0.102	0.082	6014	1127	1,111	897
10 – 1 <sup>st</sup> order Factor, 2 higher order Factors	0.865	0.860	0.059	0.057 – 0.061	0.075	5430	2068	527	44
10 – 1 <sup>st</sup> order Factor, 3 – higher order Factors	0.875	0.870	0.057	0.055 – 0.059	0.068	5198	2066	295	42

*Note:* CFI = comparative fit index; TLI = Tucker-Lewis index; RMSEA = root-mean-square residual; SRMR = standard root mean square residual;  $\Delta\chi^2$  = change in chi square between the alternative models and the a priori 11 model;  $\Delta df$  = change in degrees of freedom between the alternative models and the a priori 11 factor model.

**TABLE 5.4: Standardized Factor Loadings for the 10-Factor MERGE**

<b>Factor</b>	<b>Item</b>	<b>Standardized Loading</b>
<b>Neglect</b>		
Inacc1	My mentor responds when I contact them (R)	0.53
Inacc2	My mentor is too busy to meet with me	0.62
Inacc3	My mentor often forgets about my research progress	0.83
Inacc4	My mentor gives me their full attention when we meet (R)	0.64
Inacc5	My mentor's personal demands limit the time they have to mentor me	0.55
Sup7	My mentor wants me to become independent before I am ready	0.50
Sup8	My mentor keeps up with my research progress (R)	0.75
Sup9	My mentor is not involved enough in my research	0.80
<b>Limited Expertise</b>		
Exp1	My mentor is unfamiliar with my research topic	0.67
Exp2	My mentor is unable to provide guidance on my research	0.79
Exp3	My mentor lacks the technical knowledge to guide me in my research	0.71
Exp4	My mentor has limited management expertise	0.69
Exp5	My mentor lacks mentoring competence	0.86
<b>Deceit</b>		
Deceit1	My mentor says one thing and does another	0.78
Deceit2	My mentor likes to stretch the truth in front of others	0.75
Deceit3	My mentor is only nice to me when they need me	0.86
Deceit4	My mentor was nicer to me before I committed to work with them	0.78
Deceit5	My mentor lies to me	0.84
Deceit6	My mentor intentionally misleads me	0.83
<b>Limited Interpersonal Abilities</b>		
Inter1	My mentor has an unpredictable personality	0.84
Inter2	My mentor is impatient	0.84
Inter3	My mentor tells me information about their personal life that makes me uncomfortable	0.62
Inter4	My mentor gives me advice on topics that are none of their business	0.65
Inter5	My mentor gets annoyed easily	0.87
Inter6	My mentor thinks they are better than others	0.79
Inter7	My mentor is hot tempered	0.86
Inter8	My mentor does not take responsibility for their mistakes	0.81
<b>Abusive Supervision</b>		
Sup1	My mentor encourages competition between lab members	0.54
Sup2	My mentor makes me do tasks not related to our lab's research	0.52
Sup3	My mentor threatens me	0.78
Sup4	My mentor calls me insulting names	0.77
Sup5	My mentor yells at me	0.82
Sup6	My mentor takes their stress out on me	0.83

TABLE 5.4, cont.

<b>Micromanagement</b>		
Sup10	My mentor is too controlling	0.84
Sup11	My mentor micromanages me	0.91
Sup12	My mentor tries to get too involved in the day-to-day aspects of my research	0.86
Sup13	My mentor likes to approve of minor trivial decisions	0.79
Sup14	My mentor monitors my work too closely	0.87
<b>Lack of Career Support</b>		
Car1	My mentor is willing to give me feedback on my research (R)	0.62
Car2	My mentor advocates on my behalf (R)	0.79
Car3	My mentor protects me from others who might cause me professional harm (R)	0.73
Car4	My mentor has little interest in my career advancement	0.77
Car5	My mentor is reluctant to let me present my research at conferences	0.47
Car6	My mentor offers useful advice for achieving my career goals (R)	0.82
Car7	My mentor prioritizes publishing my research (R)	0.57
Car8	My mentor helps me identify ways to network (R)	0.72
Car9	My mentor makes sure I have sufficient funding to do my research (R)	0.48
Car10	My mentor helps me prepare for important milestones in my degree (R)	0.78
<b>Poor Relationship Quality</b>		
Rq1	My mentor and I do not like each other	0.91
Rq2	My mentor and I have a difficult relationship	0.94
Rq3	My mentor and I can talk about things other than work tasks (R)	0.55
Rq4	My mentor and I have a tense relationship	0.90
<b>Interpersonal Mismatch</b>		
Mis1	My mentor and I think different things are important in life	0.66
Mis2	My mentor and I have incompatible personalities	0.84
Mis3	My mentor has no respect for my career goals	0.82
Mis4	My mentor's personality works well with mine	0.80
Mis5	My mentor and I have similar work styles	0.58
Mis6	My mentor and I argue based on our differences in values	0.56
<b>Limited Psychosocial Support</b>		
Psy1	My mentor encourages me (R)	0.85
Psy2	My mentor values me as a person (R).	0.88
Psy3	My mentor checks in about my well-being (R)	0.80
Psy4	My mentor is a role model for me (R)	0.84
Psy5	My mentor makes me feel accepted (R)	0.90
Psy6	My mentor empathizes when I am struggling (R)	0.85
Psy7	My mentor is understanding when I experience difficulties (R)	0.85
Psy8	My mentor tells me when they think I have done a good job (R)	0.72

**TABLE 5.5:** Generalized Partial Credit IRT Model Parameters

Item ID	Item	$\alpha$	$\beta_1$	$\beta_2$	$\beta_3$	$\beta_4$
<b>NEGLECT</b>						
Inacc1	My mentor responds when I contact them (R)	1.439	0.247	1.843	2.281	3.547
Inacc2	My mentor is too busy to meet with me	1.657	-1.048	0.706	1.374	2.551
Inacc3	My mentor often forgets about my research progress	3.006	-0.869	0.237	0.681	1.512
Inacc4	My mentor gives me their full attention when we meet (R)	1.688	-0.028	1.165	1.681	2.712
Inacc5	<i>My mentor's personal demands limit the time they have to mentor me</i>	1.41	-1.515	-0.122	0.578	1.929
Sup7	<i>My mentor wants me to become independent before I am ready</i>	1.145	-0.983	0.401	1.271	2.446
Sup8	My mentor keeps up with my research progress (R)	2.458	-0.66	0.697	1.225	2.102
Sup9	My mentor is not involved enough in my research	2.849	-0.737	0.337	0.813	1.74
<b>LIMITED EXPERTISE</b>						
Exp1	My mentor is unfamiliar with my research topic	2.416	-0.085	0.962	1.487	2.356
Exp2	My mentor is unable to provide guidance on my research	4.17	-0.059	0.884	1.283	1.961
Exp3	My mentor lacks the technical knowledge to guide me in my research	2.934	-0.228	0.653	1.143	1.749
Exp4	<i>My mentor has limited management expertise</i>	1.541	-0.559	0.485	1.01	1.857
Exp5	My mentor lacks mentoring competence	2.233	-0.267	0.678	1.063	1.615
<b>DECEIT</b>						
Deceit1	My mentor says one thing and does another	2.761	-0.659	0.496	0.917	1.653
Deceit2	<i>My mentor likes to stretch the truth in front of others</i>	2.681	-0.246	0.758	1.088	1.687
Deceit3	My mentor is only nice to me when they need me	3.742	0.17	0.976	1.419	1.847
Deceit4	<i>My mentor was nicer to me before I committed to work with them</i>	2.786	0.059	0.736	1.003	1.465
Deceit5	My mentor lies to me	5.81	0.406	1.133	1.489	1.932
Deceit6	My mentor intentionally misleads me	5.168	0.392	1.126	1.485	1.98
<b>LIMITED INTERPERSONAL ABILITIES</b>						
Inter1	My mentor has an unpredictable personality	3.342	-0.029	0.652	0.918	1.53
Inter2	<i>My mentor is impatient</i>	3.485	-0.16	0.588	0.917	1.586
Inter3	<i>My mentor tells me information about their personal life that makes me uncomfortable</i>	1.981	0.574	1.604	2.004	2.489
Inter4	My mentor gives me advice on topics that are none of their business	2.254	0.373	1.293	1.65	2.158
Inter5	<i>My mentor gets annoyed easily</i>	4.73	-0.033	0.636	0.902	1.489
Inter6	My mentor thinks they are better than others	2.957	-0.065	0.511	0.832	1.379
Inter7	My mentor is hot tempered	4.926	0.251	0.903	1.268	1.763
Inter8	My mentor does not take responsibility for their mistakes	2.775	-0.154	0.609	1.012	1.679

Items that were cut from measurement model are bold faced, italic.

TABLE 5.5, continued.

<b>ABUSIVE SUPERVISION</b>						
Sup1	My mentor encourages competition between lab members	1.514	-0.268	1.023	1.867	2.800
Sup2	My mentor makes me do tasks not related to our lab's research	1.444	-0.173	1.233	1.666	2.499
Sup3	My mentor threatens me	4.223	0.906	1.492	1.758	2.232
Sup4	<b><i>My mentor calls me insulting names</i></b>	6.678	1.017	1.706	1.919	2.185
Sup5	My mentor yells at me	6.373	0.902	1.436	1.667	1.991
Sup6	My mentor takes their stress out on me	2.881	0.47	1.076	1.376	1.995
<b>MICROMANAGEMENT</b>						
Sup10	My mentor is too controlling	3.305	-0.054	0.785	1.19	1.721
Sup11	My mentor micromanages me	6.466	0.101	0.766	1.069	1.646
Sup12	<b><i>My mentor tries to get too involved in the day-to-day aspects of my research</i></b>	4.617	0.111	0.946	1.373	1.845
Sup13	My mentor likes to approve of minor trivial decisions	3.071	-0.150	0.593	0.946	1.700
Sup14	My mentor monitors my work too closely	4.277	0.046	0.902	1.423	2.153
<b>LIMITED CAREER SUPPORT</b>						
Car1	My mentor is willing to give me feedback on my research (R)	1.703	0.038	1.868	2.304	3.171
Car2	My mentor advocates on my behalf (R)	2.811	-0.305	0.710	1.502	2.171
Car3	My mentor protects me from others who might cause me professional harm (R)	2.198	-0.801	0.216	1.321	2.165
Car4	My mentor has little interest in my career advancement	2.710	-0.518	0.689	1.241	1.913
Car5	<b><i>My mentor is reluctant to let me present my research at conferences</i></b>	1.211	-0.09	1.409	2.433	3.525
Car6	My mentor offers useful advice for achieving my career goals (R)	3.123	-0.726	0.459	1.093	1.971
Car7	<b><i>My mentor prioritizes publishing my research (R)</i></b>	1.394	-0.837	0.580	1.454	2.460
Car8	My mentor helps me identify ways to network (R)	2.265	-1.184	-0.126	0.726	1.705
Car9	<b><i>My mentor makes sure I have sufficient funding to do my research (R)</i></b>	1.151	-0.377	1.327	2.177	3.217
Car10	My mentor helps me prepare for important milestones in my degree (R)	2.423	-0.686	0.379	1.026	1.929
<b>POOR RELATIONSHIP QUALITY</b>						
Rq1	My mentor and I do not like each other	5.302	0.097	0.961	1.642	2.302
Rq2	My mentor and I have a difficult relationship	8.058	-0.046	0.703	1.119	1.645
Rq3	My mentor and I can talk about things other than work tasks (R)	1.333	-1.194	0.915	1.556	2.583
Rq4	My mentor and I have a tense relationship	4.681	-0.072	0.808	1.189	1.933

Items that were cut from measurement model are bold faced, italic.

TABLE 5.5, continued.

<b>INTERPERSONAL MISMATCH</b>						
Mis1	My mentor and I think different things are important in life	1.842	-1.527	-0.318	0.602	1.751
Mis2	My mentor and I have incompatible personalities	3.924	-0.314	0.699	1.222	1.835
Mis3	My mentor has no respect for my career goals	2.811	0.02	1.082	1.766	2.207
Mis4	My mentor's personality works well with mine	2.955	-0.951	0.370	1.075	1.765
Mis5	<b><i>My mentor and I have similar work styles</i></b>	1.555	-2.000	-0.464	0.503	1.915
Mis6	<b><i>My mentor and I argue based on our differences in values</i></b>	1.477	-0.164	1.419	2.172	3.442
<b>LIMITED PSYCHOSOCIAL SUPPORT</b>						
Psy1	My mentor encourages me (R)	3.937	-0.272	0.895	1.376	2.003
Psy2	My mentor values me as a person (R).	4.327	-0.175	0.787	1.266	1.796
Psy3	My mentor checks in about my well-being (R)	2.967	-0.551	0.355	0.764	1.379
Psy4	My mentor is a role model for me (R)	3.022	-0.637	0.308	0.874	1.430
Psy5	My mentor makes me feel accepted (R)	4.928	-0.509	0.491	1.023	1.577
Psy6	My mentor empathizes when I am struggling (R)	3.82	-0.635	0.289	0.833	1.432
Psy7	<b><i>My mentor is understanding when I experience difficulties (R)</i></b>	3.561	-0.492	0.479	0.927	1.522
Psy8	<b><i>My mentor tells me when they think I have done a good job (R)</i></b>	2.288	-0.467	0.808	1.272	1.884

Items that were cut from measurement model are bold faced, italic.

**TABLE 5.6: Results of measurement invariance analyses.**

Model	CFI	TLI	RMSEA	RMSEA 90% CI	SRMR	$\chi^2$	df	p-value
Null	0.911	0.903	0.052	0.049 - 0.054	0.062	2,709.86	1082	NA
Gender	0.893	0.884	0.064	0.061 - 0.067	0.068	4,237.330	2164	< 0.001
Race & Ethnicity	0.868	0.856	0.069	0.066 - 0.071	0.073	6,119.636	3246	< 0.001
Candidacy	0.888	0.878	0.065	0.062 - 0.068	0.068	20,164.184	2352	< 0.001
English	0.885	0.875	0.067	0.064 - 0.069	0.067	4,606.966	2164	< 0.001
International	0.890	0.880	0.061	0.059 - 0.064	0.068	4,457.603	2164	< 0.001
Economic status	0.864	0.852	0.073	0.070 - 0.075	0.073	6,124.408	3,246	< 0.001

TABLE 5.7: Bivariate correlation matrix. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

Variable	1	2	3	4	5	6	7	8	9	10	11
1. Neglect	1										
2. Limited expertise	.70***	1									
3. Deceit	.59***	.65***	1								
4. Limited interpersonal abilities	.52***	.63***	.82***	1							
5. Abusive supervision	.50***	.61***	.77***	.81***	1						
6. Micromanagement	.17***	.34***	.58***	.64***	.61***	1					
7. Limited career support	.67***	.72***	.65***	.62***	.58***	.40***	1				
8. Poor relationship quality	.58***	.63***	.77***	.74***	.69***	.54***	.70***	1			
9. Interpersonal mismatch	.57***	.65***	.72***	.75***	.68***	.57***	.75***	.85***	1		
10. Limited psychosocial support	.64***	.69***	.71***	.72***	.64***	.46***	.82***	.81***	.81***	1	
11. Unequal treatment	.55***	.58***	.63***	.67***	.65***	.46***	.62***	.65***	.65***	.65***	1
12. Sexual harassment	.20***	.28***	.24***	.38***	.37***	.32***	.25***	.29***	.32***	.25***	.24***
13. Cultural diversity awareness	-.40***	-.47***	-.44***	-.45***	-.43***	-.34***	-.62***	-.53***	-.57***	-.62***	-.47***
14. Mentorship quality	-.71***	-.77***	-.71***	-.69***	-.63***	-.42***	-.82***	-.79***	-.80***	-.87***	-.67***
15. Deep-level similarity	-.52***	-.61***	-.62***	-.63***	-.56***	-.48***	-.68***	-.72***	-.81***	-.74***	-.58***
16. Perceived organizational support	-.24***	-.26***	-.25***	-.23***	-.24***	-.16***	-.30***	-.24***	-.22***	-.28***	-.32***
17. Negative affect towards graduate research	.22***	.27***	.25***	.26***	.28***	.20***	.29***	.26***	.27***	.25***	.27***
18. Positive affect towards graduate research	-.19***	-.29***	-.19***	-.16***	-.14***	-.14***	-.33***	-.23***	-.23***	-.28***	-.17***
19. Extraversion	.02	.06	.01	.00	.04	-.01	-.02	.00	.00	.04	-.02
20. Agreeableness	.04	.00	-.01	-.01	.00	-.03	-.03	.00	.02	.02	.03
21. Conscientiousness	.02	-.03	.01	-.02	.03	-.07	.00	-.05	-.08*	-.01	.00
22. Neuroticism	.06	.04	.08*	.06	.10*	.13**	.11*	.08*	.11**	.05	.09*
23. Intellect/Imagination	-.02	-.02	-.02	.01	-.02	.00	-.03	-.07	-.04	-.05	-.06
<i>M</i>	2.18	2.02	1.84	1.98	1.68	1.96	2.23	1.98	2.29	2.25	2.60
<i>SD</i>	0.87	1.00	0.94	1.05	0.76	1.05	0.87	0.95	0.94	1.06	1.19
Cronbach's $\alpha$	.85	.86	.90	.89	.82	.91	.90	.89	.86	.94	.91

TABLE 5.7, continued.

Variable	12	13	14	15	16	17	18	19	20	21	22	23
1. Neglect												
2. Limited expertise												
3. Deceit												
4. Limited interpersonal abilities												
5. Abusive supervision												
6. Micromanagement												
7. Limited career support												
8. Poor relationship quality												
9. Interpersonal mismatch												
10. Limited psychosocial support												
11. Unequal treatment												
12. Sexual harassment	1											
13. Cultural diversity awareness	-.20***	1										
14. Mentorship quality	-.26***	.58***	1									
15. Deep-level similarity	-.27***	.56***	.78***	1								
16. Perceived organizational support	-.10**	.22***	.28***	.28***	1							
17. Negative affect towards graduate research	.09*	-.10*	-.33***	-.28***	-.22***	1						
18. Positive affect towards graduate research	-.13**	.21***	.34***	.27***	.25***	-.19***	1					
19. Extraversion	.02	.02	-.04	.01	.02	-.07	.13*	1				
20. Agreeableness	-.01	.06	-.08*	-.04	.02	.05	.10	.30***	1			
21. Conscientiousness	-.03	-.09*	.04	.07*	.06	-.18***	.16***	.05	.06	1		
22. Neuroticism	.01	-.05	-.10*	-.08*	-.21***	.25***	-.18***	-.10*	.02	-.10**	1	
23. Intellect/Imagination	-.03	.12**	.04	.07	.05	-.02	.16***	.14**	.14	-.07	-.04	1
<i>M</i>	0.07	3.30	3.49	3.27	4.63	2.24	3.31	2.95	4.11	3.79	2.93	3.86
<i>SD</i>	0.21	0.92	1.11	0.89	1.40	0.85	0.90	1.09	0.75	0.86	0.89	0.80
$\alpha$	.91	.89	.95	.92	.93	.81	.82	.87	.77	.75	.71	.73

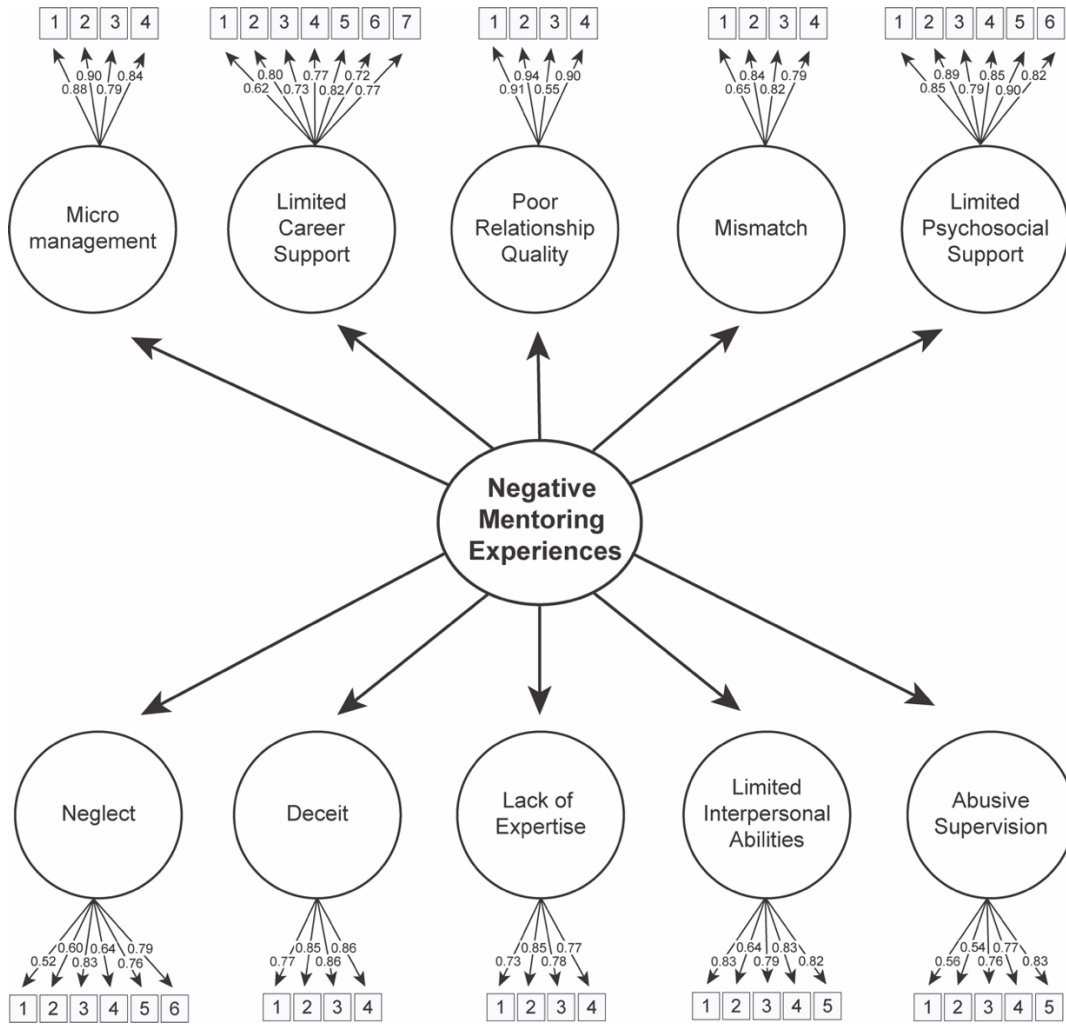
**TABLE 5.8: Final selection of items included in MERGE scale.**

<b>Neglect: 6 items, <math>\omega = 0.89</math></b>	
Inacc1	My mentor responds when I contact them (R)
Inacc2	My mentor is too busy to meet with me
Inacc3	My mentor often forgets about my research progress
Inacc4	My mentor gives me their full attention when we meet (R)
Sup8	My mentor keeps up with my research progress (R)
Sup9	My mentor is not involved enough in my research
<b>Lack of Expertise: 4 items, <math>\omega = 0.87</math></b>	
Exp1	My mentor is unfamiliar with my research topic
Exp2	My mentor is unable to provide guidance on my research
Exp3	My mentor lacks the technical knowledge to guide me in my research
Exp5	My mentor lacks mentoring competence
<b>Deceit: 4 items, <math>\omega = 0.92</math></b>	
Deceit1	My mentor says one thing and does another
Deceit3	My mentor is only nice to me when they need me
Deceit5	My mentor lies to me
Deceit6	My mentor intentionally misleads me
<b>Limited Interpersonal Abilities: 5 items, <math>\omega = 0.91</math></b>	
Inter1	My mentor has an unpredictable personality
Inter4	My mentor gives me advice on topics that are none of their business
Inter6	My mentor thinks they are better than others
Inter7	My mentor is hot tempered
Inter8	My mentor does not take responsibility for their mistakes
<b>Abusive Supervision: 5 items, <math>\omega = 0.86</math></b>	
Sup1	My mentor encourages competition between lab members
Sup2	My mentor makes me do tasks not related to our lab's research
Sup3	My mentor threatens me
Sup5	My mentor yells at me
Sup6	My mentor takes their stress out on me
<b>Micromanagement: 4 items, <math>\omega = 0.94</math></b>	
Sup10	My mentor is too controlling
Sup11	My mentor micromanages me
Sup13	My mentor likes to approve of minor trivial decisions
Sup14	My mentor monitors my work too closely

Table 5.8, continued.

<b>Lack of Career Support: 7 items, <math>\omega = 0.93</math></b>	
Car1	My mentor is willing to give me feedback on my research (R)
Car2	My mentor advocates on my behalf (R)
Car3	My mentor protects me from others who might cause me professional harm (R)
Car4	My mentor has little interest in my career advancement
Car6	My mentor offers useful advice for achieving my career goals (R)
Car8	My mentor helps me identify ways to network (R)
Car10	My mentor helps me prepare for important milestones in my degree (R)
<b>Poor Relationship Quality: 4 items, <math>\omega = 0.91</math></b>	
Rq1	My mentor and I do not like each other
Rq2	My mentor and I have a difficult relationship
Rq3	My mentor and I can talk about things other than work tasks (R)
Rq4	My mentor and I have a tense relationship
<b>Interpersonal Mismatch: 4 items, <math>\omega = 0.87</math></b>	
Mis1	My mentor and I think different things are important in life
Mis2	My mentor and I have incompatible personalities
Mis3	My mentor has no respect for my career goals
Mis4	My mentor's personality works well with mine
<b>Limited Psychosocial Support: 6 items, <math>\omega = 0.96</math></b>	
Psy1	My mentor encourages me (R)
Psy2	My mentor values me as a person (R).
Psy3	My mentor checks in about my well-being (R)
Psy4	My mentor is a role model for me (R)
Psy5	My mentor makes me feel accepted (R)
Psy6	My mentor empathizes when I am struggling (R)

**FIGURE 5.1: Final factor model for the MERGE scale.**



Squares represent observed indicators (i.e., survey items) and circles represent latent variables. Straight arrows represented factor loadings. Variances, covariances, and measurement error terms are omitted for parsimony in model.

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## Supplemental File 5.1: Study 1 Cognitive Interviews Screening Survey

Thank you for consenting to participate in this study!

The next several questions will ask you some questions about yourself. Please answer them to the best of your ability.

1. We are interested in the quality of mentoring that graduate students experience during their graduate research. How would you rate the overall quality of your mentoring relationship with your graduate advisor?

- Mostly positive
- Some positive and some negative
- Mostly negative

The following questions are about your personal characteristics and will help the researchers ensure they have received input from students who represent a broad range of personal characteristics.

7. What best describes your degree status?

- PhD Student
- PhD Candidate
- Currently Post-Doctoral
- Prefer not to respond

8. What gender do you most closely identify with?

- Woman
- Man
- Non-binary
- Other (self-describe)
- Prefer not to respond

9. With which ethnicity do you most closely identify?

- Hispanic or Latino/Latina
- Not Hispanic or Latino/Latina
- Prefer not to respond

10. With which race(s) do you most closely identify? Please choose all that apply.

- American Indian or Alaskan Native
- Asian
- Black or African American
- Native Hawaiian or other Pacific Islander
- North African or Middle Eastern

- White
- Other (self-describe)
- Prefer not to respond

11. Do you consider English to be your primary language or one of your primary languages?

- Yes
- No
- Prefer not to respond

We may want to contact you for an interview to help us refine a survey we are developing about graduate researchers' experiences with their research mentors, especially when those experiences are not so positive. If you choose to participate, you will receive a \$25 gift card to Amazon or Starbucks.

If you are willing, please enter your name and email address below. Please note that we will keep your information confidential but we need your name and contact information in order to schedule an interview.

First & Last Name:

Email Address:

Thank you for completing this survey! You will receive an email from our lab in the next 1 - 2 business days if you are selected to participate in an interview.

## Supplemental File 5.2: Study 1 Cognitive Interviews Protocol

Thank you again for your willingness to participate in our research study. The purpose of this study is to develop a survey about graduate students' mentoring experiences with their graduate research mentors. We will ask you to read and respond to ~30 statements about your research mentors' behaviors and characteristics, and the overall quality of your mentoring relationship. Your feedback will be used to ensure that the statements are understandable and clear. As a result, there are no right or wrong answers.

As a reminder, this interview will not be published, your responses will be anonymized, and the details of your interview will be kept confidential within our research team. The interview will not be transcribed and will only be used to ensure the accuracy of your comments.

Are you comfortable with me making a recording of our conversation today?

- If yes, start recorder
- If no, then explain that we will be taking notes to make sure that we capture their comments as well as possible

Great, thanks! And do you have any questions for me before we get started?

*Send link to Qualtrics survey in the chat feature of Zoom*

Please check the chat feature for a link to the survey that we will be administering to you. Also, could you please share your screen with me so that we can view your responses to the items and your progress on the survey? Please enter (*insert interview number here*) into the box labeled interview number.

Then, please read the following paragraph on the Qualtrics screen. Let me know when you have finished reading.

Great. Please continue using the red forward arrow on the bottom of the screen and provide your responses to the survey items one at a time. I will be asking your questions after each item.

*Questions to be asked after the participant reads and responds to each item:*

- What does this item mean to you?
- Why did you choose this rating?
- Would you change anything about the item to make it clearer?
- Is anything about the item confusing?

*Questions to be asked after the participant reads and responds to each item:*

- Do you have any feedback on the organization of our items on this page?

Thank you very much for your time and for participating in our research! We will be sending you a gift card by email sometime in December. Could you please complete a final question and select if you would prefer a gift card to Amazon or Starbucks? Could you also confirm the email address that you would like the gift card to be sent to?

Do you have any questions for me that I can answer before we end the interview?

### Supplemental File 5.3: Study 2 Survey and Items

Thank you for agreeing to participate in this study! This survey will ask you a series of questions about **your dissertation advisor** and their role as a mentor during your graduate research.

Although we recognize that you may or may not view this person as a mentor, we will refer to them as your "mentor" in this survey to understand the extent to which they act as a mentor. Please think of your dissertation advisor and respond to the statements with this person in mind.

If you were co-advised or had multiple dissertation advisors, please pick one person to respond about.

Q1. How would you rate the overall quality of your **relationship** with your mentor?

- Mostly positive
- Some positive and some negative
- Mostly negative
- Prefer not to respond

Q2. How would you rate the overall quality of your **graduate education** experience?

- Mostly positive
- Some positive and some negative
- Mostly negative
- Prefer not to respond

### **Mentoring Experiences in Research & Graduate Education (MERGE) Study 2 Items**

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

Dimension	Item
Inaccessibility	1. My mentor responds when I contact them. (R)
	2. My mentor is too busy to meet with me.
	3. My mentor often forgets about my research progress.
	4. My mentor gives me their full attention when we meet. (R)
	5. My mentor's personal demands limit the time they have to mentor me.
	6. My mentor treats me the same as other mentees even though I have different needs.
	1. My mentor is unfamiliar with my research topic.
	2. My mentor is unable to provide guidance on my research.

Limited Expertise	3. My mentor lacks the technical knowledge to guide me on my research.
	4. My mentor has limited management experience.
	5. My mentor lacks mentoring competence.
Deceit	1. My mentor says one thing and does another.
	2. My mentor likes to stretch the truth in front of others.
	3. My mentor is only nice to me when they need me.
	4. My mentor was nicer to me before I committed to work with them.
	5. My mentor lies to me.
	6. My mentor intentionally misleads me.
Limited Interpersonal Abilities	1. My mentor has an unpredictable personality.
	2. My mentor is impatient.
	3. My mentor tells me information about their personal life that makes me uncomfortable.
	4. My mentor gives me advice on topics that are none of their business.
	5. My mentor gets annoyed easily.
	6. My mentor thinks they are better than others.
	7. My mentor is hot tempered.
	8. My mentor does not take responsibility for their mistakes.
Supervisory Styles	1. My mentor encourages competition between lab members.
	2. My mentor makes me do tasks not related to our lab's research.
	3. My mentor threatens me.
	4. My mentor calls me insulting names.
	5. My mentor yells at me.
	6. My mentor takes their stress out on me.
	7. My mentor wants me to become independent before I am ready.
	8. My mentor keeps up with my research progress. (R)
	9. My mentor is not involved enough in my research.
	10. My mentor is too controlling.
	11. My mentor micromanages me.
	12. My mentor tries to get too involved in the day-to-day aspects of my research.
	13. My mentor likes to approve of minor trivial decisions.
	14. My mentor monitors my work too closely.
Limited Career Support	1. My mentor is willing to give me feedback on my research. (R)
	2. My mentor advocates on my behalf. (R)
	3. My mentor protects me from others who might cause me professional harm. (R)
	4. My mentor has little interest in my career advancement.

	5. My mentor is reluctant to let me present my research at conferences.
	6. My mentor offers useful advice for achieving my career goals. (R)
	7. My mentor prioritizes publishing my research. (R)
	8. My mentor helps me identify ways to network. (R)
	9. My mentor makes sure I have sufficient funding to do my research. (R)
	10. My mentor helps me prepare for important milestones in my degree. (R)
Poor Relationship Quality	1. My mentor and I do not like each other.
	2. My mentor and I have a difficult relationship.
	3. My mentor and I can talk about things other than work tasks. (R)
	4. My mentor and I have a tense relationship.
Interpersonal Mismatch	1. My mentor and I think different things are important in life.
	2. My mentor and I have incompatible personalities.
	3. My mentor has no respect for my career goals.
	4. My mentor's personality works well with mine.
	5. My mentor and I have similar work styles. (R)
	6. My mentor and I argue based on our differences in values.
Limited Psychosocial Support	1. My mentor encourages me. (R)
	2. My mentor values me as a person. (R)
	3. My mentor checks in about my well-being. (R)
	4. My mentor is a role model for me. (R)
	5. My mentor makes me feel accepted. (R)
	6. My mentor empathizes when I am struggling. (R)
	7. My mentor is understanding when I experience difficulties. (R)
	8. My mentor tells me when they think I have done a good job. (R)
Unequal Treatment	1. My mentor has favorites.
	2. My mentor shows preference to some people in the lab.
	3. My mentor treats some people better than others.
	4. My mentor is biased against certain groups of people.
<i>Content Warning: The next set of statements contains information about sexual harassment or misconduct which may be triggering to survivors. You may choose to skip this section. Support is available 24 hours a day at Project Safe Hotline: 615-322-SAFE (7233).</i>	
Sexual Harassment	1. My mentor has made sexual remarks.
	2. My mentor has made comments of a sexual nature about me.
	3. My mentor has touched me without my permission.
	4. My mentor has asked me out before.
	5. My mentor has had sex with me against my will.

**Cultural Diversity Awareness**

Byars-Winston, A., & Butz, A. R. (2021). Measuring research mentors’ cultural diversity awareness for race/ethnicity in STEM: Validity evidence for a new scale. *CBE—Life Sciences Education*, 20(2), ar15.

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

Cultural Diversity Awareness Behaviors	1. My mentor created opportunities for me to bring up issues of race/ethnicity as they arose.
	2. My mentor encouraged me to think about how the research related to my own lived experience.
	3. My mentor was willing to discuss race and ethnicity, even if it may have been uncomfortable for them.
	4. My mentor raised the topic of race/ethnicity in our research mentoring relationship when it was relevant.
	5. My mentor approached the topic of race/ethnicity with me in a respectful manner.

**Mentorship Quality & Effectiveness**

Allen, T. D., & Eby, L. T. (2003). Relationship effectiveness for mentors: Factors associated with learning and quality. *Journal of Management*, 29(4), 469-486.

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

Mentoring Relationship Quality	1. The mentoring relationship between my mentor and me is very effective.
	2. I am very satisfied with the mentoring relationship my mentor and I have developed.
	3. I am effectively utilized as mentee by my mentor.
	4. My mentor and I enjoy a high-quality relationship.
	5. Both my mentor and I benefit from our mentoring relationship.

**Deep-level similarity**

Ensher, E. A., Grant-Vallone, E. J., & Marelich, W. D. (2002). Effects of perceived attitudinal and demographic similarity on protégés' support and satisfaction gained from their mentoring relationships. *Journal of Applied Social Psychology*, 32(7), 1407-1430.

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

Deep-level similarity	1. My mentor and I see things in the same way.
	2. My mentor is similar to me in terms of our outlook and perspectives.
	3. My mentor and I are alike in a number of areas.
	4. My mentor and I analyze problems in a similar way.
	5. My mentor and I have similar values about work.
	6. My mentor and I have similar values about life in general.
	7. My mentor and I are more similar than dissimilar in important ways.

**Perceived Organizational Support**

Eisenberger, R., Cummings, J., Armeli, S., & Lynch, P. (1997). Perceived organizational support, discretionary treatment, and job satisfaction. *Journal of Applied Psychology*, 82(5), 812.

**Instructions:** Now please thinking about graduate program in general, not your mentor. Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = slightly disagree; 4 = undecided; 5 = slightly agree; 6 = agree; 7 = strongly agree; 8 = prefer not to respond

Perceived Organizational Support	1. My graduate program cares about my opinions.
	2. My graduate program really cares about my well-being.
	3. My graduate program strongly considers my goals and values.
	4. Help is available from my graduate program when I have a problem.
	5. My graduate program would forgive an honest mistake on my part.
	6. If given the opportunity, my graduate program would take advantage of me. (R)
	7. My graduate program shows very little concern for me. (R)
	8. My graduate program is willing to help me if I need a special favor.

**Affective Response to Research**

Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: the PANAS scales. *Journal of Personality and Social Psychology*, 54(6), 1063.

**Instructions:** Now please thinking about graduate research in general, not your mentor. To what extent does your graduate research generally make you feel:

**Response Scale:** 1 = not at all; 2 = a little; 3 = a moderate amount; 4 = a lot; 5 = a great deal, 6 = Prefer not to respond

Affective Response	1. Upset (negative)
	2. Hostile (negative)
	3. Alert (positive)
	4. Ashamed (negative)
	5. Inspired (positive)
	6. Nervous (negative)
	7. Determined (positive)
	8. Attentive (positive)
	9. Afraid (negative)
	10. Active (positive)

**Personality**

Donnellan, M. B., Oswald, F. L., Baird, B. M., & Lucas, R. E. (2006). The mini-IPIP scales: tiny-yet-effective measures of the Big Five factors of personality. *Psychological assessment, 18*(2), 192.

**Instructions:** Please indicate how well each of the following statements describes you and your personality in general. Describe yourself as you typically are, not as you wish to be in the future.

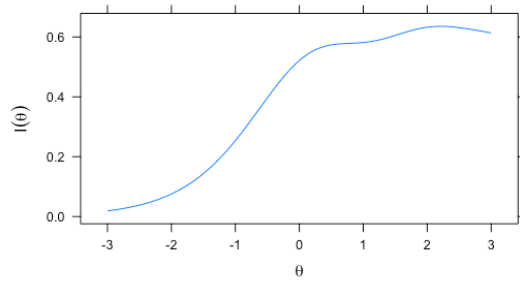
**Response Scale:** 1 = very inaccurate; 2 = moderately inaccurate; 3 = neither accurate nor inaccurate; 4 = moderately accurate; 5 = very accurate; 6 = Prefer not to respond  
 E = extraversion, A = agreeableness, C = conscientiousness, N = neuroticism, I = intellect/imagination

Big 5 Personality	1. I am the life of the party (E)
	2. I sympathize with others' feelings. (A)
	3. I get chores done right away. (C)
	4. I have frequent mood swings. (N)
	5. I have a vivid imagination. (I)
	6. I don't talk a lot. (E) (R)
	7. I am not interested in other people's problems. (A) (R)
	8. I often forget to put things back in their proper place. (C) (R)
	9. I am relaxed most of the time. (N) (R)
	10. I am not interested in abstract ideas. (I) (R)
	11. I talk to a lot of different people at parties. (E)
	12. I feel others' emotions. (A)
	13. I like order. (C)
	14. I get upset easily. (N)
	15. I have difficulty understanding abstract ideas. (I)
	16. I keep in the background. (E) (R)
	17. I am not really interested in others. (A) (R)
	18. I make a mess of things. (C) (R)
	19. I seldom feel blue. (N) (R)
	20. I do not have a good imagination. (I) (R)

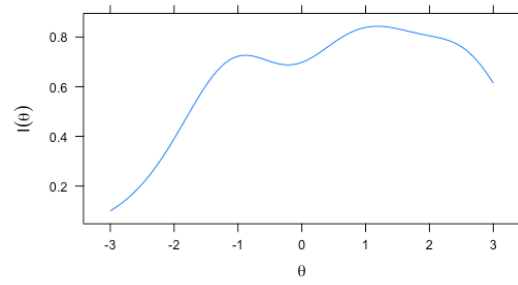
## Supplemental File 5.4: Item Information Curves for Full Item Set.

### Neglect

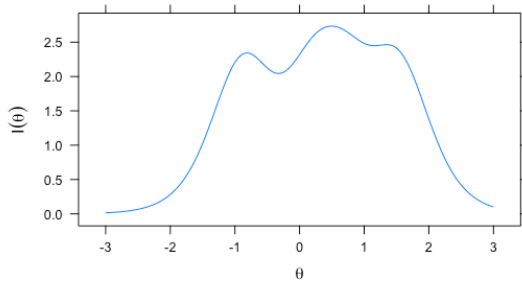
Neglect 1



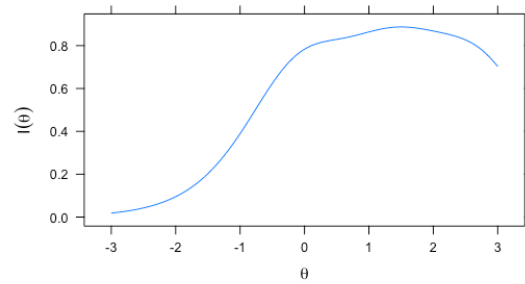
Neglect 2



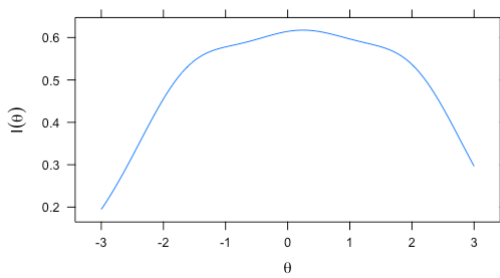
Neglect 3



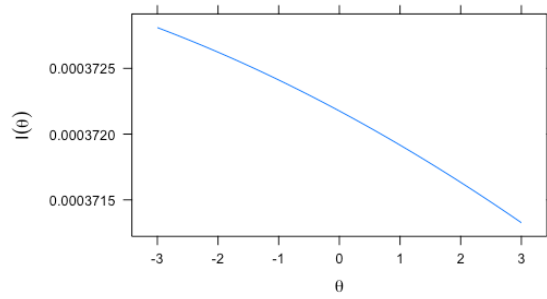
Neglect 4



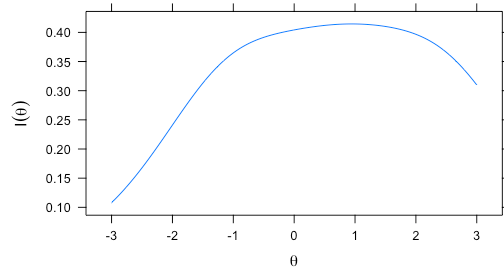
Neglect 5



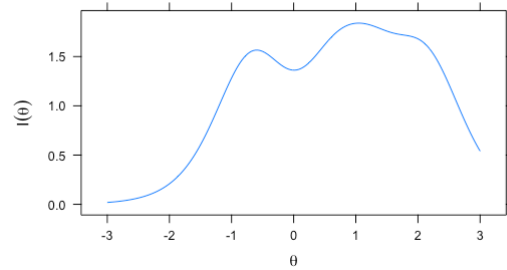
Neglect 6



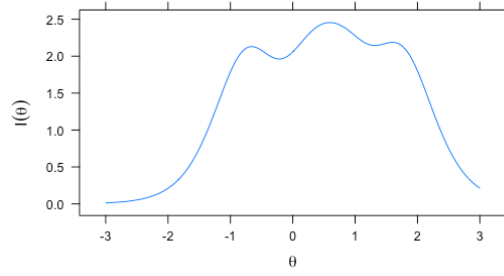
Neglect 7



Neglect 8

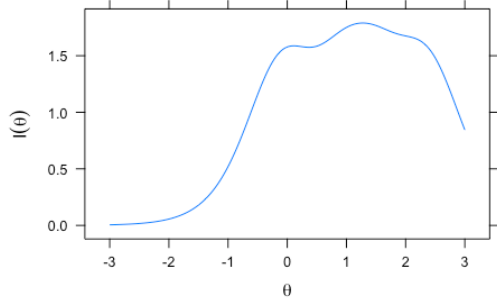


Neglect 9

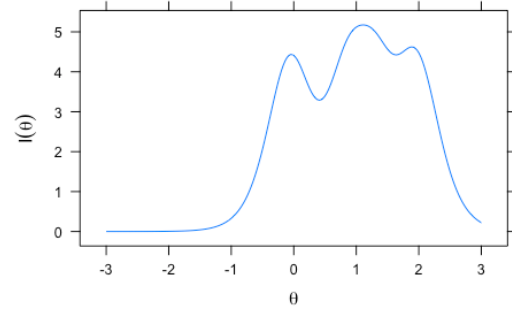


**Lack of expertise**

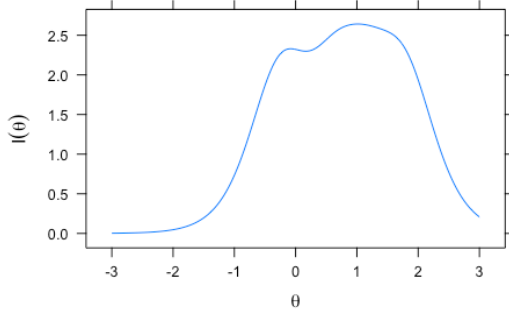
Lack of Expertise 1



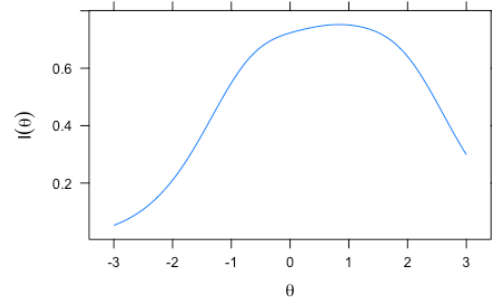
Lack of Expertise 2



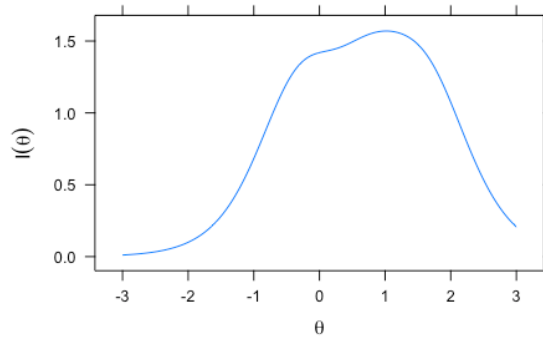
Lack of Expertise 3



Lack of Expertise 4

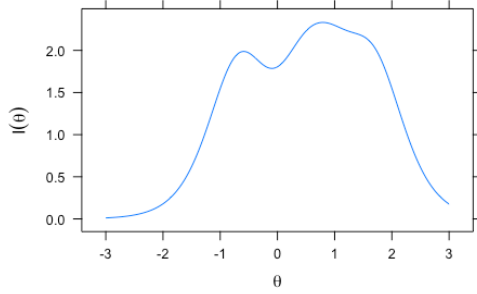


Lack of Expertise 5

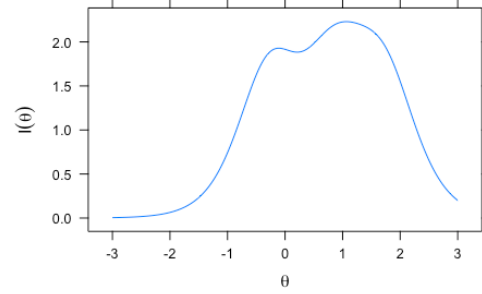


# Deceit

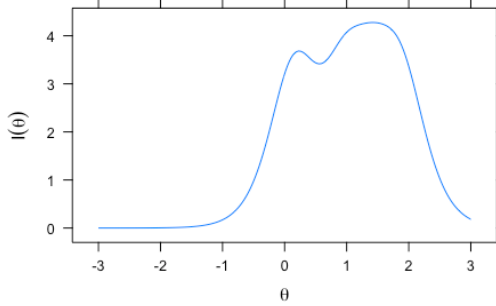
## Deceit 1



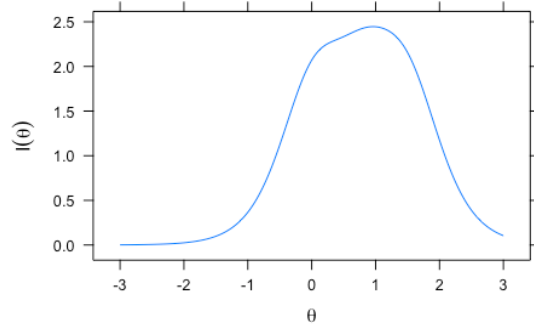
## Deceit 2



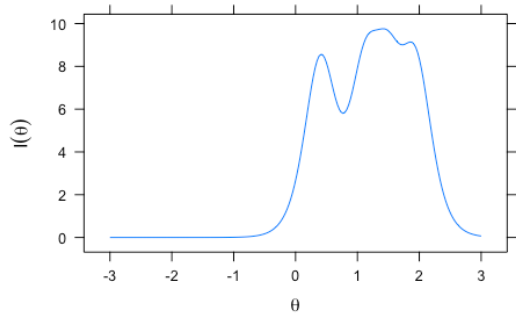
## Deceit 3



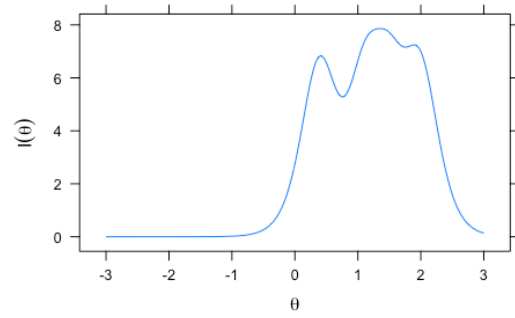
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## Deceit 5

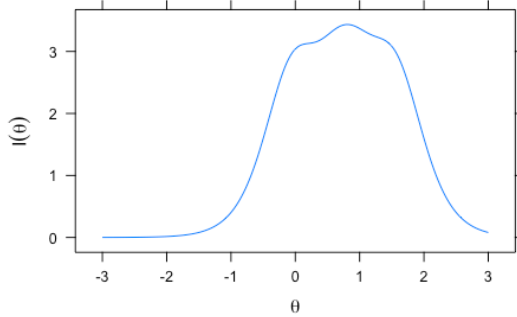


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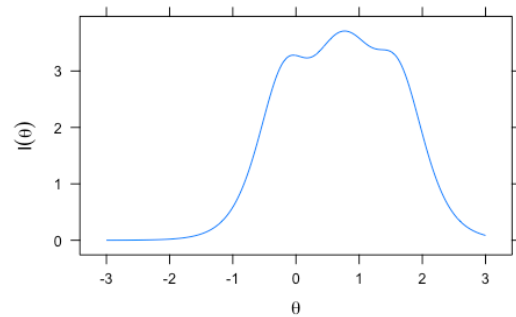


## Limited Interpersonal Abilities

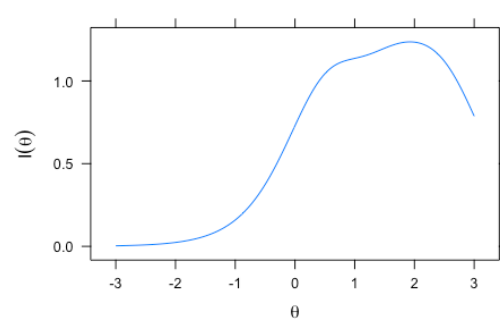
Limited Interpersonal Abilities 1



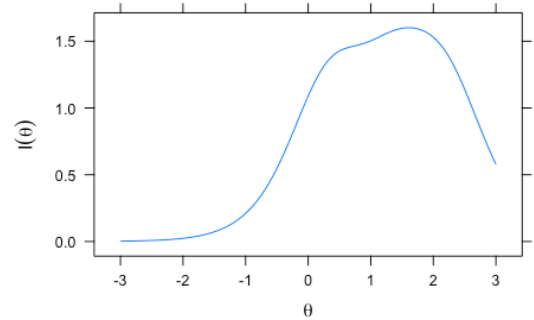
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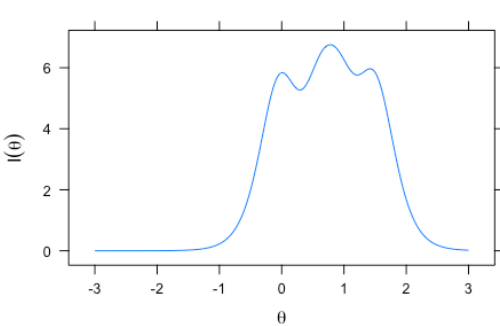
Limited Interpersonal Abilities 3



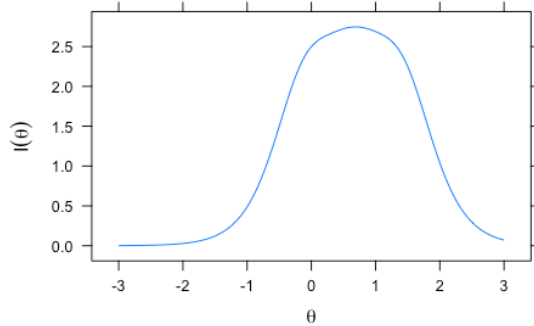
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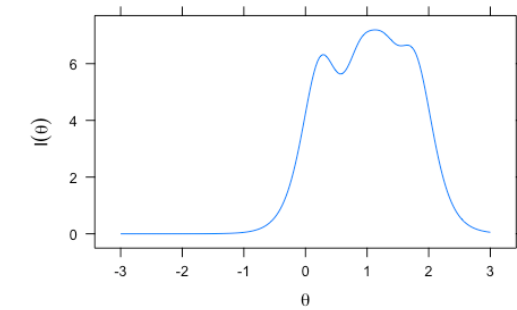
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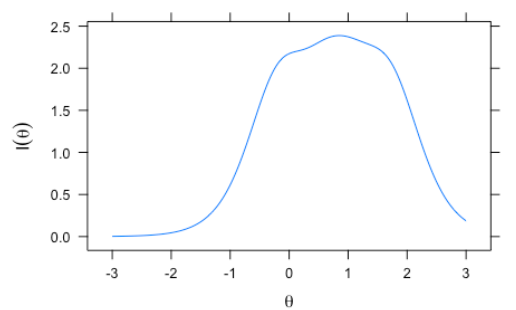
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Limited Interpersonal Abilities 7

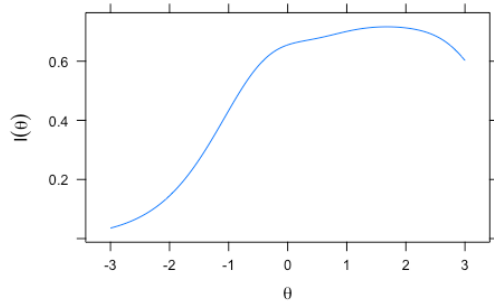


Limited Interpersonal Abilities 8

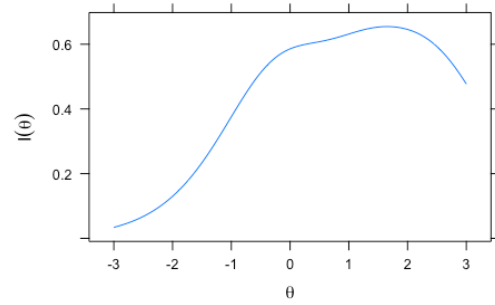


## Abusive Supervision

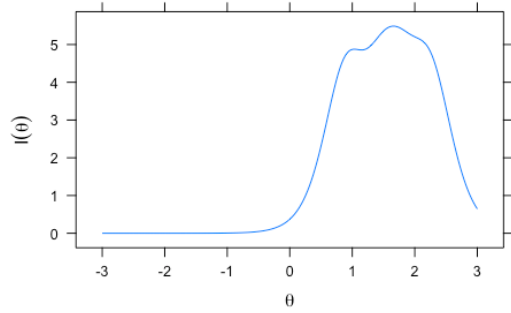
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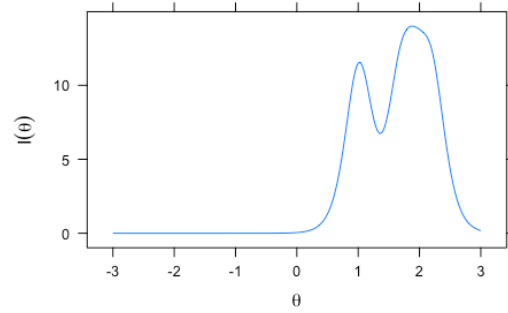
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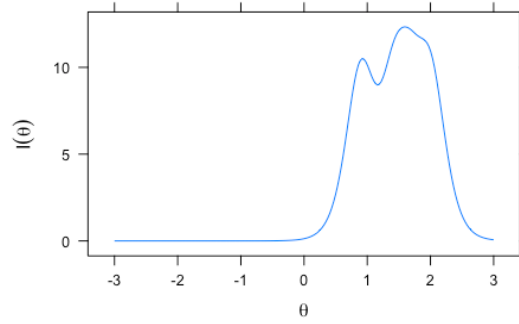
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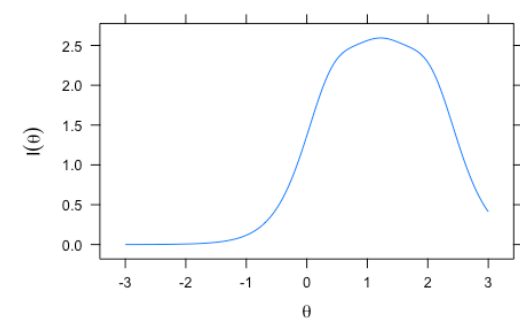
Abusive Supervision 4



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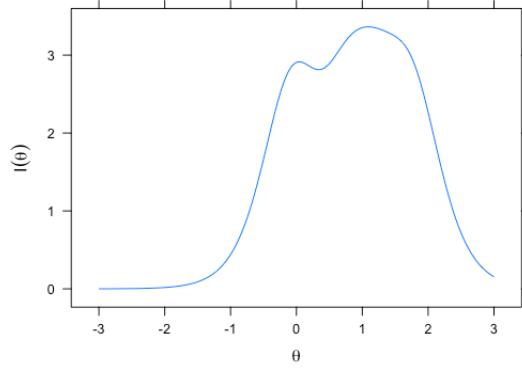


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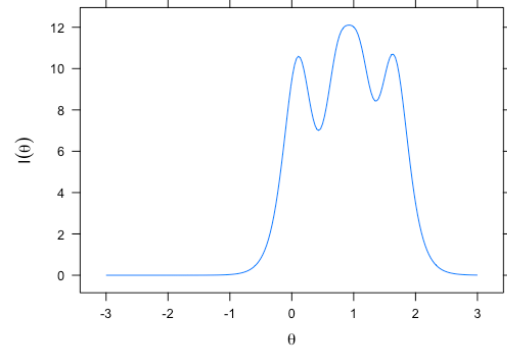


## Micromanagement

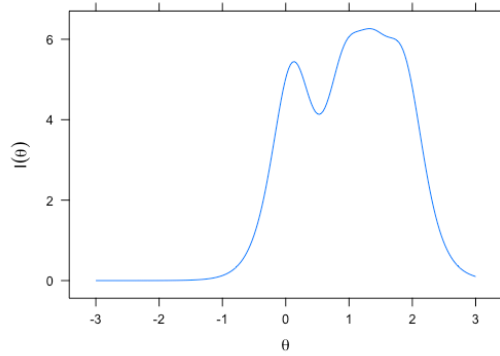
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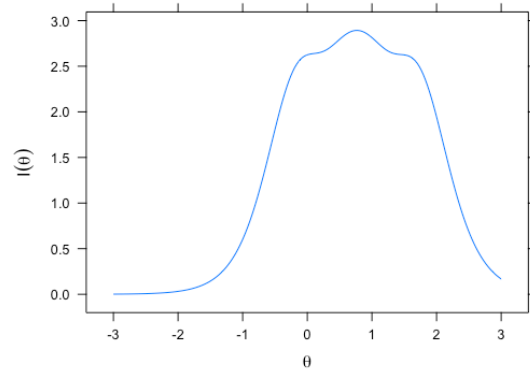
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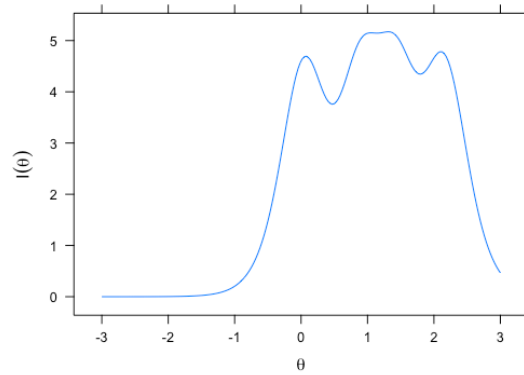
Micromanagement 3



Micromanagement 4

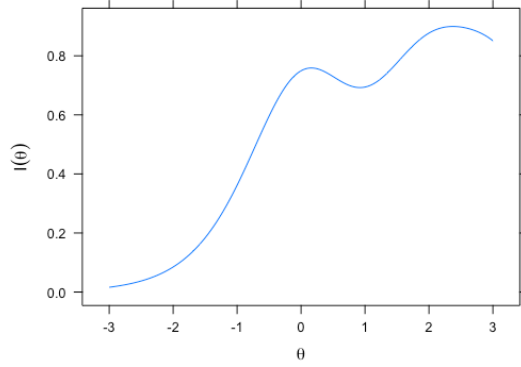


Micromanagement 5

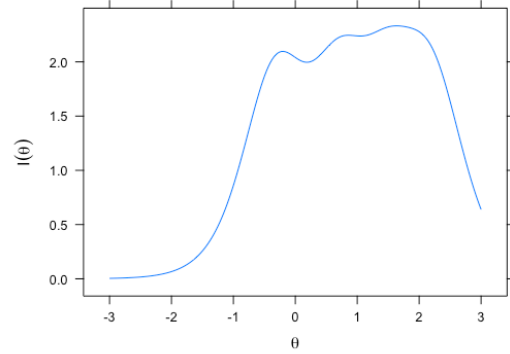


## Limited Career Support

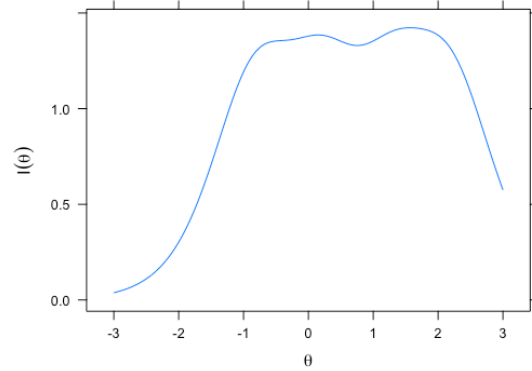
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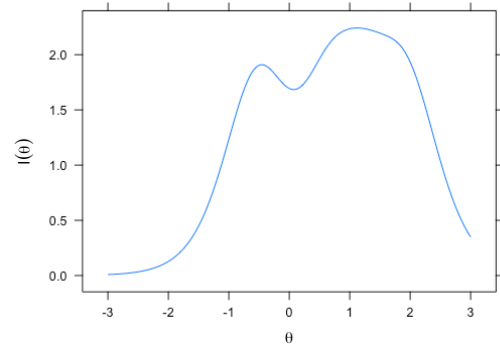
Lack of Career Support 2



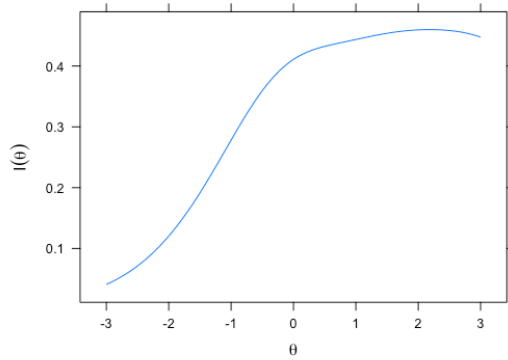
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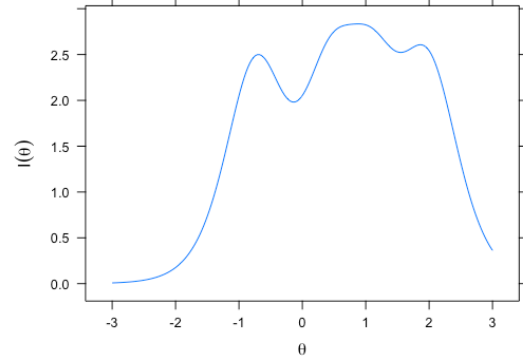
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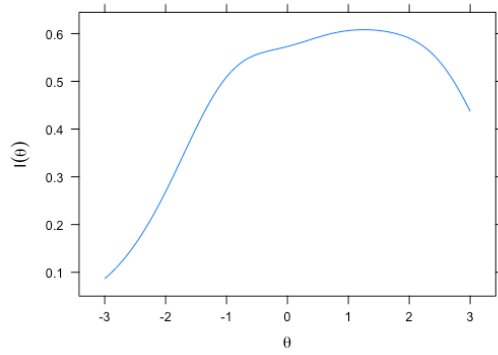
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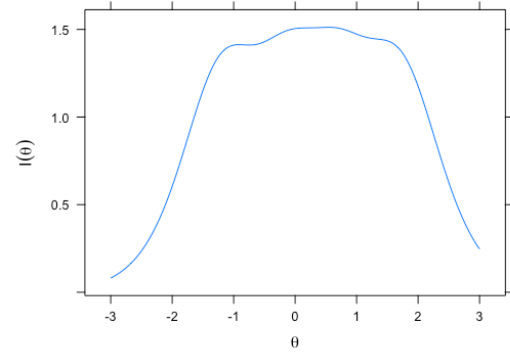
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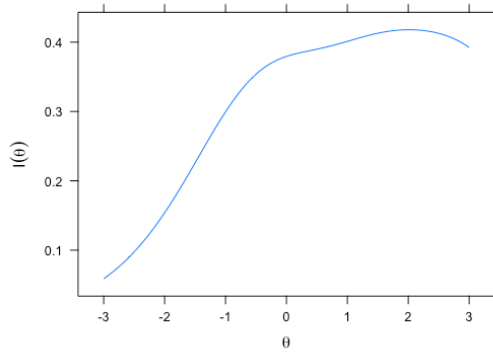
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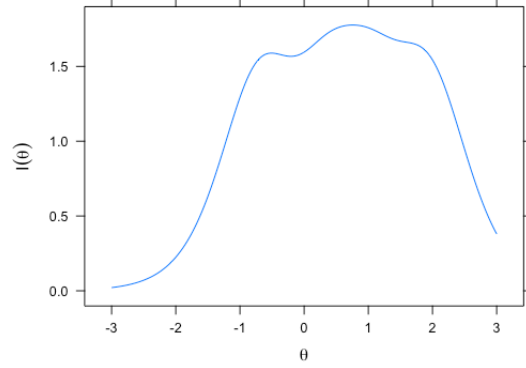
Lack of Career Support 8



Lack of Career Support 9

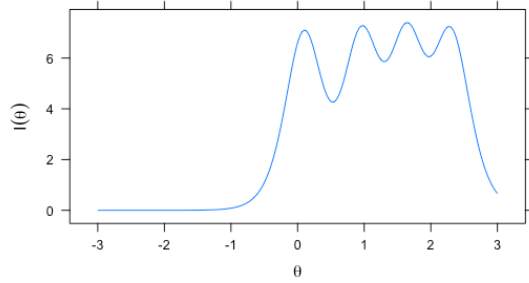


Lack of Career Support 10

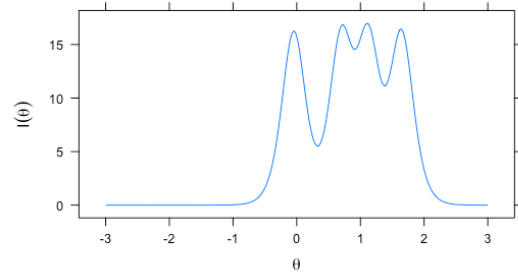


## Poor Relationship Quality

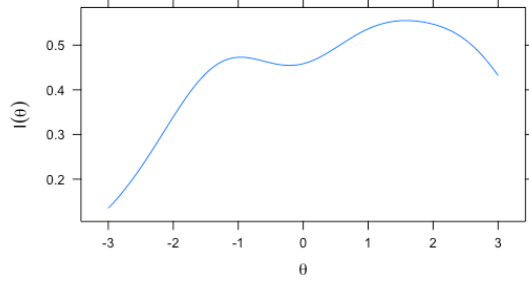
Poor Relationship Quality 1



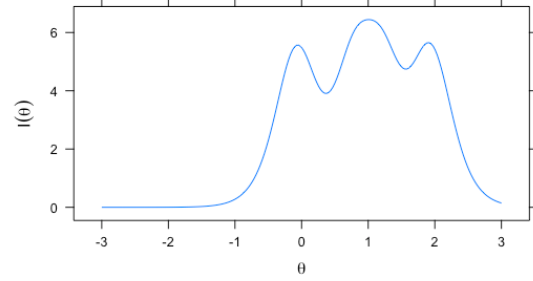
Poor Relationship Quality 2



Poor Relationship Quality 3

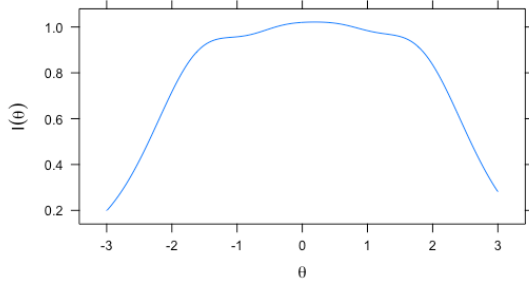


Poor Relationship Quality 4

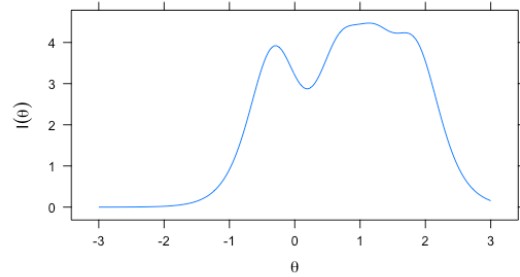


## Interpersonal mismatch

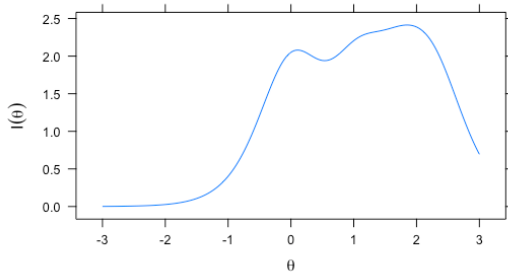
Mismatch 1



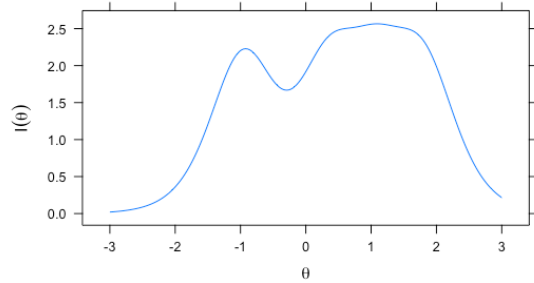
Mismatch 2



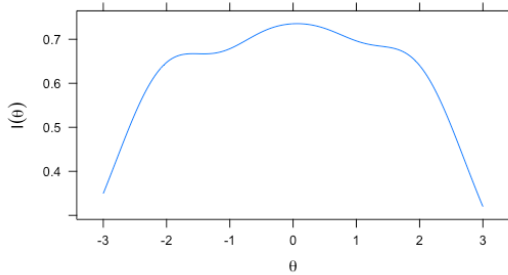
Mismatch 3



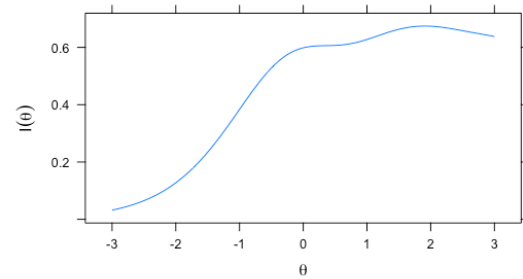
Mismatch 4



Mismatch 5

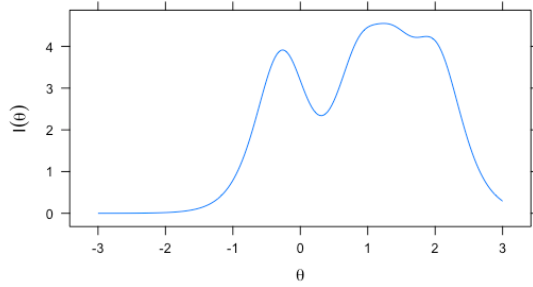


Mismatch 6

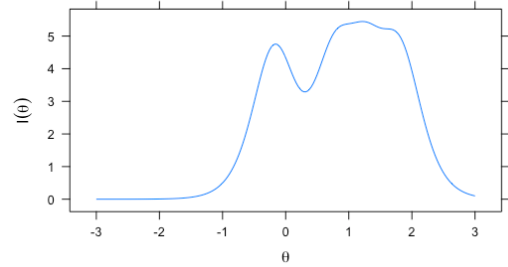


## Limited psychosocial support

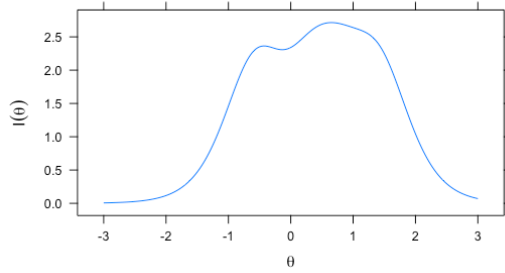
Limited Psychosocial Support 1



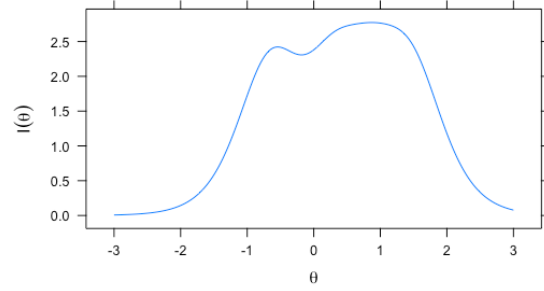
Limited Psychosocial Support 2



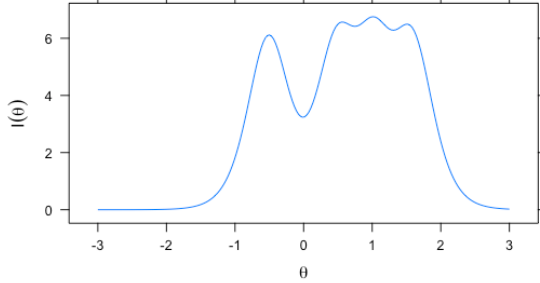
Limited Psychosocial Support 3



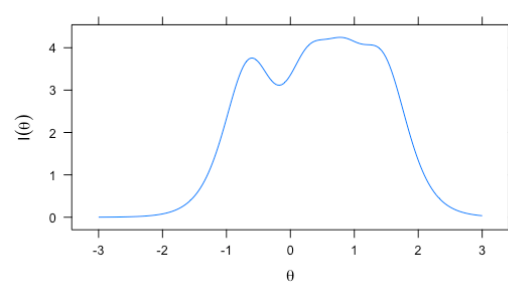
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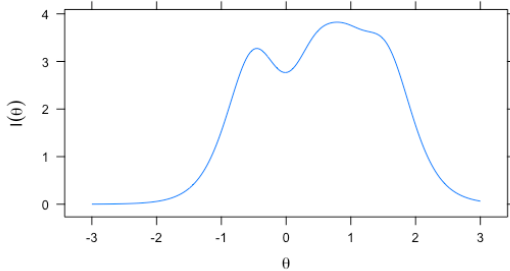
Limited Psychosocial Support 5



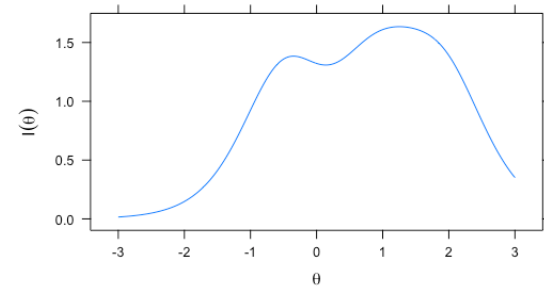
Limited Psychosocial Support 6



Limited Psychosocial Support 7

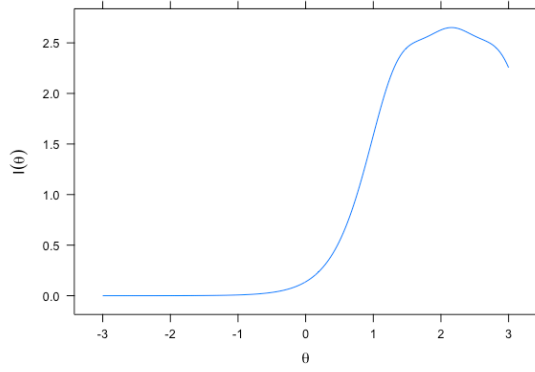


Limited Psychosocial Support 8

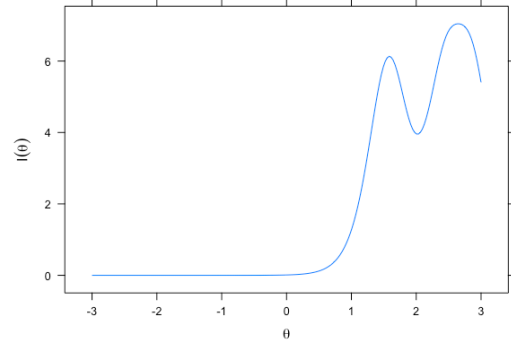


# Sexual Harassment

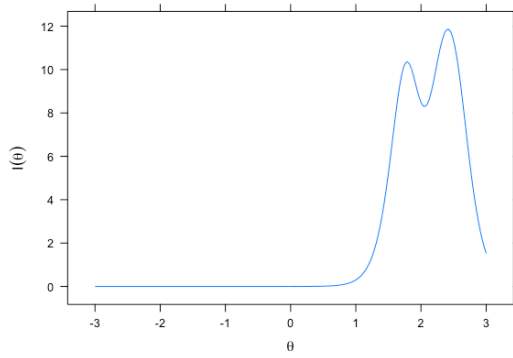
## Sexual Harassment 1



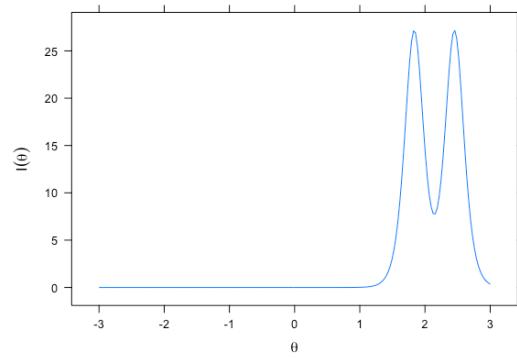
## Sexual Harassment 2



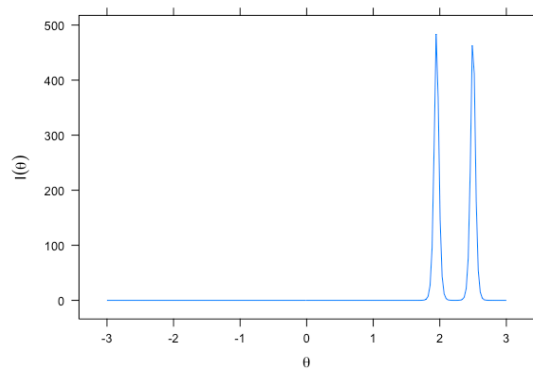
## Sexual Harassment 3



## Sexual Harassment 4

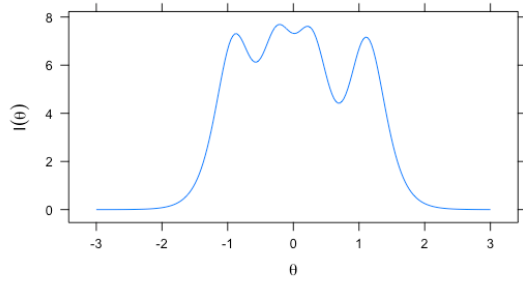


## Sexual Harassment 5

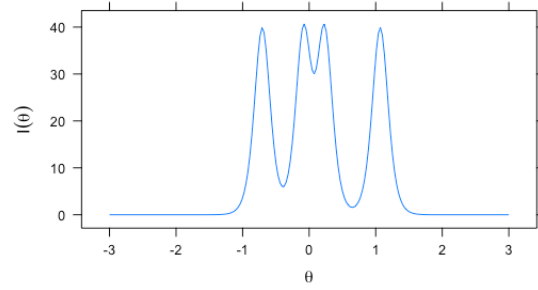


## Unequal Treatment

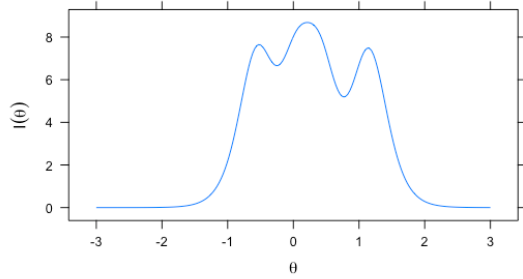
### Unequal Treatment 1



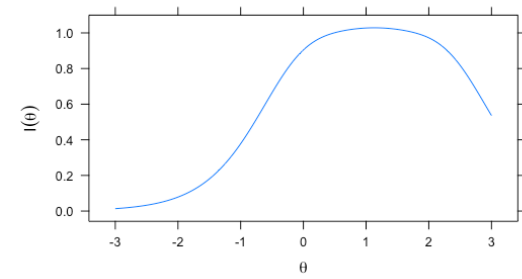
### Unequal Treatment 2



### Unequal Treatment 3



### Unequal Treatment 4



CHAPTER 6

WHAT MAKES A GOOD MATCH? PREDICTORS OF QUALITY MENTORSHIP  
AMONG SCIENCE DOCTORAL STUDENTS <sup>6</sup>

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<sup>6</sup> Tuma, T.T. & Dolan, E.L. What makes a good match? Predictors of quality mentorship among science doctoral students. Submitted to *Science Advances* on April 16<sup>th</sup>, 2023

## **ABSTRACT**

Quality mentoring promotes graduate student success, yet empirical evidence regarding how to match mentees and mentors to form quality relationships is lacking. Here we examine the influence of variables theorized to predict mentorship support and quality in a national sample of 565 science doctoral students. We found that neither mentor rank nor the matching mechanism (direct admissions, rotations) was associated with higher-quality relationships. We found no support for the widely held belief that students with demographically similar mentors experience higher quality mentorship. Rather, mentees who share deep-level similarity with mentors or have mentors with greater cultural awareness experience more supportive, higher quality mentoring. These results highlight the potential benefits of pairing mentees and mentors on the basis of deep-level similarity. Our findings also indicate that graduate students from marginalized backgrounds can be effectively mentored by faculty who are demographically dissimilar if they engage in culturally aware mentorship.

## INTRODUCTION

The United States (U.S.) National Academies of Sciences, Engineering, and Medicine have called for widespread change to graduate education in Science, Technology, Engineering, & Mathematics (STEM) (National Academies of Sciences, 2018). For decades concerns have been raised regarding the alignment between STEM graduate students' career interests and the diversity of desirable jobs present in the labor market (National Academies of Sciences, 2018). These challenges have been exacerbated by a graduate population that is not reflective of the demographic diversity in the U.S. (National Center for Science and Engineering Statistics (NCSES), 2023), resulting in a limited talent pool and lost opportunity for innovation. Moreover, STEM graduate programs are plagued with high rates of attrition and deteriorating physical and mental well-being among students (Evans et al., 2018; Levecque et al., 2017; Nagy et al., 2019; Sowell et al., 2015; Zhang et al., 2022). These persistent problems have lead policy makers and university leaders to propose changes aimed at improving graduate student training in general and the quality of mentorship that graduate students experience in particular (National Academies of Sciences, 2018).

Mentorship is a working alliance between a more experienced individual (the mentor) and a less experienced individual (mentee), and mentorship is thought to be essential for cultivating, developing, and training the next generation of scientists (National Academies of Sciences, 2019). Quality mentorship during graduate training has the potential to be an effective mechanism for recruiting talent and retaining professionals who will contribute to the national and global economy in the STEM research enterprise (National Academies of Sciences, 2019). Numerous empirical studies and robust meta-

analyses have shown that effective mentorship can lead to many desirable attitudinal, behavioral, career, and health related outcomes (Allen et al., 2004; Eby et al., 2013; Eby et al., 2008; Kammeyer-Mueller & Judge, 2008; National Academies of Sciences, 2019; O'Brien et al., 2010). Effective mentorship is thought to be particularly important for women and Racially Minoritized<sup>A</sup> individuals as they navigate through the structurally racist and inequitable norms and practices that have characterized STEM fields (Estrada et al., 2018; McGee, 2020; Ong et al., 2011). Despite the strong positive relationship between quality mentorship and desirable mentee outcomes, far less is known about the factors that predict the formation of quality mentoring relationships. The current study aims to examine the influence of key antecedents theorized to predict mentee perceptions of mentoring support and relationship quality.

**Overview of Mentoring Processes.** A graduate student's relationship with their research advisor strongly influences the quality and success of their graduate training (Sverdlik et al., 2018; Zhao et al., 2007). This is consistent with the apprenticeship model characteristic of STEM graduation education, which relies on faculty advisors to mentor graduate students as they advance in their research training and careers. Mentoring theory suggests that mentors provide at least two core forms of support to mentees (Kram, 1983). The first is *career support*, which refers to mentor behaviors aimed at facilitating the mentee's career advancement and includes the provision of career guidance,

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<sup>A</sup> We purposefully use the term "Racially Minoritized" to reflect the active role that systemic and societal racism has had and continues to have on individuals who are American Indian or Alaskan Native, Black or African American, Hawaiian or Native Pacific Islander, and Middle Eastern. We also consciously capitalize "Racially Minoritized" to recognize and affirm the cultural identities of individuals from these groups in a manner that is similar to the language used for racial and ethnic groups (e.g., Asian, Black, White).

sponsorship, and protection. The second, *psychosocial support*, refers to mentor behaviors aimed at developing the mentee's personal and social development and well-being through the provision of counseling, encouragement, acceptance, role modeling, and friendliness. Mentoring theory suggests that the mentoring *relationship quality*, or the satisfaction, liking, and trust between the mentee and mentor, acts reciprocally to reinforce mentoring support and promote desirable mentee outcomes. Studies across mentoring contexts (e.g., workplace, youth) indicate that antecedent variables (e.g., personality) and correlates (e.g., relationship length) may influence the quality of mentoring relationships and provision of career and psychosocial support, which in turn is associated with beneficial outcomes (Eby et al., 2013). Despite an abundance of conjecture, empirical studies testing the influence of such antecedent variables within the context of academic mentoring is limited. Furthermore, while mentorship is considered to be a national priority in STEM education (Crisp et al., 2017), research overall on the antecedents of quality mentorship within STEM fields is still nascent.

**Predictors of Quality Mentorship.** The mentoring of STEM graduate students presents a distinct and compelling opportunity to examine the factors associated with quality mentoring relationships for several reasons. First, different STEM disciplines and subdisciplines afford or constrain the processes through which graduate mentees are matched to faculty mentors. For instance, some graduate programs require a mentor to be identified prior to program admissions (i.e., direct admission). Mentoring matches made between mentors and mentees who are not familiar with one another are known in the mentoring literature as “formal” relationships (Ragins & Cotton, 1999). Other programs facilitate a matching process, commonly known as rotations, during which graduate

students temporarily join research groups before the mentor and mentee agree on a match. Matches based on some level of mentor-mentee familiarity is described in mentoring literature as “informal.”(Ragins & Cotton, 1999) Second, graduate mentees may consider a variety of characteristics of potential faculty mentors in the process of making a match. For instance, mentees might weigh a potential mentors’ availability to provide support, the extent of their experience mentoring graduate students, and their prestige in the field. Mentees may also weigh whether they perceive they have things in common with potential mentors, such as shared interests, values, beliefs, or personal characteristics (e.g., gender, race, ethnicity). Mentees who do not share demographic similarities with their mentor may also consider the extent to which the mentor respects and recognizes differences and is able to create an inclusive environment that is responsive to these differences. Prior research has examined the effects of these antecedents (formal vs. informal matching, mentor experience, mentor-mentee similarity) on mentoring support and relationship quality, primarily in youth and workplace mentoring. Little, if any, research has examined whether the factors currently used to match STEM graduate mentees with faculty mentors actually maximize the likelihood that these relationships will yield positive mentee outcomes. Thus, in this study, we sought to examine the effects of these antecedents on the mentoring support and relationship quality experienced by doctoral students.

**Mentee-Mentor Similarity.** A number of individual, relational, organization level variables are theorized to influence mentorship quality. Among them, similarity between the mentee and mentor is thought to be impactful. The similarity-attraction paradigm posits that individuals are attracted to and develop higher-quality relationships with

individuals who are similar to themselves (Byrne, 1961; Byrne, 1971). Multidisciplinary meta-analyses lend empirical support for the notion that similarity is associated with high-quality mentoring relationships (Eby et al., 2013; Ghosh, 2014). Yet, mentees can be similar to their mentors in many different ways, each of which is addressed below.

*Deep-level similarity.* Among all dimensions of similarity, perceived deep-level similarity—meaning shared attitudes, perspectives, interests, values, and beliefs—is most consistently and positively associated with mentoring quality (Ensher et al., 2002; Ensher & Murphy, 1997; Harrison et al., 1998; Hernandez et al., 2017, 2023; Pedersen et al., 2022; Turban et al., 2002). Evidence from one of the largest meta-analyses on mentoring found that mentee perceptions of mentorship quality were most strongly associated with deep-level similarity ( $\rho$  ranging from 0.38 to 0.59) Eby et al., 2013). In addition, moderator analyses indicate that deep-level similarity has a considerably stronger effect in academic settings than in the workplace in terms of both career support ( $\rho = 0.64$  vs.  $\rho = 0.38$ ) and psychosocial support ( $\rho = 0.75$  vs.  $\rho = 0.48$ ) Eby et al., 2013). This suggests that deep-level similarity, while positive across all contexts, may have a disproportionate influence on mentorship quality in academic settings. However, less than a quarter of the studies included in this meta-analysis were based on studies from academic settings and few were specific to graduate student-faculty mentoring relationships (Eby et al., 2013). Research is needed to understand the extent to which these findings are applicable in STEM graduate student mentoring relationships.

*Demographic similarity.* Research addressing the influence of demographic similarity on mentorship quality has produced largely inconsistent results. A common assumption is that matching mentees and mentors on the basis of demographic

similarities yields the greatest benefits, yet evidence in support of this claim is limited (Allen & Eby, 2003; Lankau et al., 2005; Turban et al., 2002). Meta-analytic results suggest that demographic similarity (e.g., gender, race/ethnicity) is, in general, not meaningfully related mentorship quality ( $\rho$  ranging from .00 to .09) (Eby et al., 2013). Yet, these results do not account for changing demographics among mentors (i.e., the majority of mentors have been disproportionately White and male), which raises questions about their relevance and generalizability as STEM faculty and student populations diversify. In addition, at least some research indicates that diversified mentoring relationships (i.e., dyads that differ on the basis of gender, race/ethnicity, sexual orientation, ability status, religion, socioeconomic status, or nationality) may yield distinct benefits (Ragins, 1997). For example, cross-race relationships are a unique form of social contact that can have a transformative impact on individuals. Furthermore, cross-race relationships can lead to the development of antiracist attitudes and reduced prejudice towards individuals of a dissimilar identity (Davies et al., 2011; Ragins & Ehrhardt, 2021). Although diversity in organizations and STEM fields has been a prominent topic for decades (Roberson, 2019), research on diversified mentoring relationships remains quite limited and has focused primarily on exploring the influence of gender and race/ethnicity on mentoring relationships.

*Gender similarity.* Despite persistent debate over how mentee-mentor gender<sup>B</sup> influences mentorship, current consensus is that neither mentor nor mentee gender

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<sup>B</sup> We recognize that sex and gender are distinct terms and that the language used to capture these distinctions continues to evolve. However, much of the prior research has conflated these terms. Given our interest in the ways that gender (i.e., an individual's lived experience identifying as a woman, man, non-binary, etc.) influences mentoring relationship dynamics, we balance the language used by previous studies with our own purposeful language.

influences the provision of mentoring or the quality of mentoring relationships (O'Brien et al., 2010; Ragins, 1999; Ragins & Cotton, 1999). Some evidence indicates that same-gender relationships afford greater mentoring support than cross-gender relationships (Morales et al., 2021; Scandura & Williams, 2001), perhaps because they facilitate greater interpersonal comfort, closeness, and shared experiences than cross-gender relationships (Allen et al., 2005; Ragins, 1997). Cross-gender relationships may limit the benefits of mentorship if majority group members do not recognize, respond to, or value the gender difference. Members of cross-gender relationships may intentionally limit social interactions in an attempt to maintain professional boundaries and minimize the potential for misconstrual that the interaction is romantic in nature (Tuma et al., 2021). Collectively, studies of gender similarity in mentoring relationships have found small or negligible associations with mentorship quality (Eby et al., 2013; O'Brien et al., 2010).

*Racial and ethnic similarity.* Research on racial and ethnic similarity in mentoring dyads has produced ambiguous and even conflicting results. For instance, one study found that African American, Hispanic, and Native American graduate students with mentors of color reported greater relational satisfaction and more career and psychosocial support than those with racially dissimilar mentors, yet these associations were small (Ortiz-Walters & Gilson, 2005). Another study of >1,000 racially diverse undergraduate and graduate students in STEM found that individuals in same-race relationships received greater psychosocial and career support than those in cross-race relationships (Blake-Beard et al., 2011). However, the provision of greater mentoring support for individuals in these dyads did not result in improved mentee outcomes (Blake-Beard et al., 2011). Rather, mentees preferred to have a mentor who matched their racial background and felt

that mentors, regardless of their race/ethnicity, should recognize how a mentee's background could affect their professional development. Another study of 220 doctoral student-faculty dyads at a single university observed that same-race/ethnicity relationships were not meaningfully associated with levels of mentoring support (Turban et al., 2002). Yet, the majority of the mentees in this study (>65%) were White, raising the question of whether racial/ethnic similarity may be more influential for people of color. In summary, some research suggests that mentees may prefer to have a mentor who shares similar demographics (Bailey et al., 2016; Blake-Beard et al., 2011; Grant-Thompson & Atkinson, 1997; Patton, 2009), yet there is little evidence that matching on the basis of demographics is a requirement for quality mentorship and studies to date have been limited by the lack of diversity among faculty mentors (Eby et al., 2013).

*Culturally aware mentoring.* Given the limited diversity amongst STEM faculty (Matias et al., 2022) and the growing proportion of STEM graduate students from Racially Minoritized backgrounds (National Center for Science and Engineering Statistics (NCSES), 2023), many mentoring relationships in STEM fields occur between racially well-represented faculty members and Racially Minoritized mentees. Furthermore, the small proportion of faculty from Racially Minoritized backgrounds engage in a greater number mentoring relationships and offer a deeper, stronger level of support to Racially Minoritized students' (Baez, 2000; Griffin, 2013; Griffin & Reddick, 2011). This creates a form of "cultural taxation" in which faculty of color expend more time and effort on mentoring work that is not incentivized, valued, or rewarded (Padilla, 1994), further magnifying identity-related inequities observed in faculty workloads (O'Meara et al., 2017). Aiming to match mentees and mentors on the basis of

demographic similarity has the potential to be troublesome given the limited number of minoritized STEM faculty and the increasing number of graduate students from Racially Minoritized backgrounds (Fries-Britt & Snider, 2015; Griffin, 2012). Thus, even if the evidence were clear that demographically matched mentorships resulted in more positive mentee outcomes, it is not just or feasible to ask minoritized faculty to serve as mentors to all minoritized mentees.

To meet the mentoring needs of graduate students of color and avoid overburdening faculty of color, some work has focused on equipping mentors of all backgrounds with knowledge, skills, and training to effectively support mentees from different backgrounds – what is referred to as culturally aware mentorship (Byars-Winston et al., 2018). Culturally aware mentorship, where mentors demonstrate interest in and value of students’ cultural knowledge, frames of reference, and identities (e.g., race/ethnicity, sexual orientation, religion, cultural identity), may be important for fostering quality mentoring relationships in dyads who differ in their demographic characteristics (Merriweather, 2012; Reddick & Pritchett, 2015; Syed et al., 2011). Cultural aware mentorship moves beyond individual mentors’ good will and altruistic values by preparing mentors with skills to recognize and respond to issues relating to race, power, and privilege in their mentoring relationships. Thus, culturally aware mentoring may be a critical factor in ensuring that minoritized mentees can thrive in their academic and professional pursuits. Some evidence suggests that mentorship that addresses cultural diversity is positively associated with mentee science identity (Camacho et al., 2021; Haeger & Fresquez, 2016), satisfaction with research (Haeger & Fresquez, 2016), and perceived mentoring effectiveness (Black et al., 2022; Pfund et al.,

2022). While culturally aware mentorship may be particularly beneficial for individuals of Racially Minoritized backgrounds, it may also be advantageous for individuals of other marginalized backgrounds. For instance, deaf mentees with research mentors who were responsive to their deaf or hard of hearing status but were not deaf themselves reported similar mentoring outcomes to mentees with a deaf mentor (Braun et al., 2017). Yet, very little research has investigated the influence of culturally aware mentoring on mentoring support and relationship quality.

*Mentor rank.* STEM faculty members who differ in their levels of experience as reflected in their rank may also differ in their knowledge, skills, prestige, and connections in ways that influence their relationships with mentees and subsequent mentoring outcomes. The term “human capital” refers to a person’s cumulative knowledge, competencies, educational, and professional experiences that can enhance their career attainment and success (Schultz, 1961). Mentor human capital is important to consider because mentors with greater human capital may positively influence their mentees. For instance, mentors who are viewed as rising stars and successful in their careers positively influence the subsequent likelihood their mentees will also be successful and high performing (Judge et al., 2004; Tonidandel et al., 2007). Alternatively, mentors who are more junior in their positions may have fewer competing demands on their time and greater motivation to provide mentorship, and thus may provide greater mentoring support to their mentees (Eby et al., 2013; Kammeyer-Mueller & Judge, 2008). Some studies have documented that midcareer mentors report greater motivation to mentor than more senior and late-career mentors (Allen et al., 1997; Morales et al., 2017), suggesting

that senior career mentors may have greater demands on their ability or reduced motivation to mentor.

*Mentee capital.* Mentee human capital may also be associated with the amount of mentoring support received. Mentors may provide greater mentoring support to mentees who possess higher potential (e.g., greater levels of experience, higher achievements) because they anticipate that high-performing mentees will be more productive and require less effort to support, which will ultimately result in greater outcomes for the mentor (Allen et al., 1997). Indeed, research suggests that mentors look for indicators of a mentee's potential for success and evaluate a mentee's credentials before choosing to engage in a mentoring relationship (Allen et al., 2000; Joy et al., 2015; Olian et al., 1993). For example, graduate students perceived to have greater potential have been shown to receive greater mentoring support from their advisors than students perceived to have less potential (Green & Bauer, 1995). This is concerning because mentors may be selecting mentees who are already primed for success, rather than providing mentorship to those who could benefit most from developmental support.

*Relationship initiation.* Finally, relationship initiation, or the mechanism by which a mentoring relationship is established, may also influence mentoring outcomes. In the workplace and youth mentoring literature, formal mentoring relationships are commonly initiated by assigning or matching by a third-party (Ragins & Cotton, 1999). In contrast, informal mentoring relationships develop spontaneously between mentors and mentees and on the basis of mutual liking, attraction, and perceived interpersonal comfort (Kram, 1985; Ragins & Cotton, 1999). Informal relationships have been shown to confer greater benefits than formal relationships (Chao et al., 1992; Inzer & Crawford, 2005; Ragins &

Cotton, 1999), but the differences are small in magnitude (Eby et al., 2013). Some research suggests that graduate students develop and maintain formal and informal mentoring relationships with faculty members, post-docs, and their peers (Feldon et al., 2019; Griffin et al., 2018). To our knowledge, the effects of relationship initiation have not been studied in academic mentoring relationships.

In some science graduate programs, relationship initiation occurs through laboratory rotations, which allow both students to explore research lab environments of several potential mentors and mentors to get to know students before both commit to a match (Artiles et al., 2023; National Academies of Sciences, 2018). Matching after developing some familiarity (i.e., following rotations) is akin to informal relationship initiation in organizational and youth settings. Other graduate programs rely on direct admissions, a process through which a student expresses an interest in working with a particular faculty member and the faculty member then agrees to sponsor them for admissions (or not). In this process, the prospective student and faculty member may have limited interaction before the student joins a mentor's research group, more akin to formal mentoring in organizational and youth settings. These different approaches to relationship initiation may influence a mentee's receipt of mentoring support. Rotations may provide time and space to develop some level of familiarity, liking, and shared interests, which may foster greater closeness, higher relationship quality, and greater provision of support. Alternatively, direct admissions may limit opportunities for students to evaluate their compatibility with a faculty mentor prior to committing to the relationship. Despite the differences in the initiation of these mentoring relationships, no

studies have directly investigated the relationship between laboratory rotations and direct admissions on mentorship quality and support.

**The Present Study.** Mentorship is touted by scholars (Crisp et al., 2017; National Academies of Sciences, 2019) and the popular literature (Heemstra & Garg, 2022; Martin & Haar, 2021) as a high-impact practice that is key for success. Yet, our understanding of variables associated with high-quality graduate student-faculty mentoring relationships is limited. Despite this knowledge gap, mentorship efforts continue to gain popularity without the benefit of evidence regarding how to match mentees and mentors in order to achieve maximum effectiveness. In the present study, we sought to address this by examining the influence of theorized antecedents on the formation of high-quality doctoral student-faculty mentoring relationships. Guided by the similarity attraction paradigm, we hypothesized that greater deep-level similarity and demographic similarity in a mentoring relationship will positively predict mentoring support and relationship quality. Furthermore, we extrapolated that cultural aware mentoring will uniquely and positively predict mentoring outcomes. We also hypothesized that mentor capital, but not mentee capital, would demonstrate small associations with mentorship quality. Finally, we hypothesized that mentoring relationships initiated informally (i.e., through rotations rather than direct admissions) would display small, positive associations with mentorship quality. To test these hypotheses, we used structural equation modeling (SEM) to test relationships between mentoring antecedents and the career and psychosocial support and relationship quality that a national sample of science doctoral students reported receiving from their research advisors.

## METHODS

The data presented are part of a larger study examining mentoring relationships between science doctoral student mentees and faculty research advisor mentors during graduate education. Here, we sought to examine the theorized mentoring antecedents on doctoral students' perceptions of the career and psychosocial support they receive from their mentors and the quality of their mentoring relationship. This study was approved and determined to be exempt by the University of Georgia Institutional Review Board (PROJECT00003604). All of the raw data will be made available on the Open Science Framework depository once the larger study is complete.

**Participants.** Participants were U.S. doctoral students currently conducting or who had done research as a graduate student for at least one year within the past year and were pursuing or had earned a PhD in a life science discipline. We focused on doctoral students in life sciences fields for three reasons. First, the life sciences represent the largest and most demographically diverse sub-field within STEM graduate education in the U.S (National Center for Science and Engineering Statistics (NCSES), 2023). Given in our interest in examining the influence of demographic similarity on mentorship support, limiting our sample to the life sciences enabled analyses that were not likely to be possible in other STEM disciplines with more the limited demographic diversity. Second, mentoring norms and practices as well as the nature of graduate education differ across STEM disciplines, thereby making it necessary to control for disciplinary differences. Finally, given the diverse subdisciplines (e.g., synthetic biology, ecology, biophysics) and range of research approaches used (e.g., bench work, field work,

computational, theoretical) the life sciences are, in many ways, a microcosm of the broader natural sciences.

We recruited doctoral students directly to minimize potential biases from graduate coordinators or programs choosing to share the study information with individuals who had exclusively favorable mentoring relationships. We contacted doctoral students directly by email at their university-affiliated addresses. All participants received a recruitment email and invitation with a link to an online survey on the secure survey service, Qualtrics. In order to ensure the sample was reflective of the diversity of the science doctoral talent pool, we purposefully recruited from Hispanic-Servicing Institutions (HSIs), Historically Black Colleges and Universities (HBCUs), and from graduate fellowship programs aimed at advancing diversity and inclusion in STEM fields (e.g., Howard Hughes Medical Institute Gilliam Fellows, The National Academies of Sciences Ford Foundation Fellows). To incentive study participation, eligible doctoral students who completed the survey accurately (i.e., passed attention checks) and in its entirety received a \$15 gift card of their choice to Amazon, Chipotle, REI, or Starbucks. In addition, we utilized a modified tailored panel management recruitment approach (Estrada et al., 2014) that included compensation, personalized emails, and study branding to encourage participation.

We received a total of 601 responses with varying degrees of completion. Sixteen of these respondents completed <25% of the items and were removed due to incomplete responses. Fifteen students failed to pass attention checks and these responses were also removed (DeSimone & Harms, 2018). Our final analytic sample consisted of 565 doctoral students who represented 70 public and private institutions, and 38 states from

varied geographic regions across the United States. An average of 8 participants ( $SD=6.5$ , range = 1-39) responded from each institution. Participants represented predominantly R1 (highest research activity; 89.7%) institutions with comparably fewer from R2 (higher research activity; 10.3%) institutions according to the Carnegie Classification of Institutions of Higher Education. Approximately 69% of participants represented public universities, 31% were from private institutions, and 10% were from institutions serving Racially Minoritized student populations.

Additional demographic information for doctoral students and their mentors are summarized in Tables 2 and 3, respectively. Students were asked to report on their mentors' demographics (e.g., gender, race/ethnicity) and career stage (e.g., assistant, associate, or full professor). We used separate items to measure race and ethnicity on the survey. Participants could identify with multiples races: American Indian or Alaskan Native, Asian, Black or African American, Hawaiian or Native Pacific Islander, Middle Eastern, or White. We recognize that these groups are not monolithic in their experiences, but we opted to combine individuals who identified as American Indian or Alaskan Native, Black or African American, Hawaiian or Native Pacific Islander, and Middle Eastern in to one composite variable termed, "Racially Minoritized," to allow for adequate statistical power. Although distinct, individuals of these Racially Minoritized backgrounds collectively as a group have both historically and currently face the structurally racist systems endemic in STEM higher education. Thus, individuals of these backgrounds collectively are Racially Minoritized in STEM education.

**Measures.** We collected data using a cross-sectional study design and established survey measures. Specific details about the measures are described below. A complete list

of the measures and items are included in the Supplemental materials. Participants were instructed to think about their dissertation advisor and their role as a mentor during their graduate research while responding to the statements. If participants were co-advised or had multiple dissertation advisors, they were asked to pick one individual to respond about. Unless otherwise noted, variables were measured using five-point Likert scales (i.e., 1 = “strongly disagree”; 5 = “strongly agree”) and items were coded so that higher values represent greater amounts of the construct.

*Cultural aware mentoring.* We used a five-item scale (Byars-Winston & Butz, 2021) to measure the extent to which mentees perceived their advisors’ mentoring behaviors reflected racial and ethnic cultural awareness, such as being aware of and willing to discuss racial and ethnic differences. We modified the response format of this scale from a five-point frequency response (i.e., 1 = “never”; 5 = “all of time”) to an agreeability response (i.e., 1 = “strongly disagree”; 5 = “strongly agree”) format because we were interested in mentees perceptions of their mentor’s ability to act with awareness of race and ethnicity in their mentoring relationship. A sample item is “*My mentor was willing to discuss race and ethnicity, even if it may have been uncomfortable for them.*”

*Deep-level similarity.* We used an eight-item scale (de Janasz & Godshalk, 2013; Ensher et al., 2002) to measure the degree to which mentees perceived their mentor to be similar to themselves in terms of their attitudes, perspectives, and values. Sample items include “*My mentor and I see things in the same way*” and “*My mentor and I are more similar than dissimilar in important ways.*”

*Gender similarity.* We created a dummy-coded, binary measure of gender similarity between mentors and mentees using the gender designations (e.g., man, non-

binary, woman) reported by the mentee for themselves and their mentor. Mentees who reported being in cross-gender (differing gender match within the dyad) relationships were coded as 0 (cross gender) and same-gender (matching gender within the dyad) relationships were coded as 1 (same gender).

*Mentor human capital.* We operationalized mentor human capital from participant reports of faculty member rank. We used these data to create a mentor human capital score, ranging from less to more human capital where: 1 = Assistant Professor, 2 = Associate Professor, 3 = Professor or Administrator (e.g., department head).

*Mentee capital.* We used the MacArthur Scale of Subjective Social Status (i.e., the MacArthur ladder) as a subjective measure of social and economic status (Adler et al., 2000). We used this single item measure of subjective social status because we predicted that an individual's subjective social status could be interpreted as a general indicator of a mentee's potential and ability by a mentor. We presented participants a drawing of a ladder with 10 rungs and the following description: "Think of the ladder as representing where people stand in our society. At the top of the ladder are the people who are the best off, who have the most money, most education, and best jobs. At the bottom are the people who are the worst off, those who have the least money, least education, worst jobs, or no job." Participants were asked to place themselves on the ladder based on a 10-point scale (1 = *bottom, worst off*; 10 = *top, best off*), and the scores were used as indicators of mentee capital.

*Race/ethnicity similarity.* We created a dummy-coded, binary measure of racial similarity between mentors and mentees using the race/ethnicity designations (e.g., Asian, Racially Minoritized, White) reported by the mentee for themselves and their mentor.

Mentees' who reported being racially and/or ethnically heterogeneous (differing race/ethnicity match within the dyad) were coded as 0 (i.e., cross-race/ethnicity), and mentees in racially homogeneous (the same race/ethnicity match within the dyad) relationships were coded as 1 (same-race/ethnicity).

*Relationship initiation.* We operationalized relationship initiation by asking participants to indicate whether they joined their graduate research mentor's lab via direct admission or following rotations, or through another scenario. Mentees who were direct admits were dummy-coded as 0 (i.e., formal relationship initiation), and mentees who joined a laboratory following rotations were coded as 1 (i.e., informal relationship initiation).

*Perceived career support.* We used a ten-item scale to measure the perceived career-related (e.g., coaching, sponsorship, protection, networking, visibility, appropriately challenging tasks) support received from the mentor. Sample items include "My mentor offers useful advice for achieving my career goals" and "My mentor helps me prepare for importance milestones in my degree."

*Perceived psychosocial support.* We used an eight-item scale to measure the perceived psychosocial-related (e.g., counseling, encouragement, friendship, role modeling, acceptance) support received from the mentor. Sample items include "My tells me when they think I have done a good job" and "My mentor values me as a person."

*Perceived relationship quality.* We used a four-item scale to measure the perceived quality of the mentoring relationship (i.e., the general satisfaction and overall quality and reciprocity of the relationship). A sample item is "My mentor and I can talk about things other than work tasks."

**Data Analysis.** We followed a two-phase structural equation modeling (SEM) process (i.e., assessment of measurement model followed by evaluation of a structural model specifying how mentoring antecedent variables related to mentoring support and quality) to address our research questions (Kline, 2015; Zyphur et al., 2023). SEM utilizes a set of statistical techniques to model complex relationships between multiple latent variables simultaneously, enabling the testing of multiple hypotheses and competing theoretical models and controlling for measurement error variance. Thus, SEM allows for more robust and accurate estimates of effects (MacCallum & Austin, 2000; Zyphur et al., 2023).

*Preliminary Analyses.* We conducted an *a priori* power analysis in order to determine the number of observations necessary to yield sufficient power in order to reject the null hypothesis and detect associations among the latent variables. We used the *semPower* package (Jobst et al., 2021) and the RMSEA fit index to assess model misspecification. The power analysis indicated that, in order to achieve an 80% chance of correctly rejecting the null hypotheses ( $\beta = 0.20$ ) with an  $\alpha$  of 0.05 and a *df* of 589,  $n = 63$  observations were required to detect model misspecification with a RMSEA of 0.05. Our final sample size of 565 observations is well above this number, indicating robust statistical power.

Prior to assessing our structural models, we conducted a series of preliminary analyses to evaluate the plausibility of statistical assumptions for our structural models. We began by determining if the patterns of data missingness were missing completely at random (MCAR), missing at random, or missing not at random by conducting Little's MCAR test (Little, 1988). The results revealed that the missing data were consistent with

missingness completely at random,  $\chi^2(1420) = 1395, p = 0.31$ . We therefore used maximum-likelihood estimation without adjustments to address missing data. The majority of items had a skewness and kurtosis below  $|1.0|$  and all items had a skewness below  $|1.70|$  and kurtosis below  $|2.50|$ , thereby meeting assumptions for multivariate normality. Finally, we examined the degree to which our responses were nested within 70 institutions, thereby violating the assumption of independence between observations in our sample (i.e., students clustered by institution). We calculated intraclass correlation coefficients (ICC) for each outcome variable to determine the clustering at the institutional level using the *lme4* linear mixed-effects model package (Bates, 2010). The ICC values (career support = 0.010, psychosocial support = 0.029 and relationship quality = 0.016) were low, suggesting very little variability at the institution level. Therefore, we opted not to pursue a multilevel SEM (Stapleton et al., 2016).

*Assessment of Measurement Models.* We evaluated our measurement models (e.g., cultural aware mentoring, deep-level similarity, career support, psychosocial support, and relationship quality) using confirmatory factor analysis (CFA) with robust maximum likelihood estimation to determine how adequately our model reproduced the variance-covariance matrix. We assessed measurement model fit by examining both incremental (e.g., Comparative Fit Index (CFI), Tucker-Lewis Index (TLI)) and absolute (e.g., Root Mean Square of Approximation (RMSEA), Standardized Root Mean Square Residual (SRMR), Chi-Square Test ( $\chi^2$ )) indices of model fit. We further assessed the goodness of measurement model fit with equivalence testing (Marcoulides & Yuan, 2017; Peugh & Feldon, 2020) and adjusted, “T-size” fit statistics (e.g.,  $RMSEA_T$ ,  $CFI_T$ ). In general, our analyses revealed good model fit and confirmed unidimensionality of the scales. To

provide evidence of reliability, we used coefficient omega ( $\omega$ ) to evaluate the internal consistency of the scales (Dunn et al., 2014). A comprehensive description of our approaches and model fit indices are reported in the Supplemental Materials.

*Assessment of Structural Models.* We tested our structural model by specifying the hypothesized relationships between our variables of interest (i.e., path analysis) as depicted in Figure 1. All of the analyses were conducted in R version 4.1.0 (R Core Team, 2016) using the lavaan package for latent variable modeling (Rosseel, 2012). We used the maximum likelihood robust method to examine the degree to which our conceptual model fit the data, with the theorized antecedents as predictors of our outcome variables of interest. Specifically, we modelled the extent to which cultural diversity awareness, deep-level similarity, mentor human capital, mentee capital, gender similarity, race/ethnic similarity, and relationship initiation predicted mentee perceptions of career support, psychosocial support, and relationship quality. We used adjusted  $p$  values to account for multiplicity with the Benjamini-Hochberg method to control the false discovery rate (Benjamini & Hochberg, 1995). Specifically, we calculated a critical value for each  $p$ -value using the formula  $(i/m)*Q$ , where  $i$  is the rank of the  $p$ -value from lowest to highest,  $m$  is the total number of tests run, and  $Q$  is our chosen false discovery rate. Variables were considered significant at an FDR rate of 5%, which corresponded to  $P_{adj} < 0.019$ .

## RESULTS

The means, standard deviations, and zero-order correlations of all variables are reported in Table 3. Doctoral students in our study reported receiving moderate amounts of career ( $M = 3.81$ ;  $SD = 0.80$ ) and psychosocial ( $M = 3.76$ ;  $SD = 1.04$ ) support from

their mentors and indicated that their relationships were of generally high quality ( $M = 4.02$ ;  $SD = 0.95$ ; Table 1). As expected, the zero-order correlations showed positive associations between career and psychosocial support and relationship quality. Two antecedent variables (i.e., cultural diversity awareness and deep-level similarity) were strongly positively associated ( $r = 0.70 - 0.81$ ) with all three mentoring support variables. Finally, the association between mentee capital and deep-level similarity was small and positive ( $r = 0.16$ ). Our structural model had good to fair model fit -  $\chi^2(1592) = 653$  ( $p < 0.001$ ),  $CFI = 0.94$ ,  $TLI = 0.93$ ,  $SRMR = 0.04$ ,  $RMSEA = 0.05$ . In terms of equivalence testing, the  $CFI_T$  was 0.928 and the  $RMSEA_T$  was 0.054 with adjusted fit values<sup>c</sup>. The T-Size CFI indicated fair model fit, while the T-Size RMSEA indicated close model fit. Given that our model that adequate fit, we proceeded with our hypothesis testing and interpretation of the structural paths in the model. Additional measurement and structural model fit results are reported in the Supplemental Materials.

Doctoral students' perceptions of deep-level similarity with their research advisors had the largest positive effect on their reports of career support ( $\beta = 0.32$ ,  $P_{adj} = 0.004$ ), psychosocial support ( $\beta = 0.66$ ,  $P_{adj} = 0.009$ ), and relationship quality ( $\beta = 0.69$ ,  $P_{adj} = 0.014$ ) (Figure 1). Students' perceptions that their advisors engaged in culturally aware mentoring also had significant positive effects beyond that of deep-level similarity, although the effects were more modest. Specifically, students' reports of culturally aware mentoring were positively associated with career support ( $\beta = 0.19$ ,  $P_{adj} = 0.002$ ), psychosocial support ( $\beta = 0.26$ ,  $P_{adj} = 0.007$ ), and relationship quality ( $\beta = 0.14$ ,  $P_{adj} =$

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<sup>c</sup> The rescaled fit statistic values derived from equivalence testing for the structural model indicated for  $CFI_T$ : "poor"  $\leq 0.885$ , "mediocre"  $= 0.885 - 0.907$ , "fair"  $= 0.907 - 0.939$ , "close"  $= 0.939 - 0.983$ , and "excellent" are  $\geq 0.983$  and for  $RMSEA_T$ : "poor"  $\geq 0.112$ , "mediocre.

0.016) (Figure 1). In contrast, race/ethnicity match exhibited a negligible association with mentee reports of career support ( $\beta = -0.07, P_{adj} = 0.021$ ) and a significant, negative association with mentee reports of psychosocial support ( $\beta = -0.20, P_{adj} = 0.011$ ) and relationship quality ( $\beta = -0.17, P_{adj} = 0.019$ ) (Figure 1). Given this unexpected effect and the fact that our study sample included dyads that differed in their racial and ethnic composition, we sought to explore the role of potential moderators on the relationship between race/ethnic similarity and mentorship quality. Existing mentoring theory proposes that demographic similarity may be particularly salient for individuals of certain demographic groups (Ragins, 1997; Ragins & Cotton, 1999), yet there is virtually no empirical research that tests this directly.

To protect against bias and enhance the transparency of these exploratory analyses we preregistered these post-hoc analyses (<https://osf.io/5j8dv>). Descriptive statistics regarding levels of mentoring support and relationship quality broken down by racial/ethnic composition of different dyads are presented in Figure 2. Because our sample was underpowered to detect significant differences using a multi-group SEM framework, we explored how race/ethnicity moderated the effect of similarity on career and psychosocial support and relationship quality using a series of one-way analyses of variance (ANOVA) paired with a post-hoc Tukey-Kramer test. Racially Minoritized mentees did not differ in any of their mentoring outcomes, regardless of the composition of their dyad (career support:  $F(2, 142) = 1.42, p = 0.23$ ; psychosocial support:  $F(2, 142) = 1.27, p = 0.28$ ; relationship quality:  $F(2, 142) = 0.77, p = 0.46$ ) (Figure 2). The same was true for White mentees (career support:  $F(2, 276) = 11.04, p = 0.35$ ; psychosocial support:  $F(2, 276) = 0.44, p = 0.64$ ; relationship quality:  $F(2, 276) =$

0.20,  $p = 0.81$ ). Only Asian students reported different levels of support based on their dyad composition. Specifically, post hoc analyses using the Tukey-Kramer post hoc criterion for significance showed that Asian students with Asian or White mentors reported significantly lower levels of career support ( $F(2, 119) = 6.13, p = 0.002$ ) than Asian mentees with Racially Minoritized mentees (Asian-RM vs. Asian-Asian: difference = 0.74 [95% CI: 0.21-1.28],  $p_{adj} = 0.003$ ; Asian-White vs. Asian-Asian: difference = 0.13 [95% CI: -0.24-0.51],  $p_{adj} = 0.68$ ; Asian-White vs. Asian-RM: difference = -0.61 [95% CI: -1.06- -0.15],  $p_{adj} = 0.005$ ). Furthermore, Asian students with Asian mentors reported lower levels of psychosocial support ( $F(2, 119) = 4.57, p = 0.01$ ) than Asian mentees with White or Racially Minoritized mentors (Asian-Asian vs. Asian-RM: difference = 0.86 [95% CI: 0.19-1.54],  $p_{adj} = 0.008$ ; Asian-Asian vs. Asian-White: difference = 0.33 [95% CI: -0.15-0.82],  $p_{adj} = 0.23$ ; Asian-White vs. Asian-RM: difference = -0.53 [95% CI: -1.11-0.04],  $p_{adj} = 0.08$ ). However, the race/ethnicity of the mentor was not significantly related to Asian mentees reports of relationship quality ( $F(2, 119) = 2.54, p = 0.08$ ).

Gender match also exhibited a negligible association with mentee reports of career support ( $\beta = 0.06, P_{adj} = 0.026$ ) and no significant association with psychosocial support ( $\beta = -0.02, P_{adj} = 0.038$ ) or relationship quality ( $\beta = -0.03, P_{adj} = 0.040$ ) (Figure 1). Gender composition of mentoring dyads was also unrelated to mentor reports of career support ( $F(3, 541) = 1.11, p = 0.340$ ), psychosocial support ( $F(3, 541) = 0.61, p = 0.60$ ), and relationship quality ( $F(3, 541) = 1.15, p = 0.32$ ). Descriptive statistics regarding levels of mentoring support and relationship quality broken down by gender composition of different dyads are presented in Figure 3.

Mentor rank exhibited a small, negative association with mentee reports of career support ( $\beta = -0.03$ ,  $P_{adj} = 0.028$ ) and no association with mentee reports of psychosocial support ( $\beta = -0.01$ ,  $P_{adj} = 0.045$ ) or relationship quality ( $\beta = 0.03$ ,  $P_{adj} = 0.050$ ) Figure 1. Similarly, mentee capital had little or no association with mentee reports of career support ( $\beta = 0.01$ ,  $P_{adj} = 0.030$ ), psychosocial support ( $\beta = 0.01$ ,  $P_{adj} = 0.042$ ), and relationship quality ( $\beta = -0.01$ ,  $P_{adj} = 0.899$ ) (Figure 1). Finally, relationship initiation also showed little or no association with mentee reports of career support ( $\beta = -0.05$ ,  $P_{adj} = 0.023$ ), psychosocial support ( $\beta = 0.03$ ,  $P_{adj} = 0.035$ ), and relationship quality ( $\beta = 0.01$ ,  $P_{adj} = 0.047$ ) (Figure 1).

## DISCUSSION

In the present study, we used SEM to examine whether antecedent variables often considered, either explicitly or implicitly, in the process of matching graduate student mentees with research advisor mentors affect the support that mentees experienced and the quality of their mentoring relationships. Consistent with studies of mentoring at the undergraduate level and in the workplace, our results provide some of the most robust evidence to date showing that deep-level similarity is strongly and positively associated with the provision of career and psychosocial support and with relationship quality in doctoral mentoring relationships (Eby et al., 2013; Ensher et al., 2002; Hernandez et al., 2017; Pedersen et al., 2022; Turban et al., 2002). These results are encouraging because deep-level similarity can be identified and cultivated. For instance, mentees can work to identify potential advisors who share their outlook, perspectives, and values before selecting them as a mentor. In addition, mentees and mentors can work together to find and affirm commonalities (e.g., non-linear paths into research, areas they care about and

value outside of research/work, etc.). Mentors can also choose to share an appropriate level of information about their personal lives (Tuma et al., 2021), such as their hobbies or their weekend plans, to the extent that they feel comfortable doing so. These kinds of self-disclosure can foster closeness in a relationship, which in turn can enhance the quality of the relationship. This may be particularly critical for creating stronger perceptions of similarity between mentors of well-represented backgrounds and mentees from marginalized backgrounds.

Our results also indicate that certain antecedents had large effects on psychosocial support and relationship quality and comparatively smaller effects on career support. These results suggest that deep-level similarity and, to a lesser extent, cultural awareness may be more impactful for forming strong emotional connections and impactful high-quality mentoring relationships while being less predictive of career-related support. One explanation for these findings is that other antecedents, such as mentee motivation, performance, or personality traits, may have a greater influence on the provision of career support. For example, mentees who are perceived as hard-workers, diligent, detail oriented, and reliable (e.g., more conscientious individuals) may be perceived as more skillful, talented, and able to produce higher-quality work, which may result in a greater provision of career support from their mentor. Given that mentoring relationships in STEM often focus on research training and fostering mentees' career development, mentorship that focuses on developing kindness, social inclusion, and emotional support may be particularly impactful for improving the outcomes students realize from mentoring.

We also found that mentees reported greater support and higher relationship quality with mentors who demonstrated willingness and ability to discuss race and ethnicity in a respectful way. This finding adds to the documented outcomes associated with culturally aware mentoring (Black et al., 2022; Byars-Winston et al., 2018; Pfund et al., 2022) to provide the first empirical link between culturally aware mentoring and mentorship quality. Our results suggest that racially well-represented mentors can establish positive and supportive mentoring relationships with students from Racially Minoritized backgrounds and ultimately contribute to diversifying STEM fields by developing their culturally aware mentoring skills. Future research should examine the how the presence or absence of mentors' cultural awareness influences marginalized individuals' ability to navigate STEM fields and thrive in their professional pursuits.

These results are promising because cultural aware mentoring is a skill that can be learned and improved over time. Professional development efforts, which require only a modest time investment, are already underway to equip faculty with these skills (NIH Award #5U01GM132372-04). However, mentoring professional development is likely not a 'magic bullet' for achieving effective mentoring relationships. Participation in mentoring professional development is largely not incentivized or rewarded (Tuma et al., 2021; White-Lewis et al., 2022). In fact, only 7% of faculty report engaging in significant mentor professional development (Stolzenberg et al., 2019). Without reward systems in place for participation in mentoring professional development and provision of quality mentorship, change efforts may be limited (National Academies of Sciences, 2019). Given the decentralized structure of graduate education (i.e., departments, labs, and dyads operate mostly independently), there is also potential for idiosyncrasies in the extent to

which mentors feel it is necessary to address cultural differences in their research mentoring relationships. This underscores the need for institutions to shift the current systems towards incentivizing, recognizing, supporting, and rewarding quality mentorship (National Academies of Sciences, 2019).

Using one of the largest and most demographically diverse samples of science doctoral students, we found little support for the widely held belief that mentees who share demographic characteristics with their mentors experience greater mentoring support or higher relationship quality than demographically dissimilar dyads. We found no significant effects of dyadic gender compositions, and we found a negative association between racial/ethnic similarity and mentee reports of psychosocial support and relationship quality. The notion that racial/ethnic similarity may have a negative effect is unexpected. While speculative, it is possible that mentors may be less intentional about cultivating relationships with same-race mentees and thus may not develop the same level of interpersonal comfort, empathy, and disclosure with mentees who are racially similar to themselves. Mentors with cross-race mentees may enter their mentoring relationships with heightened awareness of differences, which may increase their willingness to provide emotional support, counseling, and acceptance, ultimately developing what the mentee experiences as a higher quality, more supportive relationship. This possibility is important to consider given that data for the present study was collected during a period of national reckoning with systemic racism and heightened racial consciousness, which may have influenced mentor behaviors in racially dissimilar dyads.

Given the potentially complex relational dynamics that can occur in cross-race relationships, future research should determine the characteristics and processes that

distinguish high-quality, cross-race relationships from cross-race relationships of poorer quality. Although our sample has greater racial and ethnic diversity proportional to the national STEM graduate population, it remains limited in terms of diversity. Furthermore, we opted to combine all Racially Minoritized individuals into one composite variable to allow for sufficient statistical power. While this prevents exploration of the individual experiences of Racially Minoritized groups, individuals from Racially Minoritized backgrounds are likely to share some lived experience. By grouping all Racially Minoritized into one group, we test this argument and the hypothesis that matching based on demographics leads to quality relationships.

We also observed that Racially Minoritized and White mentees reported similar levels of support and relationship quality regardless of whether they were in racially similar or dissimilar dyads. However, Asian mentees with racially similar mentors reported lower mentoring support than Asian mentees with racially dissimilar mentors. These results are noteworthy because we anticipated that gender or race may have moderated the relationship between demographic match and mentoring support for certain groups, particularly for those with minoritized identities in STEM fields. Yet, the results that Asian students report less desirable outcomes with faculty mentors than other racial/ethnic groups is consistent with prior studies (Aikens et al., 2017; Kim et al., 2009). These findings could be due to cultural differences, particularly that Asian-Asian dyads may feel more compelled to focus on research related tasks and less so on the emotional aspects or quality of the relationship. We did not disaggregate students by nationality, and we treated Asian students as a monolith, despite significant cultural and historical differences between countries in Asia. Given that the vast majority of

international students are of Asian nationalities, this effect may reflect a confounding of nationality with race. We caution readers from overinterpreting these results given the potential confounds and the fact that our sample sizes between groups are unbalanced and limited. Future research should first determine whether these findings are replicable. If so, further research should aim to understand the specific factors underpinning these effects and the mechanisms through which they influence the establishment of quality mentoring relationships.

Our results also indicated that two factors that commonly influence how graduate student mentees in the sciences match with their research mentors – namely relationship initiation and mentor rank – are not meaningfully related to mentee reports of support or relationship quality. These results suggest that, in terms of setting graduate students up for quality mentorship, graduate programs are justified in allowing for both rotations and direct admissions. In addition, mentees can be reassured that the rank of their faculty mentor is not likely to limit their likelihood of developing a quality mentoring relationship. This result is somewhat surprising; we anticipated that mentors with greater human capital would provide a greater breadth and depth of resources to their mentees, thereby improving their mentees' perceptions of mentoring support. However, our results complement work from prior meta analyses which found little support for capital as a predictor of mentorship quality (Eby et al., 2013; Kammeyer-Mueller & Judge, 2008). Rather, human capital may be a better predictor of outcomes of mentorship, such as graduate students' scholarly productivity or career advancement, rather than mentorship processes directly. Alternatively, capital may have a greater role during different stages (e.g., initiation or termination stages) of the mentoring relationship. Future work should

examine other indicators of human capital (e.g., prestige of the mentee's undergraduate institution, mentor's years of experience as faculty member, mentor's publication record) to further explore the influence of mentor and mentee capital on mentoring processes.

Finally, future research should more closely examine predictors of deep-level similarity given its outsized influence on mentorship quality. Our measure of deep-level similarity focused predominantly on mentee-mentor similarity of attitudes, perspectives, and outlook, which is limited. Future research could explore the effects of other forms of deep-level similarity, such as value congruence and similar approaches to interpersonal attachment, both of which have been associated with quality mentoring relationships in workplace settings (Illies & Reiter-Palmon, 2018; Mitchell et al., 2015). Longitudinal study designs may be productive for understanding when and how doctoral student mentees come to recognize deep-level similarity with their research advisor mentors, including whether perceptions of deep-level similarity fluctuate across stages of doctoral training. Longitudinal studies should also be fruitful for understanding the direction of the association between deep-level similarity and mentoring support and quality in a way that is not possible based on the cross-sectional design of the current study. For example, it is plausible that mentees who receive more mentoring support may be more likely to view their mentor as a role model and develop a greater sense of identification, which may result in a greater perception of similarity. Finally, research aimed at understanding how mentors effectively engage in culturally aware mentoring is warranted. Such studies could provide empirical evidence regarding the sensitive and responsive ways mentors could approach learning about someone's life experience and traditions and start conversations about race, ethnicity, and socioeconomic status with a mentee. Such

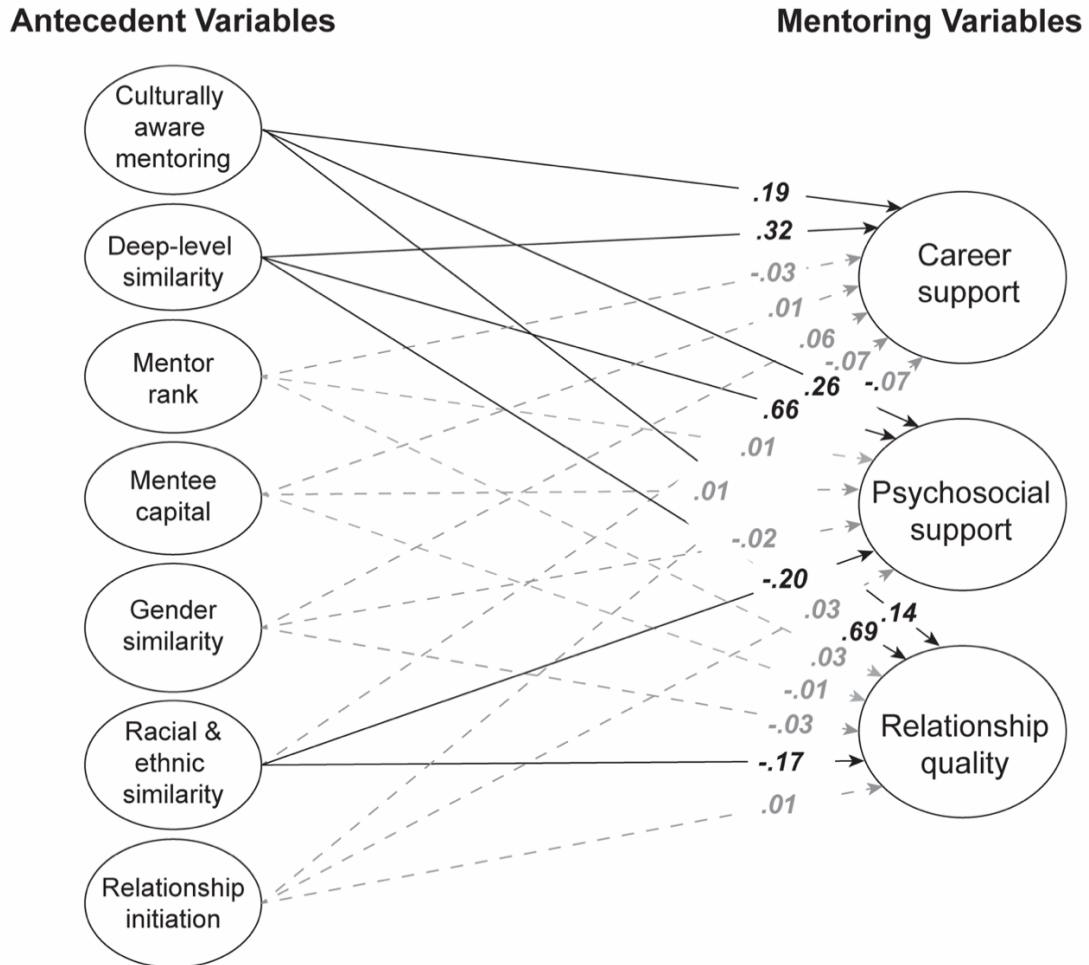
investigations may also provide insight on the mechanisms of how cultural aware mentoring affects mentoring processes and outcomes.

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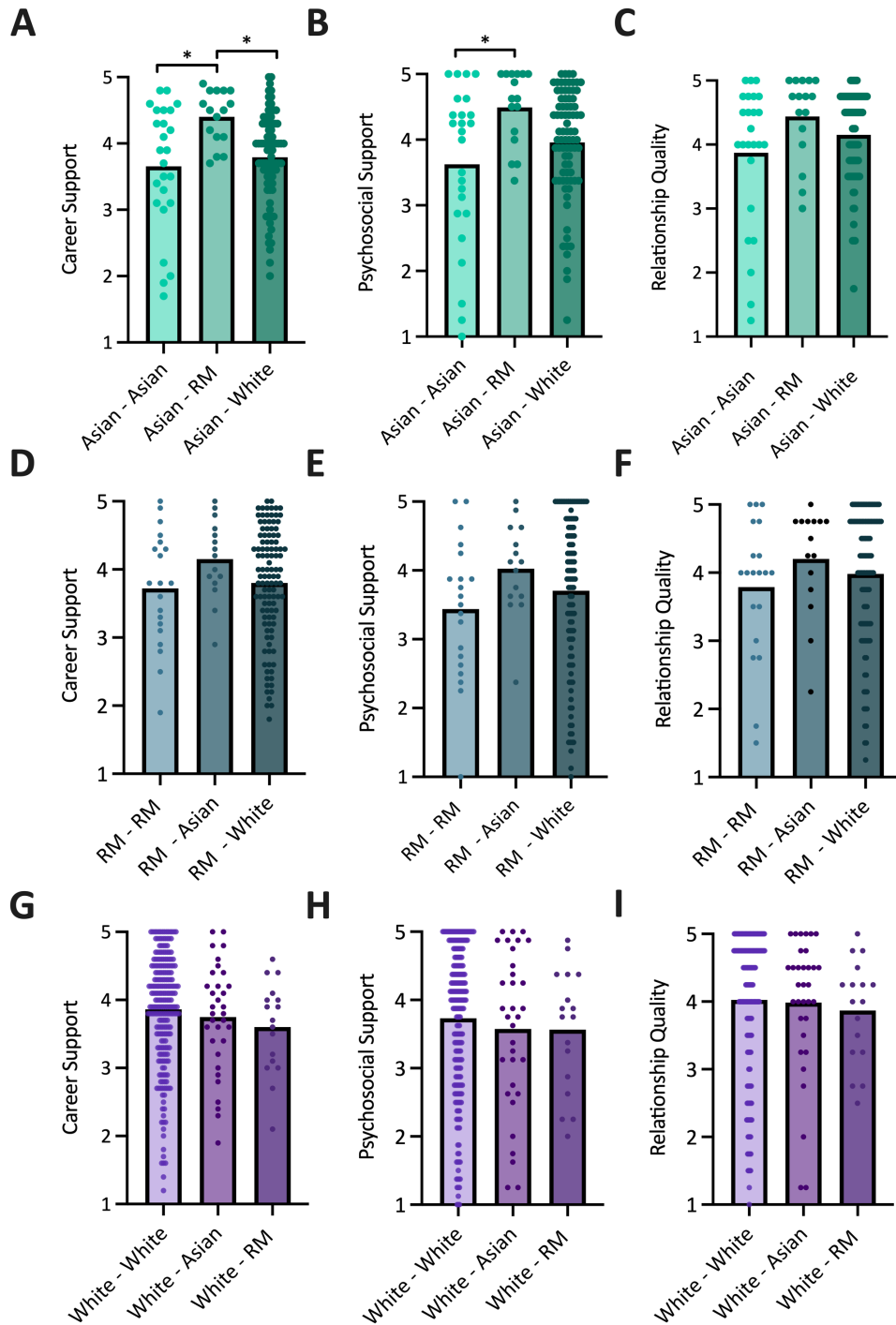
## FIGURES, TABLES, AND LEGENDS

**FIGURE 6.1: Final structural model testing relationships between mentoring antecedents and mentoring support and relationship quality.**



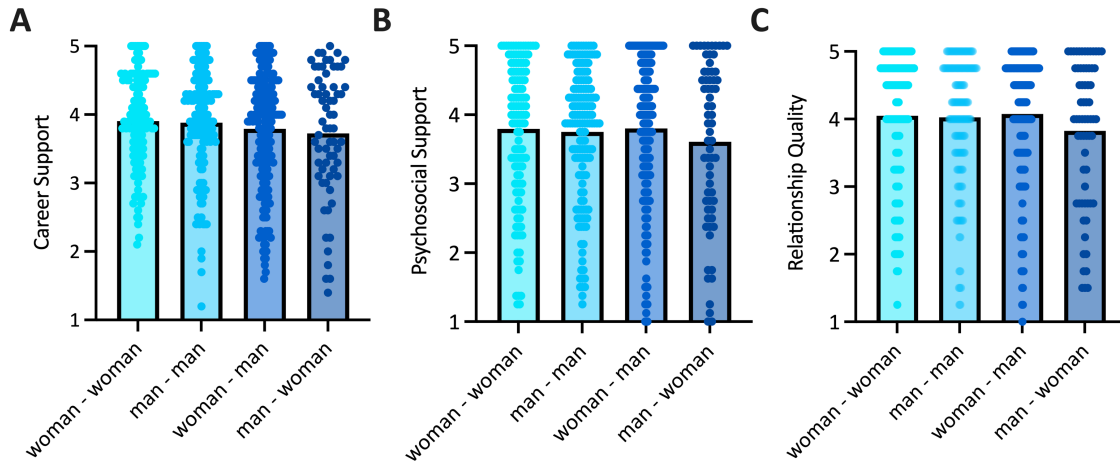
This simplified structural model illustrates tested relationships between hypothesized mentoring antecedents, forms of mentoring support (i.e., career and psychosocial support), and relationship quality. Solid black lines indicate statistically significant relationships based on Benjamini-Hochberg corrected  $p$ -values. Dashed grey lines indicate statistically non-significant paths. Numerical values presented on paths/arrows in the model indicate standardized coefficients to facilitate comparisons of the influence of exogenous variables on endogenous variables.

**FIGURE 6.2: Career support, psychosocial support, and relationship quality in racially similar and diverse mentoring dyad pairs.**



(A-C) Asian mentees and mentors of similar or different racial/ethnic backgrounds; (D-F) Racially Minoritized mentees and mentors of similar or different racial/ethnic backgrounds; and (G-I) White mentees and mentors of similar or different racial/ethnic backgrounds. Significance was derived from a one-way ANOVA with a Tukey-Kramer post-hoc test. \*  $p < 0.05$ .

**FIGURE 6.3: Career support, psychosocial support, and relationship quality in gender similar and dissimilar mentoring dyad pairs.**



(A) Perceived career support, (B) perceived psychosocial support, (C) perceived relationship quality (C) by mentee-mentor dyad gender composition. Significance was derived from a one-way ANOVA. No significant differences between groups was found.

**TABLE 6.1: Demographic characteristics of doctoral students ( $n = 565$ )**

<sup>1</sup> Counts do not sum up to 100% because some participant's research integrated multiple research contexts.

<b>Description</b>	<b><i>n</i> (%)</b>
<b>Gender</b>	
Woman	325 (58%)
Man	225 (40%)
Non-binary	13 (2%)
Prefer not to respond	2 (<1%)
<b>Race</b>	
American Indian or Alaskan Native	10 (2%)
Asian	131 (23%)
Black or African American	49 (8.5%)
Hawaiian or Native Pacific Islander	3 (<1%)
Middle Eastern	14 (2.5%)
White	319 (56%)
Prefer to self-describe	21 (3.7%)
Prefer not to respond	22 (3.8%)
<b>Ethnicity</b>	
Hispanic or Latinx/Latine	86 (15%)
Not Hispanic	465 (82%)
Prefer not to respond	14 (3%)
<b>Degree status</b>	
Pre-Candidacy	208 (37%)
Post-Candidacy	314 (55%)
Currently Post-Doctoral	40 (7%)
Prefer not to respond	3 (0.5%)
<b>International status</b>	
Yes	121 (21%)
No	443 (78%)
Prefer not to respond	1 (<1%)
<b>English First-Language</b>	
Yes	472 (84%)
No	89 (16%)
Prefer not to respond	4 (<1%)

Table 6.1, continued.

<b>Description</b>	<b><i>n</i> (%)</b>
<b>Research context<sup>1</sup></b>	
Bench	425 (75%)
Computational	277 (49%)
Fieldwork	167 (30%)
Theoretical	55 (10%)
Prefer not to respond	1 (<1%)
<b>Years completed</b>	
1	96 (17%)
2	110 (19%)
3	125 (22%)
4	89 (16%)
5	85 (15%)
6	43 (7%)
7+	13 (2%)
Prefer not to respond	4 (<1%)
<b>Relationship initiation</b>	
Direct admission	235 (42%)
Following laboratory rotations	304 (52%)
Other scenario	26 (5%)
<b>Subjective socioeconomic status</b>	
1 (bottom, worst off)	2 (<1%)
2	10 (2%)
3	32 (6%)
4	77 (14%)
5	91 (16%)
6	109 (19%)
7	147 (26%)
8	70 (12%)
9	18 (3%)
10 (top, best off)	2 (<1%)

**TABLE 6.2: Demographic characteristics of doctoral student mentors ( $n = 565$ )**

<b>Description</b>	<b><i>n</i> (%)</b>
<b>Gender</b>	
Woman	196 (35%)
Man	364 (64%)
Prefer not to respond	5 (<1%)
<b>Race</b>	
American Indian or Alaskan Native	3 (<1%)
Asian	72 (13%)
Black or African American	12 (2%)
Hawaiian or Native Pacific Islander	1 (<1%)
Middle Eastern	12 (2%)
White	427 (76%)
Prefer to self-describe	10 (2%)
Prefer not to respond	31 (5%)
<b>Ethnicity</b>	
Hispanic or Latinx/Latine	28 (5%)
Not Hispanic	517 (92%)
Prefer not to respond	20 (3%)
<b>Rank</b>	
Assistant Professor	114 (20%)
Associate Professor	138 (24%)
Full Professor	292 (52%)
Other	14 (2%)
Prefer not to respond	7 (1%)

**TABLE 6.3: Means, Standard Deviations, & Correlations of Variables.  $*p < 0.05$**

Variable	<i>M</i>	<i>SD</i>	Variable												
			1	2	3	4	5	6	7	8	9	10			
1. Career support	3.81	0.80	-												
2. Psychosocial support	3.76	1.04	.79*	-											
3. Relationship quality	4.02	0.95	.70*	.81*	-										
4. Culturally aware mentoring	3.28	0.93	.61*	.62*	.54*	-									
5. Deep-level similarity	3.27	0.89	.68*	.75*	.73*	.57*	-								
6. Mentor rank	2.34	0.82	-.12	-.08	-.06	-.10	-.07	-							
7. Mentee capital	5.92	1.65	.14	.12	.10	.07	.16*	-.02	-						
8. Gender similarity	0.50	0.50	.08	.01	.02	.03	.04	.01	.06	-					
9. Racial & ethnic similarity	0.50	0.50	.00	-.06	-.03	.06	.04	.04	.12	.01	-				
10. Relationship initiation	0.56	0.50	-.03	.03	.00	-.01	-.01	-.01	-.03	-.05	-.13	-			

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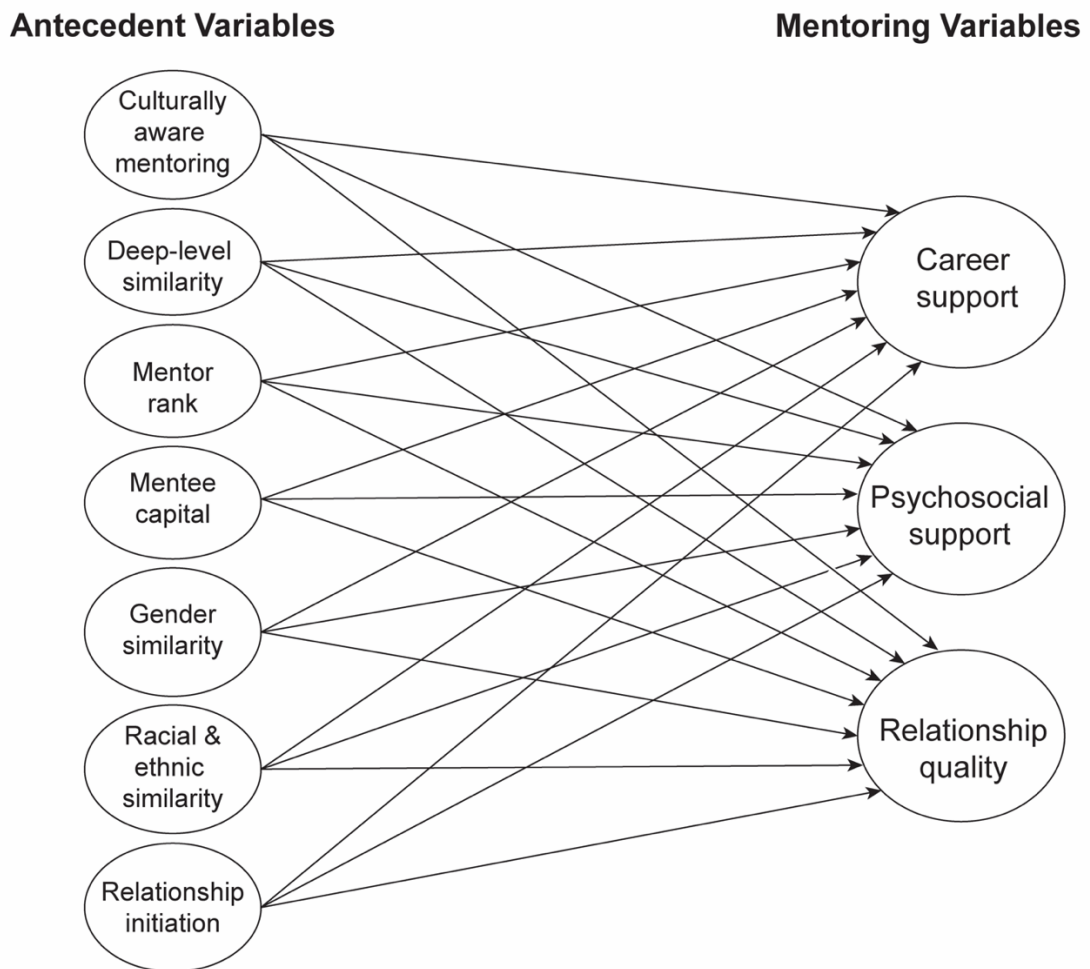
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**Supplemental Figure 6.S1: Conceptual model between antecedent variables and indicators of quality mentorship tested in the present study.**



**Supplemental Table 6.S1: Doctoral student-faculty member characteristics in the analyses by gender match.**

<b>Similar Gender</b>	<b>Mentee</b>	<b>Mentor</b>	<b><i>n</i> (%)</b>
	Woman	Woman	126 (22%)
Man	Man	154 (27%)	
Total Similar			280 (49%)
<b>Dissimilar Gender</b>	Woman	Man	199 (35%)
	Man	Woman	65 (12%)
	Non-binary	Man	9 (2%)
	Non-binary	Woman	5 (1%)
Total Dissimilar			264 (46%)
Incomplete Data			7 (1%)

**Supplemental Table 6.S2: Doctoral student-faculty member characteristics in the analyses by race/ethnicity match.**

	<b>Mentee</b>	<b>Mentor</b>	<b><i>n</i> (%)</b>
<b>Similar Race/Ethnicity</b>	White	White	229 (40%)
	Racially Minoritized	Racially Minoritized	20 (4%)
	Asian	Asian	25 (4%)
Total Similar			274 (48%)
<b>Dissimilar Race/Ethnicity</b>	White	Racially Minoritized	17 (3%)
	White	Asian	33 (6%)
	Racially Minoritized	White	110 (20%)
	Racially minoritized	Asian	15 (3%)
	Asian	White	81 (14%)
	Asian	Racially Minoritized	16 (3%)
Total Dissimilar			271 (48%)
Incomplete Data			20 (4%)

**Supplemental Table 6.S3: Descriptive statistics of indicators of quality mentorship by gender dyad composition.**

Variable	Same gender dyad				Cross gender dyad			
	Man mentee – man mentor <i>n</i> = 154 (27%)		Woman mentee – woman mentor <i>n</i> = 126 (22%)		Man mentee – woman mentor <i>n</i> = 65 (12%)		Woman mentee – man mentor <i>n</i> = 199 (35%)	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Career support	3.88	0.75	3.90	0.68	3.73	0.93	3.79	0.84
Psychosocial support	3.75	0.97	3.79	1.03	3.61	1.20	3.80	1.04
Relationship quality	4.02	0.92	4.05	0.97	3.83	1.07	4.07	0.93

**Supplemental Table 6.S4: Descriptive statistics of indicators of quality mentorship by race/ethnicity dyad composition.**

		<b>Same race/ethnicity dyad</b>		<b>Cross race/ethnicity dyad</b>			
		Asian mentee – Asian mentor <i>n</i> = 25 (4%)		Asian mentee – RM mentor <i>n</i> = 16 (3%)		Asian mentee – White mentor <i>n</i> = 81 (14%)	
<b>Variable</b>		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Career support		3.66	0.96	4.40	0.38	3.79	0.66
Psychosocial support		3.62	1.20	4.49	0.57	3.95	0.83
Relationship quality		3.87	1.08	4.43	0.66	4.15	0.71
		RM <sup>7</sup> mentee – RM mentor <i>n</i> = 20 (4%)		RM mentee – Asian mentor <i>n</i> = 15 (3%)		RM mentee – White mentor <i>n</i> = 110 (20%)	
<b>Variable</b>		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Career support		3.72	0.84	4.15	0.58	3.80	0.82
Psychosocial support		3.43	1.01	4.02	0.67	3.70	1.13
Relationship quality		3.78	1.01	4.20	0.78	3.98	1.00
		White mentee – White mentor <i>n</i> = 229 (40%)		White mentee – Asian mentor <i>n</i> = 33 (6%)		White mentee – RM mentor <i>n</i> = 17 (3%)	
<b>Variable</b>		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Career support		3.86	0.81	3.75	0.79	3.60	0.65
Psychosocial support		3.73	1.08	3.58	1.15	3.57	0.90
Relationship quality		4.03	1.04	3.98	1.00	3.87	0.76

<sup>7</sup> RM = Racially Minoritized. We purposefully use the term “racially minoritized” to reflect the active role that systemic and societal racism has had and continues to have on individuals who are American Indian or Alaskan Native, Black or African American, Hawaiian or Native Pacific Islander, and North African or Middle Eastern.

**Supplemental File 6.1: Scales used to measure latent variables.**

**Culturally aware mentoring behaviors**

Byars-Winston, A., & Butz, A. R. (2021). Measuring research mentors’ cultural diversity awareness for race/ethnicity in STEM: Validity evidence for a new scale. *CBE—Life Sciences Education*, 20(2), ar15.

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

<b>Culturally aware mentoring behaviors</b>	1. My mentor created opportunities for me to bring up issues of race/ethnicity as they arose.
	2. My mentor encouraged me to think about how the research related to my own lived experience.
	3. My mentor was willing to discuss race and ethnicity, even if it may have been uncomfortable for them.
	4. My mentor raised the topic of race/ethnicity in our research mentoring relationship when it was relevant.
	5. My mentor approached the topic of race/ethnicity with me in a respectful manner.

**Deep-level similarity**

Ensher, E. A., Grant-Vallone, E. J., & Marelich, W. D. (2002). Effects of perceived attitudinal and demographic similarity on protégés' support and satisfaction gained from their mentoring relationships. *Journal of Applied Social Psychology*, 32(7), 1407-1430.

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

<b>Deep-level similarity</b>	1. My mentor and I see things in the same way.
	2. My mentor is similar to me in terms of our outlook and perspectives.
	3. My mentor and I are alike in a number of areas.
	4. My mentor and I analyze problems in a similar way.
	5. My mentor and I have similar values about work.
	6. My mentor and I have similar values about life in general.
	7. My mentor and I are more similar than dissimilar in important ways.

**Career support<sup>1</sup>**

Tuma TT, Adams, JD, Choi S, & Dolan EL (in progress) Measuring Negative Mentoring Experiences: Development & Nomological Validation of the Mentoring Experiences in Research & Graduate Education (MERGE) Scale<sup>8</sup>

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

<b>Career support</b>	1. My mentor is willing to give me feedback on my research.
	2. My mentor advocates on my behalf.
	3. My mentor protects me from others who might cause me professional harm.
	4. My mentor has little interest in my career advancement. (R)
	5. My mentor is reluctant to let me present my research at conferences. (R)
	6. My mentor offers useful advice for achieving my career goals.
	7. My mentor prioritizes publishing my research.
	8. My mentor helps me identify ways to network.
	9. My mentor makes sure I have sufficient funding to do my research.
	10. My mentor helps me prepare for important milestones in my degree.

**Psychosocial support<sup>1</sup>**

Tuma TT, Adams, JD, Choi S, & Dolan EL (in progress) Measuring Negative Mentoring Experiences: Development & Nomological Validation of the Mentoring Experiences in Research & Graduate Education (MERGE) Scale.

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

	1. My mentor encourages me.
	2. My mentor values me as a person.

<sup>8</sup> This measure is currently being developed to measure doctoral students' negative mentoring experiences. Validity and reliability evidence based on the test content, response process, internal structure, and relationships with other variables has been collected and the resulting measurement validation manuscript is in preparation.

<b>Psychosocial support</b>	3. My mentor checks in about my well-being.
	4. My mentor is a role model for me.
	5. My mentor makes me feel accepted.
	6. My mentor empathizes when I am struggling.
	7. My mentor is understanding when I experience difficulties.
	8. My mentor tells me when they think I have done a good job.

**Relationship quality<sup>1</sup>**

Tuma TT, Adams, JD, Choi S, & Dolan EL (in progress) Measuring Negative Mentoring Experiences: Development & Nomological Validation of the Mentoring Experiences in Research & Graduate Education (MERGE) Scale.

**Instructions:** Please indicate the extent to which you agree or disagree with each of these statements.

**Response Scale:** 1 = strongly disagree; 2 = disagree; 3 = undecided; 4 = agree; 5 = strongly agree, 6 = Prefer not to respond

<b>Relationship quality</b>	1. My mentor and I do not like each other. (R)
	2. My mentor and I have a difficult relationship. (R)
	3. My mentor and I can talk about things other than work tasks.
	4. My mentor and I have a tense relationship. (R)

## **Supplemental File 6.2: Results from measurement model fitting and model modifications.**

We began the first phase of our SEM by evaluating the relationships between our measured indicators and the underlying latent variables (i.e., measurement model). We performed confirmatory factor analysis (CFA) using the R software (R Core Team, 2016) for statistical computing and the ‘lavaan’ package (Rosseel, 2012) for cultural aware mentoring, deep-level similarity, career support, psychosocial support, and relationship quality. We used robust maximum likelihood (MLR) estimation to correct for potential non-normality in our data.

Then, we assessed how well our measurement models reproduced their variance-covariance matrices using several goodness of fit indices. First, we examined the model’s chi-square test ( $\chi^2$ ) of goodness of fit and its degrees of freedom and  $p$ -value to evaluate the discrepancy between a hypothesized model and the data. It is generally agreed upon best practice to report the chi-square test despite its limitations (e.g., sensitivity to sample size, unrealistic null hypothesis in a population). Consistent with current measurement standards, we also evaluated multiple model fit indices (e.g., absolute, parsimonious, incremental) relative to recommended “cut-off” values (Hu & Bentler, 1999). The comparative fit index (CFI) and Tucker-Lewis index (TLI) are both incremental fit measures and values  $\geq .90$  indicate acceptable data-model fit. In addition, we also examined the root mean square error of residuals (RMSEA) value. RMSEA is a parsimony-adjusted fit index and approximates how well the model estimates the population covariance matrix while penalizing more complex models, with higher RMSEA values indicating poorer data-model fit. We used 0.01, 0.05, and 0.08 to indicate excellent, good, and mediocre model fit. Finally, we evaluated the standardized root mean square residual (SRMR) which examines the standardized difference between the observed correlation and the predicted correlation, thus giving further insight into misspecified covariance structures. The SRMR is an absolute fit indice, with higher values ( $< 0.08$ ) indicating poor model fit. For all model fit indices, values close to the cut-off are categorized as indicating fair fit. In sum, high values ( $\geq .90$ ) of the CFI and TLI and low values of the RMSEA and SRMR provide evidence that the hypothesized measurement models are plausible explanations of the data.

Finally, in addition to traditional null hypothesis testing, we used equivalence testing (Marcoulides & Yuan 2017; Peugh & Feldon, 2020; Yuan et al., 2016). We calculated adjusted, or “T-size” fit statistics, to compare the amount of misspecification in our model to a tolerable size of specification with adjusted cutoffs. Adjusted cutoffs and T-size fit statistics are reported below for  $CFI_T$  and  $RMSEA_T$ .

We report coefficient Omega values, which is considered to be a more sensible indicator of internal consistency than Cronbach’s alpha, as an indicator of reliability (Dunn et al.,

2014). We also encourage interested readers to consult the items comprising the scales to judge their face equivalence (i.e., the extent to which the items appear to elicit the same underlying latent variable).

### **Cultural aware mentoring behaviors**

We ran a CFA with cultural diversity awareness behaviors indicated by five items. The majority of the model fit statistics indicated excellent fit,  $\chi^2 (5) = 21.552$  ( $p < 0.001$ ), CFI = 0.982, TLI = 0.965, SRMR = 0.022, with the exception of RMSEA = 0.099 90% CI [0.059, 0.144] which indicated inadequate fit. Furthermore, the CFI<sub>T</sub> demonstrated close fit and the RMSEA<sub>T</sub> indicated fair fit with adjusted fit values<sup>A</sup>,  $\chi^2 (5) = 21.552$  ( $p < 0.001$ ), CFI<sub>T</sub> = 0.951, RMSEA<sub>T</sub> = 0.111. Therefore, we opted to proceed without adjusting the measurement model. The scale demonstrated high internal consistency ( $\alpha = 0.86$ ) and ( $\omega = 0.90$ ).

<sup>A</sup> The rescaled fit statistic values for the measurement model indicated for CFI<sub>T</sub>: “poor”  $\leq 0.832$ , “mediocre” = 0.832 – 0.860, “fair” = 0.860 – 0.905, “close” = 0.905 – 0.968 and “excellent” are  $\geq 0.968$  and for RMSEA<sub>T</sub>: “poor”  $\geq 0.137$ , “mediocre” = 0.117 – 0.137, “fair” = 0.088 – 0.117, “close” = 0.059 – 0.088, and “excellent” are  $\leq 0.059$ .

### **Deep-level similarity**

We ran a CFA with deep-level similarity indicated by seven items. The majority of the model fit statistics indicated excellent fit,  $\chi^2 (14) = 139.466$  ( $p < 0.001$ ), CFI = 0.945, TLI = 0.917, SRMR = 0.034, with the exception of RMSEA = 0.136 90% CI [0.116, 0.157] which indicated inadequate fit. Furthermore, the CFI<sub>T</sub> demonstrated fair fit and the RMSEA<sub>T</sub> indicated poor fit with adjusted fit values<sup>B</sup>,  $\chi^2 (14) = 139.466$  ( $p < 0.001$ ), CFI<sub>T</sub> = 0.903, RMSEA<sub>T</sub> = 0.145. To determine the source of misfit, we checked for correlated residuals using modification indices as a guide. Using a backwards selection process, we first identified the largest modification index (MI) value and ensured that the potential parameter modification was theoretically supported. We then respecified the model with the additional correlated residuals and examined the goodness of fit indices of the revised model. Our modification indices recommended allowing the residual values of item 6 and item 7 to correlate (MI=45.192), item 3 and item 7 (MI=32.005), and item 5 and item 6 (MI=23.501). Adding these paths to the model improved model fit  $\chi^2 (11) = 57.850$  ( $p < 0.001$ ), CFI = 0.980, TLI = 0.962, SRMR = 0.023, RMSEA = 0.092, 90% CI [0.069 - 0.115]. These modifications were further supported with CFI<sub>T</sub> demonstrating close fit and the RMSEA<sub>T</sub> indicating mediocre fit with adjusted fit values<sup>C</sup>,  $\chi^2 (11) = 57.850$  ( $p < 0.001$ ), CFI<sub>T</sub> = 0.955 RMSEA<sub>T</sub> = 0.109. The scale demonstrated high internal consistency ( $\alpha = 0.92$ ) and ( $\omega = 0.94$ ).

<sup>B</sup> The rescaled fit statistic values for the measurement model indicated for CFI<sub>T</sub>: “poor”  $\leq 0.848$ , “mediocre” = 0.848 – 0.875, “fair” = 0.875 – 0.915, “close” = 0.915 – 0.972 and “excellent” are  $\geq 0.972$  and for RMSEA<sub>T</sub>: “poor”  $\geq 0.121$ , “mediocre” = 0.101 – 0.121, “fair” = 0.072 – 0.101, “close” = 0.042 – 0.072, and “excellent” are  $\leq 0.042$ .

<sup>C</sup> The rescaled fit statistic values for the measurement model indicated for CFI<sub>T</sub>: “poor”  $\leq 0.848$ , “mediocre” = 0.848 – 0.875, “fair” = 0.875 – 0.915, “close” = 0.915 – 0.972 and

“excellent” are  $\geq 0.972$  and for  $RMSEA_T$ : “poor”  $\geq 0.124$ , “mediocre” =  $0.104 - 0.124$ , “fair” =  $0.075 - 0.141$ , “close” =  $0.046 - 0.075$ , and “excellent” are  $\leq 0.046$ .

### **Career support**

We first ran a CFA with perceived career support indicated by ten items. The fit indices of the model were acceptable,  $\chi^2 (35) = 186.86$  ( $p < 0.001$ ),  $CFI = 0.927$ ,  $TLI = 0.906$ ,  $SRMR = 0.041$ , with the exception of  $RMSEA = 0.099$ , 90% CI [0.085, 0.113]) which indicated inadequate fit. Furthermore,  $CFI_T$  demonstrated mediocre fit and  $RMSEA_T$  indicated mediocre fit with adjusted fit values <sup>D</sup>,  $\chi^2 (20) = 128.89$  ( $p < 0.001$ ),  $CFI_T = 0.881$ ,  $RMSEA_T = 0.100$ . To determine the source of misfit, we checked for correlated residuals using modification indices as a guide. Using a backwards selection process, we first identified the largest modification index (MI) value and ensured that the potential parameter modification was theoretically supported. We then respecified the model with the additional correlated residuals and examined the goodness of fit indices of the revised model. Our modification indices recommended allowing the residual values of item 2 and item 3 to correlate (MI=88.176), then item 1 and item 8 (MI=31.451). Adding these paths to the model improved model fit  $\chi^2 (33) = 92.240$  ( $p < 0.001$ ),  $CFI = 0.971$ ,  $TLI = 0.961$ ,  $SRMR = 0.032$ ,  $RMSEA = 0.064$ , 90% CI [0.048 0.079]). These modifications were further supported with  $CFI_T$  demonstrating close fit and the  $RMSEA_T$  indicating fair fit with adjusted fit values <sup>E</sup>,  $\chi^2 (33) = 92.240$  ( $p < 0.001$ ),  $CFI_T = 0.943$ ,  $RMSEA_T = 0.070$ . The scale demonstrated high internal consistency ( $\alpha = 0.89$ ) and ( $\omega = 0.92$ ).

<sup>D</sup> The rescaled fit statistic values for the measurement model indicated for  $CFI_T$ : “poor”  $\leq 0.860$ , “mediocre” =  $0.860 - 0.885$ , “fair” =  $0.885 - 0.923$ , “close” =  $0.923 - 0.976$ , and “excellent” are  $\geq 0.976$  and  $RMSEA_T$ : “poor”  $\geq 0.112$ , “mediocre” =  $0.092 - 0.112$ , “fair” =  $0.064 - 0.092$ , “close” =  $0.032 - 0.064$ , and “excellent” are  $\leq 0.032$ .

<sup>E</sup> The rescaled fit statistic values for the measurement model indicated for  $CFI_T$ : “poor”  $\leq 0.861$ , “mediocre” =  $0.861 - 0.885$ , “fair” =  $0.885 - 0.923$ , “close” =  $0.923 - 0.976$ , and “excellent” are  $\geq 0.976$  and for  $RMSEA_T$ : “poor”  $\geq 0.112$ , “mediocre” =  $0.093 - 0.112$ , “fair” =  $0.064 - 0.093$ , “close” =  $0.033 - 0.064$ , and “excellent” are  $\leq 0.033$ .

### **Psychosocial support**

We ran a CFA with perceived psychosocial support indicated by eight items. The majority of the model fit statistics indicated excellent fit,  $\chi^2 (20) = 149.094$  ( $p < 0.001$ ),  $CFI = 0.948$ ,  $TLI = 0.928$ ,  $SRMR = 0.028$ , with the exception of  $RMSEA = 0.137$ , 90% CI [0.116, 0.157]) which indicated inadequate fit. Furthermore, the  $CFI_T$  demonstrated fair fit and the  $RMSEA_T$  indicated poor fit with adjusted fit values <sup>F</sup>,  $\chi^2 (20) = 149.10$  ( $p < 0.001$ ),  $CFI_T = 0.916$ ,  $RMSEA_T = 0.123$ . To determine the source of misfit, we checked for correlated residuals using modification indices as a guide. Using a backwards selection process, we first identified the largest modification index (MI) value and ensured that the potential parameter modification was theoretically supported. We then respecified the model with the additional correlated residuals and examined the goodness of fit indices of the revised model. Our modification indices recommended allowing the residual values of item 6 and item 7 to correlate (MI=105.537), then item 1 and item 2 (MI=27.226), and then item 1 and item 8 (27.981). Adding these paths to the model

improved model fit  $\chi^2 (17) = 57.264$  ( $p < 0.001$ ), CFI = 0.985, TLI = 0.975, SRMR = 0.019, RMSEA = 0.080, 90% CI [0.058 - 0.103]). These modifications were further supported with CFI<sub>T</sub> demonstrating close fit and the RMSEA<sub>T</sub> indicating fair fit with adjusted fit values <sup>G</sup>,  $\chi^2 (33) = 92.240$  ( $p < 0.001$ ), CFI<sub>T</sub> = 0.966, RMSEA<sub>T</sub> = 0.083. The scale demonstrated high internal consistency ( $\alpha = 0.95$ ) and ( $\omega = 0.96$ ).

<sup>F</sup> The rescaled fit statistic values for the measurement model indicated for CFI<sub>T</sub>: “poor”  $\leq 0.853$ , “mediocre” = 0.853 – 0.879, “fair” = 0.879 – 0.918, “close” = 0.918 – 0.974, and “excellent” are  $\geq 0.974$  and for RMSEA<sub>T</sub>: “poor”  $\geq 0.117$ , “mediocre” = 0.097 – 0.117, “fair” = 0.069 – 0.097, “close” = 0.038 – 0.069, and “excellent” are  $\leq 0.038$ .

<sup>G</sup> The rescaled fit statistic values for the measurement model indicated for CFI<sub>T</sub>: “poor”  $\leq 0.854$ , “mediocre” = 0.854 – 0.879, “fair” = 0.879 – 0.918, “close” = 0.918 – 0.974, and “excellent” are  $\geq 0.974$  and for RMSEA<sub>T</sub>: “poor”  $\geq 0.118$ , “mediocre” = 0.099 – 0.118, “fair” = 0.070 – 0.099, “close” = 0.040 – 0.070, and “excellent” are  $\leq 0.040$ .

### **Relationship quality**

We ran a CFA with perceived relationship quality indicated by four items. The majority of the model fit statistics indicated excellent fit,  $\chi^2 (2) = 19.856$  ( $p < 0.001$ ), CFI = 0.989, TLI = 0.967, SRMR = 0.018, with the exception of RMSEA = 0.130, 90% CI [0.082, 0.185]) which indicated inadequate fit. Furthermore, the CFI<sub>T</sub> demonstrated close fit and the RMSEA<sub>T</sub> indicated poor fit with adjusted fit values <sup>H</sup>,  $\chi^2 (2) = 19.856$  ( $p < 0.001$ ), CFI<sub>T</sub> = 0.946, RMSEA<sub>T</sub> = 0.178. To determine the source of misfit, we checked for correlated residuals using modification indices as a guide. Using a backwards selection process, we first identified the largest modification index (MI) value and ensured that the potential parameter modification was theoretically supported. We then respecified the model with the additional correlated residuals and examined the goodness of fit indices of the revised model. Our modification indices recommended allowing the residual values of item 2 and item 4 to correlate (MI = 21.326). Adding this path to the model improved model fit  $\chi^2 (1) = 0.365$  ( $p = 0.546$ ), CFI = 1.000, TLI = 1.002, SRMR = 0.002, RMSEA = 0.000, 90% CI [0.000 - 0.098]). These modifications were further supported with CFI<sub>T</sub> demonstrating excellent fit and the RMSEA<sub>T</sub> indicating excellent fit with adjusted fit values <sup>I</sup>,  $\chi^2 (1) = 0.365$ , ( $p < 0.001$ ), CFI<sub>T</sub> = 0.991 RMSEA<sub>T</sub> = 0.09. The scale demonstrated high internal consistency ( $\alpha = 0.89$ ) and ( $\omega = 0.91$ ).

<sup>H</sup> The rescaled fit statistic values for the measurement model indicated for CFI<sub>T</sub>: “poor”  $\leq 0.815$ , “mediocre” = 0.815 – 0.846, “fair” = 0.846 – 0.894, “close” = 0.894 – 0.963, and “excellent” are  $\geq 0.963$  and for RMSEA<sub>T</sub>: “poor”  $\geq 0.159$ , “mediocre” = 0.139 – 0.159, “fair” = 0.110 – 0.139, “close” = 0.082 – 0.110, and “excellent” are  $\leq 0.082$ .

<sup>I</sup> The rescaled fit statistic values for the measurement model indicated for CFI<sub>T</sub>: “poor”  $\leq 0.807$ , “mediocre” = 0.807 – 0.838, “fair” = 0.838 – 0.888, “close” = 0.888 – 0.960, and “excellent” are  $\geq 0.960$  and for RMSEA<sub>T</sub>: “poor”  $\geq 0.183$ , “mediocre” = 0.163 – 0.183, “fair” = 0.133 – 0.163, “close” = 0.133 – 0.108, and “excellent” are  $\leq 0.108$ .

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## CHAPTER 7

### CONCLUSIONS & DISCUSSION

This chapter summarizes the major contributions of the studies presented in my dissertation. This body of work represents my dual training in molecular tree biology and biology education. The major findings and directions for future research are included below.

#### **Molecular Tree Biology Research**

In my molecular tree biology research, I investigated the involvement of sucrose transport proteins in the intracellular trafficking of sucrose in trees. More specifically, my work focused on their roles in processes that required carbohydrate remobilization from reserves. The work presented here extends our understanding of the mechanisms by which sucrose trafficking influences carbohydrate remobilization under carbon limiting conditions in woody trees. By leveraging two complementary and dual approaches, this research contributes to our understanding of the dynamics of carbohydrate allocation in woody perennial trees. This work can be utilized for tree improvement efforts to produce hardier and more resilient trees for use as a biofuel feedstock and bioenergy source.

Chapter 2 utilized a common silviculture practice, coppicing, to determine how perturbed sucrose transport impacts tree growth and carbohydrate allocation. This work found that even under extreme carbon limiting conditions, poplar trees prioritized and retained their carbohydrate reserves. This finding suggests that carbohydrate utilization may not be a limiting factor in the growth responses of trees when faced with carbon

deficit conditions. The findings from my research also suggest that the non-structural carbohydrate remobilization processes were influenced heavily by seasonal dynamics and by the involvement of SUT4 as a mediator for reserve remobilization under carbon limiting processes. Taken together, this work demonstrates how intracellular sucrose dynamics contribute to stored carbon mobilization, primary growth productivity, and defense in poplar trees.

Chapter 3 extended this research by characterizing the roles of winter-biased *SUTs*, *SUT4*, *SUT5*, and *SUT6*, under natural field conditions. Using CRISPR knockout mutants of winter biased *SUTs* in hybrid poplar, the seasonal growth response of these transmembrane sucrose transport proteins was investigated under natural field conditions through a multi-year field trial. To date, functional characterization of sucrose transporters under field conditions was relatively limited. By leveraging CRISPR knockout 717 mutants under field conditions, we found that perturbation of winter biased *SUTs* in poplar resulted in altered growth rates, metabolic properties, water use strategies, and phenology. For example, subtle growth differences were observed between the *sut* mutants and their respective controls during the first growing season, but stem diameter and height were compromised in the *sut4* trees following spring growth resumption. Altered phenological traits were observed in the *sut4* mutants which resulted in a reduced leaf area duration compared to the *sut5/6* mutants and controls. Metabolite profiling revealed altered sugar partitioning and reductions in tricarboxylic acid cycle intermediates and oligosaccharides associated with cold tolerance in the *sut4* mutant trees. These phenotypes are in strong contrast to greenhouse grown *sut* poplar mutants, which exhibit subtle phenotypic changes. In contrast, the *sut5/6* mutants had modest differences in

terms of tree growth, biomass yield and environmental sensing when compared to their respective controls and the *sut4* mutants. The results of Chapter 3 suggest that despite their similar winter biased expression patterns, *SUT4* may have a comparatively greater involvement in winter survival than *SUT5* and *SUT6*. Our observations also suggest that changes to carbohydrate allocation and remobilization will also be influenced under a rapidly changing climate. Finally, our work highlights the importance of field trials for understanding biological processes that are hallmarks of the perennial growth cycle which may be limited in their application and utility if studied solely under laboratory and greenhouse conditions.

Taken together, these two chapters laid the ground work for multiple directions of future research. Based on the results of Chapter 2, several potential avenues could be pursued to gain a deeper insight on the role of sucrose transport during carbon limiting conditions. First, future work could examine transcriptome and gene network responses during coppicing, across different seasons, and throughout various developmental stages of tissue re-growth. The utilization of the *sut4* mutants could provide further insights on the role of vacuolar sucrose trafficking in these physiological processes. The results could also be leveraged to identify *cis*-regulatory elements, such as promoters and enhancers, associated with these candidate genes that could provide additional understanding of the transcriptional regulation occurring during carbon limiting conditions. In line with this, once candidate genes are identified, future studies using functional genomics could target preferentially expressed genes and *cis*-regulatory elements for CRISPR/Cas9 mutagenesis. Finally, future work could over-express *SUT4* and determine how increased vacuolar sucrose export from the vacuole and in to the cytosol affects overall tree growth

and in particular, during carbon limiting conditions. The results of such work would allow for greater resolution in our understanding on the molecular, biochemical and physiological processes involved in carbohydrate remobilization.

Based on the results of Chapter 3, future work could attempt to understand processes responsible for the functional divergence of the *SUT* gene family. For instance, future research is warranted in using comparative genomics and phylogenetic analyses to identify and explore the specific evolutionary events that could affirm or refute the possibility of functional divergence amongst the gene family. In addition, given how little is known about the roles of *SUT5* and *SUT6* and their involvement in sucrose transport, functional characterization of these genes appears to be low hanging fruit. The results of this work also provides evidence to suggest that *SUT5* and *SUT6* may be involved in stem secondary cell wall growth. To test this possibility further, future research should examine the *sut5/6* mutant lines cell wall assembly to determine if *SUT5* and *SUT6* perturbation results in changes to ligninocellulosic composition and contributes to altered *p*-hydroxyphenyl (H), syringyl (S), or guaiacyl (G) lignin ratios, and if such alterations are also associated with variation in hemicellulose (e.g., xylan, glucomannan) and/or cellulose abundance within the cell walls. These results also suggest that studies examining the morphology of the xylem cells in the stem and potential for collapsed or perturbed vessels within these mutant lines could provide further insight. Both anatomical and biochemical changes to the secondary cell walls may also hinder the water transport efficiency, resulting in a greater susceptibility to drought and increase the *sut5/6* mutants susceptibility to cavitation and recovery from embolism. Thus, drought studies may be particularly beneficial for providing additional insights on the functional roles of *SUT5*

and *SUT6*. Finally, given the alterations in raffinose and galactinol abundance that were observed in the *sut4* mutants, future research should test how the reductions in these metabolites compromise, if at all, the poplar mutant's ability to cope with cold temperatures and desiccation stress under more extreme environmental conditions or under varying latitudinal gradients. These results have the potential to provide greater insight on the relationships between sucrose transport, metabolite abundance, and stress tolerance under changing environmental conditions.

### **Biology Education Research**

In my biology education research, I investigated how mentoring experiences influence the development of graduate students in STEM fields. Effective mentorship is thought to be critical for success. Yet, the quality of student-faculty mentoring relationships can vary. My research addressed this by characterizing the dysfunctional and problematic experiences that graduate students can have with their research mentors. Chapter 4 defined and characterized the content domain of the construct of negative mentoring experiences in STEM graduate research. Through an exploratory, study my findings revealed that graduate students do experience negative mentoring that influences their career and psychosocial outcomes. The results of this chapter were used to define the content domain of negative mentoring experiences, thereby serving as the basis for the item content in a survey scale. Chapter 5 extended these results by developing and collecting validity evidence for a quantitative survey scale of negative mentoring experiences. By collecting an extensive body of validity and reliability evidence, I developed a psychometrically sound measure. Finally, Chapter 6 provided empirical evidence regarding how to match mentees and mentors to allow for the development of

fulfilling and effective mentoring relationships during STEM graduate research. The results of this work provided groundbreaking insights on variables that can be cultivated and developed in mentoring relationships.

Based on the results of this body of research, future work should determine the antecedents, correlates, and consequences and outcomes of negative mentoring experiences for mentees, mentors, and programs and organizations. For example, future research could involve conducting a large-scale, national, longitudinal study to examine the influence of negative mentoring experiences on graduate students' personal and professional outcomes. This research could test how negative mentoring experiences influence graduate students' well-being, self-efficacy, career intentions, science identity, scholarly productivity, and commitment to the organization and discipline. The measure could also be used to examine base rates of negative mentoring, including whether and how mentees from different backgrounds experience negative mentoring differently. Future research could also explore the mentor's perspective on negative mentoring, including the possibility that mentees behave in less than ideal ways that can hinder the benefits mentors realize from engaging in mentoring relationships. Finally, scholars could also design and conduct intervention studies to test the effectiveness of mentoring professional development programs aimed at reducing or preventing negative mentoring experiences.

This dissertation provides unique contributions to tree biology and biology education research. The first half investigated the roles of sucrose transport proteins in the intracellular trafficking of sucrose in trees with a particular focus on their roles in processes that require non-structural carbohydrate mobilization from reserves. The

second half examined the role of mentoring relationships in promoting the development and training of students in STEM fields and how these mentoring relationships have the potential to be ineffective or dysfunctional. Together, this dissertation highlights barriers to growth for both trees and scientists in training.