RICHARD THOMAS OLSEN

Effects of Light Intensity and Nitrogen Nutrition on Growth and Photoinhibition of Container-grown *Illicium* L. Taxa

(Under the direction of DR. JOHN M. RUTER)

There are conflicting reports as to the ability of Illiciums, a genus of broad-leaf evergreens popular in the United States, to grow and survive in high light intensities, during production and in the landscape. We used photosynthetic light response curves to investigate taxon differences in photosynthetic gas-exchange of plants produced in high and low light. In general, all taxa had highest rates of photosynthesis when produced in low light. A second study investigated the influence of light intensity and rate of nitrogen application on the growth of Illicium taxa. In general, increasing nitrogen application rate did not promote growth, or ameliorate growth reductions of either taxa grown in high light. Optimal growth and nutrient uptake occurred in the lowest light treatment. We concluded that Illicium taxa studied benefited from production at low light intensities, and suggest all taxa be grown in low light to optimize growth and fertilizer efficiency.

INDEX WORDS: *Illicium anisatum, Illicium floridanum* ‘Pebblebrook’, *Illicium henryi, Illicium lanceolatum, Illicium parviflorum* ‘Forest Green’, Carotenoids, Xanthophyll cycle, SPAD chlorophyll meter, Nursery production, Nutrient allocation, Nutrient recovery

EFFECTS OF LIGHT INTENSITY AND NITROGEN NUTRITION ON GROWTH AND PHOTOINHIBITION OF CONTAINER-GROWN *ILLICIUM* L. TAXA

by

RICHARD T. OLSEN

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RICHARD T. OLSEN

Approved:

Major Professor: John M. Ruter

Committee: Mark W. Rieger
Robert O. Teskey

Electronic Version Approved:

Gordhan L. Patel
Dean of the Graduate School
The University of Georgia
December 2001

DEDICATION

By the time my grandparents were twenty-six, they had endured our country's longest depression, the attack at Pearl Harbor, and the atrocities of World War II. My mother's father flew in missions from North Africa, to D-Day, and finally Berlin, while my dad's father was island hopping in the South Pacific. I am now 26 and have walked freely over most of our country, and visited many others around the world. My shoulders have not born the weight that my grandparents felt, with my short life being one of carefree adventure in pursuit of learning and personal betterment. My pursuits pale in comparison to those of the "greatest generation", and would not be possible without their sacrifices. Again, I thank you for the world of opportunity you opened for my generation and me. May we never let you down.

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Has it been just two years? Time fades away faster than the memories, as does deadlines for writing abstracts and articles. Somehow, in the last two years I managed to take numerous classes, participate in half a dozen meetings and conferences, go skiing in California, get married, travel to England, and of course finish this degree. I have no idea how it is possible, as my wife, Erin, can attest to the paucity of time management present in my average day. Erin's productivity is unbelievable, and I can only hope that our future children inherit more of her mother in this regard than me. Her patience and undying loyalty are some of her best virtues. I asked her to move to the "Peach State", leaving her family home of twenty-five years and all the friends made during the first quarter of her life. For what? Just so I could pursue an advanced degree and satisfy one of my life goals. Erin's unselfishness surpasses her patience, not only with me but also with her family and friends. Thank you, Erin, from the bottom of my heart for allowing me to pursue my dreams while putting yours on hold.

Well, family always comes first, and to that end, I seem to have garnered a rather extended family while studying at the University of Georgia. Thank you Dr. Ruter for giving me the opportunity to study under your tutelage, and for letting me into your family. I am a better scientist for it, but more importantly, I am a better person. To Nancy Hand and Bruce Tucker, my research was not possible without your able assistance, and I enjoyed those brief moments of free time were we could relax and have fun!

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Sounding off to your professors always seems like the kosher thing to do, but not so when it comes to your fellow graduate students. Despite the number of nationalities and cultures present in our department, our graduate students were a fun, tight bunch. To those already processed like David and Mandy, thank you for leading the way. To those of you trying to finish as fast as possible, Godspeed and good luck (Oren and Tim, this means you!). To me office mate and best mate, Jeff Adkins, the time we spent at UGA was a pleasure, and I look forward to finishing our formal education together at NC State. See you there.

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CHAPTER 1

INTRODUCTION

The genus *Illicium* L. (Illiciaceae) is composed of broad-leaved evergreen trees and shrubs native to eastern North America, Mexico, the West Indies, and southeastern Asia into the Malay archipelago (Keng et al., 1993; Saunders, 1995; Smith, 1947). In the past decade, Illiciums, or star-anises, have become increasingly popular ornamentals for landscape use. Ease of propagation, lack of pests and diseases, and durability in the landscape and nursery production have led to their widespread use in the landscape industry (Dirr, 1986; Fantz et al., 1991). Increased demand has prompted many nurseries to seek out new *Illicium* species and forms to introduce to the nursery trade, often before best cultural practices have been established.

There are conflicting views as to the ability of various *Illicium* species to survive in full sun. Fantz et al. (1991) suggest that cultivated *Illicium* species grow well and flower more profusely in full sun than in shade. However, Dirr (1993; 1998) observed color loss in foliage of plants when grown in full sun. A distinct yellowing or bleaching of foliage in high light intensities is one symptom of prolonged photoinhibition (Lambers et al., 1998) resulting from photooxidation of plant pigments (Minkov et al., 1999; Xu and Shen, 1999). Plant stresses such as temperature, drought, nutrition, and salt decrease photosynthetic energy conversion and exacerbate photoinhibition in the presence of high light (Demmig-Adams and Adams, 1992; Long et al., 1994; Streb et al., 1993; Xu and Shen, 1999). When photoinhibition is prolonged or light intensities are high enough to evoke photooxidative damage, substantial decreases in carbon gain and plant growth can be expected

Nitrogen is often the mineral nutrient most limiting to plant growth, with increased productivity occurring in both natural and managed ecosystems upon nitrogen fertilization (Field and Mooney, 1986). Nitrogen is required for protein synthesis, such that under nitrogen deficiencies, there is a general decline in leaf proteins (Evans, 1996). Photosynthesis requires a large investment of proteins and enzymes, thus photosynthetic capacity is highly correlated with nitrogen investment in these compounds (Evans, 1989; Evans, 1996; Evans and Seemann, 1989; Field and Mooney, 1986). Several studies have shown that N nutrition plays a critical role in acclimation of plants upon short-term exposure to high light when transferred from low light intensities (Ferrar and Osmond, 1986; Khamis et al., 1990; Skillman and Osmond, 1998). During container-production of Illiciums, however, some taxa are subjected to long-term exposures to high light during their cropping cycle. Although it has been suggested that N plays a role in long-term acclimation of tropical broad-leaf evergreens to high light (Castro et al., 1995; Ramalho et al., 1997), no long-term study has been performed on either tropical or temperate broad-leaf evergreen species.

The increased popularity of Illiciums in southeastern U.S. nurseries and landscapes has not been supported by research pertaining to light intensity, photoinhibition, and fertility for container-grown plants. Therefore, the objectives of my work were to use container-grown Illiciums and i) determine the optimal light intensity for maximum growth and ii) quantify the effects of nitrogen supply and light intensity on growth and survival of various Illicium taxa during nursery production.

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CHAPTER 2

LITERATURE REVIEW

I. Taxonomy

The genus *Illicium* L. [Illiciaceae de Candolle (A.C. Smith)] is composed of broad-leaved evergreen trees and shrubs native to eastern North America, Mexico, the West Indies, and southeastern Asia into the Malay archipelago (Qi, 1995; Saunders, 1995; Smith, 1947). The Illiciaceae originated in the warm, wet mountains of Laurasia during the Cretaceous period, became widespread in subsequent geological eras, but now represents a typical disjunct distribution between Asia and the Americas (Qi, 1995).

In the only monograph of the genus, Smith (1947) described 42 species. However, since then several regional taxonomic studies of the genus have reduced the number of species (Guerrero, 1997; Qi and Yin, 1995; Saunders, 1995). Current estimates place the number of species at 34 (Qi, 1995). The genus, as a whole, is in need of an updated monograph.

Illiciums are among the most primitive living angiosperms (Keng, 1964; Wood, 1958) and have been extensively studied for the purpose of understanding the evolution of flowering plants. Like other primitive angiosperms, the Illiciaceae are a subclass of the Magnoliidae (Cronquist, 1988) and are placed in their own order, the Illiciales (Igersheim and Endress, 1997; Takhtajan, 1969).

II. History of cultivation

Illiciums have a relatively long history of anthropological uses. Fruits of the star-anise, (*Illicium verum* Hook. f.) are a traditional component of Chinese cooking and medicine (Duke and Ayensu, 1985; Keng et al., 1993). Subsequently, the star-anise was

the first Illicium introduced to Europe, in 1588, when fruits arrived as spice cargo with Cavendish who was returning from the Phillipines (Smith, 1947). Star-anise was subsequently identified by Clusius in 1601 and given the pre-Linnean trinomial, *Anisum phillipinarum insularum*. However, Linnaeus in 1759 described Japanese star-anise, *Illicium anisatum* L., as the type species for the genus (Smith, 1947). Due to taxonomic synonymy, *Illicium verum* was not recognized as a distinct species until 1888, after a specimen flowered at the Royal Botanic Gardens, Kew (Hooker, 1888; Smith, 1947).

The medicinal and toxic properties of Illiciums have interested chemists and pharmaceutical companies since the last century (Dymock et al., 1890; Schlotterbeck and Eckler, 1901). Current research by chemists on Illiciums involves the isolation of novel and useful phytochemicals from all parts of the plant (Schmidt, 1999; Sy and Brown, 1998; Tucker and Maciarello, 1999; Yang et al., 1990). At one time, oil of anise collected from the fruits of *I. verum* flavored food and liqueurs, but it has mostly been superseded by oil collected from the true anise plant, *Pimpinella anisum* (Hopkins, 1972).

The introduction of Illiciums into cultivation for landscaping is not well documented. Although *I. verum* was first described from its fruits in 1601, it was not cultivated in Europe until plants were sent to England by Charles Ford, superintendent of the Hong Kong Botanic Garden, in 1883 (Cox, 1945; Hooker, 1888; Smith, 1947). Likewise, *I. anisatum* was described in 1759, but not cultivated until 1790 (Bean, 1978). The honor of being the first Illicium cultivated in Europe therefore falls to the Florida star-anise, *I. floridanum* Ellis., which was introduced in 1771 by John Bartram (Bean, 1978). The swamp star-anise, *I. parviflorum* Michx. ex. Vent, from central Florida, was described in 1789 from a French herbarium specimen (Smith, 1947), and may have been the next species introduced. Active botanical exploration of Florida was commensing at the time (Wunderlin and Hansen, 2000), but I have not seen the type herbarium specimen, and am not sure if it represents wild collected material or originated from a seed grown introduction. Regardless of their date of introduction, Illiciums fell into relative obscurity, with little mention in gardening literature and were thus relegated to

botanical gardens or arboretum collections. Poor performance in the cool English and European climates further guaranteed their obscurity (Bean, 1978; Hopkins, 1972; Watson, 1895). In Japan and Southeast Asia, *I. anisatum* is still used in its traditional landscape and religious role. *Illicium anisatum*, a plant sacred to Buddha, can be found planted around Buddhist temples, cemeteries, and private gardens for use in religious ceremonies (Hopkins, 1972; Sargent, 1894; Smith, 1947).

Today, a handful of Illicium species are in general cultivation in the United States and Europe. The species native to the southeastern United States, *I. floridanum* and *I. parviflorum*, are common components of new landscapes. Their durability and hardiness in the landscape were established after severe winters of the mid-1980s, when less hardy landscape plants perished (Dirr, 1986; Fantz et al., 1991). *Illicium anisatum* has been grown in the United States since the last century, with Nehrling (1894) reporting large specimens in the Drayton Gardens, near Charleston, South Carolina. Three other species are now known to be in cultivation, but are rarely encountered: *I. henryi* Diels, *I. lanceolatum* A.C. Sm., and *I. mexicanum* A.C. Sm. (Dirr, 1998; Fantz et al., 1991; Hopkins, 1972). Two new species have recently been brought into cultivation, *I. simonsii* Maxim. and *I. oligandrum* Merr. & Chun. *Illicium simonsii* is growing successfully at Quarry Hill Botanic Garden, California, where it is currently being evaluated for future introduction (Lewandowski, 2000; Sanchez, 1998). *Illicium oligandrum*, native to Hainan in China, was recently acquired by the Stephen F. Austin Aboretum, Nagodochees, Texas (personal observation).

III. Culture

Ease of propagation, nursery production, and durability in the landscape have led to widespread use of Illiciums in the landscape industry (Dirr, 1986; Fantz et al., 1991). Originally considered disease and pest free, nurserymen are beginning to report anthracnose and root rot problems with *I. floridanum* and tea-scale infestations on *I. henryi* (Ruter, personal communication). Cuttings are the usual means of propagation,

with firm-wooded cuttings rooting in high percentages during most of the year (Dirr and Heuser, 1987). Illicium seeds have been described as requiring no pretreatment (Dirr, 1986; Dirr and Heuser, 1987; Hartmann et al., 1997; Raulston and Tripp, 1995), although new data suggest cold-stratification is necessary for optimal germination (Olsen and Ruter, 2001).

Hopkins (1972) noted the lack of information pertaining to Illicium culture, and hypothesized that all species prefer moist, acid soils in light shade. Because of their tropical origin, Illiciums are most suitable for landscapes in areas with hot summers and warm winters, although the genus has exhibited greater hardiness than predicted (U.S.D.A. Hardiness Zones 7-9; Dirr, 1986; Fantz et al., 1991). In their native habitats, Illiciums are understory shrubs or sub-canopy trees (Gibson, 1992; Nitta and Ohsawa, 1997; Takhtajan, 1969; White and Thien, 1985). Both American species are found growing in low, moist areas: *I. floridanum* in flood plains and stream corridors of the Gulf Coast (Gemborys and Hodgkins, 1971; Smith, 1947; personal observation) and *I. parviflorum* along springs and seepage slopes in the St. Johns river watershed in central Florida (Mohlenbrock, 1976; Smith, 1947; personal observation). Illiciums tend to thrive in shady and sheltered positions in cultivation (Bean, 1978; Dirr, 1998; Hopkins, 1972). However, there are conflicting views as to the capability of various *Illicium* species to survive in full sun. Fantz et al. (1991) suggest that cultivated *Illicium* species grow well and flower more profusely in full sun than in shade. However, Dirr (1993; 1998) observed color loss in foliage of plants when grown in full sun.

Although nurseries in the southeastern United States have grown several *Illicium* species for a number of years, little horticultural research exists pertaining to their production. Laboratory experiments have determined the theoretical cold hardiness of *I. floridanum* and *I. parviflorum* (Lindstrom and Dirr ; 1989), and *I. anisatum* and *I. mexicanum* (Johnson and Hirsch; 1995). Research by Ingram and Buchanan (1981) investigated direct heat injury to roots in container crops and included *I. anisatum* in their

study. A subsequent study performed by Ingram et al. (1986) examined the thermostability of excised *I. parviflorum* roots.

IV. Light intensity studies

The range of light intensity to which a plant can acclimate is determined by an individual species genetic adaptation to the light environment of its native habitat (Boardman, 1977; Pearcy, 1998). Numerous changes in leaf morphology, physiology, and biochemistry are required for adaptation and acclimation of photosynthesis to various light intensities (for reviews see Björkman, 1981; Boardman, 1977; Givnish, 1988). Plants native to high-light environments are capable of higher photosynthetic rates at high-light intensities than plants from low-light environments. Sun plants are able to increase light-saturated photosynthetic capacity by increasing protein synthesis, Rubisco activity, and components of the electron-transport chain. Shade plants have inherently low photosynthetic rates, and lack the ability to effectively increase their capability of light-saturated photosynthesis (Björkman, 1981).

Photosynthetic light-response curves are a crucial tool in understanding adaptations to sun and shade (Givnish, 1988). Models for relating photosynthesis to light intensity consist of variations in the equations for rectangular or non-rectangular hyperbolas (Evans et al., 1993; Ogren and Evans, 1993; Pachepsky et al., 1996). However, these models are complex, employing variables and conditions useful for investigating intrinsic properties and functions of the curve. For general predictive models, photosynthetic light-response curves are fitted using simpler equations based on non-linear regression procedures (Groninger, et al., 1996; Hashimoto, 1993; Laing, 1985; Marler et al., 1994).

A typical photosynthetic light-response curve is shown in Fig. 2.1. The initial point represents dark respiration, where the photon flux density is zero and there is a net production of CO_2 evolved from the leaf through respiration. As the photon flux density

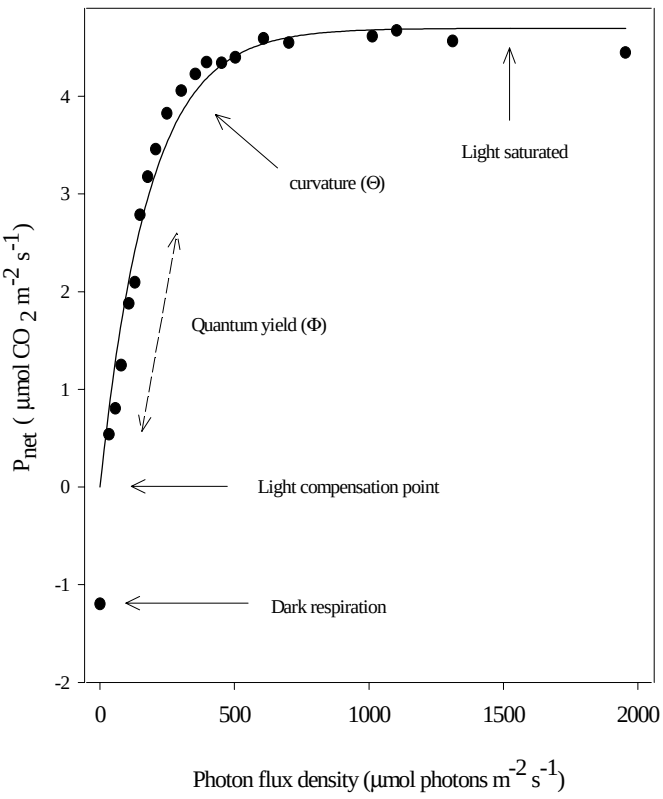

Fig. 2.1. Photosynthetic light-response curve of a mature leaf of *Illicium anisatum* grown at 1200 μmol $m^{-2}s^{-1}$ (Olsen, unpublished data).

increases, photosynthesis and CO_2 fixation begin while dark respiration decreases. The photon flux density, where assimilated CO_2 equals the CO_2 respired, is known as the light compensation point. Above the light compensation point, photosynthesis is light-limited, such that increasing the light intensity results in a proportional increase in photosynthesis. This results in a linear part of the curve where quantum yield of photosynthesis is measured. Quantum yield (ϕ) is the efficiency of light use in photosynthesis, or the amount of absorbed photons used for photochemical electron transport (Long et al., 1996; Pearcy, 1998). Above the linear portion of the curve, photosynthesis transitions from a light-limitation to a Rubisco-limitation. As the photon flux density increases further,

there is no longer a significant proportional response in photosynthetic rates. Photosynthesis is light-saturated and the rates begin to level-off.

Dark respiration and maximum photosynthetic rates are measured directly during generation light-response curves. However, most parameters are empirically derived. Light compensation points and quantum yield are calculated by fitting the data points in the linearly increasing portion of the curve to a linear regression function, where photon flux density is the independent variable (Bazzaz and Carlson, 1982; Leverenz, 1987). Quantum yield is measured using photon flux densities between 20 and 130 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in order to avoid the influences of the Kok effect, a decrease in quantum yield near the compensation point due to dark respiration (Sharp et al., 1984) and Rubisco limitations (Long et al., 1996). When light-response curves are based on absorbed light, the true quantum yield is measured. Quantum yield based on incident light is the apparent quantum yield (Φ_i) and varies with chlorophyll concentration, nutrient status, and damage to the photosynthetic apparatus (Lambers et al., 1998; Pearcy, 1998). The curvature (Θ) of the photosynthetic light-response curve refers to the non-linear portion where photosynthesis is transitioning from a light-limitation to a Rubisco limitation. It is also derived from calculations, but its interpretation is complex, encompassing interactions between chlorophyll content, gradients of light absorption and photosynthetic capacity in the leaf, as well as internal CO_2 partial pressures (Evans et al., 1993; Leverenz, 1987; Ogren and Evans, 1993).

V. Light Stress

Light intensities in excess of those necessary to saturate photosynthesis result in absorbed photons that cannot be used in photochemistry. Excess light, or light stress, is induced when the ratio of photon flux density to photosynthesis is high (Demmig-Adams and Adams, 1992). Any plant stress which lowers photosynthesis to a point that carbon

metabolism limits photosynthesis can result in a shift from saturated light to excessive light conditions and photoinhibition (Krause, 1988).

Plants have evolved mechanisms to maximize light absorption and photosynthesis, while at the same time minimizing the potential for damage from excess energy capture (Long et al., 1994). Plants, terrestrial and aquatic, live in dynamic environments where ambient light conditions can change rapidly during the day (e.g., sunflecks) or slowly, over the lifetime of the leaf or the plant (e.g., mutual or competitive shading). Plant species inhabiting environments where light is not limiting for growth must balance absorbed radiation with factors that do limit growth, such as nitrogen or water availability. Leaf morphological features designed to decrease absorption by reflecting incident light are common, and include waxy cuticles, pubescence, and salt deposition (Long et al., 1994; Powles, 1984; Vogelmann, 1993). Leaf orientation can increase or decrease leaf absorption, and is an adaptation to the light intensity experienced during growth and development of each leaf. Leaves oriented perpendicular to incident light maximize the absorption of photons. Thus, leaves produced in low light intensity, where light limits photosynthesis, maximize light absorption by producing horizontally oriented leaves. Excess light during growth results in more vertically oriented leaves, reducing the amount of absorbed photons (Demmig-Adams and Adams, 1992; Mc Millen and Clendon, 1979) and reducing the total thermal radiation load (Lambers et al., 1998) . The ability to alter leaf arrangement is genetically controlled, with some species showing little response to excess light, while others, like members of the legume family (Ludlow and Björkman, 1984) possess highly developed, dynamic leaf movements (diahelio- and paraheliotropism).

The morphological features of a leaf are determined by the light intensity during leaf development. Leaf thickness, mesophyll area, and stomatal density are fixed features during development that influence photosynthesis. There are, however, cellular functions the plant can alter in order to regulate photosynthesis during changes in light intensity. The amount of chloroplast surface area exposed to incident light is altered through

chloroplast movements (Brugnoli and Björkman, 1992; Demmig-Adams and Adams, 1992; Powles, 1984). Typically, increased synthesis of electron transport chain and Calvin-cycle components result in increased photon absorption (Demmig-Adams and Adams, 1992; Krause, 1988; Xu and Shen, 1999) but in plants with inherently low photosynthetic rates this ability is limited (Demmig-Admams and Adams, 1992; Powles, 1984).

VI. Photoinhibition

Plant adaptations that decrease light absorption, or increase light use are considered long term genetic responses to excess light. Plants have also evolved photoprotective mechanisms that rapidly and safely dissipate energy from excess absorbed photons. The decrease in photochemical efficiency due to the activation of these mechanisms is known as photoinhibition. In the past, photoinhibition was associated with damage to Photosystem II (PS II), but it is now known that damage to PS II is a secondary effect caused by severe and prolonged inhibition of electron transport (Demmig-Adams and Adams, 1992; Long et al., 1994; Powles, 1984).

The necessity to dissipate energy from excess absorbed photons safely is because they facilitate the creation of active oxygen species (AOS) (Minkov et al., 1999). Absorbed photons in the antennae complexes of Photosystem I and II excite chlorophyll, which initiates electron transport and the chemical reactions necessary to assimilate CO_2. Inhibition of electron transport decreases the rate at which excitation energy is transferred from excited chlorophyll to the quinnone acceptors (QA and QB), which can lead to the formation of triplet chlorophyll (Demmig-Adams and Adams, 1992; Xu and Shen, 1999). Triplet chlorophyll reacts with oxygen to produce singlet oxygen and oxygen radicals, both capable of damaging proteins, pigments, and thylakoid membranes (Minkov et al., 1999). Maintaining high levels of electron transport decreases the production of AOS and protects the photosynthetic apparatus. Energy inefficient metabolic processes such as photorespiration, the Mehler reaction, nitrate and sulfate reduction, and cyclic electron

flow allow for the continuation of electron transport (Demmig-Adams and Adams, 1992; Long et al., 1994; Xu and Shen, 1999) through the consumption of excess energy.

When electron flow is maintained, but carbon metabolism and photosynthesis are inhibited, a trans-thylakoid pH gradient develops. Low rates of carbon metabolism and ATP use in the stroma results in a build-up of ATP and an inhibition of H+ pumping across the thylakoid membrane. ATP concentrations in the lumen increase, with the splitting of water in the Hill reaction of photosynthesis contributing more H+ and further decreasing the acidity of the lumen. This trans-thylakoid pH gradient triggers the enzymatic reactions of the xanthophyll cycle, the major thermal energy dissipation process in photosystems (Demmig-Adams and Adams, 1992; Long et al., 1994).

VII. Carotenoids and the Xanthophyll Cycle

Carotenoids are found in the photosynthetic membranes of all photosynthetic organisms. In higher plants carotenoids are bound to proteins in the thylakoid membranes (Siefermann-Harms, 1985; Yamamoto, 1979). Carotenoids are involved in both light-harvesting and protection of the photosynthetic apparatus. Light energy in blue-green wavelengths, where chlorophyll absorbs poorly, is absorbed and transferred to chlorophyll via the carotenoids. In higher plants, there is a distinct spatial partitioning of the various carotenoids within the light-harvesting complexes (LHC). Carotenes are localized in the reaction center cores (Demmig-Adams and Adams, 1996), while the xanthophylls are the major carotenoids in the peripheral light harvesting proteins (Siefermann-Harms, 1985; Evans and Seemann, 1989). The heterogeneity of the LHCs allows for the regulation of energy transfer and energy dissipation. Under optimal conditions, 85% of the energy from antennae excited states is used in photochemistry, with the remaining energy lost as triplet chlorophyll formation (10%), fluorescence (4.5%), and heat (0.5%) (Owens, 1996). Triplet chlorophyll formation occurs most readily in the antennae, where it is quenched through a triplet energy transfer with a carotenoid, which subsequently dissipates the energy as heat. If triplet chlorophyll has

time to react with O_2 and form singlet O_2, then the carotenoids are able to quench the singlet O_2 directly (Minkov et al., 1999; Owens, 1996).

The xanthophylls are a subclass of carotenoids that contain oxygenated-functional groups (epoxy groups). Under limiting light conditions, violaxanthin (V), a diepoxide xanthophyll, acts as an antennae pigment, with a singlet excited state that is higher than the ground state of chlorophyll (Frank et al., 1994; Owens, 1996). During excess light intensities, the acidification of the lumen activates the chloroplastic enzyme violaxanthin de-epoxidase to convert violaxanthin (V) to the monoepoxide antheraxanthin (A) and then to the epoxide-free zeaxanthin (Z)(Demmig-Adams and Adams, 1992; Long et al., 1994; Minkov et al., 1999; Owens, 1996; Yamamoto, 1979). The ground state of Z is lower than the excited state of chlorophyll, reversing the transfer of energy away from the reaction center cores and dissipating the energy as heat (Frank et al., 1994; Owens, 1996). When the lumen pH increases (return to limiting light conditions or darkness), Z is epoxidized back to V via a Z epoxidase. The interconversions of the xanthophylls constitute the xanthophyll cycle (V cycle) and can be found in all higher plants (Demmig-Adams and Adams, 1992; Long et al., 1994).

Although the light driven interconversions of the xanthophylls had been known for some time (Yamamoto, 1979), their direct role in photoprotection has only recently been established. Demmig and co-workers (1987) were able to show a linear relationship between Z formation in high light and nonradiative energy dissipation. It has also been shown that Z formation and accumulation under high light intensities accounts for the largest increase in V cycle components, and thus the observed increases in total carotenoids (Demmig et al., 1987; Demmig-Adams et al., 1989; Demmig-Adams et al., 1995a; Demmig-Adams, 1998; Thayer and Björkman, 1990). Sun tolerant, or high light adapted plants and leaves exhibit higher concentrations of V cycle components than shade species and leaves (Demmig-Adams et al., 1989; Demmig-Adams et al., 1995b; Demmig-Adams and Adams, 1992; Thayer and Björkman, 1990). The lower concentration of V cycle components in shade leaves, and lower ability of shade species

to form and accumulate Z, is reflected in their lower potential for photoprotective energy dissipation (Demmig-Adams et al., 1995a).

VIII. Nitrogen and photoinhibition

Nitrogen is often the mineral nutrient most limiting to plant growth, with increased productivity occurring in both natural and managed ecosystems upon nitrogen fertilization (Field and Mooney, 1986). Nitrogen is required for protein synthesis, such that under nitrogen deficiencies, there is a general decline in leaf proteins (Evans, 1996). Photosynthesis requires a large investment of proteins and enzymes, thus photosynthetic capacity is highly correlated with nitrogen investment in these compounds (Evans, 1989; Evans, 1996; Evans and Seemann, 1989; Field and Mooney, 1986). Evans and Seemann (1989) divided leaf nitrogen associated with photosynthesis into two pools: thylakoid membrane-bound proteins (light reactions) and soluble proteins (dark reactions). Leaf nitrogen is partitioned between these pools to balance light harvesting with CO_2 assimilation, thus maximizing leaf photosynthesis. This partitioning of nitrogen depends on nitrogen supply and temperature, among other factors (Evans, 1989).

Leaves grown in high irradiances have a greater proportion of leaf nitrogen invested in soluble protein, while leaves in low light have more nitrogen allocated to the thylakoid proteins (Evans, 1989; Evans, 1996; Evans and Seemann, 1989; Hikosaka and Terashima, 1995). At irradiances above light-saturation, Rubisco limits photosynthesis, and allocation of more nitrogen to this rate-limiting step increases the photosynthetic capacity of the leaf. In low irradiances, light absorption limits photosynthesis, which results in more nitrogen being invested in the light harvesting pigment-protein complexes in the thylakoids (Evans, 1989; Evans, 1996; Evans and Seemann, 1989; Hikosaka and Terashima, 1995). Leaves in low light, however, contain less total leaf nitrogen than sun leaves (Evans and Seemann, 1989), contributing to lower respiration and the maintanence of positive carbon balance in shade plants (Evans, 1996; Hikosaka and Terashima, 1995).

The effect of nitrogen availability on photosynthesis depends on the light intensity experienced by the leaf. In high light intensities, increased nitrogen leads to higher total leaf nitrogen, with a higher proportion of nitrogen in soluble protein than thylakoid protein (Evans 1989; Evans, 1996). Again, by allocating more nitrogen to Rubisco and the Calvin cycle enzymes, leaves can increase net photosynthesis under high light and high nitrogen. In low light intensities, nitrogen supply may not be the limiting factor for growth (Evans and Seemann, 1989). Hikosaka and Terishima (1995) constructed a theoretical model to explain nitrogen partitioning on a cost-benefit basis. Their model showed that as total leaf nitrogen increases, the light intensity required to maximize daily carbon gain increases. Thus under increased nitrogen supply, increased leaf nitrogen is not advantageous for maintaining positive carbon balance in low light. Under high nitrogen and low light, total leaf nitrogen decreased, while the proportion allocated to chlorophyll-protein complexes increases (Hikosaka and Terishima, 1995). By increasing the chlorophyll-protein ratio, the leaf increases the ability to absorb light, the rate limiting step in photosynthesis for shade leaves.

Nitrogen deficiency decreases leaf proteins in a coordinated response, such that a balance is maintained between the light reactions and the dark reactions (Evans, 1996). A down regulation of photosynthesis occurs, resulting in lower maximum photosynthetic rates and increased excess light absorption. Ferrar and Osmond (1986) demonstrated that nitrogen nutrition was necessary for acclimation to high light in *Solanum dulcamara*. Nitrogen-rich plants, after an initial decrease in photosynthesis, recovered faster and increased net photosynthesis in high light. Nitrogen-poor plants recovered slowly in high light, and showed no increase in photosynthesis in high light (Ferrar and Osmond, 1986). Khamis et al. (1990) showed that decreased growth and photosynthesis in nitrogen depleted maize plants was accompanied by increased production of xanthophyll cycle components and non-photochemical quenching. Similar results have been attained across plant life traits, as in the C_4 sun-plant, maize, *Zea mays* (Lu and Zhang, 2000); the C_3 sun-plant, spinach, *Spinacia oleracea* (Logan et al., 1999; Verhoeven et al., 1997); the

evergreen shade herb, *Heuchera americana* (Skillman and Osmond, 1998); and the evergreen shade shrub, *Coffea arabica* (Ramalho et al., 1997; 1998; 1999; 2000).

IX. Nitrogen application in container-grown plants

Container-grown plants have similar nutrient requirements as field grown plants. However, the means by which nutrients are made available may differ, due to the differences between mineral soils and the soilless substrates used in nurseries. An ideal substrate provides the same functions necessary for plant growth as soils, including support, drainage and aeration, and nutrient availability (Preece and Reed, 1993).

In the southeastern United States, milled and composted pine bark is the primary component in substrate used by the container-grown ornamental nursery industry. Specific mixes will differ depending on a particular nursery or crop species, but usually consists of pine bark amended with sand or peat. Sand and peat contain few to no available nutrients for plant growth (Preece and Reed, 1993). However, pine bark provides adequate levels of most micronutrients (Niemiera, 1992; Ogden et al., 1987; Rose and Wang, 1999; Wright and Hinesley, 1991). Therefore, nurseries must supply all of the macronutrients necessary for plant growth. As in soil, the availability of nutrients in container substrate is determined by the texture and structure, and thus the cation exchange capacity (CEC) of the substrate (Preece and Read, 1993). Pine bark has a low to moderate CEC (Handreck and Black, 1994; Ogden et al., 1987), which contributes to the difficulty of maintaining adequate levels of nutrients available in cationic forms. Low CEC and frequent watering results in significant losses of nutrients via leaching from containers (Wright and Niemiera, 1987).

Nitrogen, the nutrient required in the highest amount for plant growth, is often the most limiting in container-grown plants due to leaching. Urea, ammonium, and nitrate nitrogen are the most common forms used in container fertilization programs (Ogden et al., 1987; Wright and Niemiera, 1987). Urea is essentially an ammoniacal form of nitrogen, being hydrolyzed rapidly to ammonium upon application to pine bark substrates

(Ogden et al., 1987). Ammonium (NH_4^+) is a cation and binds to cation exchange sites until those sites are saturated, at which point ammonium can be leached (Foster et al., 1983; Thomas and Perry, 1980). Nitrate (NO_3^-), however, is an anion and is readily leached from substrate during irrigation events. Although nitrate-N is the form most readily taken up by plants, its expense and ease of leaching have lead nurseries to rely more on ammoniacal-N in their fertilization programs. The oxidation of ammonium via nitrification occurs rapidly in pine bark substrate, with most of the ammonium nitrified within two days (Wright and Niemiera, 1987) and complete nitrification by five days (Niemiera and Wright, 1987a). Cox (1993) found, that regardless of nitrogen source, nitrate-N was the predominate form found in leachate fractions from potted marigolds (*Tagetes erecta* L.). Similar results have been found by other researches using various crop species and fertilizer forms (Cabrera, 1997; Jarrell et al., 1983; Niemiera and Wright, 1986a). Therefore the rate of nitrification of ammoniacal forms of nitrogen, and the factors affecting nitrification, such as temperature (Niemiera and Wright, 1987b; Walden and Wright, 1995) and pH (Niemiera and Wright, 1986b) are important factors influencing the availability and leaching of nitrogen in container-grown plants.

Although numerous methods of applying fertilizers exist, most nurseries use controlled release fertilizers (CRF) supplemented with water-soluble or liquid fertilizers (Cobb, 1986; Sanderson, 1987). Controlled release fertilizers release nutrients at a slow or controlled rate and are classified by their mode of release, type of coating, solubility, or nutrient material (Sanderson, 1987; Sharma, 1979; Shaviv and Mikkelsen, 1993). The use of CRF's confers several benefits to nurseries over more soluble forms of fertilizers, including longer periods of availability, reduced labor costs, and reduced losses due to leaching (Sharma, 1979). Nitrogen management in nurseries has improved with the widespread use CRF's. Numerous studies have shown decreased levels of nitrogen in leachates with CRF's (Broschat, 1995; Hershey and Paul, 1982; Jarrell et al., 1983; Mikkelsen et al., 1994; Rathier and Fink, 1989) with one study showing increased nitrogen uptake efficiency when using CRF's (Catanzaro et al., 1998).

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CHAPTER 3

PHOTOSYNTHETIC RESPONSES OF CONTAINER-GROWN *ILLICIUM* L. TAXA TO SUN AND SHADE[1]

[1] Olsen, Richard T., John M. Ruter, and Mark W. Rieger. To be submitted to the Journal of the American Society for Horticultural Science.

Abstract. Illiciums, or star-anises, have increased in popularity in the nursery and landscape industries, however, confusion exists as to which taxa are tolerant of high light intensities during production and subsequent establishment in the landscape. We investigated the effect of two light intensity treatements, 45% and 100% ambient light, on gas-exchange parameters of five Illicium taxa: *Illicium anisatum* L., *I.floridanum* Ellis. 'Pebblebrook', *I. henryi* Diels., *I. lanceolatum* A.C. Sm., and *I. parviflorum* Michx. Ex. Vent. 'Forest Green'. Light-response curves were determined for individual leaves, and mean response parameters calculated. Chlorophyll and total carotenoids were analyzed by extraction in acetone, with total chlorophyll also estimated with a SPAD chlorophyll meter. In general, highest rates of CO_2 assimilation (A_{max}) and lowest rates of dark respiration (R_d) were found in the 45% light treatment for all taxa. Both *Illicium anisatum* and *I. floridanum* 'Pebblebrook' had substantial reductions in A_{max} in 100% light, 94% and 81% respectively, compared to A_{max} of plants grown in 45% of full sun light. *Illicium henryi* failed to survive the high light treatment. *Illicium lanceolatum* and *I. parviflorum* 'Forest Green' where least affected by high light. Severe photooxidative bleaching was noted and confirmed by SPAD and pigment data, although SPAD readings were a poor predictor of total chlorophyll. For taxa of Illicium in our study, photosynthetic gas-exchange parameters, and foliage pigment characteristics were improved in the low light treatment, suggesting optimal growth occurs in shaded conditions.

Additional index words. *Illicium anisatum*, *Illicium floridanum* 'Pebblebrook', *Illicium henryi*, *Illicium lanceolatum*, *Illicium parviflorum* 'Forest Green', star-anise, photoinhibition, carotenoids, SPAD chlorophyll meter

Introduction

The genus *Illicium* [Illiciaceae (de Candolle) A.C. Smith] is native to subtropical and temperate regions of southeastern Asia, the Malay archipelago, southeastern United States, Mexico, and the Caribbean (Smith, 1947; Qi, 1995). In the past decade, Illiciums (star-anises), have become increasingly popular ornamentals for landscape use. Ease of propagation, lack of pests and diseases, and durability in the landscape and nursery production have led to their widespread use in the landscape industry (Dirr, 1986; Fantz et al., 1991). Increased demand has prompted many nurseries to seek out new *Illicium* species and forms to introduce to the nursery trade, often before best cultural practices have been established.

There are conflicting views as to the capability of various *Illicium* species to survive in full sun. Fantz et al. (1991) suggest that cultivated *Illicium* species grow well and flower more profusely in full sun than in shade. However, Dirr (1993; 1998) observed color loss in foliage of plants when grown in full sun. A distinct yellowing or bleaching of foliage in high light intensities is one symptom of prolonged photoinhibition resulting from photooxidation of plant pigments (Minkov et al., 1999; Xu and Shen, 1999). Photoinhibition is an adaptive process, whereby plants regulate electron transport and energy dissipation in times of excessive excitation of their photosynthetic apparatus (Long et al., 1994). The xanthophyll cycle plays the primary role in thermal energy dissipation, and like other sun-shade acclimations, responds to differences in light intensities. Sun-tolerant, or high light tolerant plants exhibit greater concentrations of xanthophyll cycle components, and carotenoids in general, than shade-adapted species, and likewise, sun leaves contain greater concentrations of these carotenoids than leaves developed in low light on the same plant (Demmig et al., 1987; Demmig-Adams et al., 1989; Demmig-Adams et al., 1995; Demmig-Adams, 1998; Thayer and Björkman, 1990).

The range of light intensity to which a plant can acclimate is determined by an individual species genetic adaptation to the light environment of its native habitat

(Boardman, 1977; Pearcy, 1998). Numerous changes in leaf morphology, physiology, and biochemistry are required for acclimation of photosynthesis to various light intensities (Björkman, 1981; Boardman, 1977). Plants native to high light environments are capable of higher photosynthetic rates at high-light intensities than plants from low-light environments. Sun plants are able to increase light-saturated photosynthetic capacity by increasing protein synthesis, Rubisco activity, and components of the electron-transport chain. Shade plants have inherently low photosynthetic rates, and lack the ablility to effectively increase light-saturated photosynthesis (Björkman, 1981).

Illiciums are generally understory shrubs or sub-canopy trees in their native habitats (White and Thien, 1985; Gibson, 1992; Nitta and Ohsawa, 1997), suggesting photosynthetic responses indicative of shade-adapted species. Genetic adaptations for survival in low light intensities may preclude sufficient acclimation by Illiciums when grown in high light intensities. Therefore, our objectives were i) to quantify the photosynthetic responses of various Illicium taxa to two light intensity treatments, and ii) determine if photoinhibition and photooxidation occurs in Illiciums grown in high light intensities.

Materials and Methods

Five Illicium taxa, *Illicium anisatum, I. floridanum* 'Pebblebrook', *I. henryi, I. lanceolatum,* and *I. parviflorum* 'Forest Green', currently available in the nursery industry were studied. Terminal cuttings were taken from plants growing at the Coastal Plain Experiment Station, Tifton, Ga., on 20 Sept. 1999 and transported to Wight Nurseries, Cairo, Georgia, for propagation. Well-rooted liners were transported to the Coastal Plain Experiment Station, where they were potted into 2.8-L black plastic containers on 22 May 2000. The substrate consisted of an 8 milled pine bark : 1 sand mix (by volume) amended with dolomitic lime at 1.2 $kg \cdot m^{-3}$ and Osmocote Plus 15.0N-4.0P-9.9K (The Scotts Company, Marysville, Ohio) applied as a top-dressing at 1.2 kg

$N \cdot m^{-3}$ (20.2 g $container^{-1}$). Plants were randomly placed in one of two light intensity treatments, either 100% or 45% ambient photosynthetic photon flux (PPF), in a randomized split-plot design. Plants in 100% PPF were grown in full sun on a nursery container pad. Plants in 45% PPF were grown in hoop houses covered in black woven polypropylene fabric of the desired light transmittance. Plants were watered as needed.

Beginning in July, plants with one flush of growth hardened under either of the two light treatments were transported to Athens, Ga. for gas-exchange measurements. Plants were placed under the same light treatments in Athens under similar nursery conditions. Plants were well watered the night before measurements were made. Plants were brought into the laboratory between 0600 and 0700 HR and allowed to acclimate one hour before measurements began. Gas-exchange measurements were made using a LI-COR 6200 portable photosynthesis system (LI-COR, Lincoln, Nebr.) with a 250 mL leaf chamber. A QB6200 LED lighting system (Quantum Devices, Barneveld, Wis.) attached to the top of the leaf chamber provided light for all measurements. A metal halide light provided supplemental light (between 350 and 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF) to the remaining plant during the single leaf measurements. Measurements were determined on a fully expanded, mature leaf below the terminal bud on hardened new growth. Measurements began at 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and proceeded in distinct increments to 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF. The QB6200 was calibrated with a LI-COR 189 Quantum Radiometer/Photometer (LI-COR, Lincoln, Nebr.) to attain the desired increment PPF levels. Leaf chamber CO_2 concentration was maintained at 365 ± 10 mg L^{-1} and leaf temperatures between 25 and 30 °C. Because of low relative humidity in the laboratory (40%) and low photosynthetic rates of Illiciums, leaf chamber relative humidity was low resulting in moderate vapor pressure deficits (VPD) of 2.0 ± 0.5 kPa.

After the final gas-exchange measurement, the leaf was removed from the chamber and the leaf area enclosed in the chamber was measured using a LI-3000 portable area meter (LI-COR, Lincoln, Nebr.). A SPAD-502 chlorophyll meter (Minolta,

Ramsey, N.J.) reading was taken. SPAD readings have been shown to be a useful, non-destructive tool for estimating leaf chlorophyll (Markwell et al., 1995; Marquard and Tipton, 1987; Yadava, 1986). Two readings per leaf were taken midway between the leaf mid vein and the margin and averaged. One leaf disk per leaf was punched out using a # 9 (13 mm) cork borer and fresh weight recorded. Leaf disks were stored at −80°C until pigment analyses were performed.

Chlorophyll *a* and *b*, and total carotenoids were extracted using 80% acetone following the methods of Bruinsma (1963) with the following exceptions. Because of poor extraction after 24 hours in the dark at 4°C, leaf disks were homogenized in the acetone solution and extracted for another 24 hours at room temperature and centrifuged. The extinction of the supernatant was measured with a Spectronic ® Genesys ™ 5 spectrophotometer (Spectronic Instruments, Rochester, New York, N.Y.) at 470, 646, and 663 nm using the specific absorption coefficients of Lichtenthaler and Wellburn (1983).

Individual photosynthetic-response curves were analyzed by non-linear regression (SigmaPlot® 4.0 for Windows, SPSS, Chicago, Ill.). Cardinal points were calculated from the fitted equations or taken directly as data points. Dark respiration (R_d) was measured at 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and maximum net CO_2 assimilation (A_{max}) was the highest measured rate of net CO_2 assimilation (A_{net}) for each plant. The photosynthetic saturation point (A_{sat}) was estimated as 95% of A_{max} (Norcini et al., 1991). Apparent quantum yield (Φ_I) and light compensation points (A_0) were calculated by fitting data for A_{net} from PPF <150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to a linear regression, with PPF as the independent variable (Leverenz, 1987), where the slope of the linear regression function equals Φ_I and the light compensation point is $A_{net} = 0$. Data for the entire experiment were analyzed as a split plot design using a general linear model (PROC GLM; SAS version 8.0 for Windows, Cary, N.C.). Light transmittance was the main plot with an error term of block × light. Taxa was the subplot factor with an error term of block × taxa + block × taxa × light. Standard error of difference between two means (SED) was calculated for all

treatment combinations. The relationship between total chlorophyll (Chl_{tot}) and SPAD data were analyzed using regression analysis.

Results

A significant light × taxa interaction ($P < 0.05$) occurred for each photosynthetic and pigment parameter except A_0 and Φ_I (data not shown). The light compensation point (A_0) and Φ_I were not calculated for *I. anisatum* and *I. floridanum* 'Pebblebrook' grown in the 100% light level treatment because of negative photosynthetic rates at the low light levels (<150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF) used for calculation of these response variables, as shown in Fig. 3.1. Light had no effect on Φ_I and A_0, however, there was a significant (P <0.001) taxa effect for both parameters (data not shown).

In general, the highest A_{max} values for each taxa studied occurred in the 45% light treatment (Table 3.1). Although A_{sat} varied by taxa and light treatment, saturation of photosynthesis occurred at similar intercellular CO_2 (C_i) levels, between 200 and 230 mg L^{-1}. However, plants of *I. anisatum* and *I. floridanum* 'Pebblebrook' in 100% light that exhibited inhibited photosynthetic rates, saturated at higher C_i levels, between 300 and 350 mg L^{-1} (data not shown).

No plants of *I. henryi* survived the 100% light treatment, and plants in the 45% light treatment had low A_{max}, A_{sat}, and Φ_I relative to the other taxa in the 45% light treatment (Table 3.1). Dark respiration (R_d) was also low, and thus the low Φ_I was the main contributing factor to the high A_0 for shade plants of *I. henryi*.

Illicium anisatum and *I. floridanum* 'Pebblebrook' had similar responses to light treatments (Table 3.1). For both species in the 100% light treatment, A_{max} and A_{sat} were greatly reduced compared to rates in the 45% light treatment. Maximum rates of net CO_2 assimilation (A_{max}) decreased by 94% and 81% for *I. anisatum* and *I. floridanum* 'Pebblebrook', respectively. Dark respiration rates varied between species, from -2.11 ± 0.36 and -1.19 ± 0.17 $\mu mol \cdot m^{-2} \cdot s^{-1}$, for *I. anisatum* and *I. floridanum*

'Pebblebrook', respectively. Both species had comparable rates of A_{max} and A_{sat} in the 45% light treatment. *Illicium anisatum*'s high Φ_I and low R_d contributed to a low A_0. *Illicium floridanum* 'Pebblebrook's low Φ_I and high R_d resulted in a high A_0.

Illicium lanceolatum and *I. parviflorum* 'Forest Green' can also be grouped together according to their similar responses to the light treatments, even though photosynthetic rates differed (Table 3.1). Maximum rates of net CO_2 assimilation (A_{max}) and A_{sat} decreased by 33% and 17% for *I. lanceolatum* and *I. parviflorum* 'Forest Green', respectively, in the 100% light treatment compared with the 45% light treatment. A low Φ_I and high R_d led to a high A_0 for *I. lanceolatum* in the 100% light treatment. In the 45% light treatment Φ_I was higher and R_d remained high, leading to a relatively high A_0 for *I. lanceolatum*. *Illicium parviflorum* 'Forest Green' maintained a high Φ_I in both light treatments. Increased R_d resulted in a higher A_0 for *I. parviflorum* 'Forest Green' in the 100% light treatment. Leaves of *I. parviflorum* 'Forest Green' in 100% PPF had vertically disposed leaves, much more so than on leaves of plants in 45% PPF. This response was not observed in the other Illicium taxa.

No consistent pattern was observed in Chl_{tot} due to light treatments (Table 3.2), and is not uncommon in light intensity studies (Pearcy, 1998). Chlorophyll *a* : *b* ratios were low and remained within a narrow range of 0.58 to 0.87 between light treatments and taxa (Table 3.2). In general, carotenoid levels increased in the 100% light treatment for all taxa. *Illicium anisatum* and *I. floridanum* 'Pebblebrook' demonstrated the greatest percent increases in carotenoid concentrations of 326% and 127%, respectively. *Illicium lanceolatum* and *I. parviflorum* 'Forest Green' showed the smallest percent increases of 78% and 42%, respectively. Plants of *I. floridanum* 'Pebblebrook' and *I. henryi* in 45% light treatment had high levels of carotenoids relative to other taxa in the 45% light treatment. SPAD readings were poorly fitted with total chlorophyll ($R^2 = 0.03$), but did confirm visual observations of foliage color during the experiment. Plants of *I. anisatum* and *I. floridanum* 'Pebblebrook' in the 100% light treatment appeared bleached and

yellow, as shown in their low SPAD readings and high carotenoid levels (Table 3.2). Severe bleaching was observed, though not recorded, on plants of *I. henryi* subsequent to plant death in the 100% light treatment. SPAD readings for *I. lanceolatum* were lower in the 100% treatment than in the 45% treatment. SPAD readings were not influenced by light treatment for *I. parviflorum* 'Forest Green'.

Discussion

Maximum rates of net CO_2 assimilation (A_{max}) observed for Illicium taxa in this study are similar to rates reported for broad-leaf evergreen species adapted to low light environments (Andersen et al., 1991a; 1991b; Langenheim et al., 1984; Luttge, 1997). Low rates of CO_2 assimilation in shade-adapted plants are not attributed to differences in rates of stomatal conductance between sun and shade plants (Björkman, 1981). The inability of shade-adapted species to increase rates of net CO_2 assimilation when grown in high light is also not attributable to stomatal limitations. Langenheim et al. (1984) showed that for several species of tropical shade-tolerant evergreens, stomatal conductance decreased in high light, however, C_i remained similar between light treatments. They suggested that low photosynthetic capacity, rather than low stomatal conductance, resulted in a lack of acclimation to increased growth PPF. A similar trend was observed for *Aucuba japonica* 'Variegata', a shade-adapted, broad-leaved evergreen native to temperate Asia, in a container-production study in Florida (Andersen et al., 1991a). Saturation of Illicium taxa in our study occurred from 200 to 230 mg L^{-1} C_i, regardless of light treatment and taxa. This C_i level for A_{sat} implies the inability of Illicium taxa in this study to increase A_{max} when grown at 100% light is due to an inherent low capacity of photosynthesis. The failure to increase rates of photosynthesis with increasing light is a direct result of an inability to increase rate-limiting steps of photosynthesis, including Rubisco synthesis and activation (Seemann, 1989) and electron transport (Boardmann, 1977; Bjorkman, 1981).

Excess light, or light stress, is induced when the ratio of photon flux density to photosynthesis is high (Demmig-Adams and Adams, 1992). Thus, for plant species unable to increase A_{max} with increases in light, long-term exposure to high light will result in prolonged light stress and photoinhibition, the decrease in photosynthetic activity induced by light in excess of that used in photosynthesis (Xu and Shen, 1999). Substantial decreases in photosynthetic activity were observed for most Illicium taxa in the 100% light treatment. The smallest decline in A_{max} (17%) was observed with *I. parviflorum* 'Forest Green'. However, Φ_I, a measure of photosynthetic efficiency which often declines with light stress (Long et al., 1994; Pearcy, 1998), remained unchanged between light treatments for *I. parviflorum* 'Forest Green', suggesting this taxon was able to avoid light stress. The vertical leaf arrangement of plants in 100% light may have effectively decreased the absorption of incident light, possibly to levels observed by plants in the 45% light treatment, a strategy used by mangrove species to avoid high levels of incident PPF (Lovelock and Clough, 1992), and implied here by the low A_0 values plants grown in 100% light. Although photosynthesis appeared to acclimate to high light for *I. parviflorum* 'Forest Green', R_d increased by 97% in high light, suggesting increased maintenance costs, perhaps from increased protein turnover in high light (Pearcy, 1998). Increased respiration, without an increase in photosynthesis, would have a negative effect on carbon-use efficiency, suggesting optimal growth for *I. parviflorum* 'Forest Green' would occur in light intensities below 100% light.

The decline in A_{max} for *I. lanceolatum* in the 100% light treatment was accompanied by a decline in Φ_I and increased levels of carotenoids. Declines in photosynthesis due to photoinhibition are the result of declines in photosynthetic efficiency, as energy from absorbed quanta is dissipated as heat instead of being used in photochemistry (Long et al, 1994). The xanthophyll cycle is recognized as the major thermal energy dissipation process in plants (Long et al., 1994; Xu and Shen, 1999) with increases in total carotenoid concentrations in high PPF due to increases in xanthophyll

cycle components (Demmig et al., 1987; Demmig-Adams et al., 1989; Demmig-Adams et al., 1995; Demmig-Adams, 1998; Thayer and Bjorkman, 1990). However, shade-adapted species have a low capacity for xanthophyll cycle mediated energy dissipation compared to sun-adapted species (Demmig-Adams et al., 1995), and when combined with their low rates of photosynthesis, predispose shade-adapted plants to photoinhibition. Prolonged inhibition in the transfer of excitation energy from excited chlorophyll to the quinnone acceptors results in triplet chlorophyll formation, which reacts with oxygen to produce singlet oxygen and oxygen radicals. Both are active oxygen species capable of damaging proteins, pigments, and thylakoid membranes, which results in photooxidative bleaching (Minkov et al., 1999). The responses of *I. anisatum* and *I. floridanum* 'Pebblebrook' to 100% light is indicative of this type of severe damage to the photosynthetic apparatus. Both species exhibited significant decreases in A_{max} and Φ_I decreased to immeasurable rates. Intercellular CO_2 rates remained high, decreasing little below ambient CO_2 levels, indicating a reduced demand for carbon. This decrease may occur if there is a massive accumulation of damaged reaction centers, which instead of transferring absorbed light energy for use in carbon assimilation, dissipate absorbed energy as heat (Pearcy, 1998).

The SPAD readings and increases in carotenoids concentrations confirmed visual observations of photooxidative bleaching in leaves of 100% light grown *I. anisatum* and *I. floridanum* 'Pebblebrook' plants. However, the chlorophyll pigment data are not consistent with regard to expected chlorophyll losses from photooxidation. *Illicium anisatum* had substantially lower Chl_{tot} combined with increased carotenoids in 100% PFD, corroborating evidence for photooxidative bleaching. *Illicium floridanum* 'Pebblebrook', on the other hand, had high Chl_{tot}, but low SPAD readings in 100% light. These inconsistencies led to the poor relationship between SPAD and chlorophyll data. Campbell et al. (1990), using a SPAD-501 chlorophyll meter showed that growing conditions affect the relationship of SPAD readings to total chlorophyll, due in part to

differences in leaf morphology. In a recent study, SPAD readings were highly correlated to total chlorophyll levels and visual observations for greenhouse grown St. Augustinegrass, but correlated poorly in field grown plants (Rodriguez and Miller, 2000). The authors attributed the poor correlation of field grown plants to a lack of uniformity in ontogenetic age of the samples, and sampling error. Re-analysis of our data, attempting to account for the above possibilities, failed to improve the relationship of SPAD readings to chlorophyll data. The low Chl *a* : *b* ratios observed for Illicium taxa in this study are substantially lower than published ratios for other broad-leaved evergreen taxa (Del Hierro et al., 2000; Demmig-Adams, 1998; Thompson et al., 1992) and C_3 plants in general (Demmig-Adams, 1998). These low ratios may be indicative of poor extraction of chlorophyll by acetone in Illicium leaves, and would also confound the relationship of SPAD readings to chlorophyll pigment data.

Failure of *I. henyri* to survive the 100% light treatment represents the most severe example of the inability to acclimate to high light by a shade-adapted species. Plants were visible bleached and necrotic within one month, and all were dead by the end of the second month (July). In a light intensity study with *Rhododendron* × 'Pink Ruffles', Andersen et al. (1991b) suggested that photoinhibition and photooxidation damage was responsible for reduced growth and chlorosis of plants in 100% sunlight. They concluded *Rhododendron* ×'Pink Ruffles' required partial shade, with no amount of acclimation preventing chlorosis and dieback when plants were transplanted from various light intensities into full sun. In a similar study using the broad-leaved evergreen *Aucuba japonica* 'Variegata', plants grown in 100% sun became chlorotic and necrotic in just 30 days, with complete defoliation occurring by the end of the summer (Andersen et al., 1991a). They classified *Aucuba japonica* 'Variegata' as a shade obligate, where optimum plant growth occurs in light intensities of less than 47% of full sun. Although *I. henryi* was the only taxon that failed to survive the 100% light treatment, it is highly probable that *I. anisatum* and *I. flordanum* 'Pebblebrook' would fail to survive the rest of

the growing season in full sun, given their poor acclimation by mid-season. High temperature and excess light often occur together in nature, where heat induced disruption of the thylakoid membrane can impair the ability to dissipate excess absorbed light (Al-Khatib and Paulsen, 1989). Plants grown in 100% of full sunlight would have been exposed to a combination of high light and high temperatures during the growing season. Our experimental design precluded the partitioning of damage between excess light absorption and differences in foliage temperature expected between the 45% and 100% light treatments.

The photosynthetic responses of Illicium taxa reflected the light levels prevalent in their native habitats. Optimal rates of photosynthesis occurred in 45% PPF, with significant decreases occurring for most taxa when grown at 100% PPF. Photoinhibitory responses, varying in severity, were documented for all taxa, suggesting optimal growth in container-nursery production should occur in light levels below 100% PPF. *Illicium lanceolatum*, a new introduction from China, out performed the taxonomically and morphologically similar *I. henryi* in sun and shade, and is recommended as a substitute for the more popular *I. henryi.*

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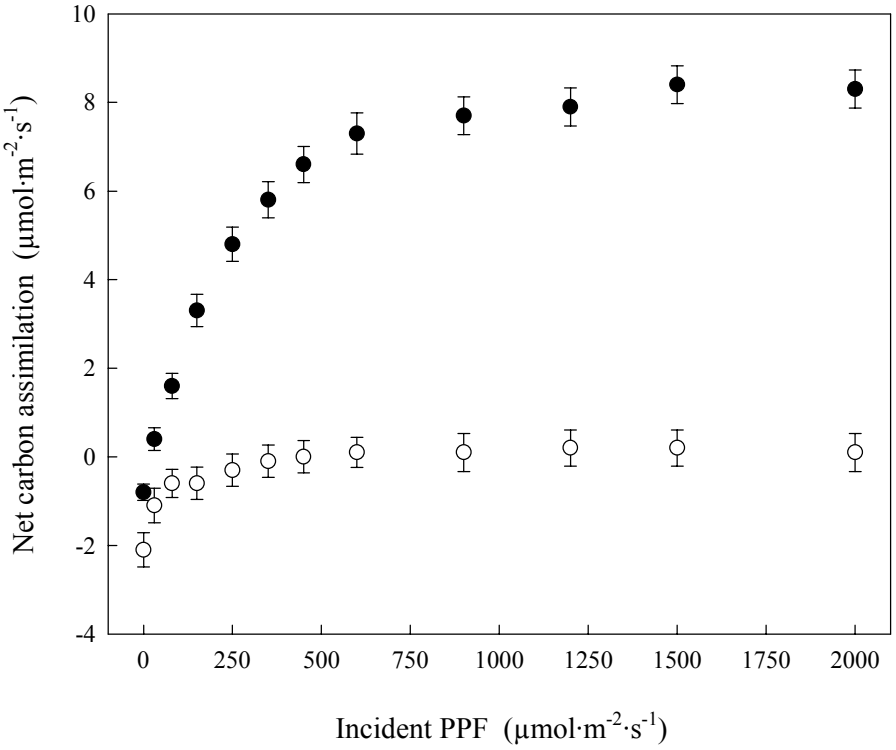

Fig. 3.1. Photosynthetic light response curves for *Illicium anisatum* grown in 45% (●) and 100% (○) of full sunlight. Measurements were made at a CO_2 concentration 365 ± 10 mg L^{-1}, leaf temperatures between 25 and 30 °C, and a vapor pressure deficit of 2.0 ± 0.5 kPa. Negative photosynthetic rates beyond 150 μmol·m^{-2}·s^{-1} PPF for plants grown in 100% light precluded comparison of quantum yields (Φ_I) and light compensation points (A_0) between treatments. Data points represent means, with n = 6. Error bars represent standard errors for the means.

Table 3.1. Photosynthetic gas-exchange parameters for five *Illicium* taxa grown in 100% and 45% of ambient photosynthetic photon flux. Mean of six replications except *I. floridanum* 'Pebblebrook' in 45% light where n=5.

Taxa	Growth light level (%)	Photosynthetic gas-exchange parameters[z]				
		A_{max}	A_{sat}	R_d	A_0[y]	Φ_I[y]
		(μmol CO_2 $m^{-2}\cdot s^{-1}$)			(μmol photons $m^{-2}\cdot s^{-1}$)	
I. anisatum	100	0.51	0.48	-2.11	--	--
	45	8.39	7.97	-0.78	22.2	0.0261
I. floridanum	100	1.55	1.47	-1.19	--	--
'Pebblebrook'	45	7.48	7.11	-1.33	56.6	0.0202
I. henryi[x]	100	--	--	--	--	--
	45	3.05	2.90	-1.05	57.9	0.0146
I. lanceolatum	100	3.78	3.59	-2.07	81.9	0.0197
	45	5.67	5.38	-1.81	55.9	0.0295
I. parviflorum	100	9.07	8.62	-1.20	29.4	0.0330
'Forest Green'	45	10.90	10.37	-0.61	16.1	0.0327
SED[w]						
between light treatments, same taxa		0.73	0.70	0.30	--	--
between taxa, same light treatment		0.76	0.72	0.31	--	--

[z] Abbreviations: Maximum net leaf CO_2 assimilation (A_{max}), net leaf CO_2 assimilation at light saturation (A_{sat}), dark respiration (R_d), light compensation point (A_0), and apparent quantum yield of leaf photosynthesis (Φ_I).

[y] A_0 and Φ_I were not calculated for *I. anisatum* and *I. floridanum* 'Pebblebrook' grown in the 100% light treatments due to severe inhibition of photosynthesis at the low light levels used for calculation of these parameters.

[x] No *I. henryi* survived the 100% light treatment.

[w] No significant interaction or light effect was observed for A_0 and Φ_I. A significant ($P <$ 0.001) taxa effect occurred for both parameters. SED for taxa comparison are 6.5 and 0.00265 for A_0 and Φ_I, respectively.

Table 3.2. Leaf pigment data for five *Illicium* taxa grown in 100% and 45% ambient photosynthetic photon flux. Mean of six replications except *I. floridanum* 'Pebblebrook' in 45% light where n=5.

Taxa	Growth light level (%)	Leaf pigment concentrations[z]					
		Chl_{tot}	Chl *a*	Chl *b*	Chl *a*:*b*	Chl_{x+c}	SPAD
		($\mu g\ cm^{-2}$)					
I. anisatum	100	47.0	17.9	29.1	0.61	9.8	17.5
	45	85.1	32.2	53.0	0.61	2.3	65.7
I. floridanum	100	83.8	31.9	51.9	0.61	17.3	27.8
'Pebblebrook'	45	56.8	22.2	34.6	0.64	7.6	59.8
I. henryi[y]	100	--	--	--	--	--	--
	45	51.5	23.9	27.6	0.87	6.3	51.5
I. lanceolatum	100	64.6	26.8	37.8	0.71	7.5	46.9
	45	55.3	25.6	29.7	0.85	4.2	58.9
I. parviflorum	100	38.3	14.5	23.8	0.60	4.0	54.8
'Forest Green'	45	35.5	13.0	22.5	0.58	2.7	57.8

SED						
between light treatments, same taxa	8.1	3.5	4.7	0.04	1.7	8.6
between taxa, same light treatment	8.2	3.6	4.8	0.04	1.8	4.2

[z] Abbreviations: total chlorophyll (Chl_{tot}), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll *a*:*b* ratio (Chl *a*:*b*), total xanthophylls and carotenoids (Chl_{x+c}), SPAD-502 chlorophyll meter reading (SPAD).

[y] No *Illicium henryi* survived the 100% light treatment.

CHAPTER 4

LIGHT INTENSITY AND RATE OF NITROGEN APPLICATION INFLUENCE GROWTH AND NUTRIENT RECOVERY OF CONTAINER-GROWN *ILLICIUM* L. TAXA[1]

[1]Olsen, Richard T. and John M. Ruter. To be submitted to HortScience.

Abstract. Production of Illiciums, a popular genus of broad-leaf evergreens in the southeastern United States, is currently depended on species-specific responses to high light intensities during growth. Nitrogen is known to increase tolerance of short-term exposure to high light, but its role in acclimation of Illicium to high light is not known. We investigated differences in growth responses of two taxa (*Illicium floridanum* Ellis. 'Pebblebrook' and *I. parviflorum* Michx. ex. Vent. 'Forest Green') to factorial combinations of light intensity (100, 70, and 45% ambient light) and nitrogen application rate (1.2, 1.5, and 1.8 kg $N \cdot m^{-3}$) under typical nursery production conditions. Nitrogen rate had no effect on various growth parameters for *I. floridanum* 'Pebblebrook' in any light intensity, and only limited effect for *I. parviflorum* 'Forest Green' in 45% light. Increased nitrogen application rate did not increase survival of *I. floridanum* 'Pebblebrook' in high light. Optimal growth occurred in the 45% light intensity for both taxa. Foliage color, as indicated by SPAD chlorophyll meter readings, improved in low light for *I. floridanum* 'Pebblebrook'. Light intensity had no effect on SPAD readings for *I. parviflorum* 'Forest Green', whereas increased nitrogen application rate increased readings to some extent. Recovery rates for nitrogen, phosphorus, and potassium were highest in low light and the lowest nitrogen application for both taxa. Optimal growth, combined with high SPAD readings and nutrient recovery rates in low light, indicates nurseries should produce both taxa under shade to optimize growth and fertilizer efficiency.

Additional index words. *Illicium floridanum* 'Pebblebrook', *Illicium parviflorum* 'Forest Green', star-anise, SPAD chlorophyll meter, nitrogen allocation, nutrient recovery

Introduction

The genus Illicium [Illiciaceae (de Candolle) A.C. Smith] is a popular genus of landscape plants native to subtropical and temperate regions of southeastern Asia and

North America (Smith, 1947; Qi, 1995). Although Illiciums, or star-anises, are understory shrubs or sub-canopy trees in their native habitats (White and Thien, 1985; Gibson, 1992; Nitta and Ohsawa, 1997), in cultivation several species have demonstrated considerable sun tolerance (Dirr, 1993; Fantz et al., 1991). In a study investigating the influence of light intensity on five Illicium taxa currently available in the nursery industry, Olsen (2001) found that only *Illicium parviflorum* 'Forest Green' demonstrated adequate acclimation to growth in full sun by maintaining similar photosynthetic rates as shade grown plants. Growth rates were not measured, but Olsen (2001) suggested that optimal growth for Illicium taxa occurs in conditions of less than full sun. Currently, many nurseries in the southeastern United States grow selections of *I. floridanum* under shade, while producing *I. parviflorum* in full sun.

Photosynthesis requires a large investment of proteins and enzymes, thus photosynthetic capacity is highly correlated with nitrogen investment in these compounds (Evans, 1996; Evans and Seemann, 1989; Field and Mooney, 1986). The effect of nitrogen availability on photosynthesis depends on the light intensity experienced during growth. In high light intensities, increased nitrogen leads to higher total leaf nitrogen in soluble protein, due to increased allocation to Rubisco and Calvin cycle enzymes (Evans, 1996). Light-saturated rates of photosynthesis in apple increases curvilinearily with increasing N content (Cheng and Fuchigami, 2000), and at a given light intensity, low N leaves have lower photosynthetic efficiency and greater photoinhibition than high N leaves (Cheng et al., 2000). Several studies have shown that N nutrition plays a critical role in acclimation of plants upon short-term exposure to high light when transferred from low light intensities (Ferrar and Osmond, 1986; Khamis et al., 1990; Skillman and Osmond, 1998). During container-production of Illiciums, however, some taxa are subjected to long-term exposures to high light during their cropping cycle. Although it has been suggested that N plays a role in long-term acclimation of tropical broad-leaf evergreens to high light (Castro et al., 1995; Ramalho et al., 1997), no long-term study has been performed on either tropical or temperate broad-leaved evergreen species.

Therefore, our objectives were to investigate the effects of light intensity and nitrogen on growth, nutrient recovery, and survival of two Illicium taxa under nursery production conditions typical in the southeastern United States.

Materials and Methods

Illicium floridanum 'Pebblebrook' and *I. parviflorum* 'Forest Green', cultivars representing two popular Illicium species in the nursery industry, were studied. Terminal cuttings were taken from plants growing at the Coastal Plain Experiment Station, Tifton, Ga., on 20 Sept. 1999 and transported to Wight Nurseries, Cairo, Georgia, for propagation. Well-rooted liners were transported to the Coastal Plain Experiment Station, where they were potted into 2.8-L black plastic containers on 22 May 2000. The substrate consisted of an 8 milled pine bark : 1 sand mix (by volume) amended with dolomitic lime at 1.2 $kg \cdot m^{-3}$ and Osmocote Plus 15.0N-4.0P-9.9K 8-9 month Southern formula (The Scotts Company, Marysville, Ohio) was applied as a top dressing at 1.2 kg $N \cdot m^{-3}$ (20.2 g $container^{-1}$). Treatments consisted of factorial combinations of light intensity (100%, 70%, and 45% of ambient photosynthetic photon flux (PPF)) and nitrogen application rate (1.2, 1.5, and 1.8 kg $N \cdot m^{-3}$). Nitrogen beyond the base rate of 1.2 kg $N \cdot m^{-3}$ per container was applied as Polycoated Urea 38.5N-0P-0K 8-9 month formula (Harrell's, Lakeland, Fla.) as a top-dressing at 2.0 and 4.0 g $container^{-1}$ for the 1.5 and 1.8 kg $N \cdot m^{-3}$ treatments, respectively. Plants in 100% PPF were grown in full sun on a nursery container pad. Plants in 70% and 45% PPF were grown in hoop houses covered in black woven polypropylene fabric with the desired light transmission. Plants were watered as needed using overhead irrigation such that each plant received ≈84 mm per irrigation event for a leaching fraction of <0.2.

Initial plant height was ≈12 and ≈20 cm for *I. floridanum* 'Pebblebrook' and *I. parviflorum* 'Forest Green', respectively. Thereafter, plant height, width1, and width2 (plant width perpendicular to width1) were recorded on 10 July, 10 September, and 10

November. Growth index (GI) ((height + width1 + width2)/ 3) was calculated for each plant at each measurement date. A SPAD-502 chlorophyll meter (Minolta, Ramsey, N.J.) reading was taken at each measurement date. SPAD readings have been shown to be a useful, non-destructive tool for estimating leaf chlorophyll (Markwell et al., 1995; Marquard and Tipton, 1987; Yadava, 1986). A reading was taken midway between the leaf mid-vein and the margin on two, recently matured leaves per plant and averaged.

After final growth and SPAD measurements were made on 10 November, plants were harvested for dry mass determination. Plants were separated into leaves, stems, and roots. Roots were washed free of substrate. All plant parts were dried to a constant dry mass in a forced-air oven at 80°C. Plant parts were weighed, and then ground in a Wiley mill to pass a 20-mesh sieve. Tissue nitrogen (N) was analyzed using the copper catalyst Kjeldahl method (Association of Official Analytical Chemists, 1990). Phosphorus (P), and potassium (K) were analyzed with a microwave digestion method (Kalra et al., 1998), with K being read on a Perkin Elmer AAnalyst 300 Atomic Absorbance Spectrophotometer (Perkin Elmer, Inc., Norwalk, Conn.) using an air-acetylene flame and standard operating conditions. After digestion, P was determined by the molybdovandate colorimetric method (Association of Official Analytical Chemists, 1990) using a Brinkman PC 801 colorimeter (Brinkman Instruments, Inc., Westbury, N.Y.). Total N, P, and K content per tissue were determined by multiplying the tissue nutrient concentrations by tissue dry mass. Total plant nutrient content was calculated by summing the individual nutrient content per plant tissue.

Percent recovery of N, P, and K was determined by calculating the total nutrient load applied per N treatment. Each container received the same base rate of N, P, and K from Osmocote Plus 15.0N-4.0P-9.9K at 1.2 kg $N \cdot m^{-3}$ (20.2 g $container^{-1}$). Assuming negligible rates of N, P, and K were supplied by the pine bark substrate (Ogden et al., 1987; Mills and Jones, 1996), each container received approximately 3.0 g N, 0.5 g P, and 1.7 g K. At 1.5 kg $N \cdot m^{-3}$ (20.2 g Osmocote Plus + 2.0 g Polycoated Urea), total N applied approximated 3.8 g N $container^{-1}$, and at 1.8 kg $N \cdot m^{-3}$ (20.2 g Osmocote Plus +

4.0 g Polycoated Urea), total N applied approximated 4.6 g N container^{-1}. The total plant content for each nutrient was divided by the total nutrient applied per treatment and multiplied by 100 to give percentage of total nutrient recovery.

Each taxon was analyzed separately. Data for the entire experiment were subjected to an analysis of variance, as a split plot design, and regression analysis (PROC GLM; SAS version 8.0 for Windows, Cary, N.C.). Data were tested for linear and quadratic effects for light and nitrogen where appropriate, using Type III SS at $P \leq 0.05$ or 0.01.

Results

Growth parameters. Nitrogen application rate had no effect on any measured growth parameter for *I. floridanum* 'Pebblebrook', nor were there any significant light × nitrogen interactions (data not shown). Data were pooled across N application rates for each light treatment. All measured growth parameters decreased as light level increased for all measurement dates (Table 4.1). Differences were present by the first measurement date (July), with height, GI, and SPAD readings ≈53% greater in 45% compared to 100% light. These differences increased during the study, such that by the final measurement date, plant height, GI, and SPAD readings were 100%, 136%, and 213% greater, respectively in 45% than in 100% light. Root : shoot ratios, calculated by dividing RDW by the sum of LDW and SDW (Table 4.1), ranged from 1.3 in 45% light to 4.8 in 100% light (data not shown). Seven plants died in the 100% light treatment, two each from 1.2 and 1.8 kg N·m^{-3} treatments and three from the 1.5 kg N·m^{-3} treatment. Those plants that survived in 100% full sun had bleached foliage as seen in the low SPAD readings for this treatment.

In general, measured growth parameters for *I. parviflorum* 'Forest Green' decreased as light level increased, except GI in July and SPAD readings in Sept. and Nov. (Table 4.2). July height and SPAD measurements decreased linearly as light level

increased. In September, increased light level decreased height and GI to a greater extent at 100% than at 70% or 45%, while SPAD remained unaffected. By November, height remained inversely related to light intensity, whereas GI and SPAD readings were influenced by both light level and N application rate. In 45% and 70% light levels, increased N application rate increased GI and SPAD readings to a greater extent than in 100% light. Significant light × nitrogen interactions for final leaf, stem, and total dry mass were indicated. In 45% light, N application rate increased dry mass more than increasing N rate in 70% and 100% light. Root dry mass decreased quadratically with increasing light level, with the greatest decrease occurring between the 70% and 100% light levels. Root : shoot ratios, calculated from dry mass data (Table 4.2), ranged from 0.6 to 0.8 across all treatments, and decreased with increasing N application rate in 45% and 70% light (data not shown). Plants of *I. parviflorum* 'Forest Green' in the 100% light held foliage at ≥ 45° angle to the stem (personal observation). One plant died in the 100% light and 1.5 kg $N \cdot m^{-3}$ treatment.

Tissue analysis. Nitrogen application rate did not influence tissue analysis for *I. floridanum* 'Pebblebrook', but several light × nitrogen interactions were noted (Table 4.3). Leaf N at 100% light was similar across N application rates, but as light level decreased leaf N at 1.2 kg $N \cdot m^{-3}$ decreased more than for other N application rates. Stem N was not influenced by light or N treatment. Root N in the 45% light level was not influenced by N application rate, however, in the 70% and 100% light levels root N increased with increasing N application rate. Leaf and root P had similar responses to light and N treatments. In 45% light, leaf and root P decreased as N application rate increased. In 70% light, leaf and root P increased with increasing N application rate. As light level increased, stem P decreased to a greater extent in 100% light than in 70% and 45%. Increasing N application rate increased leaf K at the 70% light level, but at 45% light leaf K remained unaffected. In 100% light, leaf K was lowest at the 1.5 kg $N \cdot m^{-3}$

application rate. Stem K increased with increasing light level. Root K was similar in 45% and 70% light but decreased in 100% light.

Leaf N was not influenced by light or N application rate in *I. parviflorum* 'Forest Green' (Table 4.4). Stem N at 45% and 70% light were similar, but in 100% light N increased to a greater extent at 1.8 kg $N \cdot m^{-3}$ than the lower N application rates. Root N was not influenced by N application rate, but responded quadratically to light level. Root N was similar at the 45% and 70% light treatments but increased in 100% light. Leaf P increased with decreasing N application rate but responded quadratically to light, decreasing more at 100% light than in the lower light levels. Stem P responded similarly to 45% and 70% light, but in 100% light stem P decreased to a greater extent in the 1.5 and 1.8 kg $N \cdot m^{-3}$ application rates than in the 1.2 kg $N \cdot m^{-3}$ rate. As light level increased, root P decreased quadratically. Root P decreased as light level and N application rate increased. Leaf K was not influenced by light level but responded quadratically to increasing N. For stem K, values increased with increasing N application rate in 45% and 100% light, but decreased in 70% light. Root K remained similar in 45% and 70% light but increased in 100% light.

Total nutrient accumulation. Nitrogen application rate did not influence N, P, or K accumulation for *I. floridanum* 'Pebblebrook' and there were no light × nitrogen interactions (data not shown). Data were pooled across N application rates for each light treatment. As light level decreased, nutrient accumulation of individual tissues increased except root N, leaf and stem P, and stem K (Table 4.5). Root P increased quadratically with light level, as a substantial increase in root P in the 45% light treatment dominated this and total P responses. Leaf K increased linearly while root and total K increased quadratically with decreasing light level. Stem K was not influenced by light or N treatment.

Nitrogen application rate did not influence total N accumulation but did influence some tissue levels of P and K in *I. parviflorum* 'Forest Green' (Table 4.6). Leaf, stem,

and total N decreased as light level increased, with root N unaffected by light level. Leaf and root P had similar responses to light treatment, with P accumulation for both tissues decreasing to a greater extent at 100% than at the 70% and 45% light levels. Stem P in 45% and 70% light was unaffected by N application rate. In 100% light, stem P increased for both 1.2 and 1.5 kg $N \cdot m^{-3}$ rates, but decreased at the 1.8 kg $N \cdot m^{-3}$ rate. Total P increased linearly as N application rate increased in the 45% light level, but decreased linearly as N application rate increased in 100% light. In 70% light, total P increased between the 1.2 and 1.5 kg $N \cdot m^{-3}$ rate and decreased slightly at 1.8 kg $N \cdot m^{-3}$ rate. Both leaf and stem K decreased quadratically as light level increased. Stem K also decreased linearly with increasing N application rate. Root and total K were not influenced by light or N treatment.

Nutrient recovery. Nitrogen application rate had no influence on nutrient recovery in *I. floridanum* 'Pebblebrook', and there were no light × nitrogen interactions (data not shown). Data were pooled across N application rates for each light treatment. Percent recovery of N, P, and K decreased as light level increased (Table 4.7). Percent recovery of N decreased linearly as light level increased. Percent recovery of N was 135% greater in 45% light compared to full sun. Phosphorus recovery declined the greatest between 45% and 70% light, with P recovery in 45% light 365% greater than in 70% light and 622% greater than in 100% light. Percent recovery of K declined the greatest between 70% and 100%. In 45% light, K recovery was 155% greater than in 100% light.

Nitrogen application rate alone did not influence nutrient recovery for *I. parviflorum* 'Forest Green' (Table 4.8), but a significant light × nitrogen interaction occurred for N recovery. Recovery of N in 45% and 70% light were similar, and for each light level N recovery decreased as N application rate increased. In 100% light, N recovery rates for each N application rate were lower than in 45% and 70% light, with the lowest N percent recovery occurring in the 1.5 kg $N \cdot m^{-3}$ rate. Recovery percents for P

and K decreased linearly as light level increased. Recovery of P was 133% greater in 45% light compared to 100% light while K recovery was 65% greater.

Discussion

Nitrogen is often the mineral nutrient most limiting to plant growth, with increased productivity occurring in both natural and managed ecosystems (Field and Mooney, 1986) and nursery production (Ogden et al., 1987) upon N fertilization. The response to increased nitrogen depends upon the irradiance during growth and the photosynthetic characteristics of a particular plant species. Broad-leaf evergreens possess lower rates of photosynthesis per unit leaf nitrogen on a leaf area basis than most other plant species (Field and Mooney, 1986; Evans, 1989). As N availability increases and leaf N increases, the photosynthetic nitrogen use efficiency is expected to decline (Garnier et al., 1995) as more leaf N is stored than utilized in photosynthesis (Marschner, 1995). Thus, photosynthetic nitrogen use efficiency plays a substantial role in determining leaf and whole plant productivity (Garnier et al., 1995).

For *I. floridanum* 'Pebblebrook', tissue analysis revealed that percent leaf N increased with increasing N application rate at lower light intensities (Table 4.3). However, this effect was lost when total leaf N accumulation was calculated (Table 4.5). In either case, growth of *I. floridanum* 'Pebblebrook' remained unaffected by N application rate (Table 4.1), as did the root : shoot ratio, which normally decreases with increasing N (Marschner, 1995). If our base rate of 1.2 kg $N \cdot m^{-3}$ was sufficient to supply N for photosynthesis and growth, while not adversely affecting photosynthetic nitrogen use efficiency we would not expect a further increase in growth as N availability continued to increase. This response of *I. floridanum* 'Pebblebrook' to N application rate is in agreement with the asymptotic relationship of nitrogen and growth (Marschner, 1995) and has been noted in previous nursery container-production studies. For citrus, a tropical broad-leaf evergreen, growth plateaued at a daily N rate of ≈17 $mg \cdot L^{-1}$ (total N

applied equivalent to 1.8 kg $N \cdot m^{-3}$) in a 30-week container study in Florida (Maust and Williamson, 1994). For *Ligustrum texanum*, also a broad-leaf evergreen, maximum growth was attained between 1.2 and 1.8 kg $N \cdot m^{-3}$ when applied as slow-release fertilizers (Jarrell et al., 1983).

In our study with *I. parviflorum* 'Forest Green', tissue analysis indicated an increase in tissue percent N with increasing N application rate only for stem N (Table 4.4). However, N application rate did not increase total accumulated N in any tissue (Table 4.6). A decrease in allocation to roots, as seen in the decrease in root : shoot ratio for *I. parviflorum* 'Forest Green', would increase the allocation of photosynthates for shoot growth in 45% light. Total dry mass increased only in 45% light, such that dry mass increased ≈20% from 1.2 to 1.8 kg $N \cdot m^{-3}$ for *I. parviflorum* 'Forest Green', but GI increased only ≈8% (Table 4.2). Therefore, our N application rates appear to lie within the range where a diminished return on plant growth occurs as N availability increases, although with out growth data for an N application rate below our base rate this remains speculative.

Regardless of N application rate, growth was reduced across all measurement dates for both *I. floridanum* 'Pebblebrook' and *I. parviflorum* 'Forest Green' in 100% light. In a gas-exchange study with various Illicium taxa grown under similar conditions, maximum photosynthesis of *I. floridanum* 'Pebblebrook' was 400% greater in 45% than 100% light (Olsen, 2001). In that same study, maximum photosynthesis of *I. parviflorum* 'Pebblebrook' was not significantly affected by light level, but dark respiration increased for plants in 100% light. Thus, for *I. floridanum* 'Pebblebrook', reduced photosynthetic rates in 100% light would lead to fewer photosynthates produced in high light conditions.

Although *I. parviflorum* 'Forest Green' acclimates photosynthesis to higher light levels (Olsen, 2001), increased respiration in high light decreases photosynthates available for growth, which is illustrated by the reduced growth of *I. parviflorum* 'Forest

Green' plants in 100% light in our present study. A reduction in the photosynthate pool would affect the ability of plants in 100% light to take up N, which requires photosynthates for assimilation in the roots (Lim et al., 1990; Raper et al., 1978). The decrease in N content and decreased N percent recovery in 100% light for both taxa in our study supports this contention.

Furthermore, black plastic containers used by nurseries are exposed to direct incident solar radiation in full sun, often resulting in supraoptimal root zone temperatures of container plants in full sun (Martin, et al., 1991). Root and stem N accumulation decreased when plants of *Ilex crenata* 'Rotundifolia' were subjected to increasing root zone temperatures from 28 to 40°C, with increasing N application rates unable to alleviate decreases in total plant growth at higher root-zone temperatures (Yeager, et al., 1991). Both root and stem N decreased with increasing light intensity in our study, indicating root-zone temperatures likely played a role in declining plant performance in high light. Root respiration increases with increasing root-zone temperature, with current photosynthates supplying the major source of carbon (Ruter and Ingram, 1990). The loss of membrane stability that accompanies increased root temperatures in *I. parviflorum* (Ingram et a., 1986) would increase maintenance respiration in the roots. Ruter and Ingram (1990; 1991) found increased respiration of current photosynthates, as well as increased root exudation of carbon as root-zone temperature increased from 38 to 42°C in *Ilex crenata* 'Rotundifolia'. In our study, the increased light levels would also have been paralleled by increases in root-zone temperature in 100% light, thus increased respiration of roots in high light would have added another competing sink for photosynthates and contributed to decreased growth and N assimilation in high light plants in our study.

Illicium floridanum 'Pebblebrook' in this study, and a previous study (Olsen, 2001), had much-reduced growth flushes in 100% light compared to lower light levels. Furthermore, in our study there was a 29% mortality rate for *I. floridanum* 'Pebblebrook' across N treatments in 100% light. For seedlings of *Tsuga canadensis*, a shade tolerant

evergreen conifer, survival upon transfer from low to high light conditions requires the production of new shoots and foliage (Mohammed and Parker, 1999). The inability of *I. floridanum* 'Pebblebrook' to produce new shoots restricted acclimation to high light intensities by limiting photosynthetic leaf area of the plant acclimated to the growth light intensity. The high root : shoot ratio noted for plants of *I. floridanum* 'Pebblebrook' was a result of this poor shoot growth, rather than increase in allocation to roots, since root mass was lower than in 70% and 45% light (Table 1). *Illicium parviflorum* 'Forest Green', however, exhibited a continuously flushing growth pattern, resulting in continued growth throughout the study (Table 4.2).

The response of SPAD meter readings further illustrates differences between taxa. SPAD readings for *I. floridanum* 'Pebblebrook' decreased with increasing light for all measurement dates, where *I. parviflorum* 'Forest Green' showed only an initial decrease at the July date. By Sept., SPAD readings for *I. parviflorum* 'Forest Green' in 100% light were similar to plants grown in lower light levels, presumably due to the continued growth and acclimation of new shoots and leaves acclimated to the high light intensity. By Nov., SPAD readings increased significantly as N application rate increased, although the values only ranged between 51.4 and 59.8 (Table 4.2) supporting a previous study where increasing N improved foliage color for the type species *I. parviflorum* (Ruter, unpublished data). However, within this small range of SPAD readings, visual differences between treatments are not readily discernable, and therefore, we see no benefit from increasing N to increase foliage color in *I. parviflorum* 'Forest Green'.

Percent recovery of N, P, and K for each taxon was dependant upon treatment, however, highest percent recovery occurred at the 45% light level for both taxa. Although percent tissue P and total accumulated P appear low for both taxa in our study (Tables 4.3 –4.6), they are within the range for healthy Illicium taxa (0.12% to 0.29%) surveyed by Mills and Jones (1996). Few studies have investigated nutrient recovery and uptake rates during container production of woody ornamentals. Struve (1995) calculated recovery rates for *Quercus rubra* and *Nyssa sylvatica* fertilized with combinations of

fertilizer release types and application rates and found recovery rates from 4.1% to 37.8%, depending on nutrient and species. In our study, percent recovery for the N, P, and K for both taxa decreased as light level increased. Although each treatment received the same amount of water during each irrigation event, the 100% light treatment were often watered twice during the day due to higher rates of evapotranspiration in full sun. Increased irrigation frequency increases leaching losses (Wright and Niemiera, 1987) and would have contributed to differences in nutrient recovery between treatments, however other factors were also present. With decreasing growth rates as light level increased (Tables 4.1 and 4.2), and decreased photosynthetic performance in high light (Olsen, 2001), it is not surprising that recovery rates for each nutrient also declines with increasing light level. The competition for photosynthates, as discussed earlier for N would also apply for P, which requires energy for uptake by the root (Marschner, 1995; Mills and Jones, 1996), and also for K where uptake is directly correlated to metabolic activity (Marschner, 1995). If our base rate of 1.2 kg $N \cdot m^{-3}$ is assumed to approximate the plateau N level where a limited return on growth occurs with a further increase in N application rate (Marschner, 1995; Maust and Williamson, 1994), then for both taxa in our study we would expect N uptake rates to decrease upon further addition of N. Previous studies have shown increased leaching of N with increased N application rate (Jarrell et al., 1983; Mikkelsen et al., 1994; Ruter, 1992). In *Ligustrum texanum*, N recovery rates increased up to 1.8 kg $N \cdot m^{-3}$, at which point growth plateaued and recovery rates decreased upon further N application (Jarrell et al., 1983). If photosynthate supply limits energy necessary for nitrogen assimilation (Lim et al., 1990; Raper et al., 1978) and subsequent plant growth, then plants growing in conditions of limited photosynthate production would have lower percent recovery of N. This occurred in our study for plants of both taxa grown in 70% and 100% light for N, P, and K.

The high percent recovery of N, P, and K in the 45% light treatment has tremendous application to the nursery industry in terms of increasing fertilizer efficiency

and decreasing leaching losses to the environment. Both NO_3^- and PO_4^- are highly mobile in container substrates, levels of which can be high in nursery runoff (Jarrell et al., 1983; Struve, 1995). The increased recovery of N, P, and K by both taxa in the low light coincides with optimal growth of these taxa. Rates of recovery suggest that nurseries may actually be able to reduce the levels of these nutrients applied in low light with out adversely affecting growth. The ratios of N-P-K have been suggested as more important than the level of any one nutrient in plants, due to interactions that occur between nutrients within the plant and substrate (Mills and Jones, 1996; Wright, 1983; Wright and Niemiera, 1987). Recommended ratios of N-P-K for woody ornamental nursery crops range from 3-1-1 up to 8-1-4 (Sanderson, 1987; Wright and Niemiera, 1987). The ratio for *I. floridanum* 'Pebblebrook', calculated from whole plant tissue content (Table 3), was closer to 10-1-4 for plants in 45% light where optimal growth occurred. The N-P-K ratio for *I. parviflorum* 'Forest Green' in 45% was 3-1-2 for all N application rates. These results support the suggestion by Struve (1995) that N-P-K ratios for a given crop should be based on ratios of actual N-P-K required by that crop. It is also important to note that increasing N alone in our study appeared to have no adverse effects on tissue levels of P and K.

Excellent growth for both taxa occurred at the rate of 1.2 kg $N \cdot m^{-3}$ and maximum growth was in the lowest light level (45%) for both taxa. Although there was a slight increase in dry mass and total N tissue content at the higher N levels for *I. parviflorum* 'Forest Green', there was no visual benefit to plant quality with higher N application rates at any light level. Furthermore there was greater loss of N, as seen in the reduced N recovery, as N application rate increased. Optimal recovery rates for N, P, and K were found at the 45% light level, coinciding with maximum growth. Increased application N application rate ultimately did not improve acclimation, plant growth or survival in high light during production for *I. floridanum* 'Pebblebrook'. Although *I. parviflorum* 'Forest Green' survived and grew sufficiently in high light, optimal growth occurred in low light, as predicted by Olsen (2001). For production purposes in the southeastern

United States, it is recommended that nurseries grow both *I. floridanum* ‘Pebblebrook’ and *I. parviflorum* ‘Forest Green’ in light levels of 45% ambient light.

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Table 4.1. Growth parameters for *Illicium floridanum* 'Pebblebrook' across three measurement dates and final harvest as influenced by light level during growth. For all treatments n=24, except 100% in July where n=23 and in September and November where n=17 due to plant death.

Light	July			September			November			Final dry mass			
level (%)	Height (cm)	GI[z] (cm)	SPAD	Height (cm)	GI (cm)	SPAD	Height (cm)	GI (cm)	SPAD	Leaves (g)	Stems (g)	Roots (g)	Total (g)
45	19.4	17.7	42.3	26.1	23.7	52.2	28.3	24.8	72.6	8.4	4.8	16.9	30.0
70	17.7	15.8	38.8	21.0	18.7	44.0	22.8	19.3	39.8	5.1	3.1	13.8	22.0
100	12.8	11.3	27.2	14.2	11.5	29.4	14.1	10.5	23.2	0.9	1.2	10.1	12.3
Significance[y]													
Light													
Linear	**	**	**	*	**	**	**	**	NS	**	**	**	**
Quadratic	NS	*	NS	NS	NS	*	NS	NS	**	NS	NS	NS	NS

[z] Growth Index (GI) = (height + width1 + width2)/3.

[y] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

Table 4.2. Growth parameters for *Illicium parviflorum* 'Forest Green' across three measurement dates and final harvest as influenced by light level and nitrogen treatments during growth. For all treatment combinations n=8, except 100% light at 1.5 kg $N \cdot m^{-3}$ where n=7 due to plant death.

Light		July			September			November			Final dry mass			
level	Nitrogen	Height	GI[z]	SPAD	Height	GI	SPAD	Height	GI	SPAD	Leaves	Stems	Roots	Total
(%)	($kg \cdot m^{-3}$)	(cm)	(cm)		(cm)	(cm)		(cm)	(cm)		(g)	(g)	(g)	(g)
45	1.2	32.5	26.4	42.6	47.6	38.8	57.4	51.9	37.6	55.8	25.0	11.6	26.4	63.0
	1.5	30.0	27.3	41.0	50.3	39.1	60.8	56.9	40.0	55.1	29.8	13.4	26.2	69.4
	1.8	34.4	28.3	42.9	50.5	41.1	60.1	54.9	40.4	59.8	32.1	15.8	27.7	75.7
70	1.2	28.6	24.2	43.6	43.9	36.2	61.2	49.1	34.3	51.4	27.0	10.7	26.8	64.6
	1.5	34.0	26.4	47.0	49.1	39.2	62.0	55.1	37.0	53.6	28.5	12.6	26.3	67.4
	1.8	29.4	24.4	46.7	47.8	36.4	63.2	56.2	37.4	57.8	28.1	11.9	23.9	63.9
100	1.2	25.8	22.4	34.0	33.1	27.3	54.9	37.9	28.1	56.3	17.7	6.6	18.6	42.9
	1.5	24.9	20.8	31.4	36.0	27.8	62.0	40.4	28.0	55.4	16.1	6.3	17.5	39.9
	1.8	24.2	22.3	31.4	35.5	27.3	61.8	42.5	28.5	57.0	18.3	7.4	18.9	44.6

Significance													
Light													
Linear	*	NS	**	**	**	NS	*	**	NS	**	**	**	**
Quadratic	NS	NS	**	*	**	NS	*	**	NS	**	**	**	**
Light × nitrogen	NS	NS	NS	NS	NS	NS	NS	**	*	**	*	NS	*

[z] Growth Index (GI) = (height + width1 + width2)/3.

[y] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

Table 4.3. Final tissue analysis for *Illicium floridanum* 'Pebblebrook' as influenced by light level and nitrogen treatment during growth. For all treatment combinations n=8, except for 100% light at 1.2 and 1.8 kg $N \cdot m^{-3}$ where n=6 and 100% light at 1.5 kg $N \cdot m^{-3}$ where n=5, due to plant death.

Light level (%)	Nitrogen ($kg \cdot m^{-3}$)	Nitrogen (%)			Phosphorus (%)			Potassium (%)		
		Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
45	1.2	2.36	1.65	2.64	0.24	0.37	1.07	1.74	0.38	1.27
	1.5	2.56	1.80	2.65	0.17	0.37	1.03	1.82	0.34	1.17
	1.8	2.51	2.12	2.75	0.16	0.30	1.04	1.77	0.31	1.03
70	1.2	2.28	1.92	2.40	0.16	0.28	0.16	1.93	0.44	1.26
	1.5	2.51	2.18	3.01	0.22	0.27	0.20	2.09	0.43	1.37
	1.8	2.64	2.65	2.84	0.22	0.41	0.20	2.16	0.39	1.11
100	1.2	2.80	1.54	2.38	0.14	0.23	0.18	0.92	0.52	0.62
	1.5	2.70	1.88	2.74	0.13	0.18	0.11	0.69	0.68	0.69
	1.8	2.82	1.84	2.92	0.15	0.32	0.19	1.20	0.67	0.67

Significance[z]									
Light									
Linear	NS	NS	**	*	**	**	NS	**	**
Quadratic	NS	NS	**	*	*	**	NS	**	**
Light × nitrogen	**	NS	**	*	NS	**	*	NS	NS

[z] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

Table 4.4. Final tissue analysis for *Illicium parviflorum* 'Forest Green' as influenced by light level and nitrogen treatment during growth. For all treatment combinations n=8, except 100% light at 1.5 kg $N \cdot m^{-3}$ where n=7 due to plant death.

Light level	Nitrogen	Nitrogen (%)			Phosphorus (%)			Potassium (%)		
(%)	($kg \cdot m^{-3}$)	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
45	1.2	1.54	1.12	1.34	0.15	0.23	0.93	1.37	0.51	0.89
	1.5	1.66	1.12	1.51	0.10	0.14	1.06	1.09	0.51	1.01
	1.8	1.70	1.08	1.49	0.14	0.28	0.92	1.28	0.60	0.78
70	1.2	1.45	1.00	1.29	0.29	0.26	0.30	1.22	0.42	0.91
	1.5	1.57	0.99	1.30	0.11	0.23	0.95	1.00	0.38	0.73
	1.8	1.69	1.10	1.60	0.09	0.31	0.92	1.03	0.35	0.82
100	1.2	1.41	0.88	1.60	0.11	0.92	0.15	0.93	0.59	1.08
	1.5	1.55	0.74	1.69	0.08	0.74	0.15	0.87	0.55	1.08
	1.8	1.79	1.19	1.89	0.07	0.41	0.14	0.86	0.51	1.08

Significance[z]									
Light									
Linear	NS	NS	**	*	**	**	NS	NS	**
Quadratic	NS	NS	**	*	*	**	NS	**	**
Nitrogen									
Linear	NS	NS	NS	*	NS	**	**	NS	NS
Quadratic	NS	*	NS	NS	NS	**	**	NS	NS
Light × nitrogen	NS	**	NS	NS	*	NS	NS	*	NS

[z] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

Table 4.5. Total plant nutrient accumulation in *Illicium floridanum* 'Pebblebrook' as influenced by light level during growth. For all treatments, n=24, except 100% light where n=17 due to plant death.

Light Level	Nitrogen (mg)				Phosphorus (mg)				Potassium (mg)			
(%)	Leaf	Stem	Root	Total	Leaf	Stem	Root	Total	Leaf	Stem	Root	Total
45	207	87	441	735	16	17	176	208	149	56	193	399
70	125	67	378	571	11	9	25	45	111	58	170	342
100	25	20	273	316	2	4	18	30	13	62	68	144
Significance[z]												
Light												
Linear	*	**	NS	*	NS	NS	**	**	**	NS	**	**
Quadratic	NS	NS	NS	NS	NS	NS	**	**	NS	NS	**	*

[z] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

Table 4.6. Total plant nutrient accumulation in *Illicium parviflorum* 'Forest Green' as influenced by light level and nitrogen treatment during growth. For all treatment combinations n=8, except 100% light at 1.5 kg $N \cdot m^{-3}$ where n=7 due to plant death.

Light level	Nitrogen	Nitrogen (mg)				Phosphorus (mg)				Potassium (mg)			
(%)	($kg \cdot m^{-3}$)	Leaf	Stem	Root	Total	Leaf	Stem	Root	Total	Leaf	Stem	Root	Total
45	1.2	388	129	352	869	34	27	246	307	340	136	233	710
	1.5	497	148	396	1046	31	18	273	323	330	134	260	724
	1.8	546	167	408	1122	44	43	256	343	408	165	215	789
70	1.2	392	106	338	836	77	30	76	183	332	115	241	689
	1.5	450	124	339	918	30	29	248	308	284	100	193	578
	1.8	480	131	382	992	27	38	219	283	287	84	196	568
100	1.2	254	57	291	603	21	147	26	179	163	109	201	473
	1.5	242	48	292	564	14	108	27	149	139	97	187	423
	1.8	320	88	353	762	12	48	27	87	160	93	200	454

Significance[z]												
Light												
Linear	***	**	NS	**	**	**	**	NS	**	*	NS	NS
Quadratic	**	NS	NS	*	**	*	*	NS	*	**	NS	NS
Nitrogen	NS	NS	NS	NS	NS	**	NS	NS	NS	*	NS	NS
Light × nitrogen	NS	NS	NS	NS	NS	**	NS	*	NS	NS	NS	NS

[z] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

Table 4.7. Percent recovery of applied N, P, and K by *Illicium floridanum* 'Pebblebrook' as influenced by light level during growth. For all treatments n=24, except 100% light where n=17 due to plant death.

Light level (%)	Recovery (%) N	P	K
45	19.6	41.9	23.5
70	15.6	9.0	20.0
100	8.6	5.8	9.2
Significance[z]			
Light			
Linear	*	**	**
Quadratic	NS	**	*

[z] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

Table 4.8. Percent recovery of N, P, and K by *Illicium parviflorum* 'Forest Green' as influenced by light level and nitrogen treatment during growth. For all treatment combinations n=8, except 100% light at 1.5 kg $N \cdot m^{-3}$ where n=7 due to plant death.

Light level (%)	Nitrogen ($kg \cdot m^{-3}$)	Recovery (%) N	P	K
45	1.2	28.7	61.9	41.7
	1.5	27.4	65.1	42.6
	1.8	24.5	69.2	46.4
70	1.2	27.6	37.0	40.5
	1.5	24.2	62.0	34.0
	1.8	21.7	57.1	33.4
100	1.2	19.9	36.6	27.8
	1.5	14.8	30.0	24.9
	1.8	16.7	17.6	26.7
Significance[z]				
Light				
Linear		**	*	*
Quadratic		*	NS	NS
Light × nitrogen		*	NS	NS

[z] Significance tests based on Type III SS; NS >0.05, * ≤ 0.05, and ** ≤ 0.01.

CHAPTER 5

CONCLUSION

The increased popularity of Illiciums in Southeastern nurseries and landscapes has not been followed by a concomitant increase in research pertaining to the physiological and cultural requirements of Illicium species. Our research is of immediate use and pertinent to the nursery industry, with four new species of Illicium introduced in the last 10 years and several new cultivars being selected of species currently in the trade. Unfortunately, individual personal observations and professional opinions have perpetuated a cloud of confusion pertaining to the cultural needs of Illiciums in both the landscapes and nurseries of the southeastern United States. Our research sought to penetrate this cloud using sound scientific inquiry and experimentation.

Our studies have elucidated species-specific responses to light intensity that have perhaps led to inconsistencies in production and planting practices for Illiciums. *Illicium parviflorum* 'Forest Green', a selection of perhaps the most popular Illicium species, demonstrated the most plasticity with regard to light intensity during growth. It was able to maintain high levels of photosynthesis, comparable to levels in low light, perhaps owing to the vertical orientation of leaves grown under high light. However, respiration rates were higher, indicating optimal growth would occur in low light due to a better carbon use efficiency rate. *Illicium lanceolatum* exhibited some ability to acclimate to high light, but photosynthesis and foliage quality improved when grown in low light. *Illicium anisatum, I floridanum* 'Pebblebrook', and *I. henryi* failed to acclimate successfully to high light, with varying degrees of photooxidative bleaching from chronic photoinhibition evident.

Our second study sought to elucidate the interactions of light and nitrogen on growth and performance of Illiciums during a long-term container-container production study. Unfortunately, increasing nitrogen application rates is often seen as an option for nurseries to improve growth and foliage characteristics during production. However, in Illiciums, there is a limited response to nitrogen application rate. Growth and foliage color for *Illicium floridanum* 'Pebblebrook' was not improved with increasing nitrogen availability. The effect of nitrogen on growth of *Illicium parviflorum* 'Forest Green' was not as great as growth increases due to decreasing light intensity. For both taxa, recovery rates of nitrogen and other macronutrients decreased as light intensity increased. Optimal growth, combined with improved foliage characteristics and nutrient recovery rates in low light, indicates nurseries should produce both taxa under shade to optimize growth and fertilizer efficiency.

The results of our research, when disseminated, should prompt nurseries to change their production practices for container-grown Illiciums. Currently, *Illicium parviflorum* clones are grown in full sun, which our research has shown to be less than optimal for growth and nutrient management. In general it appears that all Illicium taxa in cultivation in the southeastern United States should be grown in light intensities of less than full sun, in agreement with the light intensities present in their native habitats.