POTENTIAL CLIMATE CHANGE EFFECTS ON DEEP SOIL CARBON AND HYDROLOGY IN LOBLOLLY PINE PLANTATIONS OF THE SOUTHEAST U.S.

by

JI QI

(Under the Direction of Daniel Markewitz)

ABSTRACT

Forests in the Southeast U.S. are predicted to experience more variable precipitation in the future with more extreme daily precipitation events. Within these forests, the loblolly pine (*Pinus taeda* L.) is the most extensively planted and productive commercial pine species. Changes in climate could create more severe drying and re-wetting cycles in the forest soil profile to greater depths affecting stocks of soil C. To addresses this effect, a soil incubation experiment was established using soils from four loblolly pine plantations which span the full temperature and precipitation range of the species. Soils were incubated from as many as eight layers up to a depth of three meters. Results indicated that there were no significant changes to soil respiration in deep soils under repeated drying-wetting cycles.

Change in precipitation could result in drought during the growing season. Deep soils help forests buffer the effects of water deficits during drought but the extent of deep rooting and quantity of plant available water at depth needs better quantification. Throughfall reduction x fertilization treatments were applied in a loblolly pine plantation in Taliaferro County, Georgia. Multiple layers of soil moisture were monitored to a depth of three meters from March 2013 to July 2015. Results demonstrated soil water storage could satisfy evapotranspirational demand in the face of increasing dryness in the clay rich Piedmont soil of this research site when considering the whole soil profile.

Possible climate change scenarios also include seasonal and frequency precipitation change. A hydrological model was used to quantify water fluxes and to test alternative precipitation regimes. Model outputs under year round reductions indicated sustained evapotranspiration to the detriment of soil drainage. With more seasonal precipitation redistribution and heavy storms, both evapotranspiration and drainage decreased, while surface runoff increased. Although root biomass measured both before and after the treatment had no significant difference between treatments, evapotranspiration increased with deeper roots under evenly reduced precipitation and seasonal precipitation redistribution scenarios. How deep root buffering capacity will persist in the face of changing precipitation may depend less on seasonal redistribution than rainfall frequency.

INDEX WORDS: Southeast loblolly pine, climate change, deep soil carbon, drying-wetting cycles, drought, fertilization, deep soil hydrology, HYDRUS

POTENTIAL CLIMATE CHANGE EFFECTS ON DEEP SOIL CARBON AND HYDROLOGY IN LOBLOLLY PINE PLANTATIONS OF THE SOUTHEAST U.S.

by

JI QI

BS, Beijing Forestry University, China, 2011

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2016

POTENTIAL CLIMATE CHANGE EFFECTS ON DEEP SOIL CARBON AND HYDROLOGY IN LOBLOLLY PINE PLANTATIONS OF THE SOUTHEAST U.S.

by

JI QI

Major Professor:	Daniel Markewitz
Committee:	Lawrence Morris
	David Radcliffe
	Robert Teskey

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
December 2016

DEDICATION

To my parents and husband

My love, strength and inspiration

In loving memory of

My grandfathers

ACKNOWLEDGEMENTS

My deepest gratitude to my advisor, Dr. Daniel Markewitz, for his guidance and encouragement through my time at the University of Georgia. His mentoring and advice have helped me to grow not only as a research scientist, but also as a person. I am especially grateful to Drs. Lawrence Morris, David Radcliffe, and Robert Teskey for serving on my advisory committee and sharing their extensive knowledge with me.

My gratitude to Madison Akers, Anchal Bangar, Brandon Crouch, Maryam Foroughi, Ruan Mateus Guimaraes Dias, Carla Gann, Christian Hoadley, Aaron Joslin, George Matthew, Dr. Mary Anne McGuire, Lee Ogden, Rachel Ryland, Jenna Stockton, Dr. Lori Sutter, Brandon Varner, Greg Ward and my intern Doris Laguer Martinez. I greatly appreciate your generous efforts to the extensive field and laboratory work involved with this research.

I am very grateful to the funding made possible by The Pine Integrated Network: Education, Mitigation, and Adaptation project funded by the USDA National Institute of Food and Agriculture, Award #2011-68002-30185, and the University of Georgia, Warnell School of Forestry and Natural Resources.

.

TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Forests in the Southeast U.S. are predicted to experience more variable precipitation in the future with up to 3 times more extreme daily precipitation events (a daily amount that occurs once in 20 years) (Meehl et al. 2007, Kunkel et al. 2013) and a 2.5% or more per decade decrease in water yield (Sun 2013). Summertime precipitation may decline by 10 to 30% in the Southeast U.S. (Meehl et al. 2007, Solomon et al. 2007). Uncertainty in future precipitation patterns still remains, however, because the Southeast is located in the transition zone between projected wetter conditions to the north and drier conditions to the southwest (Kunkel et al. 2013).

Within forests of the Southeast U.S. region, the native loblolly pine (*Pinus taeda* L.) is the most extensively planted and productive commercial pine species (Fox et al. 2007) covering ~14 million hectares (USDA Forest Service, 2015). These forests contain 1/3 of the contiguous U.S. forest carbon and form the backbone of an industry that supplies 16% of global industrial wood, 5.5% of the jobs, and 7.5% of the industrial economic activity of the region (pinemap.org). Loblolly pine is an early successional species that grows across a broad range of soil types throughout the Southeast, although it is not highly drought tolerant.

Changes in climate in this region could create more severe drying and re-wetting cycles in the soil profile. Soil drying-wetting cycles can result in a pulse of respiration, which may exceed the respiration rate of constantly moist soils by as much as 500% (Birch 1958, Orchard and Cook 1983). Previous research on drying-wetting cycles has mainly focused on surface (0-20 cm) soil C (Mikha et al. 2005, Wu and Brookes 2005, Butterly et al. 2010, Butterly et al. 2011). Fewer studies, however, have looked at subsurface (20-100 cm) and particularly deep (>100 cm) soil C. Globally, more than 50% of soil organic C is found in subsoil horizons (>20 cm) (Batjes 1996). Deep soils are different from surface soils in both states of soil C (i.e., particulate or hydrolysable) and mineralization rates. As the soil C pool is the largest pool of terrestrial C globally, it is important to study the effect of drying-wetting cycles on deep soil C.

Chapter two of this dissertation addresses the effect of drying-wetting cycles on deep soil carbon. A soil incubation experiment was established using soils from loblolly pine plantations in Florida, Georgia, Oklahoma, and Virginia, which span the full temperature and precipitation range of the species (pinemap.org). Soils were incubated from as many as eight layers up to a depth of 3 m. Soil respiration was measured repeatedly during three cycles of imposed drying-wetting incubations. In addition, soil carbon was fractionated (water extractable, light, hydrolysable, and residual) in all samples to better interpret controls on soil respiration rates in the surface and at depth.

Another possible effect of climate change is drought during the growing season, a critical period for plant growth (Markewitz et al. 2010). During the growing season, loblolly pine rely on soil water as transpiration often exceeds precipitation (McNulty et al. 1996). Low soil water availability could reduce net photosynthesis (Wertin et al. 2010), decrease both above and below ground growth, and shift root distribution (Torreano and Morris 1998). Access to water reserves in deep soil (>1 m) during drought periods helps forests buffer the effects of precipitation deficits (Nepstad et al. 1994, Fensham and Fairfax 2007, Padilla and Pugnaire 2007, Maeght et al. 2013). Positive relationships between rooting depth and resistance to drought have been demonstrated (Fensham and Fairfax 2007, Padilla and Pugnaire 2007). In pine plantations, in particular, one common forest management practice to increase productivity is fertilization (Fox et al. 2007);

however, when combined with low soil water availability, plants may exhibit little response to fertilization (Tang et al. 2004, Goldstein et al. 2013), or even intensify the impact of drought (Bartkowiak et al. 2015, Ward et al. 2015).

Chapter three focuses on throughfall reduction x fertilization effects on deep soil water usage. A throughfall reduction treatment (ambient versus ~30% throughfall reduction) and a fertilization treatment (no fertilization versus fertilization) were applied in a 6-year-old loblolly pine plantation in Taliaferro County, Georgia. Multiple layers of soil moisture were monitored to a depth of three meters from March 2013 to July 2015.

Soil moisture measurements alone, however, do not describe the magnitudes and rates of water fluxes because two layers may contain the same water volume within a given soil volume, but have different rates of fluid movement through them. This means that model estimates of water fluxes are required in order to fully quantify the hydrologic system. Furthermore, our throughfall exclusion experiment was limited in reducing input equally year round while many models predict more variable temporal changes in precipitation inputs. As such, I use a site specific model calibration to test water fluxes under different precipitation scenarios. Chapter four enhances our understanding of hydrologic processes within the loblolly pine plantation on well-drained, deep Ultisol by using Hydrus 1-D (Šimůnek et al. 2016) to simulate changes in the vertical distribution of soil water to the depth of three meters. The model is calibrated and validated with the experimental data before being used to simulate three scenarios: (1) evenly reduced precipitation throughout the experimental period; (2) less precipitation in summer, more in winter; (3) the same amount of precipitation with less frequency, but heavier storms; and (4) how deeper rooting depth interacts with the above three scenarios. Understanding the physical processes driving the observed soil water dynamics at the site enhances our ability to predict future hydrologic effects of a changing climatic regime.

The last chapter summarizes and highlights the important findings in this study.

REFERENCES

Bartkowiak, S. M., L. J. Samuelson, M. A. McGuire, and R. O. Teskey. 2015. Fertilization increases sensitivity of canopy stomatal conductance and transpiration to throughfall reduction in an 8-year-old loblolly pine plantation. Forest Ecology and Management 354:87-96.

Batjes, N. H. 1996. Total carbon and nitrogen in the soils of the world. European Journal of Soil Science 47:151-163.

Birch, H. F. 1958. Pattern of humus decomposition in East African soils. Nature 181:788-788.

Butterly, C. R., P. Marschner, A. M. McNeill, and J. A. Baldock. 2010. Rewetting CO_2 pulses in Australian agricultural soils and the influence of soil properties. Biology and Fertility of Soils 46:739-753.

Butterly, C. R., A. M. McNeill, J. A. Baldock, and P. Marschner. 2011. Changes in water content of two agricultural soils does not alter labile P and C pools. Plant and Soil 348:185-201.

Fensham, R. J., and R. J. Fairfax. 2007. Drought-related tree death of savanna eucalypts: Species susceptibility, soil conditions and root architecture. Journal of Vegetation Science 18:71-80.

Fox, T. R., E. J. Jokela, and H. L. Allen. 2007. The development of pine plantation silviculture in the southern United States. Journal of Forestry 105:337-347.

Goldstein, G., S. J. Bucci, and F. G. Scholz. 2013. Why do trees adjust water relations and hydraulic architecture in response to nutrient availability? Tree Physiol 33:238-240.

Kunkel, K. E., L. E. Stevens, S. E. Stevens, L. Sun, E. Janssen, D. Wuebbles, C. E. Konrad, II , C. M. Fuhrman, B. D. Keim, M. C. Kruk, A. Billet, H. Needham, M. Schafer, and J. G. Dobson. 2013. Regional Climate Trends and Scenarios for the U.S. National Climate Assessment:

Part 2. Climate of the Southeast U.S. NOAA Technical Report 142-2 Page 103. National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service Washington D.C. .

Maeght, J. L., B. Rewald, and A. Pierret. 2013. How to study deep roots - and why it matters. Frontiers in Plant Science 4:14.

Markewitz, D., S. Devine, E. A. Davidson, P. Brando, and D. C. Nepstad. 2010. Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. New Phytologist 187:592-607.

McNulty, S. G., J. M. Vose, and W. T. Swank. 1996. Loblolly pine hydrology and productivity across the southern United States. Forest Ecology and Management 86:241-251.

Meehl, G. A., C. Tebaldi, H. Teng, and T. C. Peterson. 2007. Current and future U.S. weather extremes and El Nino. Geophysical Research Letters 34:1-6.

Mikha, M. M., C. W. Rice, and G. A. Milliken. 2005. Carbon and nitrogen mineralization as affected by drying and wetting cycles. Soil Biology & Biochemistry 37:339-347.

Nepstad, D. C., C. R. Decarvalho, E. A. Davidson, P. H. Jipp, P. A. Lefebvre, G. H. Negreiros, E. D. Dasilva, T. A. Stone, S. E. Trumbore, and S. Vieira. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372:666-669.

Orchard, V. A., and F. J. Cook. 1983. Relationship between soil respiration and soil-moisture. Soil Biology & Biochemistry 15:447-453.

Padilla, F. M., and F. I. Pugnaire. 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology 21:489-495.

Šimůnek, J., M. T. van Genuchten, and M. Šejna. 2016. Recent developments and applications of the HYDRUS computer software packages. Vadose Zone Journal 15.

Solomon, S., D. Qin, M. Manning, M. Marquis, K. Averyt, M. M. B. Tignor, H. L. Miller, Jr., and Z. Chen. 2007. Climate change 2007; the physical science basis; contribution of Working Group I to the Fourth Assessment Report of the Intergovernamental Panel on Climate Change. Cambridge University Press : Cambridge, United Kingdom, United Kingdom.

Sun, G. 2013. Impacts of Climate Change and Variability on Water Resources in the Southeast USA. Pages 210-236 in K. T. Ingram, K. Dow, L. Carter, and J. Anderson, editors. Climate of the Southeast United States: Variability, Change, Impacts, and Vulnerability. Island Press/Center for Resource Economics, Washington, DC.

Tang, Z. M., M. A. Sayer, J. L. Chambers, and J. P. Barnett. 2004. Interactive effects of fertilization and throughfall exclusion on the physiological responses and whole-tree carbon uptake of mature loblolly pine. Canadian Journal of Botany-Revue Canadienne De Botanique 82:850-861.

Torreano, S. J., and L. A. Morris. 1998. Loblolly pine root growth and distribution under water stress. Soil Science Society of America Journal 62:818-827.

Ward, E. J., J.-C. Domec, M. A. Laviner, T. R. Fox, G. Sun, S. McNulty, J. King, and A. Noormets. 2015. Fertilization intensifies drought stress: Water use and stomatal conductance of *Pinus taeda* in a midrotation fertilization and throughfall reduction experiment. Forest Ecology and Management 355:72-82.

Wertin, T. M., M. A. McGuire, and R. O. Teskey. 2010. The influence of elevated temperature, elevated atmospheric CO_2 concentration and water stress on net photosynthesis of loblolly pine (*Pinus taeda* L.) at northern, central and southern sites in its native range. Global Change Biology 16:2089-2103.

Wu, J., and P. C. Brookes. 2005. The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. Soil Biology & Biochemistry 37:507-515.

CHAPTER 2

DRYING-WETTING CYCLES: EFFECT ON DEEP SOIL CARBON IN LOBLOLLY PINE PLANTATIONS OF THE SOUTHEAST U.S.

---

[1] J. Qi, D. Marekwitz, M. Foroughi, E. Jokela, B. Strahm and J. Vogel. To be submitted to *Soil Science Society of American Journal*.

ABSTRACT

In the Southeast U.S., the climate is predicted to be warmer and have more severe drought in the summer. Decreasing rainfall in summer months should create more severe drying that will eventually affect re-wetting cycles deeper in the soil profile. Changing drying-wetting cycles in this deeper portion of the profile may impact the soil C pool; the largest pool of terrestrial C globally. The aim of this research is to study the effect of drying-wetting cycles on deep soil C. A soil incubation experiment was established using four soils that are part of a simulated drought experiment in Florida, Georgia, Oklahoma, and Virginia. Soils were incubated from as many as eight layers up to a depth of 3.0 m. During incubations, soil respiration was generally greatest in surface soils and declined with depth. Compared to soils that were kept constantly moist, drying-wetting cycles did not consistently stimulate more soil respiration. Cumulative CO_2-C as a proportion of total soil C, however, was higher in soils below 1 m than above. Total C and water extractable C were the best indicators for cumulative CO_2-C ($p = 0.82$). Assuming that there was no other factor (i.e., new carbon inputs) affecting soil C mineralization at depth other than soil moisture cycles, this study indicated that there would be no significant change to soil CO_2 respiration in deep soils under more severe drying-wetting cycles.

Key Words: Southeast loblolly pine, deep soil carbon, climate change, drying-wetting cycles, soil carbon respiration

INTRODUCTION

Climate change models predict that summertime precipitation may decline by 10 to 30% in the Southeast U.S. (Meehl et al. 2007, Solomon et al. 2007), although uncertainty in, and disagreement between, projections remain (Seager et al. 2009). Drought may stress soil microbes and plants; and may have implications for nutrient availability, plant productivity, biogeochemical processes, gaseous fluxes and the C pool in soils (Borken and Matzner 2009). Understanding how drought induced drying-wetting cycles affect C mineralization is important in predicting the effects of climate change on forest soils and estimating potential changes in the soil C pool (Borken and Matzner 2009).

Soil drying-wetting cycles can result in a pulse of soil respiration (known as the Birch effect), which may exceed the respiration rate of constantly moist soils (Birch 1958, Orchard and Cook 1983, Kieft et al. 1987a). After a rewetting, soil respiration can be elevated by as much as 500% compared with samples that are kept constantly moist, with the CO_2 pulse lasting from 2 days to 2 weeks (Birch 1958, Jager and Bruins 1975, Clein and Schimel 1994, Franzluebbers et al. 2000, Fierer and Schimel 2002, Mikha et al. 2005, Beare et al. 2009, Butterly et al. 2010).

Previous research on drying-wetting cycles has mainly focused on surface (0-20 cm) soil C (Mikha et al. 2005, Wu and Brookes 2005, Butterly et al. 2010, Butterly et al. 2011). Fewer studies, however, have looked at subsurface (20-100 cm) and particularly deep (>100 cm) soil C. Globally, more than 50% of soil organic C is found in subsoil horizons (>20 cm) (Batjes 1996). One estimate found that 27-77% of mineral soil C was below 20 cm depth when soils were sampled to more than 80 cm (Harrison et al. 2011). Shallow soil sampling can result in an underestimate of soil C storage and an inability to adequately measure the impacts of other changes over time in whole-ecosystem studies (Harrison et al. 2011).

Presently, it is unknown if the mechanisms controlling drying-wetting responses in topsoil differ from those in deeper soil. There is, however, clear evidence that the forms of soil C can differ in these two portions of the profile. In a study conducted on a sandy clay loam soil in California, the proportion of soil organic matter with a density < 1.6 g/cm3 (primarily undecomposed plant material and charcoal) decreased with depth, making up 20% or more of the total C in the upper 18 cm, but less than 10% for the deeper soil (Trumbore et al. 1989). Another study in Amazonian forest soils found similar results; soil organic C with a density <2 g/cm3 comprised about 30% of the total soil C pool for the upper 10 cm but the proportion dropped rapidly with depth to <5% (Trumbore et al. 1995). For soil organic matter with density >2 g/cm3 (e.g., altered plant matter, microbial cell wall debris and organic matter adsorbed to clay) the ratio of hydrolysable C (removable by acid treatment, e.g., amino acids, proteins, carbohydrates, and simple sugars) to non-hydrolysable C (not removable by acid treatment) also decreased from 2:1 in the upper soil to 1:1 in the deeper soil (Trumbore et al. 1989). One study directly addressing dynamic soil C properties found that soil respiration at 50, 100 and 200 cm responded differently to changes in water, temperature, and nutrient availability relative to the surface soil (0-25 cm) (Fierer et al. 2003). Due to the different forms of C in deep soils, it is possible that the mechanisms controlling the response of soil respiration to drying-wetting differ as well.

In addition to differences in states of soil C (i.e., particulate or hydrolysable) with depth, different mineralization rates have also been observed. Subsurface soil organic C mineralization rates are generally lower and have longer mean residence times than surface soil organic C (Trumbore 2000). One study conducted in a grassland soil in France showed that surface soil C has a mean residence time of ~300 years, while subsurface soil C has a mean residence time of ~3000 years (Fontaine et al. 2007). Fractionation of soil organic C by physical or chemical properties has been demonstrated to relate to mineralization rate. Low density C fractions (<2 g/cm^3), except charcoal, turns over on a time scale of decades or less (Trumbore and Zheng 1996). The mean residence time of hydrolysable C is several centuries, while the age of non-hydrolysable material could be thousands of years (Trumbore et al. 1989). It is uncertain, however, which C fraction is a good indicator of potential soil C respiration at depth.

This study tested the hypothesis that more severe drying-wetting cycles will stimulate deep soil respiration and potentially soil C loss. Soil samples from four locations across the Southeast U.S. that are part of a study simulating increased drought (i.e., throughfall exclusion, see Will et al. (2015)) were utilized. Multiple depths from 0 to 3 m were incubated for three drying-wetting cycles. Soil respiration was measured during all rewetting periods, and then compared to total soil C content, water extractable C content, light, hydrolysable, and residual C fractions.

METHODS

Site descriptions

The soils used in this incubation study came from four loblolly pine plantations that comprise a largescale throughfall reduction x fertilization experiment. The four plantations were established at the edges of the loblolly pine range, which span the full temperature and precipitation range of the species (Figure 2.1). The sites are located in Taliaferro County, Georgia; Taylor County, Florida; McCurtain County, Oklahoma, and Buckingham County, Virginia. Among these four locations, the 30 year (1981-2010) average annual precipitation ranged from 1.1 to 1.4 m and annual temperature ranged from a low of 6.7°C to a high of 27.3°C (http://www.ncdc.noaa.gov) (Table 2.1).

For this incubation experiment soils were sampled in the control plots of each research site. More details of the field experiment can be found in Will et al. (2015). Soils in each location were comprised of Cecil-Lloyd complex (Taliaferro, Georgia), Ruston (McCurtain, Oklahoma), Littlejoe (Buckingham, Virginia), and Melvina-Moriah-Lutterloh complex (Taylor, Florida). The first three complexes are largely Ultisols, while Florida consists of a Spodosol and Alfisol. Soil samples from Georgia, Oklahoma, and Virginia contain clay to loam texture argillic or kandic horizons, while soils from Florida contain sand texture with a spodic horizon. All samples were acidic, with pH ranging from 3.6 to 6.2 (Table 2.2).

Soils were sampled at eight depths (when possible): 0-10, 10-20, 20-50, 50-100, 100-150, 150-200, 200-250 and 250-300 cm. In Georgia the Lloyd series is a fine, kaolinitic, thermic Rhodic Kanhapludult, while the Cecil series is a fine, kaolinitic, thermic Typic Kanhapludult. The Rhodic designation indicates an influence of mafic parental material on soil color. Two soil profiles were collected to 300 cm. In Oklahoma, the Ruston series is a fine-loamy, siliceous, semiactive, thermic Typic Paleudult. Two profiles were collected to 100 cm, due to shallow soil solum, with the same increments. Littlejoe is a fine, mixed, subactive, mesic Typic Hapludult. Due to shallow soil solum, two soil profiles were collected to a depth of 150 cm with the same increments. In Florida, Melvina is a sandy, siliceous, thermic Oxyaquic Alorthod; Moriah is a loamy, siliceous, superactive, thermic Aquic Arenic Hapludalf; while Lutterloh is loamy, siliceous, subactive, thermic Grossarenic Paleudalf. Due to high water table at the Florida site two soil profiles were collected to 170 cm with the same increments as used in Georgia. All these soils are typical in their respective regions. All soil series descriptions are based on USDA-NRCS Soil Survey Division (https://soilseries.sc.egov.usda.gov).

Soil physical and chemical analysis

All samples were air-dried and homogenized by sieving through a 2 mm screen. A subsample was analyzed in replicate for soil texture, pH, total C and N and water extractable C. Textural analysis followed Gee and Or (2002) and soil water pH tests followed the method of Thomas (1996) with a 1:1 soil:water ratio. For C and N analysis samples were further oven-dried at 65ºC and ball mill ground. Total C (TC) and N were analyzed on a CE Elantech NC 2100 Soil Analyzer with a detection limit of 100 ug-C/g-soil (CE Elantech Inc., Lakewood, NJ) using the Dumas method as described in Bremmer (1996).

Soil C Fractionation

All soil samples were analyzed for water extractable C (WE). Ten grams of air-dried soil was shaken with 100 ml of deionized water for one hour on a reciprocating shaker at a speed of 200 rev/min. After shaking, the extracts were filtered with Whatman No. 42 filter paper to recover solution for analysis (Jones and Willett 2006). Concentrations of dissolved organic C were determined with a Shimadzu TOC-TN analyzer (Shimadzu Corp., Kyoto, Japan). Results were then converted to mg C-WE/g soil.

Soil carbon fractionation was performed on all soil samples by combining density and hydrolytic fractionation techniques. This method was modified after Trumbore et al. (1989) and Golchin et al. (1994). Light fraction, <2.0 g/cm^3 (LF), material was physically isolated using sodium polytungstate (SPT). The remaining heavy fraction, >2.0 g/cm^3, was further fractionated by acid hydrolysis into a hydrolysable fraction (HF) and a residual fraction (RF).

Approximately 5 g of sample was placed in a 50-ml centrifuge tube with approximately 25 ml SPT. The centrifuge tubes containing soil-SPT mixture were shaken on a reciprocating shaker at 300 RPM for 15 min. Particles that were adhered to the walls and/or top of the tubes were washed back into suspension with SPT. The suspensions were allowed to stand for 30 min prior to centrifugation to prevent mechanical occlusion of light fraction particles. Suspensions were then centrifuged at 2000 RCF for 60 min. The supernatant with floating particles was decanted onto a glass fiber-filter and filtered under vacuum. Particles that had adhered to the walls of the tubes were scraped off with a spatula and washed onto the filter paper. All material was then washed off the filter paper and the LF was dried for 18 hours at 60°C and then weighed.

The remaining soil was washed with deionized water to remove SPT. Ten ml of 6 N HCl was then added to the centrifuge tubes. The tubes containing soil-acid mixture were heated in a water bath to 95°C for 18 hours. Samples were then centrifuged at 2000 RCF and supernatant decanted for analysis. The remaining residual fraction, RF, was washed repeatedly with 25 ml of deionized water and up to four of the washes were kept for analysis of residual C and N. The RF was dried at 60°C for 18 hours and weighed. The bulk samples, LF and RF were analyzed for C and N concentration by dry combustion as described above. The hydrolysable fraction was analyzed on the Shimadzu TOC-TN identified above.

Soil Incubations

Air-dried and sieved samples were used for incubation. To determine field moisture capacity for incubations soil water retention curves were determined using Tempe cells (SoilMoisture Equipment Corp., Santa Barbara, CA) and a WP4C Dewpoint PotentialMeter (Decagon Devices. Inc., Pullman, WA). Separate core samples were collected for these analyses. Tempe cells were used for <1 MPa and WP4C Dewpoint PotentialMeter was used for >1 MPa. Results from both instruments were then integrated to form soil water retention curves.

Two subsamples each weighing 100 g air-dried were placed in 1-L canning jars (Mason jars; Jarden Co., Muncie, IN) then wet to field capacity (-0.01 MPa). After wetting, jars were capped. Caps included a rubber septum for gas sampling. All samples were incubated under 35 ± 0.5°C in a Precision dual program illuminated incubator (GCA Corp., Chicago, IL). Gas samples were taken at 0, 2, 4, 8, 12, 24, 48, 72, 96 hours and so on until the CO_2 concentration in all jars stopped increasing. The jars were then opened and samples were allowed to dry. Total weight of the jar was used to assess the extent of drying. When the initial air-dry state was achieved soils were re-wetted to field capacity, capped, and re-measured for the second cycle. This cycle was repeated a third time, similar to the approach taken by Fierer et al. (2003). The 0 h reading was used as the baseline headspace CO_2 concentration. All headspace gas samples were analyzed with the LI-7000 CO_2 gas analyzer (LI-COR Inc., Lincoln, NE). Respired CO_2 during the incubations was determined by sampling the headspace gas using a 3-mL airtight syringe. Collected gas was injected into the LI-7000 CO_2 gas analyzer using compressed N_2 gas at 150 ml/min as the carrier (Zibilske 1994). Sample CO_2 concentrations were determined by using a calibration equation made by injecting the same volume of standard CO_2 gases with concentrations of 0.1, 1, 3 and 10%. To solve for CO_2 concentration in the headspace of the jar, the ideal gas equation:

$$PV = nRT$$

was used, where P is pressure in bars (constant), V is volume of gas in the jar in liters (constant), n is moles of gas in the jar, R is the gas constant in L bar/mol/K, and T is temperature in Kelvin (constant). The mass of C respired (mg) is reported.

Statistical analysis

The experimental design consisted of 4 factors: location (Georgia, Florida, Oklahoma and Virginia, fixed), depth (0-10, 10-20, 20-50, 50-100, 100-150, 150-200, 200-250 and 250-300 cm, fixed), treatment (control and drying-wetting cycles, fixed), and cycles (cycle 1, 2 and 3, fixed and repeated) with field replicates (field replicate 1 and 2, random). A mixed effect, repeated measures model was used to test for differences and account for the correlation over cycles. Tukey's significant difference test at the level of $\alpha = 0.05$ were used to separate cumulative CO_2-C/soil C content and cumulative CO_2-C/WE.

Linear regressions and stepwise regressions were used to identify soil C fractionations that significantly influenced soil respiration. All variables were transformed to obtain normal distributions before the regressions. The LF, RF, WE and TC were transformed using log transformation. The HF was transformed using square root transformation. The cumulative CO_2-C was transformed using skewed log transformation. All C fractionations and TC were analyzed for correlations. The SAS statistical package (SAS Institute Inc., Cary, North Carolina) was used for all data analyses.

RESULTS

Distribution of C

The highest TC concentrations of all four sites were in 0-10 cm soils, ranging from 1.29-3.89% C (Table 2.2). The C content dropped off rapidly in the upper 1 m to ~0.22 to 0.32%. Below 1 m, the C% remained between 0.05-0.09%, with the exception of 150-170 cm Florida soil that had a 0.33% C, indicating a spodic horizon. The surface soils (0-20 cm) contained ~41% of the total C stock, subsurface soils (20-100 cm) ~35%, and deep soils (100-300 cm) ~24%.

Of the TC in the profile, the WE proportion generally increased with depth (Table 2.3). In Georgia, the proportion of WE to TC varied from about 3% for soils above 1m to ~13% for soils below 1m. In Florida and Virginia, the proportion of WE to TC was ~1% throughout the profile, while in Oklahoma it was ~3% throughout.

The LF concentration of all profiles decreased rapidly with depth (Table 2.3). Georgia soils had the most dramatic change decreasing from 10,550 mg/kg (0-10 cm) to 22 mg/kg (250-300 cm). The LF of Oklahoma soils ranged from 4,421 – 392 mg/kg while in Florida and Virginia soils had similar LF concentrations at ~9,000 mg/kg in the surface and ~200 mg/kg in the deepest layer. The LF as a proportion of TC showed a generally decreasing trend over depth, with ~ 40% of C as LF at the surface decreasing to ~10% at depth.

The HF of all profiles varied from ~3,000 mg/kg at the surface to ~400 mg/kg at 1m (Table 2.3). In Georgia soil below 1m, HF decreased to ~ 150 mg/kg. In the Florida spodic horizon, HF was 1,105 mg/kg, much higher than the soils above. There is a generally increasing trend in the proportion of HF to TC with depth. The proportions varied from ~15% at the surface to ~40% at depth.

The RF concentration decreased with depth in all profiles (Table 2.3). Georgia 0-10 cm had the highest RF of 9,655 mg/kg and declined to 318 mg/kg at 2-3 m. RF of Florida and Oklahoma surface soils were ~3,000 mg/kg, while RF of Virginia surface soil was 7,529 mg/kg. At ~1m, RF of Oklahoma and Virginia soils were ~1,000 mg/kg, while RF of Florida dropped to ~500 mg/kg at ~1 m, then increased to 1,616 mg/kg at 150-170 cm. The proportion of RF compared with TC increased with depth. In Georgia the proportions increased from ~50% to ~60% with depth and in Oklahoma the increase was from ~20% to ~30%. In Florida and Virginia, these proportions varied from <20% at the surface to ~60% at depth.

Cumulative CO_2-C

Rates of cumulative CO_2-C differed among locations ($p=0.0434$) with fluxes in Florida generally being greatest and Georgia being lowest (Figure 2.2). For all sites, cumulative CO_2-C was greatest in 0-10 cm soils, ranging from 212 mg (Oklahoma) to 115 mg (Florida) per 100 g of soil, and generally decreased over depth to rates of <1 mg-CO_2-C/100 g of soil. The exception was for Florida 150-170 cm soil, which was the spodic horizon and had greater soil respiration than the horizons above. Difference in respiration among depths was significant ($p<0.001$). At all depths soil respiration was measurable after drying and re-wetting. This was even observed at the deepest depth: 250-300 cm in Georgia (Figure 2.2).

Carbon lost through soil respiration was generally greatest during the first cycle (accounting for 31-66% of cumulative C loss) and declined thereafter (Figure 2.2). Two exceptions were 0-10 cm soil samples from Georgia where soil released more C during the second cycle (21 mg CO_2-C/100 g of soil) than the first cycle (20 mg CO_2-C/100 g of soil) and the 0-10 cm soil samples from Florida where more C was released during the third cycle (21 mg CO_2-C/100 g of soil) compared to the earlier cycles (19 and 18 mg CO_2-C/100 g of soil). Such increases over drying-wetting cycles were not observed in the subsurface soils.

Increased soil respiration with drying-wetting cycles compared to those that were constantly moist was not consistently observed (Figure 2.2) and the treatment effect was not significant ($p=0.7594$). However, for Georgia soils below 20 cm, Florida 10-20 and 50-100 cm soils, Oklahoma soils between 0-50 cm, and Virginia soils between 10-100 and 150-200 cm, drying-wetting cycles stimulated greater (not significantly different) soil respiration than ones that were constantly moist.

CO_2-C in relation to TC

For 0-100 cm soils, cumulative CO_2-C as a proportion of TC decreased with depth (Figure 2.3). Below 100 cm, however, these proportions had increasing trends with depth (with the exception of Florida 150-170 cm soil). In general, cumulative CO_2-C as a proportion of TC content was greater below 100 cm than soil above 100 cm (Figure 2.3). In Georgia, total soil respiration over the three cycles accounted for 1.3 – 3.4% of TC in the upper 100 cm. Below this depth, total soil respiration over the three cycles accounted for 3.7-5.6% of total soil C. Soils from Florida and Virginia showed similar trends. Total soil respiration over the three cycles accounted for 0.9 – 2.9% of TC in the upper 100 cm in Florida soil but 1.1-3.1% in the soils below 100 cm. In Virginia, 1.9-2.7% of TC was released above 100 cm while soil below 100 cm respired 2.8-5.6% of TC. The depth effect was significant for all locations ($p<0.001$).

CO_2-C in relation to soil C fractions

In general, cumulative CO_2-C as a proportion of water extractable carbon decreased over repeated drying-wetting cycles and with depth (Fig. 2.4). Cumulative CO_2-C as a proportion of WE carbon exceeded 100% in 58% of all samples, including Georgia 0-10 cm, Florida 0-10, 10-20, 20-50, 150-200 cm, and all depths of Oklahoma and Virginia soils, except 100-150 cm (Fig. 4). The CO_2-C:WE carbon proportion reached 506% in Florida 0-10 cm soils.

All C fractionations were significantly correlated with each other and with TC ($p<0.0001$). All fractions were also significant predictors of soil respiration ($p<0.0001$). Across all samples WE explained ~35% of the variance in cumulative CO_2-C over 3 cycles (i.e., $R^2=0.35$) (Table 2.4 and Fig. 2.5). Among the components of the C fractionation, the LF accounted for 54%, RF for 72%, and the HF for 75% of the variance in CO_2-C respired (Table 2.4 and Fig. 2.5). TC, however, had a greater predictive value individually (R^2=0.80) than all the other C fractions. Stepwise regression indicated that the combined model of TC and WE was the best fit for cumulative CO_2-C (R^2=0.82).

DISCUSSION

Results from this study do not support the hypothesis that drying-wetting cycles in deep soil stimulate soil respiration. In many previous studies focusing on surface soils, drying-wetting cycles have increased soil respiration (Birch 1958, Jager and Bruins 1975, Clein and Schimel 1994, Franzluebbers et al. 2000, Fierer and Schimel 2002, Beare et al. 2009, Butterly et al. 2010). Increased CO_2 losses in previous studies, however, have not been universally observed. For example, Fierer and Schimel (2002) reported that total CO_2 loss during incubations significantly increased with the number of drying-wetting events for oak forest soils but not for grassland soils, where drying-rewetting events decreased total soil respiration. Similar declines in soil respiration with drying-rewetting have been observed in a loamy sand soil with shoot material of *Lolium perenne* mixed in and a silt loam soil on a farm in Kansas (Magid et al. 1999, Mikha et al. 2005).

Despite the relative acceptance of the Birch effect, previous research suggests that the effect of drying-wetting cycles on soil respiration varies greatly. There have been a few reports (Franzluebbers et al. 1994, Curtin et al. 1998, Kruse et al. 2004) that were consistent with results from this study. For example, three soil series in the Southeast U.S. studied by Kruse et al. (2004), showed mixed results similar to the current study: the drying-wetting treatment decreased cumulative soil respiration on an Orangeburg sandy loam (fine-loamy, kaolinitic, thermic, Typic Kandiudults); while it increased cumulative soil respiration on a Norfolk depressional sandy loam (fine-loamy, kaolinitic, thermic, Arenic Kandiudults); and had no effect on a Norfolk loamy sand (coarse-loamy, kaolinitic, thermic, Typic Kandiudults).

Previous research has mainly focused on surface soil (<20 cm) responses of drying-wetting (Mikha et al. 2005, Wu and Brookes 2005, Butterly et al. 2010); a few studied subsurface soils (20-100 cm) (Nelson et al. 1998, Xiang et al. 2008); and even fewer studied deep soil C (>100 cm) (Trumbore et al. 1995, Fierer et al. 2003). Data similar to that of the current study are rare in demonstrating a potentially active microbial community and active C pool, as evidenced by soil respiration, down to as much as three meters. Responses observed in surface and deep soils may differ, however, as showed by results of one previous study where moderate drought (-1.5 and -5 MPa) had a larger relative impact on the rates of C mineralization from surface compared to deep soil horizons (Fierer et al. 2003). Results of the current study also showed differences but here soils below 1 m respired more C as a proportion of the total soil C pool than soils above 1 m, indicating deep soils may respond differently to drying-wetting cycles than surface soils.

Mechanistically, surface and deep soils may differ in a number of ways. For example, the breakdown of soil aggregates in surface soils and the release of previously physically protected soil organic matter may result in increased soil respiration. In deep soil, however, aggregation does not occur to as great a degree as in surface soils (Adu and Oades, 1978). Furthermore, even in the event of physical alteration of soils by wetting and drying, deep soils may lack a supply of fresh or microbially available C that may limit soil respiration in deep soils (Fontaine et al. 2007). Finally, even if labile or microbially available C is made available at depth it is possible that microbes may be nutrient limited (note N concentrations in Table 2.2) due to extremely low soil nutrient concentrations (Fierer and Schimel, 2003). Thus, after rewetting an increase in microbial turnover may be truncated by a stoichiometric imbalance of C to required nutrients (Kieft et al. 1987b).

Considering the amount of C stored in deep soils and the potential contribution of deep soil respiration to atmospheric CO_2, there is a need to estimate the potential total respiration. To estimate the soil C respiration at any depth, TC was the best indicator for cumulative soil CO_2-C respiration (R^2=0.80), with additional information gained from WE (R^2=0.82). The WE alone only explained 35% of C respired (Table 2.4 and Figure 2.5). In the majority of these incubations, soil C respired exceeded WE carbon, the readily available C, indicating there are other microbially available C pools than WE. The LF is another rapidly cycling C pool and can contribute significantly to soil respiration (Trumbore 2000). However, there is very little LF at depth. For example, in the Georgia soil tested below 50 cm, there is <100 mg/kg LF. Therefore, the LF could not explain the total amount of C respired at depth (R^2=0.54). The RF is not thought to be particularly microbially available (Trumbore et al. 1989), however, in this study RF is well correlated with cumulative CO_2-C respired (R^2=0.72). This could be caused by the strong correlation between C fractions ($p<0.0001$). Among all C fractions, HF had the best fit for cumulative CO_2-C (R^2=0.75) (Table 2.4 and Figure 2.5). Previous research using similar acid extraction methods for HF have found this C pool to be correlated with rates of C decomposition (Rovira and Vallejo 2002, Silveira et al. 2008). As such, we suggest that in the high clay content Ultisols and Alfisols of the Southeast (Table 2) the C adsorbed to clay surfaces, which is well represented by HF, might be the best indicator for soil respiration at depth.

Despite their low C content, subsoil horizons contain more than half of the global soil C stock (Harrison et al., 2011; Koarashi et al., 2012; Harper and Tibbett, 2013). The soil C stock corresponds to 699 Pg C in the top 0.2 m layer, 716 Pg C in 0.2-1 m layer, 491 Pg C in 1-2 m layer, and 351 Pg C to the depth of 3 m. Together, this soil C pool is larger than the biomass C pool and atmospheric CO_2-C pool combined (Scharlemann et al. 2014). Specifically, for the soils tested in this study, there was an average of 41% of C stored in the top 0.2 m layer, 35% in the 0.2-1 m layer, and 24% in the 1-3 m layer. The amount of cumulative soil respiration with the drying and wetting treatments from the top 0.2 m layer contributed 50%, the 0.2-1 m layer 29%, and the 1-3 m layer 21%. Thus, although soil moisture changes in deep soil did not consistently impact soil respiration, these soils could contribute substantially to atmospheric CO_2.

CONCLUSION

Drying-wetting cycles did not have a consistent effect of enhancing soil carbon loss in these four Southeast U.S. soil profiles investigated. Many sub (0.2 – 1 m) and deep (<1 m) soils of this region have high (>30%) clay contents and low soil C concentrations that may render this deep soil carbon insensitive to more severe drying-wetting cycles. The carbon enriched, subsurface spodic horizon encountered in this study was an exception, having increased soil respiration with drying-rewetting. Spodosols are common in the coastal plains of the Southeast U.S. (and in many northern temperate forests), store significant amounts of C, and thus may deserve further attention. Across all soils studied, drying-wetting cycles in deep soils induced greater C loss as a proportion of total soil C than surface soils. Across all depths, the total C was the best predicator for soil C respiration, with water extractable C adding some information. In clay-rich subsoils, the acid extractable, hydrolysable C fraction may be most informative. Considering the amount of C stored in deep soils and the differences in responses observed here, deep soils could contribute substantially to atmospheric CO_2.

REFERENCES

Batjes, N. H. 1996. Total carbon and nitrogen in the soils of the world. European Journal of Soil Science **47**:151-163.

Beare, M. H., E. G. Gregorich, and P. St-Georges. 2009. Compaction effects on CO_2 and N_2O production during drying and rewetting of soil. Soil Biology & Biochemistry **41**:611-621.

Birch, H. F. 1958. Pattern of humus decomposition in East African soils. Nature **181**:788-788.

Borken, W., and E. Matzner. 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Global Change Biology **15**:808-824.

Bremner, J. M. 1996. Nitrogen - total. Methods of Soil Analysis Part 3—Chemical Methods **sssabookseries**:1085-1121.

Butterly, C. R., P. Marschner, A. M. McNeill, and J. A. Baldock. 2010. Rewetting CO_2 pulses in Australian agricultural soils and the influence of soil properties. Biology and Fertility of Soils **46**:739-753.

Butterly, C. R., A. M. McNeill, J. A. Baldock, and P. Marschner. 2011. Changes in water content of two agricultural soils does not alter labile P and C pools. Plant and Soil **348**:185-201.

Clein, J. S., and J. P. Schimel. 1994. Reduction in microbial activity in birch litter due to drying and rewetting events. Soil Biology & Biochemistry **26**:403-406.

Curtin, D., F. Selles, H. Wang, C. A. Campbell, and V. O. Biederbeck. 1998. Carbon dioxide emissions and transformation of soil carbon and nitrogen during wheat straw decomposition. Soil Science Society of America Journal **62**:1035-1041.

Fierer, N., A. S. Allen, J. P. Schimel, and P. A. Holden. 2003. Controls on microbial CO_2 production: a comparison of surface and subsurface soil horizons. Global Change Biology **9**:1322-1332.

Fierer, N., and J. P. Schimel. 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biology & Biochemistry **34**:777-787.

Fontaine, S., S. Barot, P. Barre, N. Bdioui, B. Mary, and C. Rumpel. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature **450**:277-U210.

Franzluebbers, A. J., R. L. Haney, C. W. Honeycutt, H. H. Schomberg, and F. M. Hons. 2000. Flush of carbon dioxide following rewetting of dried soil relates to active organic pools. Soil Science Society of America Journal **64**:613-623.

Franzluebbers, K., R. W. Weaver, A. S. R. Juo, and A. J. Franzluebbers. 1994. Carbon and nitrogen mineralization from cowpea plants part decomposing in moist and in repeatedly dried and wetted soil. Soil Biology & Biochemistry **26**:1379-1387.

Gee, G. W., and D. Or. 2002. 2.4 Particle-size analysis. Methods of Soil Analysis: Part 4 Physical Methods **sssabookseries**:255-293.

Golchin, A., J. M. Oades, J. O. Skjemstad, and P. Clarke. 1994. Study of free and occluded particulate organic-matter in soils by solid-state 13C CP/MAS NMR-spectroscopy and scanning electron-microscopy. Australian Journal of Soil Research **32**:285-309.

Harrison, R. B., P. W. Footen, and B. D. Strahm. 2011. Deep Soil Horizons: Contribution and Importance to Soil Carbon Pools and in Assessing Whole-Ecosystem Response to Management and Global Change. Forest Science **57**:67-76.

Jager, G., and E. H. Bruins. 1975. Effect of repeated drying at different temperatures on soil organic matter decomposition and characteristics, and on soil microflora. Soil Biology & Biochemistry **7**:153-159.

Jones, D. L., and V. B. Willett. 2006. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. Soil Biology and Biochemistry **38**:991-999.

Kieft, T. L., E. Soroker, and M. K. Firestone. 1987a. Microbial Biomass Response to a Rapid Increase in Water Potential When Dry Soil is Wetted. Soil Biology & Biochemistry **19**:119-126.

Kieft, T. L., E. soroker, and M. K. firestone. 1987b. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biology and Biochemistry **19**:119-126.

Kruse, J. S., D. E. Kissel, and M. L. Cabrera. 2004. Effects of drying and rewetting on carbon and nitrogen mineralization in soils and incorporated residues. Nutrient Cycling in Agroecosystems **69**:247-256.

Magid, J., C. Kjaergaard, A. Gorissen, and P. J. Kuikman. 1999. Drying and rewetting of a loamy sand soil did not increase the turnover of native organic matter, but retarded the decomposition of added C-14-labelled plant material. Soil Biology & Biochemistry **31**:595-602.

Meehl, G. A., C. Tebaldi, H. Teng, and T. C. Peterson. 2007. Current and future U.S. weather extremes and El Nino. Geophysical Research Letters **34**:1-6.

Mikha, M. M., C. W. Rice, and G. A. Milliken. 2005. Carbon and nitrogen mineralization as affected by drying and wetting cycles. Soil Biology & Biochemistry **37**:339-347.

Nelson, P. N., J. A. Baldock, and J. M. Oades. 1998. Changes in dispersible clay content, organic carbon content, and electrolyte composition following incubation of sodic soil. Soil Research **36**:883-898.

Orchard, V. A., and F. J. Cook. 1983. Relationship between soil respiration and soil-moisture. Soil Biology & Biochemistry **15**:447-453.

Rovira, P., and V. R. Vallejo. 2002. Labile and recalcitrant pools of carbon and nitrogen in organic matter decomposing at different depths in soil: an acid hydrolysis approach. Geoderma

107:109-141.

Scharlemann, J. P. W., E. V. J. Tanner, R. Hiederer, and V. Kapos. 2014. Global soil carbon: understanding and managing the largest terrestrial carbon pool. Carbon Management **5**:81-91.

Seager, R., A. Tzanova, and J. Nakamura. 2009. Drought in the Southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. Journal of Climate **22**:5021-5045.

Silveira, M. L., N. B. Comerford, K. R. Reddy, W. T. Cooper, and H. El-Rifai. 2008. Characterization of soil organic carbon pools by acid hydrolysis. Geoderma **144**:405-414.

Solomon, S., D. Qin, M. Manning, M. Marquis, K. Averyt, M. M. B. Tignor, H. L. Miller, Jr., and Z. Chen. 2007. Climate change 2007; the physical science basis; contribution of Working Group I to the Fourth Assessment Report of the Intergovernamental Panel on Climate Change. Cambridge University Press : Cambridge, United Kingdom, United Kingdom.

Thomas, G. W. 1996. Soil pH and soil acidity. Methods of Soil Analysis Part 3—Chemical Methods **sssabookseries**:475-490.

Trumbore, S. 2000. Age of soil organic matter and soil respiration: Radiocarbon constraints on belowground C dynamics. Ecological Applications **10**:399-411.

Trumbore, S. E., E. A. Davidson, P. B. Decamargo, D. C. Nepstad, and L. A. Martinelli. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochemical Cycles **9**:515-528.

Trumbore, S. E., J. S. Vogel, and J. R. Southon. 1989. AMS 14C measurements of fractionated soil organic matter: an approach to deciphering the soil carbon cycle. Radiocarbon **31**:644-654.

Trumbore, S. E., and S. H. Zheng. 1996. Comparison of fractionation methods for soil organic matter 14C analysis. Radiocarbon **38**:219-229.

Will, R. E., T. Fox, M. Akers, J. C. Domec, C. Gonzalez-Benecke, E. J. Jokela, M. Kane, M. A. Laviner, G. Lokuta, D. Markewitz, M. A. McGuire, C. Meek, A. Noormets, L. Samuelson, J. Seiler, B. Strahm, R. Teskey, J. Vogel, E. Ward, J. West, D. Wilson, and T. A. Martin. 2015. A range-wide experiment to investigate nutrient and soil moisture interactions in loblolly pine plantations. Forests **6**:2014-2028.

Wu, J., and P. C. Brookes. 2005. The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. Soil Biology & Biochemistry **37**:507-515.

Xiang, S.-R., A. Doyle, P. A. Holden, and J. P. Schimel. 2008. Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. Soil Biology and Biochemistry **40**:2281-2289.

Zibilske, L. M. 1994. Carbon mineralization 1. Methods of Soil Analysis: Part 2—Microbiological and Biochemical Properties **sssabookseries**:835-863.

Table 2.1. Research site attributes with 30-year (1981-2010) average climate data (http://www.ncdc.noaa.gov).

Location	Latitude	Longitude	Average Max Temp (°C)	Average Min Temp (°C)	Average Precipitation (m)	Soil Series
Taliaferro, Georgia	33˚37’35” N	82˚47’54” W	22.7	10.1	1.1	Lloyd-Cecil
Taylor, Florida	30˚12’22” N	83˚52’12” W	27.3	13.6	1.4	Melvina-Moriah-Lutterloh
McCurtain, Oklahoma	34 ˚01’47” N	94˚49’23” W	23.9	9.4	1.3	Ruston
Buckingham, Virginia	37˚27’37” N	78˚39’50” W	19.4	6.7	1.1	Littlejoe

Table 2.2. Physical and chemical properties of soils from research locations at Taliaferro County, Georgia; Taylor County, Florida; McCurtain County, Oklahoma, and Buckingham County, Virginia. Values given as mean ± 1SE (n=2).

Location	Depth (cm)	Texture	pH	C (%)	N (%)
Georgia	0-10	loam	5.5±0.5	1.92±0.67	0.10±0.03
	10-20	clay loam	5.4±0.2	0.87±0.26	0.06±0.01
	20-50	clay	5.4±0.1	0.44±0.13	0.04±0.00
	50-100	clay	5.2±0.4	0.25±0.02	0.03±0.00
	100-150	clay	5.8±0.0	0.07±0.03	0.00±0.00
	150-200	clay loam	5.6±0.1	0.06±0.03	0.00±0.00
	200-250	clay loam	5.4±0.3	0.05±0.02	0.00±0.00
	250-300	loam	5.3±0.2	0.05±0.01	0.01±0.00
Florida	0-10	sand	5.5±0.2	2.06±0.36	0.07±0.02
	10-20	sand	5.6±0.1	1.30±0.10	0.04±0.01
	20-50	sand	5.8±0.3	0.62±0.09	0.02±0.00
	50-100	sand	6.2±0.4	0.22±0.03	0.01±0.00
	100-150	sandy clay loam	5.2±0.1	0.07±0.01	0.00±0.00
	150-170	sandy clay loam	4.8±0.3	0.33±0.03	0.00±0.00
Oklahoma	0-10	loam	4.8±0.5	1.29±0.25	0.07±0.03
	10-20	loam	4.2±0.2	0.43±0.12	0.04±0.01
	20-50	loam	3.9±0.0	0.32±0.14	0.03±0.00
	50-100	clay loam	3.6±0.2	0.29±0.03	0.03±0.01
Virginia	0-10	silt loam	4.2±0.1	3.89±0.54	0.14±0.03
	10-20	loam	4.5±0.3	1.00±0.24	0.04±0.01

	20-50	silty clay	4.5±0.4	0.52±0.16	0.03±0.00
	50-100	silty clay loam	4.9±0.1	0.23±0.05	0.02±0.00
	100-150	silty clay loam	4.9±0.0	0.09±0.01	0.00±0.00

Table 2.3. C fractionation of soils from four research locations at Taliaferro County, Georgia; Taylor County, Florida; McCurtain County, Oklahoma, and Buckingham County, Virginia. Values given are mean ± 1SE (n=2).

Location	Depth (cm)	Water Extractable C (mg/kg)	Light Fraction (mg/kg)	Hydrolysable Fraction (mg/kg)	Residual Fraction (mg/kg)
Georgia	0-10	504±25.4	10550±2609	3411±682	9655±1793
	10-20	275±25.5	4395±958	2043±178	3193±512
	20-50	157±14.2	1711±1630	1162±365	1271±471
	50-100	94.8±9.1	92.9±37.3	327.2±87.5	594±135
	100-150	85.8±8.2	87.9±31.3	205.0±12.9	404±86.9
	150-200	82.6±7.1	68.2±9.7	230.5±29.3	381±62.2
	200-250	71.3±2.7	69.3±24.5	151.7±17.8	318±63
	250-300	68.8±5.5	21.6±22.8	126±23.8	319±12.3
Florida	0-10	117±19.3	9217±3146	2138±579	2843±1165
	10-20	86.7±8.5	4701±1631	1721±368	2153±534
	20-50	52.4±1.7	2390±1200	1188±157	1249±225
	50-100	39.8±1.1	1585±6.8	374±73.4	475±85.4
	100-150	30.1±1.0	3503±1147	370±140	481±183
	150-170	33.5±0.5	208.3±0	1105±14.9	1616±22.5
Oklahoma	0-10	299±16.2	4421±1279	2420±656	3133±625
	10-20	205±2.5	1669±468	1597±318	1439±148
	20-50	139±17.2	901±436	1211±130	1121±120
	50-100	92.2±1.7	393±334	486±315	917±265
Virginia	0-10	228±68.5	9596±8697	2726±871	7529±4754

10-20	80.4±17.2	2622±2385	1737±547	2822±1262
20-50	31.7±1.7	724±145	10909±158	1540±251
50-100	22.7±0.2	162±47.7	791±361	1032±128
100-150	20.4±0.4	135±80.3	406±53.1	610±134

Table 2.4. Models of single linear regressions and stepwise regression used to compare fractionations of C (LF, HF, RF, and WE) and TC with cumulative CO_2-C. All data were transformed into normal distributions. LF is the light fraction, HF is the hydrolysable fraction, RF is the residual fraction, WE is the water-extractable C and TC is the total C. Coefficient of determination (R^2) and root mean square error (RMSE) values are reported.

Variables	Regression Equation	R^2	RMSE
TC	$y = -3.15343 + 1.36745 * \log(TC)$	0.8002	0.40279
WE	$y = -1.10988 + 1.43943 * \log(WE)$	0.3475	0.72783
LF	$y = -0.49780 + 0.76793 * \log(LF)$	0.5369	0.61317
HF	$y = -0.00981 + 0.05358 * \text{sqrt}(HF)$	0.7527	0.44806
RF	$y = -3.77832 + 1.77580 * \log(RF)$	0.7230	0.47423
TC and WE	$y = -3.44557 + 1.23974 * \log(TC) +0.38203 * \log(WE)$	0.8177	0.38942

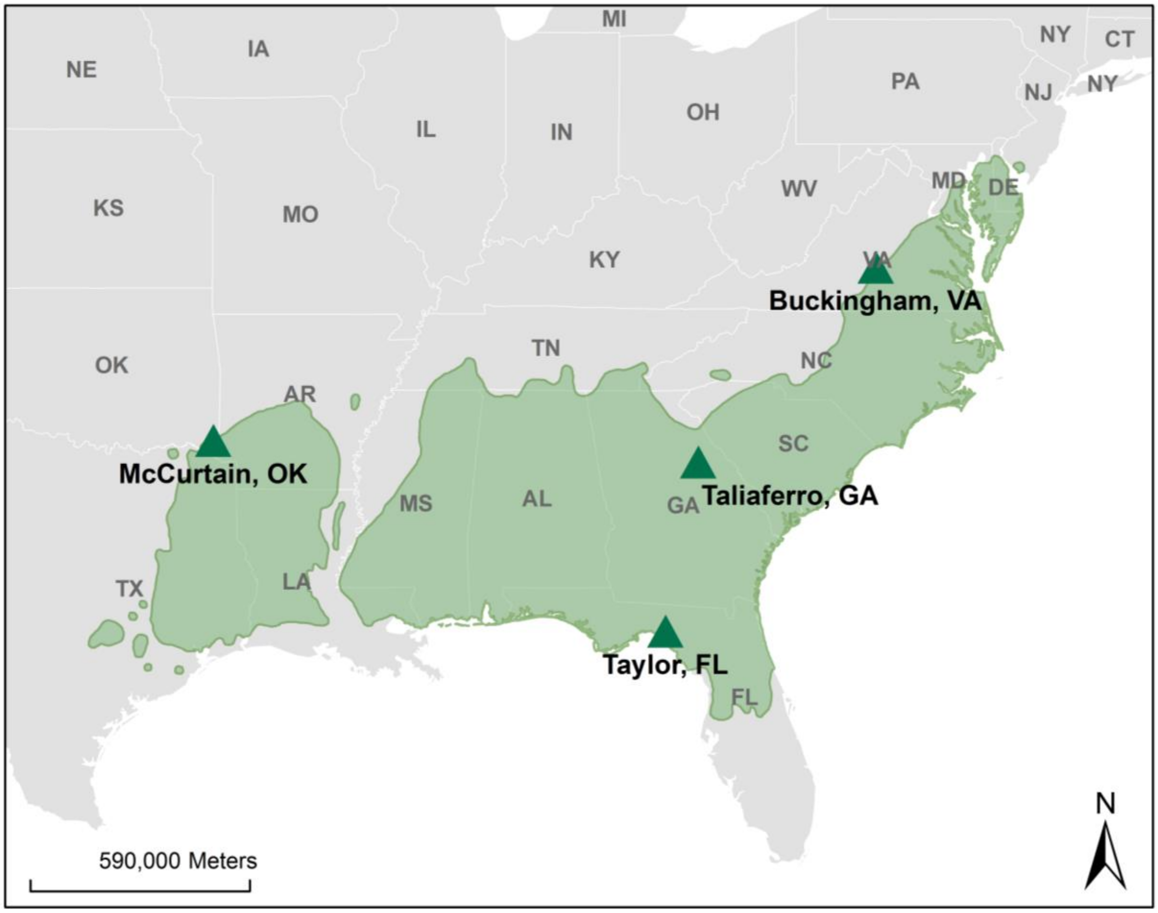

Figure 2.1. Research site locations at Taliaferro County, Georgia; Taylor County, Florida; McCurtain County, Oklahoma, and Buckingham County, Virginia indicated by dark green triangles. Light green shadow area indicates the native range of loblolly pine (http://esp.cr.usgs.gov/data/little/).

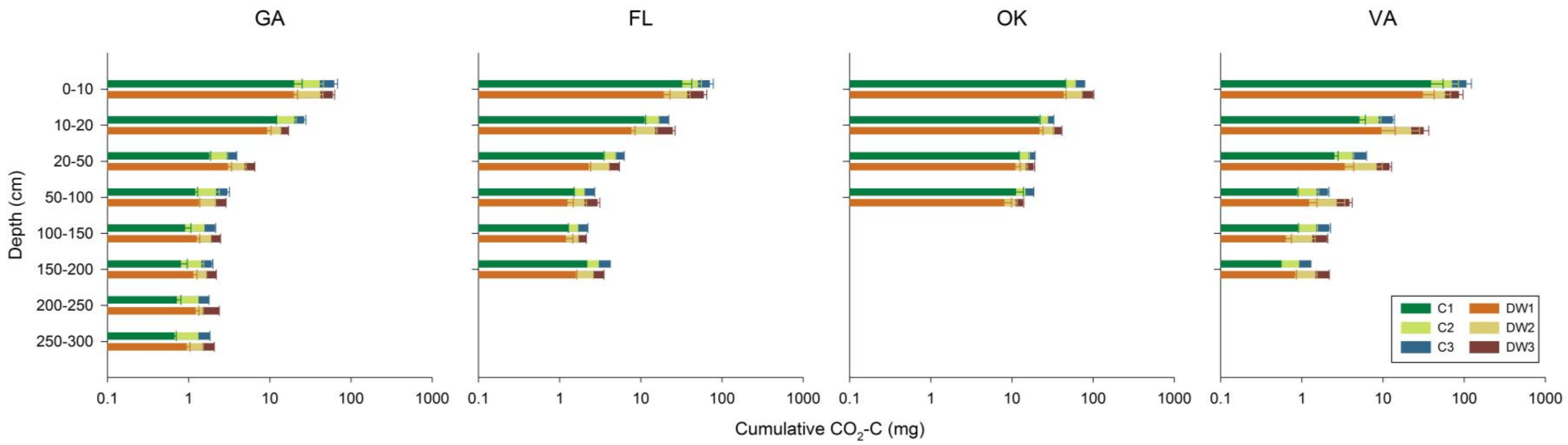

Figure 2.2. Comparison of cumulative CO2-C during soil incubations over control and three drying-wetting cycles. Three control cycles are indicated by C1, C2, and C3. Three drying-wetting cycles are indicated by DW1, DW2, and DW3. Error bars represent ±1SE (n=2).

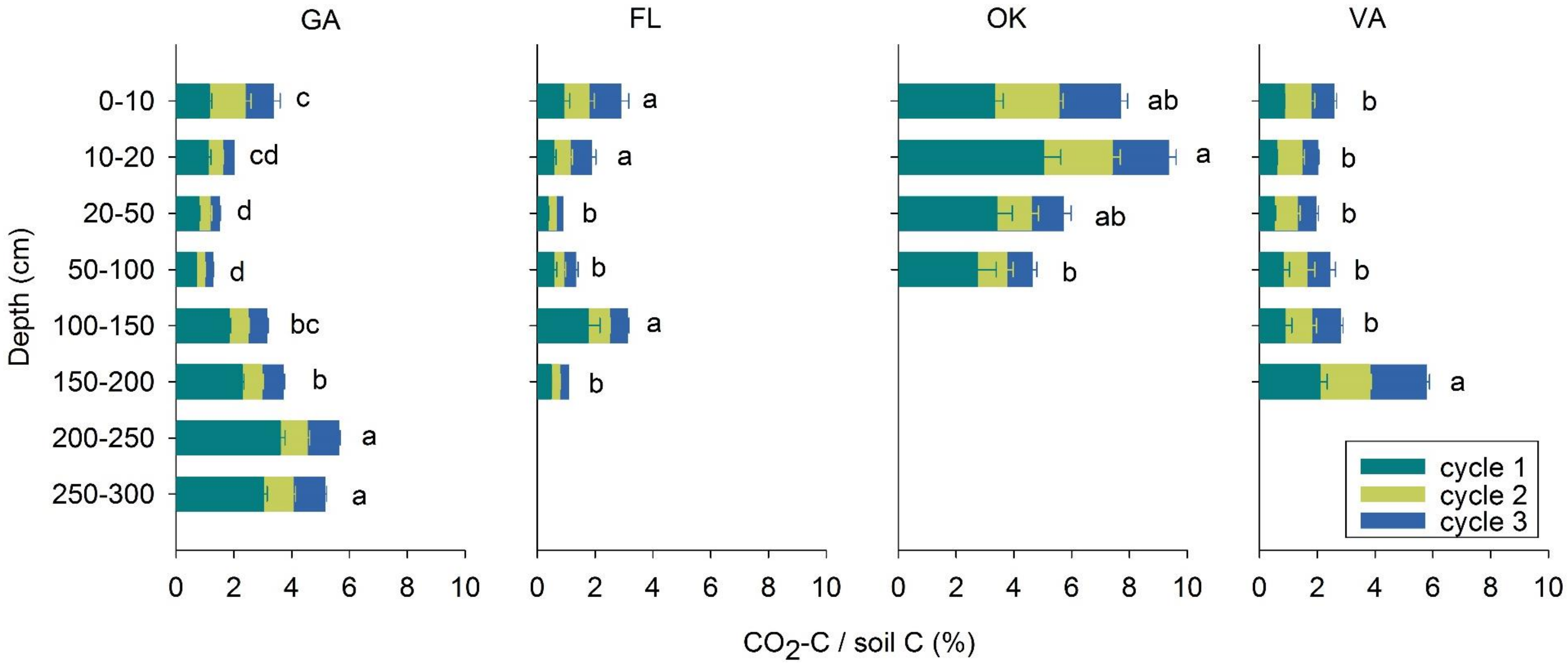

Figure 2.3. Cumulative CO_2–C as a proportion of total soil C content over drying-rewetting cycles. Three drying-wetting cycles are indicated as cycle 1, cycle 2, and cycle 3. Error bars represent ±1SE (n=2). Cumulative CO_2-C/soil C content of three cycles were separated using Tukey's significant difference test at the level of α = 0.05. The dissimilar letters next to bars are used to indicate significant differences between depths within a site.

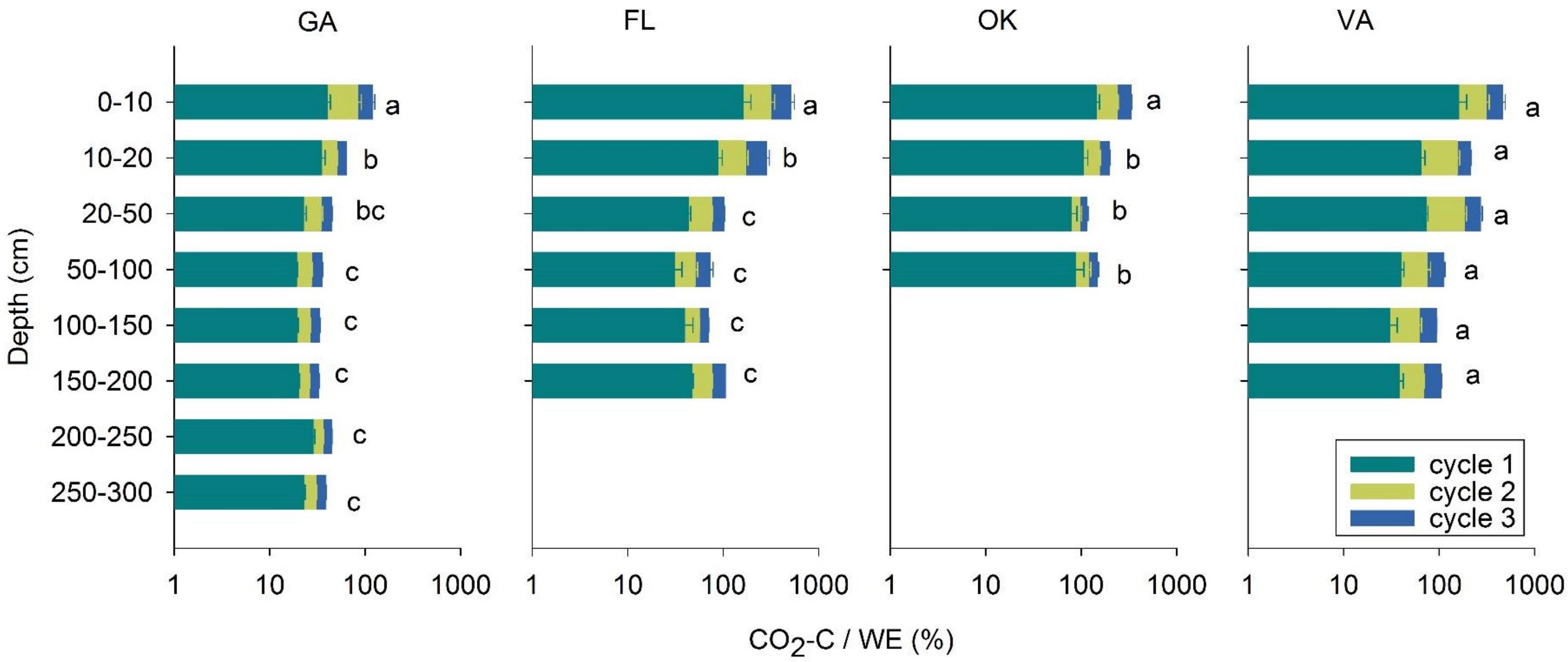

Figure 2.4. Cumulative CO_2–C as a proportion of soil water-extractable C (WE) over drying-rewetting cycles. Three drying-wetting cycles are indicated as cycle 1, cycle 2, and cycle 3. Error bars represent ±1SE (n=2). Cumulative CO_2-C/WE content of three cycles were separated using Tukey's significant difference test at the level of $\alpha = 0.05$. The dissimilar letters next to bars are used to indicate significant differences between depths within a site.

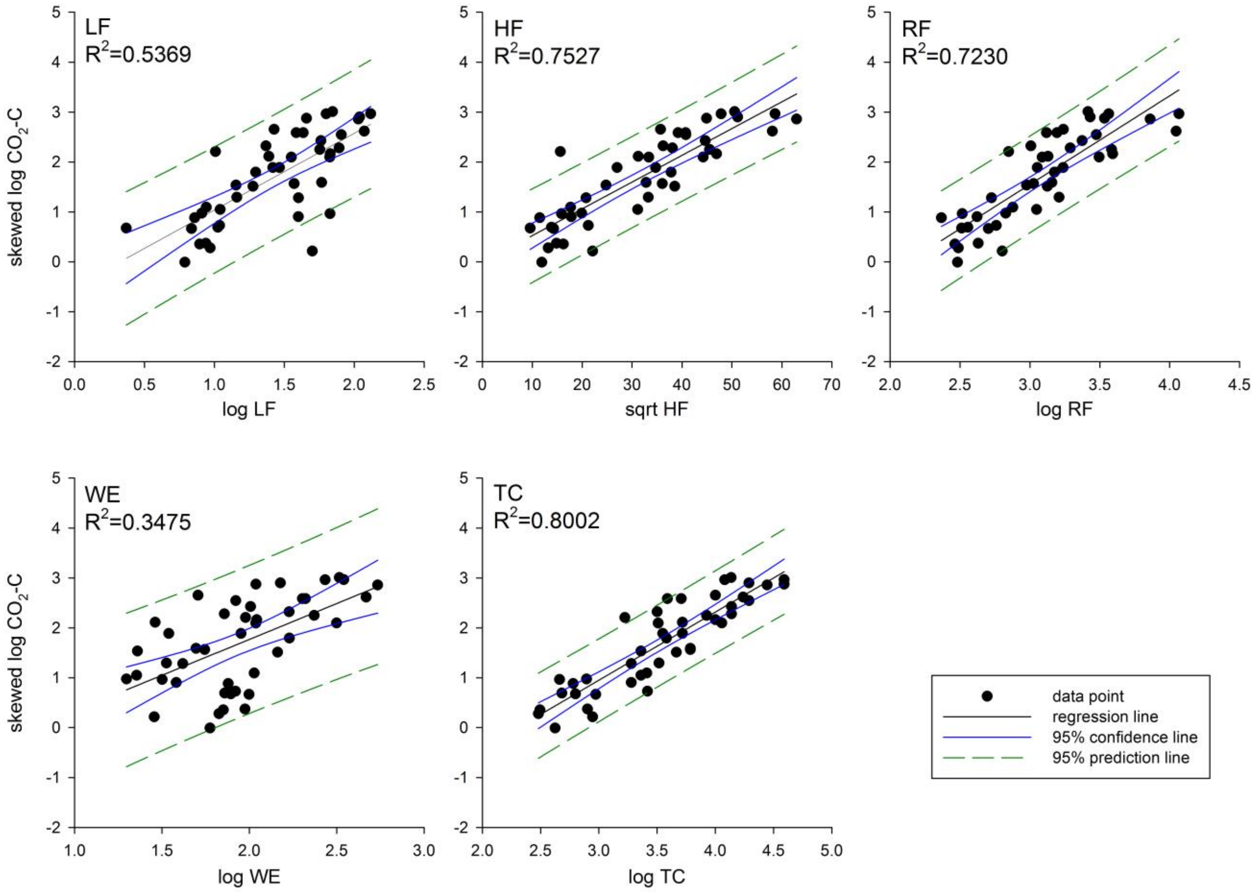

Figure 2.5. Fractionations of C: light fraction (LF), hydrolysable fraction (HF), residual fraction (RF), and water-extractable fraction (WE) and total C (TC), compared with cumulative CO_2-C using linear regression. All data were transformed to normal distributions. R^2 values are reported. Black dots indicate data points. Solid black lines indicate regression lines. Solid blue lines indicate 95% confidence lines. Dashed green lines indicate 95% prediction.

CHAPTER 3

THROUGHFALL REDUCTION X FERTILIZATION: EFFECT ON DEEP SOIL WATER USAGE IN A LOBLOLLY PINE PLANTATION OF THE SOUTHEAST U.S.

---

[1] J. Qi, D. Marekwitz, M. McGuire, L. Samuelson, and E. Ward. To be submitted to *Forest Ecology and Management*.

ABSTRACT

Forests in the Southeast U.S. are predicted to experience a moderate decrease in precipitation inputs that may result in soil water deficiency during the growing season. The potential impact of a drier climate on the productivity of managed loblolly pine plantations in the Southeast U.S. is uncertain. Access to water reserves in deep soil during drought periods may help buffer these forests from the effects of water deficits. To better understand the potential impact of drought on deep soil water, we studied the combined effects of throughfall reduction and fertilization on soil water usage to a depth of 3 m in a 6-year-old loblolly pine plantation by applying a throughfall reduction treatment (ambient versus ~30% throughfall reduction) and a fertilization treatment (no fertilization versus fertilization). Fertilization lowered soil moisture for all depths and differences were significant at 0.3-0.6 m (2.9%, $p<0.0001$) and 1.94-3.06 m (4.5%, $p<0.0001$). Throughfall reduction also lowered soil moisture for all depths and differences were significant in the surface soils (0-0.3 m) (1.2-3.6%) and deep soils (below 2 m) (2.6-3.6%). Fertilization significantly decreased 0.1-0.9 m soil water when combined with the throughfall reduction treatment. Soils of all depths were rarely depleted of plant available water, with the exception of 0-0.1 m mainly during the growing season. Under throughfall reduction treatment, soil below 0.9 m consistently accounted for more than half of the change in plant available water during months when evapotranspiration exceeded precipitation. Soil water storage can satisfy evapotranspirational demand in the face of increasing dryness in this clay rich Piedmont soil when considering the whole soil profile.

Keywords: deep soil, soil moisture, drought, fertilization

INTRODUCTION

Deep root (>1 m) water uptake plays an important role in forest ecosystems during drought (Nepstad et al. 1994, Fensham and Fairfax 2007, Padilla and Pugnaire 2007, Maeght et al. 2013). Drought stresses plants and lowers productivity (Borken and Matzner 2009) and access to deep water reserves can buffer plants from these stresses (Belk et al. 2007). Predicting plant responses to a changing climate requires an understanding of deep soil water access under drought conditions.

Forests in the Southeast U.S. are predicted to experience more variable precipitation in the future with up to three times more extreme daily precipitation events (a daily amount that occurs once in 20 years) (Meehl et al. 2007, Kunkel et al. 2013), and a 2.5% or more per decade decrease in water yield (Sun 2013). Uncertainty in future precipitation patterns still remains because the Southeast is located in the transition zone between projected wetter conditions to the north and drier conditions to the southwest (Kunkel et al. 2013). This could result in soil drying during the growing season, a critical period for plant growth (Markewitz et al. 2010). Positive relationships between rooting depth and resistance to drought have been demonstrated (Fensham and Fairfax 2007, Padilla and Pugnaire 2007). For example, in Brazilian Amazonia, about half of the closed forests rely on deep roots to maintain evergreen canopies throughout the dry season (Nepstad et al. 1994). A global review of 565 root profiles, across 15 terrestrial biomes, indicated that soil depths of 0.4, 0.7, and 1.1 m correspond to cumulative root proportions of 80, 90, and 95%, respectively (Schenk and Jackson 2002). Even though deep roots may represent a relatively small fraction of the overall root system biomass they likely fulfill much more essential functions. It was estimated in an Amazonian forest that 2.5 to 5.5 m soil contributed ~20% of water demand and 5.5 to 11.5 m contributed ~10% (Markewitz et al. 2010). Studying deep roots is critical to increase our understanding of plant water uptake and soil water availability (Harper and Tibbett 2013, Maeght et al. 2013).

Understanding the impact of a potentially drier climate is particularly important in managed loblolly pine forests and plantations in the Southeast U.S.. Loblolly pine (*Pinus taeda* L.) is the most extensively planted and productive commercial pine species in the Southeast U.S. (Fox et al. 2007) covering approximately fourteen million hectares (USDA Forest Service, 2015). Loblolly pine is an early successional species that grows across a broad range of soil types throughout the Southeast. However, it is not highly drought tolerant so is uncommon on the driest soil types (e.g., Quartzipsamments). It has been estimated that a Loblolly pine stand in Georgia use ~580-650 mm of water per year (Bartkowiak et al. 2015), about 55% of the rain this region receives (1109 mm, 30-year average) (http://www.ncdc.noaa.gov). During the growing season, loblolly pine rely on soil water storage as transpiration often exceeds precipitation (McNulty et al. 1996).

Low soil water availability could reduce net photosynthesis (Wertin et al. 2010), decrease both above and below ground growth, and shift root distribution (Torreano and Morris 1998) of loblolly pines. In a study conducted at three sites across Georgia, loblolly pine seedlings that received 25% the water inputs compared to those that were well watered had 23% lower net photosynthesis in June (Wertin et al. 2010). During an eight-week experiment on loblolly pine seedlings altering water regimes, plants watered every fourth week to a soil potential of -0.2 MPa compared with those that were watered every week to field capacity, had stem volume and root growth decline of 46 and 41%, respectively. Although the distribution of cumulative root growth was similar between the different watering regimes, by the end of this study, the pattern of growth with depth shifted as soils became drier and root growth intensified where adequate water remained (Torreano and Morris 1998).

Fertilization is often combined with other management practices in loblolly pine plantations and significantly improves productivity (Jokela et al. 1991, Kyle et al. 2005, Fox et al. 2007). However, only a few studies have examined the combined effects of fertilization and decreased water availability under controlled field conditions (Tang et al. 2004, Samuelson et al. 2014). Fertilization can increase productivity (Fox et al. 2007) but when combined with low soil water availability plants may exhibit little response to fertilization (Tang et al. 2004, Goldstein et al. 2013), or fertilization may even intensify the impact of drought (Bartkowiak et al. 2015, Ward et al. 2015).

In this research we studied how drought and fertilization, a little studied interaction, affect soil hydrological processes to a depth of 3 m. Predicting how these forests might respond to drought is critical for understanding how forests might be altered under a changing climate. This research was designed to test these hypotheses: (1) throughfall reduction treatment will reduce soil moisture for the whole soil profile, and when combined with fertilization the reduction will be greater than throughfall reduction or fertilization alone; (2) under throughfall reduction treatment, soil moisture storage change will be greater in deep soil when compared with ambient throughfall, and when combined with fertilization the change will be greater than throughfall reduction or fertilization alone.

METHODS

Site descriptions

The experiment was established in a loblolly pine plantation in Taliaferro County, Georgia owned by Plum Creek Timber Company. The study site is at an elevation of 152 m with latitude 33°37’32.61” N and longitude 82°47’56.54” W. This site was clear-cut in 2004 and both chemical and mechanical site preparation were applied in 2005. This included an aerial application of Velpar ULW herbicide (5.97 kg/ha), debris management, and combination plowing. In 2006, bare root seedlings (seed orchard mix) were hand planted at 1544 trees/ha. Herbaceous weed control was applied banded at ~220 ml/ha of Oust Extra in 2006. Refer to Will et al. (2015) for more details.

The soils of this research site are a Cecil-Lloyd complex. The Lloyd series is a fine, kaolinitic, thermic Rhodic Kanhapludult, while the Cecil series is a fine, kaolinitic, thermic Typic Kanhapludult. The Rhodic designation indicates an influence of mafic parent material on soil color. These soils are typical in the region. These soil series descriptions are based on USDA-NRCS Soil Survey Division (https://soilseries.sc.egov.usda.gov).

The 30-year (1983-2012) average annual precipitation is 1119 mm and the 30-year (1983-2012) average daily maximum and minimum temperature is 22.7°C and 10.1°C (http://www.ncdc.noaa.gov). During the study period, monthly Palmer Drought Severity Index indicated mild drought from June 2014 to June 2015 ranging from -1.00 to -1.99 and moderate drought for July 2015 with values ranging from -2.00 to -2.99 (http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/psi/201303-201507).

Experimental design

Throughfall exclusion structures (Figure 3.1) were installed to reduce throughfall by 30% which is at the extreme end of predictions for precipitation reduction associated with climate change for the region (Collins et al. 2013, Walsh et al. 2014). Furthermore, because most planted pine forests are nutrient limited and nutrient management is widespread, it is important to examine the interaction of throughfall exclusion treatment with an imposed nutritional gradient. This study was designed as a 2x2 factorial experiment with 4 blocks and the following treatments: Control (C) - no treatment; Fertilizer (F) - fertilizer additions to achieve "optimum" nutrition; Throughfall reduction (D) - panels installed in understory to divert 30% of throughfall off of the plot (Figure 3.1); Fertilizer + throughfall reduction (FD) - combined fertilizer and throughfall reduction treatments (Figure 3.2) (PINEMAP 2013). Blocks were established by tree height and basal area (Will et al. 2015). The fertilizer rates were 224 kg/ha N, 28 kg/ha P, 56 kg/ha K and micro-nutrients. The throughfall reduction structures were made of plastic troughs and were installed in the forest understory starting May 2012 (Figure 3.1). These panels capture approximately 30% of incoming throughfall, channeling the water to outside of the experimental treatment areas. The treatment area for each plot was 34 x 28 m with a 21 x 14 m measurement area in the center and a 6 m untreated buffer area between each treatment area. Refer to Will et al. (2015) for more details.

Soil texture and chemical analysis

One soil profile per plot was sampled to 3 m in the middle of each plot. Soils were collected in eight depths: 0-0.1, 0.1-0.2, 0.2-0.5, 0.5-1.0, 1.0-1.5, 1.5-2.0, 2.0-2.5 and 2.5-3.0 m. All samples were air-dried and homogenized by sieving through a 2 mm screen. A subsample was analyzed in replicate for soil texture, pH, total C and N. Textural analysis followed Gee and Or (2002) and soil water pH tests followed the method of Thomas (1996) with a 1:1 soil:water ratio. For C and N analysis samples were further oven-dried at 65ºC and ball mill ground. Total C (TC) and N were analyzed on a CE Elantech NC 2100 Soil Analyzer (CE Elantech Inc., Lakewood, NJ) using the Dumas method as described in Bremmer (1996).

Soil moisture measurements

At the approximate center of the plot, sets of 6.5 mm diameter welding rods were installed within tree rows (in all plots), between tree rows (in all plots), and under throughfall reduction structures (only in D and FD plots) to cover these 4 depth increments: 0-0.1, 0-0.3, 0-0.6 and 0-0.9 m. These rods were used for soil moisture measurements and were left exposed at the surface for later reading (Greco and Guida 2008). In addition, using these same rods, 0.12-m TDR probes were constructed with coaxial cable and epoxy (Evett 2005) and installed at 1.94-2.06 and 2.94-3.06 m with the cable exposed at the surface. On a monthly basis, soil volumetric water content (VWC) was measured by attaching a Riser Bond Model 1205CXA Coaxial Metallic TDR (Radiodetection, Raymond, Maine) to the rods or coaxial cable with alligator clips. The wave forms were measured to estimate VWC. Soil moisture probes were measured approximately monthly from May 2013 to August 2015. The surface soil moisture measurements were later partitioned into separate depths: 0-0.1, 0.1-0.3, 0.3-0.6 and 0.6-0.9 m, using:

$$D_e = \sum_{i=1}^{n} \theta_i D_i$$

where De [L] is depth of water equivalent, θ_i and D_i are the VWCs and layer thicknesses, respectively, of each layer (Radcliffe and Šimůnek 2010).

To better capture the soil moisture changes during the growing season, logging TDR probes (CS655 0.12 m Soil Water Content Reflectometer, Campbell Scientific, Inc., Logan, Utah) were installed in March 2014 at 0.54-0.66 m at the approximate center of the plots in blocks 2 and 4. They were programmed to collect data every 30 minutes from March 2014 to October 2015. These data were logged automatically (CR23X, Campbell Scientific, Inc., Logan, Utah), then downloaded and averaged by day.

Plant available water

To calculate plant available water (PAW), soil water retention curves were determined using Tempe cells (SoilMoisture Equipment Corp., Santa Barbara, CA) and a WP4C Dewpoint PotentialMeter (Decagon Devices. Inc., Pullman, WA). Core samples were collected in each plot at 0-75 mm and 100-175 mm. Core samples were also collected at 0.5, 1.0, 1.5, 2.0, 2.5 and 3.0 m from the walls of two soil pits dug on site to a depth of 3 m.

Tempe cells were used for <1MPa and WP4C Dewpoint PotentialMeter were used for >1MPa. Results from both instruments were then combined to form soil water retention curve equations following Van Genuchten (1980):

$$S_e(h) = \frac{1}{[1 + (-\alpha h)^{n^m}}$$

where α [L-1], n [-] and m [-] are fitting parameters, h is pressure [L] and $S_e(h)$ [-] is the effective soil water saturation calculated following Van Genuchten (1980):

$$S_e = \frac{\theta - \theta_r}{\theta_s - \theta_r}$$

where θ is the VWC, θ_s is the saturated VWC and θ_r is the residual VWC, defined as the VWC where hydraulic conductivity approaches zero (Van Genuchten 1980). PAW (θ_{PAW}) was calculated as the amount of soil water held at tensions between -0.01 and -1.5 MPa (θ_{wp}), determined from soil moisture retention curves. Monthly PAW of each soil layer was calculated using:

$$\theta_{PAW} = \theta - \theta_{wp}$$

where θ of 0-0.1, 0.1-0.3, 0.3-0.6 and 0.6-0.9 m soils were measured using TDR probes and later partitioned into separate depths; θ of 0.9-2 m were averaged between VWC measurements at 0.6-0.9 m and 2 m; and θ of 2-3 m were averaged between VWC measurements at 2 and 3 m.

Precipitation (PPT) and actual evapotranspiration (AET)

PPT records were obtained from six weather stations located within 90 km of the research site (www.georgiaweather.net). The mean PPT between six locations from March 2013 to August 2015 were used to estimate the water balance during the experiment. The AET under the different treatments were calculated using the sap flow data collected following the method of Bartkowiak et al. (2015). These data were collected from five trees within each measurement plot.

Statistical analysis

Soil VWC data of different depths were tested for main and interactive treatment effects ($\alpha = 0.05$). Among 5185 data points, there were 62 VWC measurements below zero, ~1% of the total data collected. These data points were not included in data analysis. The experimental unit of replication was the plot. Between rows, in row, and under trough positions (within unit repeated measurements) were averaged to represent plot level VWC. These data were also analyzed as repeated measure, using dates as the repeated factor. Tukey's significance test at the level of $\alpha = 0.05$ was used to separate treatment effect on VWCs at the same depth. The SAS statistical package (SAS Institute Inc., Cary, North Carolina) was used for all data analyses.

RESULTS

Soil Physical and Chemical Properties

Soils of all depths were acidic, with pH ranging from 5.2 to 5.8. The C concentrations ranged from 1.92% in 0-0.1 m and decreased with depth to ~0.5% below 1 m. The N concentrations were 0.1% at the surface and decreased to 0-0.01% below 1 m (Table 3.1).

The clay content ranged from 24-47%, with lowest clay contents in the 0-10 and 2.50-3.0 m layers, while 0.2-2.5 m soils had >40% clay throughout (Table 3.1). Wilting point VWCs (θ_{wp}) ranged from 10-19%. In correspondence with clay contents, θ_{wp} were highest in the middle of the soil profile but decreased towards the surface and the bottom of the profile (Table 3.2).

VWC

Soil VWCs were generally higher during winters and lower during summers (Figure 3.4), and the effect of time was significant ($p<0.0001$ for all depths). This was more obvious in surface soils, while deep soil VWC varied proportionally less over the observed time. There were no significant time by treatment interactions for any depths (p value ranged from 0.4-0.9).

The main effect of fertilization was reduced VWC for all depths (Table 3.3). The effect was more prominent below 0.30 m with 1.3 to 4.5% lower VWC in fertilized plots. The differences were significant within the 0.3-0.6 m depth increment (2.9%, $p<0.0001$) and 2.94-3.06 m increment (4.5%, $p<0.0001$). Surface soil moisture was only 0.4 to 0.5% lower in the fertilized plots, and these differences were not significant.

The main effect of throughfall reduction treatment was also lowered soil moisture for all depths, ranging from 0.8 to 3.6% VWC (Table 3.3). The differences were significant for surface soils, 0-0.1 ($p<0.0001$) and 0.1-0.3 m ($p=0.0253$), with 3.6 and 1.2% lower VWC, respectively.

Differences from 0.3-0.6 and 0.6-0.9 m were not significantly different. Deep soils did differ, 1.94-2.06 m (p=0.0006) and 2.94-3.06 m (p=0.0252) had significantly lower VWC, with 3.6 and 2.6% lower VWC, respectively.

The interaction effect of fertilization and throughfall reduction was significant at 0.1-0.3 m (p<0.0001), 1.94-2.06 m (p=0.0002), and 2.94-3.06 m (p<0.0001) soils (Table 3.3). In these cases, without fertilization throughfall reduction treatment (i.e., C vs D) significantly lowered soil moisture while with fertilization the effect of throughfall reduction (i.e., F vs FD) was not significant. For example, at 2 m, without throughfall reduction fertilization (i.e., C vs F) significantly reduced soil moisture while with throughfall reduction fertilization (i.e., D vs FD) didn't have a significant effect on soil moisture (Figure 3.5).

Water balance

Plant available water (PAW) varied with season. In general, plots with FD treatment had the lowest PAW, while C had the highest (Figure 3.6). Soils of all depths were never depleted of PAW, except for the 0-0.1 m soils under D, F and FD treatments. Among these soils, there was no PAW in 0-0.1 m soil under D treatments for 6 months, 4 months for FD plots, and 2 months for F plots (mainly being depleted during the growing season) (Figure 3.6).

AET exceeded PPT for 4-8 months in the growing seasons during the experimental period, with D plots having the longest duration of PPT deficit (May - October 2014). Soil water storage change over time showed similar trends as PPT-AET, often being negative during the growing season and positive during winter. Plots under FD treatment experienced the longest time period (11 months) with the total ΔPAW < 0, while C plots had the shortest time (8 months) (Figure 3.7).

During the months that AET exceeded PPT, the contribution of soil below 0.9 m to ΔPAW varied widely: 1.0-7.2 cm in C plots, 1.0-7.5 cm in D, 0.1-10.3 cm in F and 0.4-19.0 cm in FD (Figure 3.7). FD soils below 90 cm contributed the highest amount of water (19.0 cm), which occurred in FD plots in May 2014. During this month, VWC at 2 m changed from 54.6% to 39.7%, accounting for 78% of the total ΔPAW. The highest proportion of soil water from below 0.9 m that contributed to total ΔPAW for any month was 98%, which occurred in plots under FD treatment during November 2013 (Figure 3.7). Overall, D plots had a consistently large proportion (62-81%) of total ΔPAW coming from soils below 0.9 m, while the proportions varied widely under other treatments (C: 40-86%, F: 18-81% and FD: 11-98%) (Figure 3.7).

Growing season analysis

VWC collected by dataloggers every 30 mins followed the same trend as VWC measured monthly (Figure 3.8). Soil VWCs were generally higher during winters and lower during summers. These higher temporal resolution data better captured daily variability in VWC. Soils under all four treatments experienced a similar increase and decrease in VWC, with smaller daily variances for D and FD soils.

DISCUSSION

We hypothesized that throughfall reduction would reduce soil moisture for the whole soil profile, and when combined with fertilization the reduction would be greater than throughfall reduction or fertilization alone. Under the treatment of throughfall reduction, there were lower soil moistures throughout the whole soil profile relative to ambient throughfall plots, with both surface (0-0.3 m) and deep (2-3 m) soils having significantly lower soil moisture (Table 3.3 and Figure

3.4). In the surface, lower soil moisture might be explained by lower throughfall inputs and high fine root biomass associated with high root water uptake. In 0.3-2.0 m soils the absence of significant effects might be attributed to the high clay content, which requires a large water content difference to induce a relatively small change in water potential that may not have been statistically detectable (Table 3.1 and 3.2). In deep soil horizons, lower soil moisture could be caused by higher root water uptake or continued soil drainage. The absence of VWC values above θ_s (Table 3.2), however, suggests limited potential for drainage and therefore, lower VWC in 2-3 m soils are likely caused by higher root water uptake.

Fertilized plots also had consistently lower soil moisture than unfertilized plots. In the study conducted on the same research site in 2013, fertilization significantly increased leaf area index (Bartkowiak et al. 2015). Higher leaf area index could result in more canopy interception and thus reduced throughfall input. Sap flux data from this experiment indicated no difference in ET for these treatments (Bartkowiak et al. 2015), these data support lower VWC under fertilization was caused by higher root water uptake. These soil moisture differences between fertilized and unfertilized plots were especially prominent below 0.3 m, with significant differences at 0.3-0.6 m and 2.94-3.06 m (Table 3.3 and Figure 3.4). Finally, under throughfall reduction treatment with fertilization (FD) VWC was significantly lower in the 0.1-0.9 m depths (Figure 3.4). These results do indicate some increased drying (lower VWC) of the surface under FD (0.1-0.9 m) compared to D (0-0.3 m). On a water content basis in the upper 0.9 m this translated into a greater depletion of 2.38 cm in FD. The depletion in the upper 0.9 m compromised ~80% of depletion over the entire 3 m.

Our second hypothesis addressed deep soil moisture, proposing that under throughfall reduction treatment, soil moisture storage change (ΔPAW) would be greater in deep soil when compared with ambient throughfall, and when combined with fertilization the change would be greater than throughfall reduction or fertilization alone. We found consistently greater ΔPAW below 0.9 m under throughfall reduction treatment. During months when AET > PPT, 0-0.9 m soil rarely (5/37 months) contributed more than half of total ΔPAW. In throughfall reduction only plots, soils below 0.9 m consistently contributed more than half of ΔPAW, while the proportion varied widely in ambient throughfall soils (18-86%) (Figure 3.6). Under FD treatment, soils below 0.9 m contributed 98% of ΔPAW during November 2013, which is the maximum contribution throughout all months of the experiment under all treatments.

Within the soils of the current study site, even though we excluded 30% of throughfall, which is at the extreme end of predictions for precipitation and soil moisture variation associated with climate change for the region (Collins et al. 2013, Walsh et al. 2014), data demonstrated that there is enough PAW to support evapotranspiration. Within all the treatments, soils of all depths were rarely depleted of PAW (i.e. below θ_{wp}), with the exception of the 0-0.1 m that was dry mainly during the growing season (Table 3.2 and Figure 3.6).

The observed changes in soil moisture did not result in reduced ground level growth or evapotranspiration under the D treatment during the 2013 growing season (Bartkowiak et al. 2015). However, 2013 had 27% higher precipitation than the 30-year average in this area (http://www.ncdc.noaa.gov). Decreased soil moisture in the F treatment similarly did not have a significant effect on evapotranspiration in 2013 despite increased leaf area due to fertilization. Fertilization also increased quadratic mean DBH and basal area (Bartkowiak et al. 2015). In contrast, the combined FD treatment did decrease evapotranspiration per ha from 62 to 47 mm/month but this was not coincident with a significant decrease in growth (Bartkowiak et al.

2015). Overall, these results suggest that, at least, during the 2013 and 2014 growing season soil moisture under drought with or without fertilization was sufficient to sustain growth.

Two additional study sites were direct companions to this site in Georgia. One companion experiment in a 13-year-old loblolly pine plantation in Florida (30 ° 1’22” N, 83 ° 52’12” W) showed similar results with no impact of throughfall reduction (D) on forest productivity or water relations (Wightman 2014). The lack of response at this site was attributed to abundant rainfall and the ability of trees to access a shallow water table (1-2 m depth). In fact, the fertilizer only treatment increased monthly transpiration by 17% in the spring of 2013 and transpiration was not significantly different among treatments during the rest of the year (Wightman 2014). The results from this site similarly suggest that given higher than average precipitation or access to a shallow water table a 30% throughfall reduction may not lower soil moisture enough to stress trees in physiologically significant ways.

The second companion research site in a 13-year-old plantation in Virginia (37°27’37” N, 78 ° 39’50” W) provides some contrasting results. At this location the throughfall reduction treatment lowered evapotranspiration by 19% during the growing season even when the annual precipitation was 9% higher than the 30-year mean in the research area (Ward et al. 2015). Under fertilization, evapotranspiration also declined by 13% during the growing season and under FD evapotranspiration decreased by 29%.

These contrasting results from Georgia, Florida, and Virginia highlight the critical role of soils in identifying pine plantation responses to drought x fertilization. The soil in the Georgia site is a very deep (>3 m) and well drained Kanhapludult with >30% clay from 0.10-2.5 m. These clays are accessible to plants (i.e., rootable, Chapter 4) and at saturation may contain up 0.8 m of PAW. In Florida, soils are a complex of Spodosols and Alfisols with all being somewhat poorly drained and possessing a thick cap of fine sand (Chapter 2). All these soils, however, also possess a high water table. As such, outside consecutive years of severe drought we would expect little water limitation at this site. Finally, at the Virginia site soil is also an Hapludult with a silt loam overlying a silty clay loam subsoil but is shallow (~1.5 m) to a paralithic contact (i.e., weathered rock). Soils at the Virginia site are limited in both the depth of rooting and the soil moisture storage capacity. The soil conditions at these three sites provide unique rooting environments and supplies of PAW, thus different reactions to drought x fertilization should be expected.

The ability of pine stands in the Georgia study site to sustain evapotranspiration per ha despite decreased water input (Bartkowiak et al. 2015) should result in less water yield at this site (Sun and Liu 2013). The highest observed AET in all treatments was ~700 mm/year (Figure 3), while the 30-year average precipitation is ~1120 mm (www.ncdc.noaa.gov). Assuming 30% precipitation reduction, drainage or water yield might decline from 420 mm to ~80 mm. Water yield and ET are two offsetting components of the water balance and results here suggest that the ability of pine ecosystems to capture PAW under a future drier climate may have trickledown effects on other key ecosystem functions (Sun and Liu 2013).

The uptake of deep soil water by the root system has been indicated to be sufficient to maintain AET in several other forest ecosystems, including a temperate Eucalyptus forest and a tropical wet/dry savanna in Australia (Leuning et al. 2005), and scrub oak and pine flatwoods ecosystems in Florida (Bracho et al. 2008). In an Amazonian rainforest it was estimated that the 2.5 to 5.5 m soil contributed ~20% of water demand and 5.5 to 11.5 m contributed ~10% during an imposed throughfall exclusion (Markewitz et al. 2010). In another Amazonian study, during the severe 5.5- month dry season of 1992, PAW stored below 2 m in the soil provided >75% of the water extracted in both mature evergreen forest and nearby pasture ecosystems (Nepstad et al.

1994). Previous research supports the critical role of deep roots for plant water balance. The results from this current research specifically demonstrate the importance of deep soil water in maintaining evapotranspiration in loblolly pine plantations on deep clay rich Ultisols in the Southeast U.S., especially in the face of a changing climate.

CONCLUSION

Throughfall reduction and fertilization both lowered soil moisture for all depths (0-3 m) and the combined treatment yielded lower soil moisture than either treatment alone. Even with 30% throughfall reduction, soils of all depths were rarely depleted of plant available water, with the exception of 0-0.1 m during the growing season. During the months that evapotranspiration exceeded precipitation (i.e., when plant root uptake is depleting soil plant available water), soil below 0.9 m always contributed to the observed change in plant available water storage. Under throughfall reduction treatment, soil below 0.9 m constantly accounted for more than half of the change in plant available water storage. In this 3 m deep, clay rich Piedmont soil under 30% throughfall reduction, soil water storage was able to satisfy plant demand for evapotranspiration. Within Southeast U.S. loblolly pine plantations, deep soil water (>0.9 m) will be important in maintaining evapotranspiration on deep, clay rich Ultisols.

REFERENCES

Bartkowiak, S. M., L. J. Samuelson, M. A. McGuire, and R. O. Teskey. 2015. Fertilization increases sensitivity of canopy stomatal conductance and transpiration to throughfall reduction in an 8-year-old loblolly pine plantation. Forest Ecology and Management 354:87-96.

Belk, E. L., D. Markewitz, T. C. Rasmussen, E. J. Maklouf Carvalho, D. C. Nepstad, and E. A. Davidson. 2007. Modeling the effects of throughfall reduction on soil water content in a Brazilian Oxisol under a moist tropical forest. Water Resources Research 43:14.

Borken, W., and E. Matzner. 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Global Change Biology 15:808-824.

Bracho, R., T. L. Powell, S. Dore, J. Li, C. R. Hinkle, and B. G. Drake. 2008. Environmental and biological controls on water and energy exchange in Florida scrub oak and pine flatwoods ecosystems. Journal of Geophysical Research: Biogeosciences 113:n/a-n/a.

Bremner, J. M. 1996. Nitrogen - total. Methods of Soil Analysis Part 3—Chemical Methods sssabookseries:1085-1121.

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W. J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A. J. Weaver, and M. Wehner. 2013. Long-term Climate Change: Projections, Commitments and Irreversibility. Pages 1029–1136 in T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Fensham, R. J., and R. J. Fairfax. 2007. Drought-related tree death of savanna eucalypts: Species susceptibility, soil conditions and root architecture. Journal of Vegetation Science 18:71-80.

Fox, T. R., E. J. Jokela, and H. L. Allen. 2007. The development of pine plantation silviculture in the southern United States. Journal of Forestry 105:337-347.

Gee, G. W., and D. Or. 2002. 2.4 Particle-size analysis. Methods of Soil Analysis: Part 4 Physical Methods sssabookseries:255-293.

Goldstein, G., S. J. Bucci, and F. G. Scholz. 2013. Why do trees adjust water relations and hydraulic architecture in response to nutrient availability? Tree Physiol 33:238-240.

Greco, R., and A. Guida. 2008. Field measurements of topsoil moisture profiles by vertical TDR probes. Journal of Hydrology 348:442-451.

Harper, R. J., and M. Tibbett. 2013. The hidden organic carbon in deep mineral soils. Plant and Soil 368:641-648.

Jokela, E. J., H. L. Allen, and W. W. McFee. 1991. Fertilization of southern pines at establishment: 263-277.

Kunkel, K. E., L. E. Stevens, S. E. Stevens, L. Sun, E. Janssen, D. Wuebbles, C. E. Konrad, II , C. M. Fuhrman, B. D. Keim, M. C. Kruk, A. Billet, H. Needham, M. Schafer, and J. G. Dobson. 2013. Regional Climate Trends and Scenarios for the U.S. National Climate Assessment: Part 2. Climate of the Southeast U.S. NOAA Technical Report 142-2 Page 103. National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service Washington D.C. .

Kyle, K. H., L. J. Andrews, T. R. Fox, W. M. Aust, J. A. Burger, and G. H. Hansen. 2005. Long-term effects of drainage, bedding, and fertilization on growth of loblolly pine (*Pinus taeda* L.) in the coastal plain of Virginia. Southern Journal of Applied Forestry 29:205-214.

Leuning, R., H. A. Cleugh, S. J. Zegelin, and D. Hughes. 2005. Carbon and water fluxes over a temperate Eucalyptus forest and a tropical wet/dry savanna in Australia: measurements and comparison with MODIS remote sensing estimates. Agricultural and Forest Meteorology 129:151-173.

Maeght, J. L., B. Rewald, and A. Pierret. 2013. How to study deep roots - and why it matters. Frontiers in Plant Science 4:1-14.

Markewitz, D., S. Devine, E. A. Davidson, P. Brando, and D. C. Nepstad. 2010. Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. New Phytologist 187:592-607.

McNulty, S. G., J. M. Vose, and W. T. Swank. 1996. Loblolly pine hydrology and productivity across the southern United States. Forest Ecology and Management 86:241-251.

Meehl, G. A., C. Tebaldi, H. Teng, and T. C. Peterson. 2007. Current and future U.S. weather extremes and El Nino. Geophysical Research Letters 34.

Nepstad, D. C., C. R. Decarvalho, E. A. Davidson, P. H. Jipp, P. A. Lefebvre, G. H. Negreiros, E. D. Dasilva, T. A. Stone, S. E. Trumbore, and S. Vieira. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372:666-669.

Padilla, F. M., and F. I. Pugnaire. 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology 21:489-495.

Radcliffe, D. E., and J. Šimůnek. 2010. Soil physics with HYDRUS: Modeling and applications. CRC press Boca Raton, Florida.

Samuelson, L. J., C. J. Pell, T. A. Stokes, S. M. Bartkowiak, M. K. Akers, M. Kane, D. Markewitz, M. A. McGuire, and R. O. Teskey. 2014. Two-year throughfall and fertilization effects on leaf physiology and growth of loblolly pine in the Georgia Piedmont. Forest Ecology and Management 330:29-37.

Schenk, H. J., and R. B. Jackson. 2002. The global biogeography of roots. Ecological Monographs 72:311-328.

Sun, G. 2013. Impacts of Climate Change and Variability on Water Resources in the Southeast USA. Pages 210-236 in K. T. Ingram, K. Dow, L. Carter, and J. Anderson, editors. Climate of the Southeast United States: Variability, Change, Impacts, and Vulnerability. Island Press/Center for Resource Economics, Washington, DC.

Sun, G., and Y. Liu. 2013. Forest influences on climate and water resources at the landscape to regional scale. Landscape Ecology for Sustainable Environment and Culture. 309-334.

Tang, Z. M., M. A. Sayer, J. L. Chambers, and J. P. Barnett. 2004. Interactive effects of fertilization and throughfall exclusion on the physiological responses and whole-tree carbon uptake of mature loblolly pine. Canadian Journal of Botany-Revue Canadienne De Botanique 82:850-861.

Thomas, G. W. 1996. Soil pH and soil acidity. Methods of Soil Analysis Part 3—Chemical Methods sssabookseries: 475-490.

Torreano, S. J., and L. A. Morris. 1998. Loblolly pine root growth and distribution under water stress. Soil Science Society of America Journal 62:818-827.

Van Genuchten, M. T. 1980. A closed form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Science Society of America Journal 44:892-898.

Walsh, J., D. Wuebbles, K. Hayhoe, J. Kossin, K. Kunkel, G. Stephens, P. Thorne, R. Vose, M. Wehner, and J. Willis. 2014. Ch. 2: Our changing climate. Climate Change Impacts in the United States: The Third National Climate Assessment, JM Melillo, Terese (TC) Richmond, and GW Yohe, Eds., U.S. Global Change Research Program:19-67.

Ward, E. J., J.-C. Domec, M. A. Laviner, T. R. Fox, G. Sun, S. McNulty, J. King, and A. Noormets. 2015. Fertilization intensifies drought stress: Water use and stomatal conductance of Pinus taeda in a midrotation fertilization and throughfall reduction experiment. Forest Ecology and Management 355:72-82.

Wertin, T. M., M. A. McGuire, and R. O. Teskey. 2010. The influence of elevated temperature, elevated atmospheric CO2 concentration and water stress on net photosynthesis of loblolly pine (Pinus taeda L.) at northern, central and southern sites in its native range. Global Change Biology 16:2089-2103.

Wightman, M. 2014. The impact of fertilization and throughfall reduction on Pinus taeda water relations and growth. Master's thesis. University of Florida.

Will, R. E., T. Fox, M. Akers, J. C. Domec, C. Gonzalez-Benecke, E. J. Jokela, M. Kane, M. A. Laviner, G. Lokuta, D. Markewitz, M. A. McGuire, C. Meek, A. Noormets, L. Samuelson, J. Seiler, B. Strahm, R. Teskey, J. Vogel, E. Ward, J. West, D. Wilson, and T. A. Martin. 2015. A range-wide experiment to investigate nutrient and soil moisture interactions in loblolly pine plantations. Forests 6:2014-2028.

Table 3.1. Soil texture, pH, and C and N concentrations for all treatment plots at Taliaferro County, Georgia. Values given as mean ± 1SE (n=16). Samples were collected in May 2012.

Depth (m)	Texture	Sand %	Silt %	Clay %	pH	C (%)	N (%)
0-0.1	loam	45±12	31±6	24±12	5.5±0.5	1.92±0.67	0.10±0.03
0.1-0.2	clay loam	37±11	32±6	31±11	5.4±0.2	0.87±0.26	0.06±0.01
0.2-0.5	clay	26±7	33±6	42±9	5.4±0.1	0.44±0.13	0.04±0.00
0.5-1.0	clay	18±8	35±6	47±4	5.2±0.4	0.25±0.02	0.03±0.00
1.0-1.5	clay	21±9	36±9	42±5	5.8±0.0	0.07±0.03	0.00±0.00
1.5-2.0	clay loam	22±10	39±8	38±6	5.6±0.1	0.06±0.03	0.00±0.00
2.0-2.5	clay loam	22±11	45±8	32±7	5.4±0.3	0.05±0.02	0.00±0.00
2.5-3.0	loam	26±13	48±7	25±9	5.3±0.2	0.05±0.01	0.01±0.00

Table 3.2. Soil water retention curve parameters for Exclusion x Fertilization study in Taliaferro County, Georgia. For 0-0.1 and 0.1-0.2 m, eight samples were collected and data points from all eight samples were used to create one soil water retention curve, and for soils below 0.2 m, two samples were collected. Samples were collected in August 2013.

Depth (m)	θ_r	θ_s	α	n	m	θ_{wp}
0-0.1	0.08	0.33	8.20E-04	1.45	0.31	0.10
0.1-0.2	0.10	0.40	3.06E-03	1.28	0.22	0.13
0.2-0.5	0.10	0.39	2.23E-03	1.39	0.27	0.11
0.5-1.0	0.08	0.41	9.65E-04	1.41	0.29	0.15
1.0-1.5	0.07	0.48	7.00E-04	1.38	0.28	0.19
1.5-2.0	0.08	0.43	1.83E-02	1.28	0.21	0.16
2.0-2.5	0.10	0.39	1.92E-02	1.22	0.18	0.14
2.5-3.0	0.09	0.50	3.13E-03	1.36	0.26	0.13

θ_r is the residual volumetric water content, θ_s is the saturated volumetric water content, α [L^{-1}], n [-] and m [-] are fitting parameters, and θ_{wp} is the volumetric water content at -1.5 MPa, determined from soil moisture retention curves.

Table 3.3. Treatment effects for fertilization, throughfall reduction, and their interaction (n=4), and %VWC change.

Depth	Fertilization		Throughfall Reduction		Interaction
(m)	Δ VWC (%)	P value	Δ VWC (%)	P value	P value
0-0.1	-0.49	0.5162	-3.58	<0.0001	0.1334
0.1-0.3	-0.41	0.4221	-1.19	0.0253	<0.0001
0.3-0.6	-2.94	<0.0001	-0.8	0.2551	0.2676
0.6-0.9	-1.24	0.1202	-0.81	0.3131	0.2948
1.94-2.06	-1.27	0.223	-3.58	0.0006	0.0002
2.94-3.06	-4.51	<0.0001	-2.64	0.0252	<0.0001

Figure 3.1. Throughfall reduction structure covering ~30% of the plot area with troughs to capture and funnel throughfall away from the plots. Taliaferro County, Georgia in 2012 when trees were 6 years old.

Figure 3.2. Map of experimental treatments and blocks located in Taliaferro County, Georgia. This study was designed as a 2x2 factorial experiment with fertilization (F) and throughfall reduction (D) in four blocks. Fertilizer additions included N, P, K and micronutrients and throughfall reduction diverted 30% of throughfall off of the plot. Blocks, indicated by different border colors, were established by tree height and basal area measured in 2012.

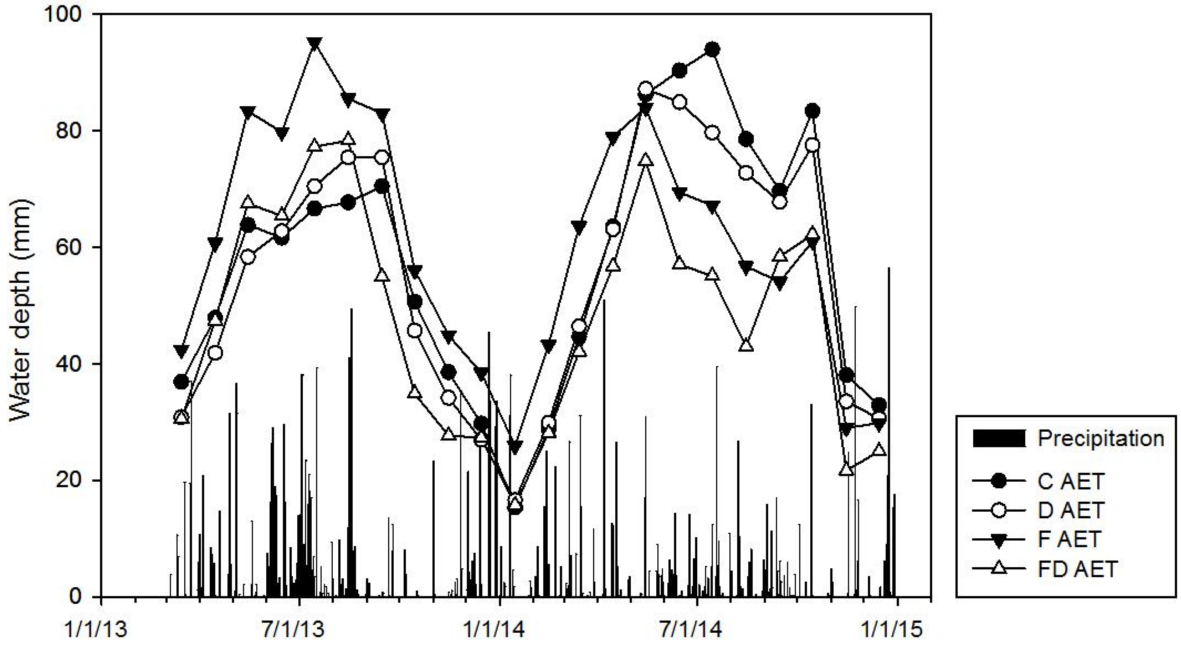

Figure 3.3. Daily precipitation (PPT) (black bars) and monthly actual evapotranspiration (AET) in treatments of Control (C), Fertilized (F), Throughfall Exclusion (D) and FxD at the throughfall exclusion experiment in Taliaferro, Georgia for the period of March 2013 to December 2014.

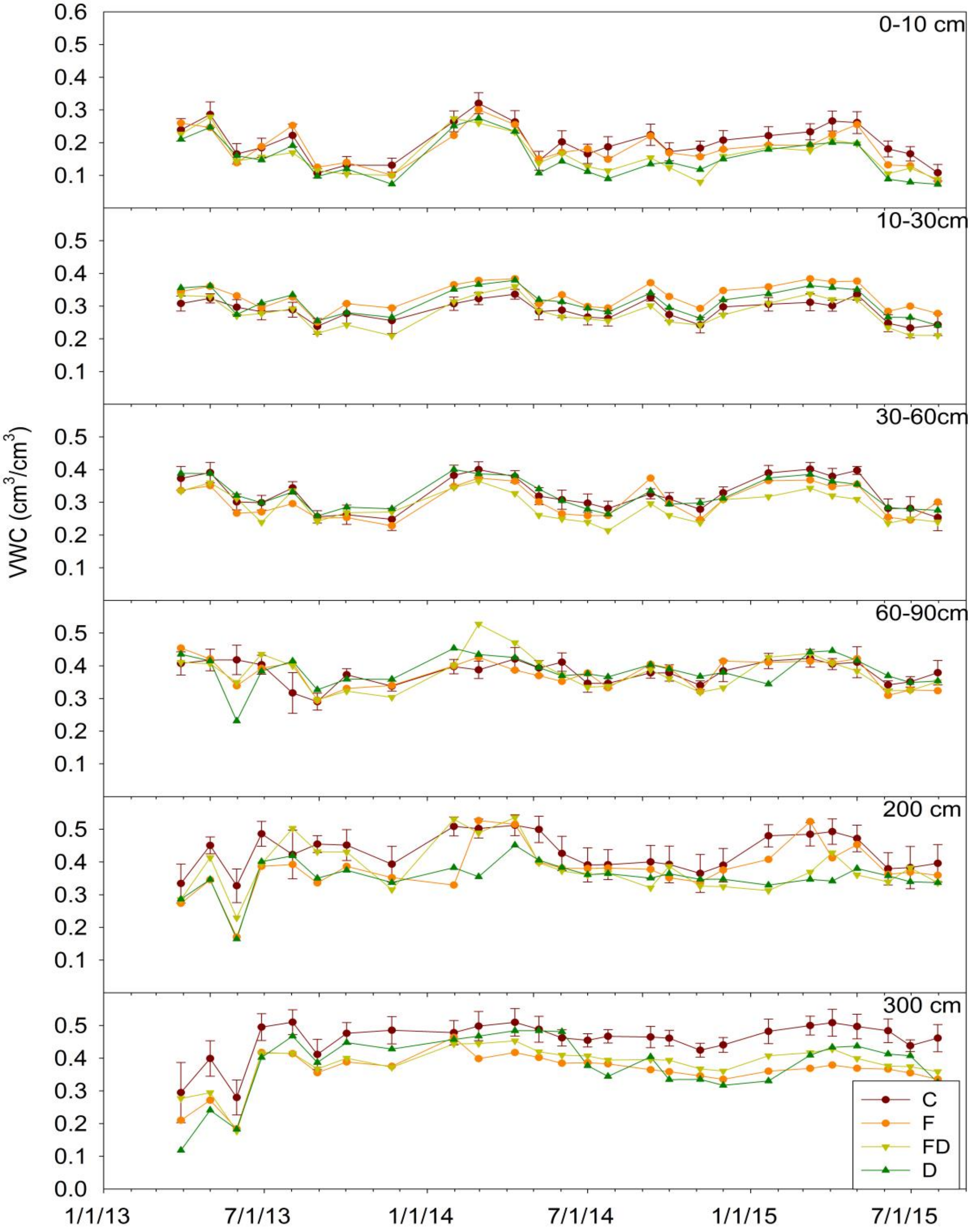

Figure 3.4. Mean soil VWC of six depths for March 2013 to July 2015. Treatments are Control (C), Fertilized (F), Throughfall Exclusion (D) and FxD. Bars representing ±1SE for four replicates are given only for C to maintain clarity (n=4).

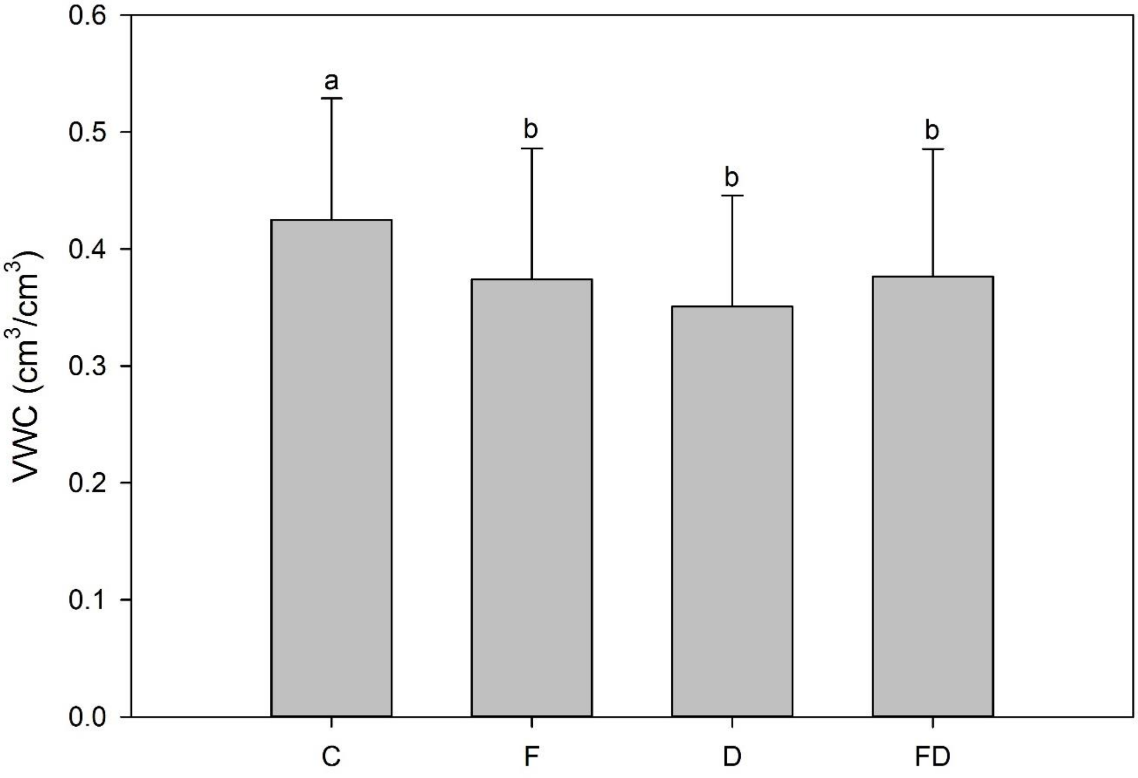

Figure 3.5. Treatment (Control (C), Fertilized (F), Throughfall exclusion (D) and FxD) effects on volumetric water content (VWC) of 1.94-2.06 m soils. Bars represent the means of VWC (over the period of March 2013 to July 2015) and error bars represent ±1SE (n=108). Letters indicate significant differences for post-hoc tests.

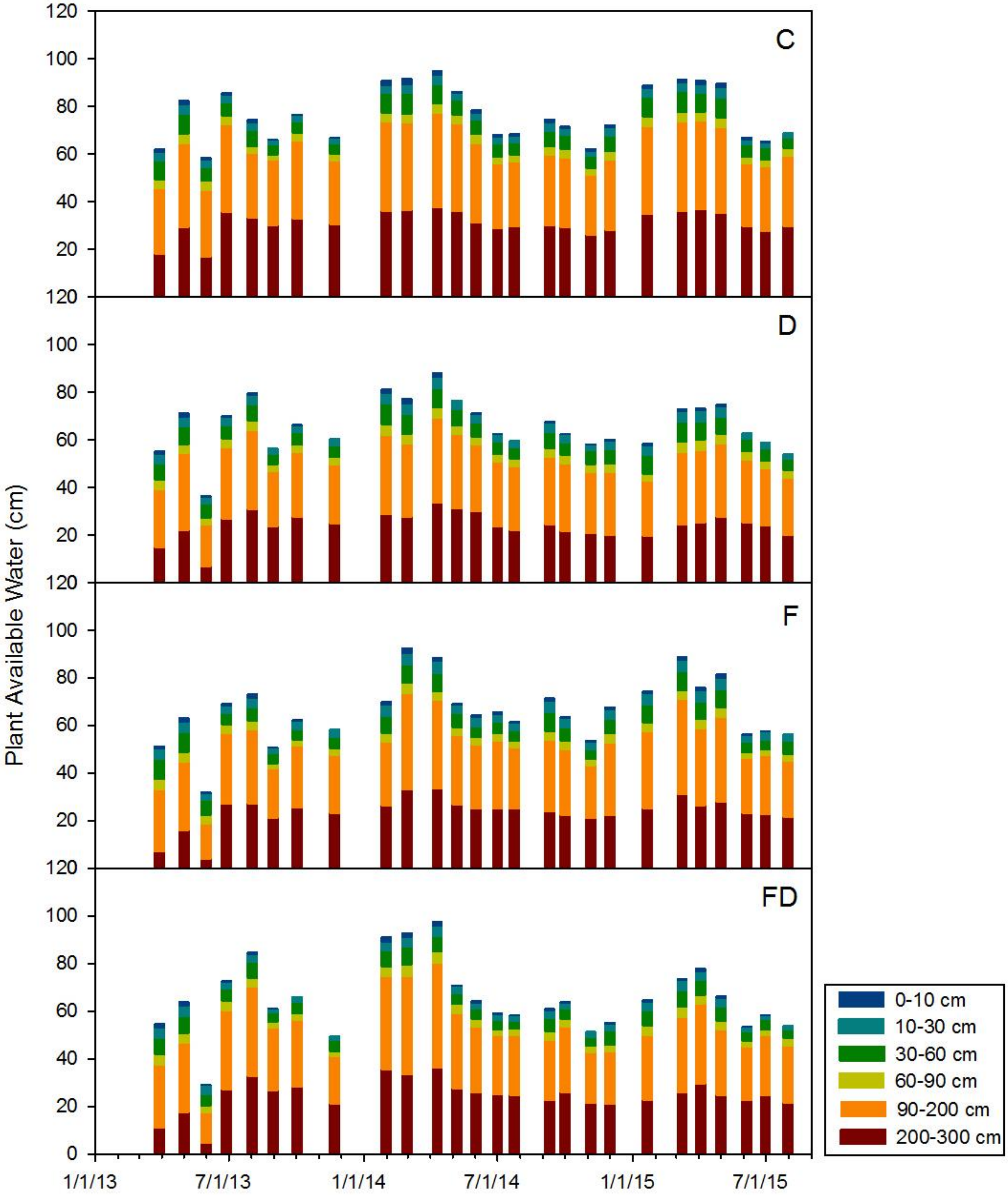

Figure 3.6. Seasonal trends in plant available water for Control (C), Fertilized (F), Throughfall exclusion (D) and FxD treatments for March 2013 to July 2015. Stacked bars represent plant available water storage of 0-0.1, 0.1-0.3, 0.3-0.6, 0.6-0.9, 0.9-2.0, and 2.0-3.0 m

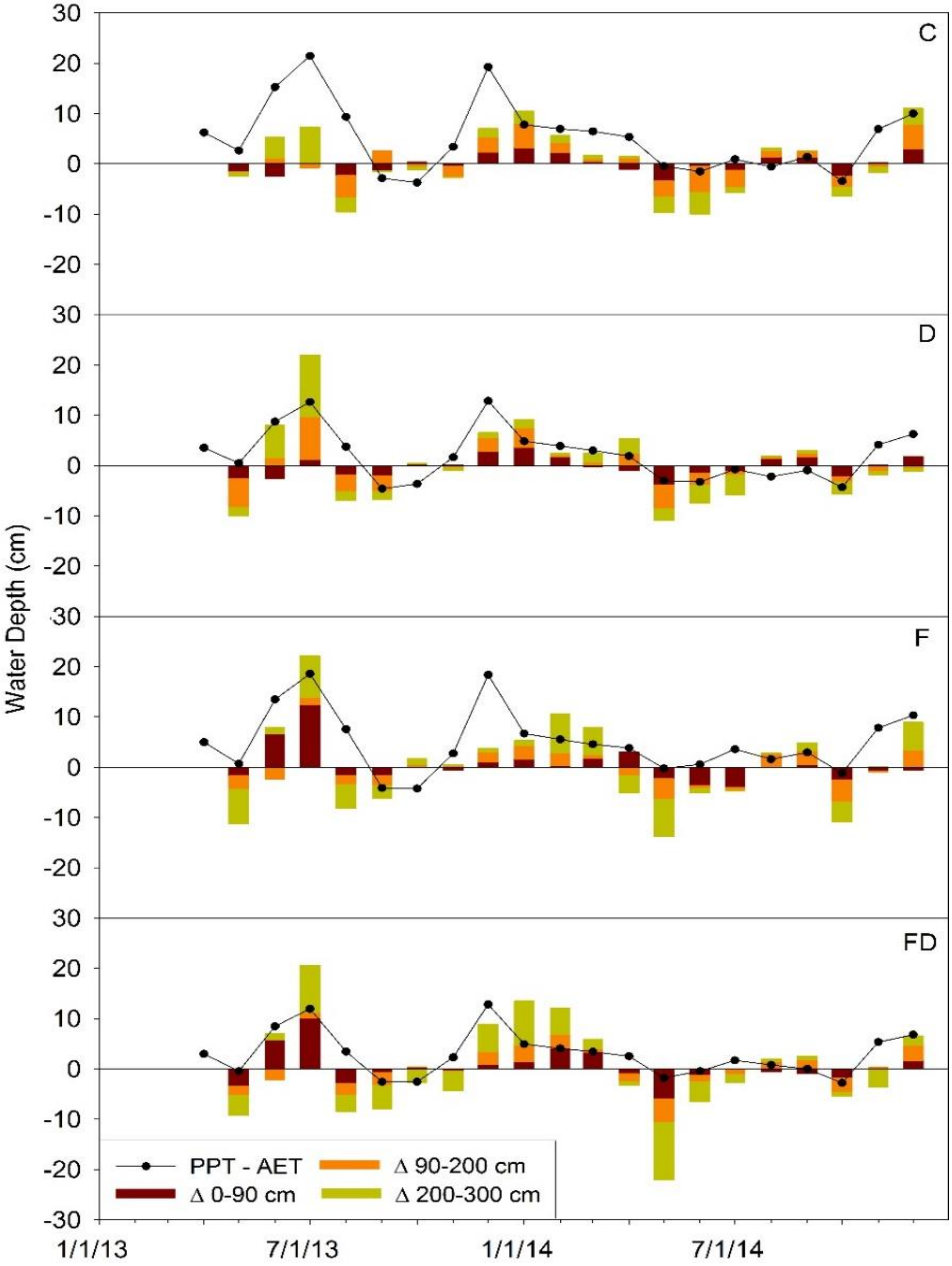

Figure 3.7. Water mass balance for April 2013 to December 2014. Solid lines are water depth of precipitation - actual evapotranspiration (PPT-AET). Stacked bars are plant available water storage change by depth. Error bars representing ±1SE were too small to show (n=4). Treatments are Control (C), Fertilized (F), Throughfall Exclusion (D), and FxD.

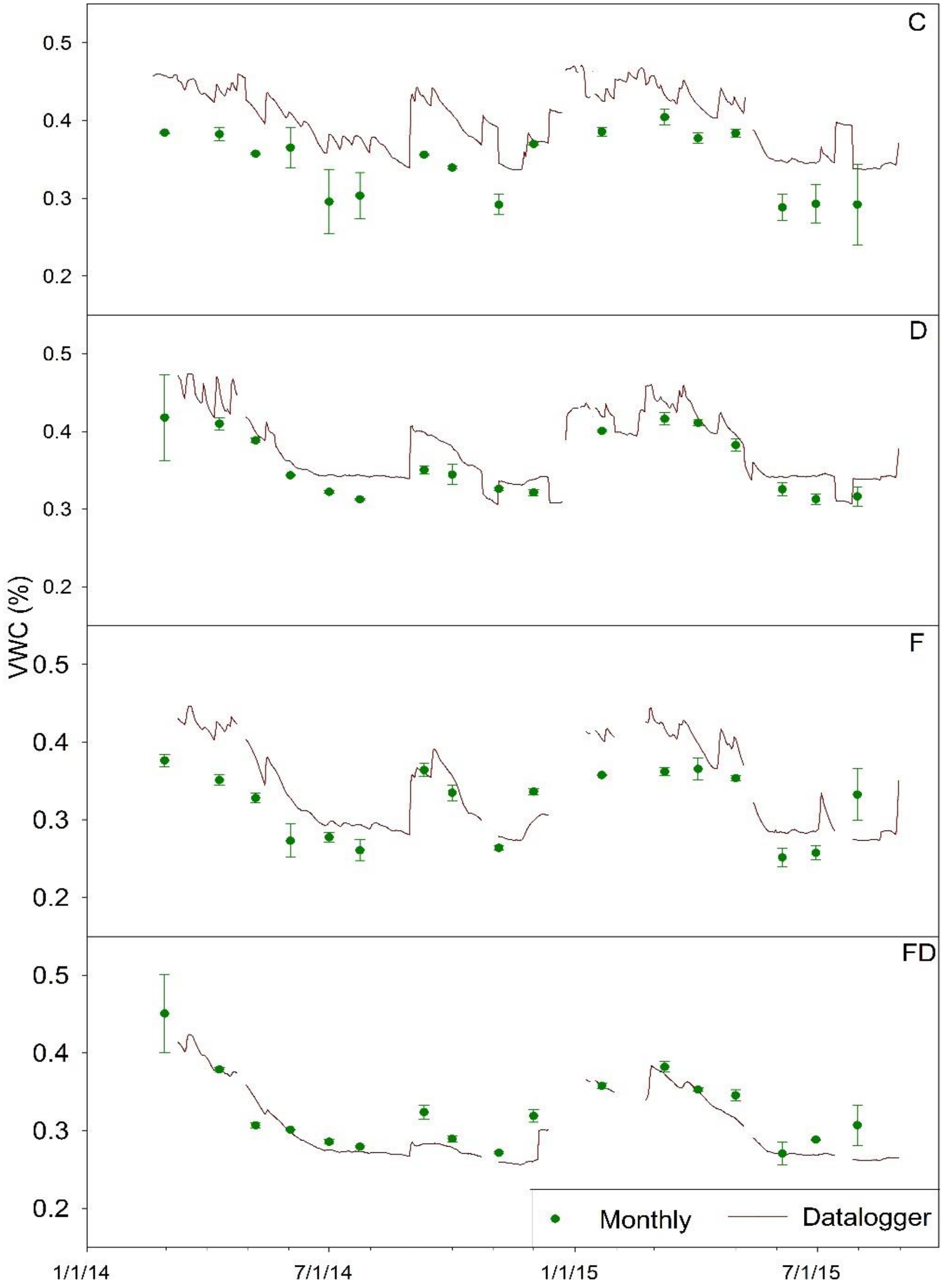

Figure 3.8. Average daily soil VWC at 0.6 m based on 30-minute readings of TDR probes (red line) and monthly point samples of VWC (mean ± 1SE) (n=4). Treatments are Control (C), Fertilized (F), Throughfall Exclusion (D), and FxD.

CHAPTER 4

MODELING THE EFFECT OF CHANGING PRECIPITATION INPUTS ON DEEP SOIL WATER UTILIZATION IN A SOUTHEAST U.S. LOBLOLLY PINE PLANTATION

---

[1] J. Qi, D. Marekwitz, and D. Radcliffe. To be submitted to *Hydrological Processes*.

ABSTRACT

Forests in the Southeast U.S. are predicted to experience future changes in seasonal patterns of precipitation inputs as well as more variable precipitation events. These climate change induced alterations could increase drought and lower water availability. Drought could also alter rooting patterns and increase importance of deep roots that access subsurface water resources. Evapotranspiration and soil water storage are linked with precipitation and discharge. To address plant response to drought in both deep rooting and soil water utilization as well as soil drainage, we utilize a throughfall exclusion experiment in a *Pinus taeda* L. plantation of the Southeast U.S. to calibrate and validate a hydrological model. The model was accurately calibrated using 914 days of data under ambient rainfall (R^2=0.84 and RMSE = 0.04 cm) and validated using 30% throughfall reduction data (R^2=0.67 and RMSE = 0.04 cm). We then test these scenarios: (1) evenly reduced precipitation; (2) less precipitation in summer, more in winter; (3) same amount of precipitation with less frequent, but heavier storms; and (4) shallower rooting depth under the above three scenarios. When less precipitation was received, drainage decreased much faster than evapotranspiration. When precipitation was reduced more than 30%, plants relied on soil water to satisfy evapotranspirational demand. Under the scenarios of seasonal precipitation redistribution and heavy storms, both evapotranspiration and bottom flux decreased, while surface runoff increased. Although root biomass measured both before and four years after the treatment did not differ among treatments, there is additional gain in evapotranspiration with deeper roots under evenly reduced precipitation and seasonal precipitation redistribution scenarios, but not when precipitation frequency was adjusted. The deep soil provides an important buffer capacity when precipitation alone cannot satisfy the evapotranspirational demand.

Key words: hydrologic model, Hydrus 1-D, precipitation change, evapotranspiration, bottom flux, surface runoff, deep root, soil moisture

INTRODUCTION

Forests in the Southeast U.S. are predicted to experience future changes (Meehl et al. 2007) in seasonal patterns of precipitation inputs (i.e., lower growing season inputs) as well as more variable precipitation events (i.e., fewer low intensity but greater high intensity events), although considerable uncertainty in projections remain (Seager et al. 2009). These climate change induced alterations could increase drought and lower water availability stressing plants and lowering productivity (Borken and Matzner 2009). Understanding how plants respond to drought is critical to predicting how a changing climate will alter plants and forests, and in the Southeast U.S. may affect how forest plantations are managed.

To cope with drought, plants have evolved both aboveground (e.g., stomatal conductance) and belowground (e.g., rooting depth) physiological responses (Breda et al. 2006). Aboveground leaf level response to water stress has received substantial research (Wertin et al. 2012, Samuelson et al. 2014); while investigation of belowground root responses have been more limited due to sampling difficulties, particular under forests (Joslin et al. 2000, Comas et al. 2013). In Amazonian rainforest under a throughfall exclusion experiment a comparison of above vs belowground controls on water uptake indicated belowground soil-to-root hydraulic resistance could contribute 10-90% of the total soil-plant-atmosphere resistance (Fisher et al. 2007).

Root traits that impact water relations include morphological traits that are relatively fixed for a given species (e.g., root architecture, depth, surface area, and anatomy), and physiological responses that are more plastic (e.g., shifts in belowground carbon allocation, and hydraulic redistribution; Phillips et al. 2016). These physiological processes depend on soil properties and spatial-temporal formation patterns of drought (Comas et al. 2013). For example, rooting depths were found to be greater in species from dry ecosystems (Schenk and Jackson 2002), in seedlings from forests with a long dry period (Paz 2003), and in seedlings growing in dry sandy soils (Yamada et al. 2005). Previous research has also shown that water stressed trees increase C allocation to roots growing deeper in the soil. For example, during an eight-week experiment on loblolly pine seedlings, the pattern of growth with depth shifted as soils became drier and root growth intensified where adequate water remained (Torreano and Morris 1998).

In the case of deep roots under mature forests, even though these roots may represent a relatively small fraction of the overall root system biomass they likely fulfill much more essential hydrological functions than shallow roots. A global review of 565 root profiles, across 15 terrestrial biomes, found that soil depths of 0.4, 0.7, and 1.1 m correspond to cumulative root proportions of 80, 90, and 95%, respectively (Schenk and Jackson 2002). Deeper rooting, however, allows trees to access subsurface water resources. Several studies have shown the importance of deep roots in maintaining canopy and mitigating drought effects (Fensham and Fairfax 2007, Padilla and Pugnaire 2007). In the Brazilian Amazon, about half of the forests rely on soil water below 100 cm to maintain evergreen canopies throughout the dry season (Nepstad et al. 1994, Stahl, Herault et al. 2013). Results from a throughfall exclusion study in the Amazon showed that during dry years, root water uptake from 250 to 550 cm soil contributed ~20% of water demand, and 550 to 1150 cm contributed ~10% (Markewitz et al. 2010). In a warm temperate pine plantation in the Southeast U.S., throughfall exclusion increased the proportion of water uptake from below 90 cm during the driest months, accounting for 30-90% of the monthly water demand (Chapter 3). Despite strong evidence that roots below 1 m facilitate water uptake, measuring increased root growth in soils in response to imposed throughfall exclusion experiments has proven difficult (Joslin et al. 2000, Phillips et al. 2016).

The throughfall exclusion experiments cited do not necessarily simulate natural drought (or climate change) so may underestimate the role of deep roots. For example, throughfall exclusion experiments often have permanent structures that exclude an equal amount of input for every month (Will et al. 2015) while droughts or, specifically, climate change may alter the seasonal input of precipitation (Meehl et al. 2007). In the Southeast U.S., for example, under a scenario of a continued CO_2 emissions increase, the region is predicted to experience up to a 20% decrease in precipitation during summer and up to a 20% increase in precipitation during winter (Melillo et al. 2014). This decreased precipitation during the summer growing season when evaporative demand is high could result in deeper soil drying and increase the role of deep roots in water uptake (Markewitz et al. 2010).

Similar to changes in seasonal distributions of rainfall, many general circulation models agree that as the climate warms, the frequency of extreme precipitation events will increase across the globe (O'Gorman and Schneider 2009). In fact, many regions of the United States have experienced a 1.4 ± 2.2 % per year increased frequency of extreme precipitation (upper 0.1% of precipitation events) over the last 50 years (Groisman et al. 2005). Forests in the Southeast U.S., in particular, are predicted to experience more variable precipitation in the future with up to three times more extreme daily precipitation events (a daily amount that occurs once in 20 years) (Meehl et al. 2007, Kunkel et al. 2013), and 10-30% increase in consecutive dry days (Melillo et al. 2014). An increase in dry days may also require a change in root distributions to sustain water supply.

The interaction between rooting depth and the amount or distribution of precipitation inputs may impact not only root water uptake but also soil drainage (and consequently stream discharge). The ecohydrological link from the mass balance

$$Q = P - ET - \Delta S$$

necessitates that if precipitation (P) declines, and evapotranspiration (ET) is sustained that soil water storage (ΔS) or discharge (Q) must decline (Vose et al. 2016). Recent experience with droughts and low flows in many areas of the United States indicate that even small changes in drought severity and frequency may have a major impact on water supply (Easterling et al. 2000, Luce and Holden 2009). Due to higher leaf area, deeper rooting, and large above-ground biomass, forests maintain relatively high evapotranspiration rates (Breuer et al. 2003). In the eastern U.S., after a typical rainfall event (>25 mm) only 10–34% of the precipitation leaves a forested watershed as streamflow (Hewlett 1982). If climate change results in a 10-30% reduction in rainfall inputs streamflow may decline in response. Throughfall exclusion experiments that remove 30 to 60% input have resulted in years of zero remaining soil storage or zero soil drainage (Joslin et al. 2000, Fisher et al. 2007, Markewitz et al. 2010). Presently, forests in the southeastern U.S. are predicted to experience a 2.5% or more per decade decease in water yield (Sun 2013).

To address plant response to drought in both deep rooting and soil water utilization as well as soil drainage we utilize a throughfall exclusion experiment in a managed pine (*Pinus taeda* L.) plantation of the Southeast U.S.. Plant water utilization (Samuelson, Pell et al. 2014) and soil water balance (Chapter 3) have previously been reported. Here we focus on belowground root response and utilize four years of exclusion with replicated treatments (n=4) to calibrate and validate a hydrological model that is then used to address hydrologic effects of changing precipitation input. We test these scenarios: (1) evenly reduced precipitation (experimental treatment); (2) less precipitation in summer, more in winter; (3) equal amounts of precipitation with less frequent, but heavier storms; and (4) shallower rooting depth under the above three scenarios.

We hypothesized that (1) with less precipitation, soil will satisfy the evapotranspirational demand first, but reduce drainage; (2) with seasonally redistributed precipitation, there will be less evapotranspiration and less bottom flux in the summer and more in the winter; (3) with the same amount of precipitation but with less frequency (i.e., heavier storms), there will be more surface runoff, and less evapotranspiration; and (4) deeper rooting and soil water uptake (1, 2, or 3m) will always result in higher ET and lower drainage. Understanding the physical processes driving the observed soil water dynamics at this site will enhance our ability to predict future hydrologic effects of changing precipitation input.

METHODS

Site descriptions

The throughfall exclusion experiment was established in a loblolly pine plantation in Taliaferro County, Georgia (33°37’32.61” N, 82°47’56.54” W). This site was clear-cut in 2004 and both chemical and mechanical site preparation were applied in 2005, including aerially applied Velpar ULW herbicide (5.97 kg/ha), debris management, and combination 2-in-1 plow. In 2006, bare root seedlings (seed orchard mix) were hand planted at 1544 trees/ha. Herbaceous weed control was applied banded at ~220 ml/ha of Oust Extra in 2006. Refer to Will et al. (2015) for more details.

The soils of this research site are a Cecil-Lloyd complex. The Lloyd series is a fine, kaolintic, thermic Rhodic Kanhapludult, while the Cecil series is a fine, kaolinitic, thermic Typic Kanhapludult (Table 4.1). The Rhodic designation indicates an influence of mafic parent material on soil color. These soils are typical in the region and descriptions are based on USDA-NRCS Soil Survey Division (https://soilseries.sc.egov.usda.gov).

The 30-year (1983-2012) average annual precipitation is 1119 mm and the 30-year (1983-2012) average daily maximum and minimum temperature is 22.7°C and 10.1°C (http://www.ncdc.noaa.gov). During the study period, monthly Palmer Drought Severity Index indicated mild drought from Jun 2014 to Jun 2015 (Palmer Drought Severity Index range from -1.00 to -1.99) and moderate drought only for Jul 2015 (values range from -2.00 to -2.99, http://www.ncdc.noaa.gov/temp-and-precip/drought/historical- palmers /psi/201303-201507).

Experimental design

Linear throughfall exclusion structures comprised of wood and plastic covering ~30% of the ground surface area were installed to reduce throughfall by 30%, which is at the extreme end of predictions for precipitation decline associated with climate change for the region (Collins et al. 2013, Walsh et al. 2014). Furthermore, because most planted pine forests are nutrient limited and nutrient management is widespread, the interaction of throughfall exclusion treatment was examined with an imposed nutritional gradient. This study was designed as a 2x2 factorial experiment with four blocks and the following treatments: Control (C) - no treatment; Fertilizer (F) - fertilizer additions to achieve "optimum" nutrition; Throughfall reduction (D) - panels installed in understory to divert 30% of throughfall off of the plot; Fertilizer + throughfall reduction (FD) - combined fertilizer and throughfall reduction treatments (PINEMAP 2013). Because nutrient management is not the focus of this research, we only use data from control and throughfall reduction plots. Blocks were established by tree height (mean ± SD; 6.34 ± 0.58 m) and basal area (mean ± SD; 8.79 ± 1.58 m2/ha) (Will et al. 2015). The fertilizer application rates were 224 kg/ha N, 28 kg/ha P, 56 kg/ha K and micro-nutrients. The throughfall reduction gutters were installed in the forest understory in May 2012. These panels cover 30% of the ground surface thus capturing ~30% of incoming throughfall. Water is channeled outside of the experimental treatment areas. The treatment area for each plot is 34 x 28 m with 21 x 14 m measurement area in the center and a 6 m untreated buffer area between each treatment area. Refer to Will et al. (2015) for more details.

Root Biomass

To assess potential changes in surface soil (0-10 and 10-20 cm) root biomass samples were collect prior to treatment initiation in Dec 2011/Jan 2012 and four years after treatment in Dec 2015/Jan 2016. Eight locations in each plot were randomly selected and sampled with a 6.5 cm diameter auger. Four of these eight samples were composited such that 2 samples were retained per plot. Roots of <2mm were handpicked from each sample for 20 minutes (Berhongaray et al. 2013). To assess potential changes in deep soil root biomass, data were collected from one soil core in each plot four years after treatment (2015). Samples were collected from 0-10, 10-20, 20-50, 50-100, 100-150, 150-200, 200-250 and 250-300 cm. Each of the 0-10 and 10-20 cm samples were handpicked for 20 min (Berhongaray et al. 2013). The rest of the samples were elutriated with a hydropneumatic elutriation system (Gillison's Variety Fabrication, Inc., Benzonia, MI) to separate roots from soil (Kosola et al. 2007). These roots were then dried, weighted and converted into root distribution data (g-root/kg-soil).

Soil Volumetric Water Content

Monthly soil volumetric water content (VWC) were measured and previously reported in Qi, 2016. VWC was measured using Riser Bond Model 1205CXA Coaxial Metallic Time Domain Reflectometer (TDR) (Radiodetection, Raymond, Maine). At the approximate center of the plot, sets of TDR probes were installed within tree-rows (in all plots), between tree rows (in all plots) and under throughfall reduction structures (only in D and FD plots) to cover these 4 depths: 0-10, 0-30, 0-60 and 0-90 cm. These soil moisture measurements were later partitioned into separate depths: 0-10, 10-30, 30-60 and 60-90cm using:

$$D_e = \sum_{i=1}^{n} \theta_i D_i$$

where D_e [L] is depth of water equivalent, θ_i and D_i are the VWCs and layer thicknesses, respectively, of each layer (Radcliffe and Šimůnek 2010). TDR probes were also installed at 200 and 300 cm. Soil VWCs were measured approximate monthly from March 2013 to July 2015.

To better capture the soil moisture changes during the growing season, a separate set of TDR probes (CS655 12 cm Soil Water Content Reflectometer, Campbell Scientific, Inc., Logan, Utah) were placed at 0.6 m at the approximate center of the plot in blocks 2 and 4. They were programmed to collect data every 30 minutes from March 2014 to July 2015. These data were logged automatically with data loggers (CR23X, Campbell Scientific, Inc., Logan, Utah), then downloaded and averaged by day.

Model structure and inputs

The model was designed to simulate daily changes (March 2013 to July 2015) in the vertical distribution of soil water using HYDRUS 1-D version 4.16 (Simunek et al. 2008), incorporating water flow and root water uptake. Using the Richards' equation for variably-saturated water and convection–dispersion type equations, HYDRUS-1D numerically solves moisture transport for a given soil, based on measured or estimated parameters (Simunek et al. 2008). This model consists of 300 cm of soil, separated into 8 soil material layers (0-10, 10-20, 20-50, 50-100, 100-150, 150-200, 200-250 and 250-300 cm) with respective soil hydraulic parameters. The hydraulic model is the modified van Genuchten-Mualem single porosity model.

Water flow parameters

Soil textural analysis followed Gee and Or (2002). Soils were sampled to 3 m in the middle of each plot. Soils were collected in eight depths as listed above. All samples were air-dried and homogenized by sieving through a 2 mm screen.

Soil water retention curves were determined using Tempe cells (SoilMoisture Equipment Corp., Santa Barbara, CA) and a WP4C Dewpoint PotentialMeter (Decagon Devices. Inc., Pullman, WA). Separate core samples were collected for these analyses. Tempe cells were used for <1MPa and WP4C Dewpoint PotentialMeter were used for >1MPa. Using the RETC program (Simunek et al. 2008), results from both instruments were integrated to form soil water retention curve equations following Van Genuchten (1980):

$$S_e(h) = \frac{1}{[1 + (-\alpha h)^n]^m}$$

where α [L^{-1}], n [-] and m [-] are fitting parameters, and $S_e(h)$ [-] is the effective soil water saturation calculated following Van Genuchten (1980):

$$S_e = \frac{\theta - \theta_r}{\theta_s - \theta_r}$$

where θ is the VWC, θ_s is the saturated VWC and θ_r is the residual VWC, defined as the VWC where hydraulic conductivity approaches zero (Van Genuchten 1980). Plant available water was calculated as the amount of soil water held at tensions between -0.01 and -1.5 MPa (θ_{wp}), determined from soil moisture retention curves.

Saturated hydraulic conductivity (K_{sat}) was measured at 20, 50, 100, 150, 200, 250 and 300 cm using a compact constant head permeameter (Eijelkamp Agrisearch Equipment, The Netherlands; Reynolds and Elrick 2002) at four locations across the research site.

Precipitation (PPT) and potential evapotranspiration (PET) records were obtained from six weather stations located within 90 km of the research site (www.georgiaweather.net; Figure 3.2). The mean PPT and PET between six locations from March 2013 to July 2015 were used to estimate the water balance during the experiment. This model assumes that there is no evaporation from the soil surface.

Actual evapotranspiration (AET) under the different treatments were calculated using sap flow data collected on site. These data were collected from five trees within the measurement plots (Bartkowiak et al. 2015). These data were not used to drive the model simulation, because daily data are not available, but are used to constrain the model outputs.

Root water uptake parameters were based on the Feddes et al. (1978) model structure. Parameters for the Feddes structure were optimized for the modeled plant species (loblolly pine) based on data from Hanson and Weltzin (2000). The root biomass data collected on the site were used to parameterize the model.

Data for inverse solution

The upper boundary condition for the model was set as an atmospheric boundary with surface run off. The lower boundary condition was set as free drainage. Precipitation inputs determine water flux to the soil surface and evapotranspiration determines water removal.

In the model, observation points were placed at 5, 20, 45, 75, 200 and 300 cm in order to compare with field observed monthly VWC data. During model calibration an inverse modelling approach was utilized based on the soil moisture using the control plot averages. The best solution was based on a minimization of R^2 and RMSE. Using this control plot calibration an initial validation was done using the more intensive temporal observation points placed at 60 cm to compare with field observed daily VWC. Thereafter, the control plot calibration parameters were applied to the exclusion plot.

RESULTS

Root distribution

Surface soil root biomass collected before treatments were initiated did not significantly differ among treatments ($p>>0.05$) and had mean values of 5.79 ± 1.49 g of root/kg of soil at 0-10 cm and 3.69 ± 0.93 g of root/kg of soil at 10-20 cm. Four years after treatments were installed, surface soil root biomass still did not significantly differ either due to fertilization or throughfall exclusion (all p-values>0.1). Surface soil C contents before and four years after treatment were also not significantly different between treatments ($p>0.5$). Similarly, no difference in root biomass at any depth through 3 m was detected four years after treatments began ($p>0.5$). The root biomass distribution followed the power function: $y=16.68x^{-0.59}$ ($R^2=0.89$), which was used to parameterize all simulations with the model (Figure 4.2).

Model Calibration

Parameters that were determined by measurements made at the site (e.g., root biomass, K_{sat}, etc) were used for the initial parameterization of the model (Table 4.2). Field VWC data from the control plots were then used for model calibration. The initial model predictions, however, did not fit well with field observations ($R^2 = 0.36$). As such, water retention parameters for each soil layer were calibrated iteratively using data from the control plot until R^2 between the model fitted and observed VWC for all depths over all dates were optimized. The resulting R^2 was 0.84, with

RMSE = 0.04 cm. Among all layers, the 300 cm layer had the poorest fit (Figure 4.3). In this layer, the model under predicted soil moisture for all months except September 2013.

Model validation

Soil VWC data were measured at the same time intervals in the throughfall exclusion only plots. These data were used for model validation and to assess changes in the depth of root water uptake with drying. Using the same optimized parameters, the R^2 between the model fitted value and field observed value was 0.67, with RMSE = 0.04 cm (Figure 4.4).

In addition to the 2.5-year record of monthly data in the throughfall exclusion only plot, the 30-minute data averaged to a daily VWC for both control and throughfall exclusion only were also used for validation. When the model was validated with these daily data, simulation results captured the same wetting and drying trends as the field observations in both control and drought treatment at the depth of 60 cm (Figure 4.5). Furthermore, the model was often, but not always, able to capture quick short-term changes in VWC. For example, the Oct/Nov 2014 increase in VWC was not well modeled while that from Jan/Feb 2015 was well represented.

Water fluxes

Compared to field observed AET, the model generally over estimated ET during months of spring and summer, and slightly underestimated AET during winter months (Figure 4.6). Model estimated ET was sometimes more than double the amount of the AET observed in the field from March to September 2013. Model estimated ET generally agreed with field observed AET during October to December in both years (Figure 4.6). The cumulative root water uptake (i.e., water use over the entire experimental period of 2 years and 5 months) under the control condition was 225.5 cm, the cumulative bottom flux was 87.7 cm, and the cumulative runoff was 6.4 cm.

Evenly reduced precipitation

Simulations of evenly reduced throughfall inputs but accounting for exclusions of 10 to 90% indicated that bottom flux decreased much faster than ET (Figure 4.7). Root water uptake followed the power function: $y=16.782x^{0.4635}$, while bottom flux followed an exponential function: $y=2.9332e^{0.011x}$, where y is water flux in cm and x is PPT in cm. Under ambient conditions of 100% PPT input, ET accounted for 75% of total PPT, while with a 30% exclusion of PPT, ET accounted for 97% (203 cm) of PPT input. Drainage (bottom flux) was 31.3 cm (36%) of drainage expected under ambient PPT. When PPT was reduced by 30% or more, total ET exceeded PPT input during the period of simulation. When exclusion was 90% or only 10% of normal PPT input was received (i.e., 30 cm of water), ET was 80 cm or 264% of PPT received.

The above simulation used 3 m of rooting depth as measured at the site. To test the importance of deep roots, root distribution was adjusted from 3 m to 2 m and then to 1 m. For these simulations, ET declined with shallower rooting (Figure 4.8). The decrease in ET was greater when more PPT was excluded. Soils below 1 m contributed <2% of ET with less than 20% PPT reduction; while more than 10% of ET came from soils below 1 m when more than 60% PPT was excluded. The 2-3 m soil layer contributed more root water uptake especially when the PPT was reduced 50-80%. The highest amount of ET (5.8 cm) that came from 2-3 m was under 70% PPT reduction.

Less precipitation in summer, more in winter

Under this scenario precipitation was adjusted seasonally. In the summer (June, July and August) PPT was reduced and in the winter (December, January and February) PPT was increased an equal percentage. Within these simulations ET generally decreased with decreased summer PPT, except for the 90% PPT redistribution (Figure 4.9). When the seasonal adjustment was 30%, compared to the control, ET decreased 4% over the 2.5-year period (Figure 4.9), bottom water flux decreased 27% (Figure 4.10), while surface runoff increased 143%. When the precipitation was seasonally adjusted by 50% patterns were similar with ET decreasing 9% (Figure 4.9), bottom water flux decreasing 48% (Figure 4.10), and surface runoff increasing 234%.

When root distribution was adjusted to 2 and 1 m, model outputs for ET decreased with shallower rooting depth (Figure 4.9). The effect of rooting depth on ET was larger when more PPT was redistributed from summer to winter. The smallest amount of water coming from below 1 m was 0.82 cm when 10% of PPT was redistributed. When 80-100% of PPT was redistributed, ET did not continue to decrease, however, the source of water uptake for ET with the different rooting depths continued to increase. At 100% PPT redistribution (i.e. no summer rainfall), 14.8 cm of water came from below 1 m and 11.1 cm came from below 2 m.

Less frequent rain events, greater rain event size

Rain event frequency was either once per week, biweek, or 4-week within this simulation scenario. The rainfall input was based on the measured amount and summed over the week, biweek, or 4-week period. As such, the one-day 4-week event was up to 4 times the size of the weekly event. With longer periods between PPT events, ET decreased (Figure 4.11), bottom flux decreased (Figure 4.12), and surface runoff increased. The amount of ET under weekly PPT interval was 98% of the ET under the control PPT (Figure 4.11), while bottom flux decreased 9% relative to control (Figure 4.12), and surface runoff increased 55%. When the PPT interval was set to bi-weekly, ET decreased 6% relative to control (Figure 4.11), bottom flux decreased 17% (Figure 4.12), while surface runoff increased 522%. When the PPT interval was set to every four weeks, ET decreased 14% (Figure 4.11), bottom flux decreased 29% (Figure 4.12), and surface runoff increased 799%.

Within this PPT regime, rooting depth did not result in a clear ET trend (Figure 4.11). When PPT was input once every 4 weeks, ET was higher with 1 m rooting depth, than with 2 m rooting depth, and 3 m rooting depth had the least amount of ET. When PPT was released once every week or once every two weeks, 2 m rooting depth resulted in the least amount of ET. The differences between rooting depths were small, less than 4 cm among all rooting depths, with one exception of 7.7 cm between 1 and 3 m when PPT was adjusted to once every 4 weeks (Figure 4.11).

DISCUSSION

Root Biomass

Four years after the throughfall exclusion x fertilization treatments were installed, root biomass over multiple depths were not significantly different among treatments (p values ranged from 0.12 at 0-10 cm to 0.74 at 100-150 cm). Measuring fine root biomass is difficult as roots have high spatial variation (Hendrick and Pregitzer 1992, Graefe et al. 2008), and during conventional washing procedures fine root loss may exceed 50% of the total root length (Pallant et al. 1993). In this study, 128 surface samples from 0-10 cm and 10-20 cm were collected (8 samples x 16 plots), but the coefficient of variation was relatively high (~25%) such that only greater differences could likely be detected. At greater depths only a single sample was collected per plot and variance at depth where root biomass is small were greater. Furthermore, some plants also increase water uptake by establishing symbiotic relationships with mycorrhizal fungi, which increase the total absorptive surface area of the root system (McCully 1999), but these changes would not be measured by the approach utilized here.

On the other hand, in a throughfall exclusion study under deciduous forest in the Southeast U.S. that utilized nearly five years of minirhizotron root elongation data, no impacts of drying on fine roots through the upper 60 cm was observed (Joslin et al., 2001). In this deciduous forest study, impacts on root to shoot ratios or fine root productivity were also not detected. Similarly, in two Amazonian throughfall exclusion studies, one on a clay rich (>70% clay) and the other on a sandy (>60% sand) Oxisol, changes in root mass were not detected (Belk et al., 2007; Fisher et al., 2007).

Soil moisture has been shown to have a clear effect of on tree root distribution. For example, root growth of loblolly pine seedlings shifted downward with depth during the growing period due to water depletion in surface soils (Torreano and Morris 1998). Similarly, an irrigation study (i.e., water augmentation rather than water reduction) in 50-yr-old Douglas Fir (*Psuedotsuga menzeisii*) did find reduced fine root production with irrigation, although production (i.e., growth and mortality) can change while standing stock (i.e., root biomass) stays constant.

Given we did not observe differences in root biomass, we considered changes in soil C as a potential means to capture changes in belowground inputs. Root detritus has been shown to be important in the formation of soil organic C (Fekete et al. 2014). Several litter removal experiments that found no significant difference in soil C content between control or litter removal, even after up to 20 years of manipulation, concluded that fine roots must be critical to sustaining soil C

(Lajtha et al. 2014, Huang and Spohn 2015). Furthermore, in a northeastern Hungary forest, with 4 years of root exclusion treatment, there was a significant decrease in soil C concentration in the upper 15 cm soil (Fekete et al. 2014). We, however, detected no change in soil C contents in 0-10 or 10-20 cm.

In a final effort to detect changes in root inputs we measured the ^{14}C age of 150-200 cm soil samples from two control plots and two throughfall exclusion only plots following the approach of Trumbore et al. (1996). We presumed that under throughfall exclusion increased root growth at depth would reduce the ^{14}C age of the soil C. Because of the limited sample size (n=2) we did not statistically test these measurements but the control samples were dated 7980 ± 30 years while the throughfall reduction plots were dated 8430 ± 35 years, contrary to our expectation. Others have demonstrated in loblolly pine and white oak seedlings that relative root elongation rates are linearly related to soil water potential (Teskey and Hinckley 1981, Torreano and Morris 1998). As such, we might interpret these ^{14}C results as suggesting that soil drying under throughfall exclusion might limit root growth rather than induce greater growth. In total, however, we found no evidence that fine root biomass was altered during four years of throughfall exclusion.

Model calibration and validation

Our initial calibrations with field measured soil water parameters (Table 4.2) did not fit well with field observations of VWC ($R^2 = 0.36$). Inconsistencies in physical soil water characteristics between laboratory and field data are not uncommon (Rasmussen et al. 1993). Reasons include alteration of soil structure during sample collection, hysteresis effects on soil moisture, spatial variability of soil properties (Belk et al. 2007), and different vegetation or organic matter content that all could lead to different soil water retention parameters (Wang et al. 2013).

After these parameters were optimized, however, model calibration improved (R^2=0.84 and RMSE=0.04 cm). The final calibrated parameters were comparable with other hydrologic research conducted in similar soils series (Bruce et al. 1983).

Using these calibrated parameters from the control treatment, a model simulation on the throughfall exclusion only treatment generated a satisfactory validation result (R^2 = 0.67, RMSE = 0.04 cm) (Figure 4.3). There are several reasons why models do not completely agree with field measurements. For example, as noted above, we may not have captured changes in root distribution during the experimental period. Similarly, the actually amount of throughfall exclusion was not measured but was presumed to equal the 30% of ground covered. However, a similar assumption in a throughfall exclusion in the Amazon was demonstrated to be valid (Nepstad et al., 2001).

Another mechanism we have not considered is hydraulic redistribution. During hydraulic redistribution water from deeper soil layers is redeposited along a hydraulic gradient in drier surface soil by flowing out through root tips. These hydraulic redistributions do not alter the total water use of the deeply rooted plants but can increase water use by shallow rooted understory. For example, in an 18-yr-old loblolly pine plantation with a complex understory located on the Lower Coastal Plain of North Carolina, hydraulic redistribution increased transpiration during a drought by 30-50% and accounted for 15-25% of measured total soil water depletion seasonally (Domec et al. 2010). In another study of hydraulic redistribution in a clay rich Oxisol under throughfall exclusion, with understory, there was clear evidence of sap flux towards root tips but the quantity of water redistributed was not quantified (Oliveira et al., 2005). In the absence of understory, this process of redistribution should not alter total ET but could result in subsurface soil drying beyond that found in this model. For example, under the throughfall reduction treatments our model underestimated soil moisture between 10-90 cm during the June to December 2014 period and at 300 cm throughout the simulation the observed soil moisture varied more than model fitted values.

Water fluxes

Model estimated ET and sap flow estimated ET generally agreed during fall and winter, while the largest differences occurred in spring and summer (Figure 4.5). Model estimated AET was sometimes more than double the amount of the AET estimated from sap flow from March to September 2013. A possible explanation for our model overestimation is canopy interception. Canopy interception of PPT can reduce the amount of water entering the soil and ET while intercepted rainfall is being evaporated off the canopy. Canopy interception accounted for an average of 15% of total ET in a coastal plain loblolly pine plantation over 10 years (Gavazzi et al. 2016) and 20% of total PPT in another loblolly pine plantation in the same region (Cao et al. 2006). In this model, we did not specifically subtract interception from ET and thus water leaving the system because of canopy intercept is counted as part of the evapotranspiration, although this water is not taken up by roots.

Disagreement between modeled ET and AET calculated from sap flow measurements are not uncommon. For example, in a deciduous forest in the Southeast U.S., sap flow estimates of transpiration were about 50% of annual evapotranspiration estimated from eddy covariance and catchment studies (Wilson et al. 2001). Similarly, when five deciduous hardwood species were investigated in a nursery in South Carolina the difference between modeled ET and measured sap flow ranged from a 35% underestimation to a 25% overestimation (Bowden and Bauerle 2008). In young loblolly pine that have little heartwood, however, sap flow is generally consider a good measure of AET.

Precipitation manipulations

Despite model uncertainty described above, our parameterization and simulation explained 70 to 80% of the observed variation in VWC across 3m of soil. As such, our goal was to use the model to expand our knowledge of the hydrologic functioning of the forest ecosystem by being able to alter throughfall exclusion (or precipitation reduction) from a constant rate to a seasonal pattern and to alter rainfall frequency and intensity. We hypothesized that with a constant rate of PPT exclusion soil will satisfy the evapotranspirational demand of plants but will reduce bottom flux (or drainage). In addition to the potential effects of droughts on plants, these changes in drainage may have a major impact on water supply (Easterling et al. 2000, Luce and Holden 2009). Forest water yield and ET are two key ecosystem functions (Xiao et al., 2008, 2010; Jung et al., 2010). As noted previously, the ecohydrological link from the mass balance necessitates that if PPT declines and ET is sustained that soil water storage (ΔS) or discharge (Q), must decline (Vose et al., 2016). At our experimental site, ground level evapotranspiration did not differ significantly between the control and the throughfall reduction treatments (Bartkowiak et al. 2015). Soil water storage, however, generally declined during the summer and increased or recharged during winter throughout the experimental period (Qi, 2016). Therefore, with decreased water input, we should expect less water yield under the throughfall reduction treatment (Sun and Liu 2013).

Results from this model supported this hypothesis. When PPT was reduced by 30% to 210 cm over 2.5-year, ET accounted for almost all of the PPT received (203 cm or 96.6%, Figure 4.8), and drainage declined to ~30 cm or 35.9% compared with control plot drainage (Figure 4.7). When evenly distributed PPT exclusion exceed 30%, PPT received could not sustain ET, and plants had to extract water from the soil. At the extreme end of this PPT manipulation scenario, when 90% of PPT was excluded, 49.4 cm of ET came from soil water storage (79.5% of plant available water storage; see Qi 2016) and drainage declined to only 4.6 cm over the whole experimental period. Given the evenly distributed reduction in PPT, these results appear intuitive and are consistent with previous research. For example, when looking at the 75 years of climate and stream data at six watersheds of the Coweeta basin in the southern Appalachian Mountains, wet and dry years correlate strongly with streamflow variability (adjusted R^2=0.99) (Ford et al. 2011).

These results are also consistent with findings in Qi (2016), that this hydrologic system can sustain the evapotranspirational demand under 30% PPT reduction when considering the whole soil profile. This research is new in demonstrating that 30% PPT reduction (which is at the extreme end of predictions for precipitation reduction associated with climate change for the region (Collin, et al. 2013, Walsh et al. 2014)) is the limit for this ecosystem. Beyond this threshold, plants will depend on soil water storage to satisfy evapotranspirational demand. It is also notable that this experiment period had more than the average amount of PPT (http://www.ncdc.noaa.gov), thus the threshold PPT reduction should be smaller if less PPT were received.

In our second hypothesis, we proposed that with more seasonal redistribution of PPT there will be less ET and less drainage in the summer but more drainage in the winter. Model results did not completely support this hypothesis. The ET generally decreased with decreased summer PPT (Figure 4.9) but drainage did not increase in the winter as hypothesized (Figure 4.10). For most of the experimental period, drainage decreased. One exception occurred between March to June 2015, where with 30% PPT redistribution, there was more drainage than under control conditions. In the face of seasonal rainfall redistribution, water did not leave this hydrological system as bottom flux but instead was routed through increased surface runoff. Surface runoff increased 143% compared to control when the redistribution was 30%, and surface runoff increased 234% when the precipitation was redistributed by 50%.

Our final hypothesis proposed that with the same amount of PPT distributed in less frequent but heavier rain events, there would be more surface runoff and less ET. Results from this modeling effort confirmed this hypothesis. When the PPT interval was manipulated, surface runoff increased 55% under a weekly PPT interval, 522% under a bi-weekly interval, and 799% when the PPT interval was set to once every four weeks. On the other hand, ET decreased (Figure 4.11), although not as much as bottom flux (Figure 4.12). These changes in water flux from drainage to surface runoff are familiar in landscapes that have suffered surface compaction and may have important consequences in shifting stream discharge from baseflow to rapid flow.

Rooting Depth

In addition to our interest in simulating different patterns of rainfall inputs, we wanted to investigate the role of deep rooting in buffering forests from the impacts of drought. To test the importance of deep roots, rooting depth was adjusted from 3 m to 2 m and then to 1 m. Under these rooting depths there was additional gain in ET with deeper roots under all evenly reduced PPT scenarios and seasonal PPT redistribution scenarios (Figure 4.8 and 4.9). Under both scenarios, soils below 1 m contributed more to ET when more PPT was excluded or redistributed. Under the evenly reduced PPT scenario the 2-3 m soils were important when PPT was reduced by 50-80% (Figure 4.8). Under the seasonal PPT redistribution scenario, more water came from below 1 m as PPT redistribution increased. The additional gain of water from below 1 m was often a small percentage compared to annual ET, however, during months when AET > PPT, the 90-300 cm soil at this research site constantly (32/37 months) contributed more than half of total change in plant available water (Qi 2016). As such, it appears that deep soil and deep roots provide an important buffer capacity (Markewitz et al. 2010) when PPT alone cannot satisfy the monthly evapotranspirational demand. This will be critical if rainfall patterns in the Southeast U.S. become more seasonal.

Deep root buffering effects were not as evident when PPT frequency was manipulated. As expected, when root depth was adjusted to 2 or 1 m, transpiration decreased when there were longer periods between PPT (Figure 4.11). However, within the same PPT regime, rooting depth did not result in clear transpiration trends (Figure 4.11). This could be caused by the availability of soil water. The soil in this experiment is clay rich in the middle section with 50-200 cm soil requiring >15% VWC to rise above the water potential of wilting point (θ_{wp} in Table 4.1). Therefore, when rooting depth is 2 m, the average θ_{wp} increased while the proportion of root distributed above 1 m decreased. Thus explain why deeper roots did not result in higher transpiration under tested PPT regimes.

CONCLUSION

The hydrologic simulation model used in this study was accurately calibrated using 914 days of VWC data under ambient rainfall of the control plots (R^2=0.84 and RMSE = 0.04 cm). Simulation of VWC under 30% throughfall exclusion provided supporting model validation (R^2=0.67 and RMSE = 0.04 cm). Using the simulation model, scenarios of precipitation input and rooting depth were evaluated for response in ET and drainage. With less precipitation (greater exclusion), drainage decreased much faster than evapotranspiration. When precipitation was reduced by more than 30%, plants relied on soil water to satisfy evapotranspirational demand. Under the scenarios of seasonal precipitation redistribution and heavy storms, both evapotranspiration and bottom flux decreased, while surface runoff increased. Root biomass measured both before and 4 years after the throughfall exclusion treatment did not differ among treatments. Simulations, however, found there is an increase in evapotranspiration with deeper roots under evenly reduced precipitation and seasonal precipitation redistribution scenarios. When precipitation frequency was manipulated deep soil did not buffer the stress of drought. Deep soil and deep rooting can provide an important buffer capacity when precipitation alone cannot satisfy the evapotranspirational demand of forests. How this buffering capacity will persist in the face of changing precipitation inputs, however, may depend less on seasonal redistribution than rainfall frequency.

REFERENCES

Bartkowiak, S. M., L. J. Samuelson, M. A. McGuire and R. O. Teskey (2015). "Fertilization increases sensitivity of canopy stomatal conductance and transpiration to throughfall reduction in an 8-year-old loblolly pine plantation." Forest Ecology and Management 354: 87-96.

Belk, E. L., D. Markewitz, T. C. Rasmussen, E. J. Maklouf Carvalho, D. C. Nepstad and E. A. Davidson (2007). "Modeling the effects of throughfall reduction on soil water content in a Brazilian Oxisol under a moist tropical forest." Water Resources Research 43(8): 14.

Berhongaray, G., J. S. King, I. A. Janssens and R. Ceulemans (2013). "An optimized fine root sampling methodology balancing accuracy and time investment." Plant and Soil 366(1-2): 351-361.

Borken, W. and E. Matzner (2009). "Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils." Global Change Biology 15(4): 808-824.

Bowden, J. D. and W. L. Bauerle (2008). "Measuring and modeling the variation in species-specific transpiration in temperate deciduous hardwoods." Tree Physiology 28(11): 1675-1683.

Breda, N., R. Huc, A. Granier and E. Dreyer (2006). "Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences." Annals of Forest Science 63(6): 625-644.

Breuer, L., K. Eckhardt and H.-G. Frede (2003). "Plant parameter values for models in temperate climates." Ecological Modelling 169(2–3): 237-293.

Bruce, R. R., J. H. Dane, V. L. Quisenberry, N. L. Powell and a. A. W. Thomas (1983). Physical characteristics of soils of the Southern Region: Cecil. Athens, Georgia: Georgia Agricultural Experiment Stations.

Cao, W., G. Sun, S. G. McNulty, J. Chen, A. Noormets, R. Skaggs and D. M. Amatya (2006). Evapotranspiration of a mid-rotation loblolly pine plantation and a recently harvested stands on the coastal plain of North Carolina, USA. Hydrology and Management of Forested Wetlands, Proceedings of the International Conference, April 8-12, 2006, New Bern, North Carolina, American Society of Agricultural and Biological Engineers.

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W. J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A. J. Weaver and M. Wehner (2013). Long-term Climate Change: Projections, Commitments and Irreversibility. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. T. F. Stocker, D. Qin, G.-K. Plattner et al. Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press: 1029–1136.

Comas, L. H., S. R. Becker, V. V. Cruz, P. F. Byrne and D. A. Dierig (2013). "Root traits contributing to plant productivity under drought." Frontiers in Plant Science 4: 16.

Domec, J. C., J. S. King, A. Noormets, E. Treasure, M. J. Gavazzi, G. Sun and S. G. McNulty (2010). "Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange." New Phytologist 187(1): 171-183.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl and L. O. Mearns (2000). "Climate extremes: Observations, modeling, and impacts." Science 289(5487): 2068-2074.

Feddes, R. A., P. J. Kowalik and H. Zaradny (1978). Simulation of field water use and crop yield, Centre for Agricultural Publishing and Documentation.

Fekete, I., Z. Kotroczo, C. Varga, P. T. Nagy, G. Varbiro, R. D. Bowden, J. A. Toth and K. Lajtha (2014). "Alterations in forest detritus inputs influence soil carbon concentration and soil respiration in a Central-European deciduous forest." Soil Biology & Biochemistry 74: 106-114.

Fensham, R. J. and R. J. Fairfax (2007). "Drought-related tree death of savanna eucalypts: Species susceptibility, soil conditions and root architecture." Journal of Vegetation Science 18(1): 71-80.

Fisher, R. A., M. Williams, A. L. Da Costa, Y. Malhi, R. F. Da Costa, S. Almeida and P. Meir (2007). "The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment." Global Change Biology 13(11): 2361-2378.

Ford, C. R., S. H. Laseter, W. T. Swank and J. M. Vose (2011). "Can forest management be used to sustain water-based ecosystem services in the face of climate change?" Ecological Applications 21(6): 2049-2067.

Gavazzi, M. J., G. Sun, S. G. McNulty, E. A. Treasure and M. G. Wightman (2016). "Canopy Rainfall Interception Measured over Ten Years in a Coastal Plain Loblolly Pine (Pinus Taeda L.) Plantation." Transactions of the Asabe 59(2): 601-610.

Gee, G. W. and D. Or (2002). "2.4 Particle-size analysis." Methods of Soil Analysis: Part 4 Physical Methods sssabookseries(methodsofsoilan4): 255-293.

Graefe, S., D. Hertel and C. Leuschner (2008). "Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons." Biotropica 40(5): 536-542.

Groisman, P. Y., R. W. Knight, D. R. Easterling, T. R. Karl, G. C. Hegerl and V. A. N. Razuvaev (2005). "Trends in intense precipitation in the climate record." Journal of Climate 18(9): 1326-1350.

Hanson, P. J. and J. F. Weltzin (2000). "Drought disturbance from climate change: response of United States forests." Science of The Total Environment 262(3): 205-220.

Hendrick, R. L. and K. S. Pregitzer (1992). "Spatial Variation in Tree Root Distribution and Growth Associated with Minirhizotrons." Plant and Soil 143(2): 283-288.

Hewlett, J. D. (1982). Principles of Forest Hydrology. Athens, Georgia, University of Georgia Press.

Huang, W. and M. Spohn (2015). "Effects of long-term litter manipulation on soil carbon, nitrogen, and phosphorus in a temperate deciduous forest." Soil Biology and Biochemistry 83: 12-18.

Joslin, J. D., M. H. Wolfe and P. J. Hanson (2000). "Effects of altered water regimes on forest root systems." New Phytologist 147(1): 117-129.

Kosola, K. R., B. A. A. Workmaster, J. S. Busse and J. H. Gilman (2007). "Sampling damage to tree fine roots: Comparin, air excavation and hydropneumatic elutriation." Hortscience 42(3): 728-731.

Kunkel, K. E., L. E. Stevens, S. E. Stevens, L. Sun, E. Janssen, D. Wuebbles, C. E. Konrad, II, C. M. Fuhrman, B. D. Keim, M. C. Kruk, A. Billet, H. Needham, M. Schafer and J. G. Dobson (2013). Regional Climate Trends and Scenarios for the U.S. National Climate Assessment: Part 2. Climate of the Southeast U.S. NOAA Technical Report 142-2 Washington D.C., National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service 103.

Lajtha, K., R. D. Bowden and K. Nadelhoffer (2014). "Litter and Root Manipulations Provide Insights into Soil Organic Matter Dynamics and Stability." Soil Science Society of America Journal 78: S261-S269.

Luce, C. H. and Z. A. Holden (2009). "Declining annual streamflow distributions in the Pacific Northwest United States, 1948-2006." Geophysical Research Letters 36.

Markewitz, D., S. Devine, E. A. Davidson, P. Brando and D. C. Nepstad (2010). "Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake." New Phytologist 187(3): 592-607.

McCully, M. E. (1999). "Roots in soil: Unearthing the complexities of roots and their rhizospheres." Annual Review of Plant Physiology and Plant Molecular Biology 50: 695.

Meehl, G. A., C. Tebaldi, H. Teng and T. C. Peterson (2007). "Current and future U.S. weather extremes and El Nino." Geophysical Research Letters 34(20).

Melillo, J. M., Terese (T.C.) Richmond and E. and Gary W. Yohe (2014). "Climate Change Impacts in the United States: The Third National Climate Assessment." U.S. Global Change Research Program: 841.

Nepstad, D. C., C. R. Decarvalho, E. A. Davidson, P. H. Jipp, P. A. Lefebvre, G. H. Negreiros, E. D. Dasilva, T. A. Stone, S. E. Trumbore and S. Vieira (1994). "The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures." Nature 372(6507): 666-669.

O'Gorman, P. A. and T. Schneider (2009). "The physical basis for increases in precipitation extremes in simulations of 21st-century climate change." Proceedings of the National Academy of Sciences of the United States of America 106(35): 14773-14777.

Oliveira, R. S., T. E. Dawson, S. S. O. Burgess and D. C. Nepstad (2005). "Hydraulic redistribution in three Amazonian trees." Oecologia 145(3): 354-363.

Padilla, F. M. and F. I. Pugnaire (2007). "Rooting depth and soil moisture control Mediterranean woody seedling survival during drought." Functional Ecology 21(3): 489-495.

Paz, H. (2003). "Root/shoot allocation and root architecture in seedlings: Variation among forest sites, microhabitats, and ecological groups." Biotropica 35(3): 318-332.

Phillips, R. P., I. Ibáñez, L. D’Orangeville, P. J. Hanson, M. G. Ryan and N. G. McDowell (2016). "A belowground perspective on the drought sensitivity of forests: Towards improved understanding and simulation." Forest Ecology and Management 380: 309-320.

Radcliffe, D. E. and J. Šimůnek (2010). Soil physics with HYDRUS: Modeling and applications, CRC press Boca Raton, Florida.

Rasmussen, T. C., D. D. Evans, P. J. Sheets and J. H. Blanford (1993). "Permeability of Apache Leap Tuff - Borehole and Core Measurements Using Water and Air." Water Resources Research 29(7): 1997-2006.

Reynolds, W. D. and D. E. Elrick (2002). 3.4.3.3 Constant Head Well Permeameter (Vadose Zone). Methods of Soil Analysis: Part 4 Physical Methods. J. H. Dane and C. G. Topp. Madison, WI, Soil Science Society of America: 844-858.

Samuelson, L. J., C. J. Pell, T. A. Stokes, S. M. Bartkowiak, M. K. Akers, M. Kane, D. Markewitz, M. A. McGuire and R. O. Teskey (2014). "Two-year throughfall and fertilization effects on leaf physiology and growth of loblolly pine in the Georgia Piedmont." Forest Ecology and Management 330: 29-37.

Schenk, H. J. and R. B. Jackson (2002). "The global biogeography of roots." Ecological Monographs 72(3): 311-328.

Schenk, H. J. and R. B. Jackson (2002). "Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems." Journal of Ecology 90(3): 480-494.

Seager, R., A. Tzanova and J. Nakamura (2009). "Drought in the Southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change." Journal of Climate 22(19): 5021-5045.

Simunek, J., M. T. van Genuchten and M. Sejna (2008). "Development and applications of the HYDRUS and STANMOD software packages and related codes." Vadose Zone Journal 7(2): 587-600.

Stahl, C., B. Herault, V. Rossi, B. Burban, C. Brechet and D. Bonal (2013). "Depth of soil water uptake by tropical rainforest trees during dry periods: does tree dimension matter?" Oecologia 173(4): 1191-1201.

Sun, G. (2013). Impacts of Climate Change and Variability on Water Resources in the Southeast USA. Climate of the Southeast United States: Variability, Change, Impacts, and Vulnerability. K. T. Ingram, K. Dow, L. Carter and J. Anderson. Washington, DC, Island Press/Center for Resource Economics: 210-236.

Sun, G. and Y. Liu (2013). "Forest influences on climate and water resources at the landscape to regional scale." 309-334.

Teskey, R. O. and T. M. Hinckley (1981). "Influence of Temperature and Water Potential on Root-Growth of White Oak." Physiologia Plantarum 52(3): 363-369.

Torreano, S. J. and L. A. Morris (1998). "Loblolly pine root growth and distribution under water stress." Soil Science Society of America Journal 62(3): 818-827.

Trumbore, S. E., E. A. Davidson, P. B. Decamargo, D. C. Nepstad and L. A. Martinelli (1995). "Belowground cycling of carbon in forests and pastures of Eastern Amazonia." Global Biogeochemical Cycles 9(4): 515-528.

Van Genuchten, M. T. (1980). "A closed form equation for predicting the hydraulic conductivity of unsaturated soils." Soil Science Society of America Journal 44(5): 892-898.

Vose, J., J. S. Clark, C. Luce and T. Patel-Weynand (2016). Effects of drought on forests and rangelands in the United States: a comprehensive science synthesis. 93b: 1-289.

Walsh, J., D. Wuebbles, K. Hayhoe, J. Kossin, K. Kunkel, G. Stephens, P. Thorne, R. Vose, M. Wehner and J. Willis (2014). "Ch. 2: Our changing climate." Climate Change Impacts in the United States: The Third National Climate Assessment, JM Melillo, Terese (TC) Richmond, and GW Yohe, Eds., U.S. Global Change Research Program: 19-67.

Wang, C., C. Y. Zhao, Z. L. Xu, Y. Wang and H. H. Peng (2013). "Effect of vegetation on soil water retention and storage in a semi-arid alpine forest catchment." Journal of Arid Land 5(2): 207-219.

Wertin, T. M., M. A. McGuire and R. O. Teskey (2012). "Effects of predicted future and current atmospheric temperature and CO2 and high and low soil moisture on gas exchange and growth of Pinus taeda seedlings at cool and warm sites in the species range." Tree Physiology 32(7): 847-858.

Will, R. E., T. Fox, M. Akers, J. C. Domec, C. Gonzalez-Benecke, E. J. Jokela, M. Kane, M. A. Laviner, G. Lokuta, D. Markewitz, M. A. McGuire, C. Meek, A. Noormets, L. Samuelson, J. Seiler, B. Strahm, R. Teskey, J. Vogel, E. Ward, J. West, D. Wilson and T. A. Martin (2015). "A range-wide experiment to investigate nutrient and soil moisture interactions in loblolly pine plantations." Forests 6(6): 2014-2028.

Wilson, K. B., P. J. Hanson, P. J. Mulholland, D. D. Baldocchi and S. D. Wullschleger (2001). "A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance." Agricultural and Forest Meteorology 106(2): 153-168.

Yamada, T., E. Suzuki, T. Yamakura and S. Tan (2005). "Tap-root depth of tropical seedlings in relation to species-specific edaphic preferences." Journal of Tropical Ecology 21: 155-160.

Table 4.1. Soils texture and soil water potential of wilting point (θ_{wp}) for all treatment plots at Taliaferro County, Georgia. Values given as mean ± 1SE (n=16).

Depth (cm)	Texture	Sand %	Silt %	Clay %	θ_{wp}
0-10	loam	45±12	31±6	24±12	0.10
10-20	clay loam	37±11	32±6	31±11	0.13
20-50	clay	26±7	33±6	42±9	0.11
50-100	clay	18±8	35±6	47±4	0.15
100-150	clay	21±9	36±9	42±5	0.19
150-200	clay loam	22±10	39±8	38±6	0.16
200-250	clay loam	22±11	45±8	32±7	0.14
250-300	loam	26±13	48±7	25±9	0.13

Table 4.2. Soil water retention curve parameters as initially estimated from field measure and as determined from model calibration. Initial values are means of 8 samples for 0-10 and 10-20 cm (n=8) and n=2 below 20 cm.

Initial parameters

Depth (cm)	θ_r	θ_s	α	n	K_{sat}
0-10	0.08	0.33	8.20E-04	1.45	164.7
10-20	0.10	0.40	3.06E-03	1.28	164.7
20-50	0.10	0.39	2.23E-03	1.39	91.8
50-100	0.08	0.41	9.65E-04	1.41	28.0
100-150	0.07	0.48	7.00E-04	1.38	19.2
150-200	0.08	0.43	1.83E-02	1.28	3.5
200-250	0.10	0.39	1.92E-02	1.22	3.9
250-300	0.09	0.50	3.13E-03	1.36	3.4

Final parameters

Depth (cm)	θ_r	θ_s	α	n	K_{sat}
0-10	0.19	0.36	4.20E-03	1.43	172.0
10-20	0.00	0.40	6.46E-03	1.21	172.0
20-50	0.08	0.38	4.27E-03	1.28	32.1
50-100	0.09	0.48	5.28E-03	1.16	3.0
100-150	0.00	0.67	1.73E-03	2.00	3.0
150-200	0.07	0.50	2.78E-03	1.97	10.0
200-250	0.10	0.55	8.93E-04	2.00	25.0
250-300	0.12	0.50	5.08E-03	1.14	100.0

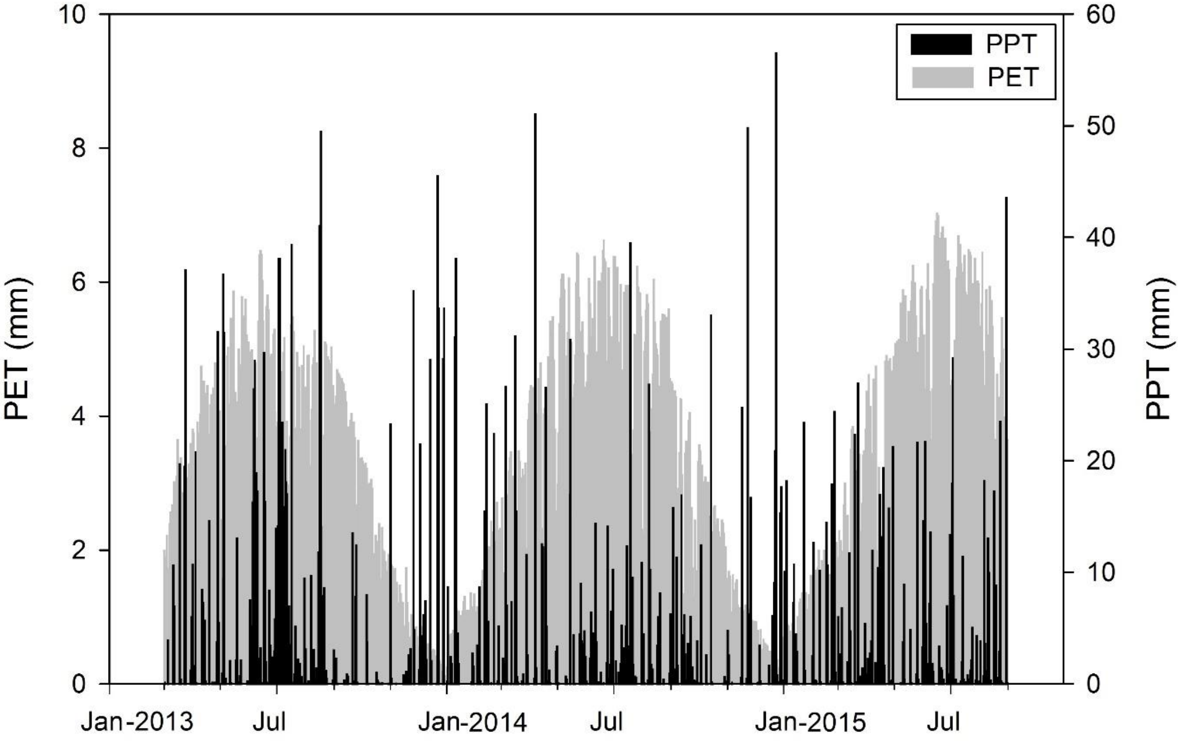

Figure 4.1. Daily precipitation (PPT) (black bars) and daily potential evapotranspiration (PET) (gray bars) at the throughfall exclusion experiment in Taliaferro County, Georgia for the period of March 2013 to July 2015.

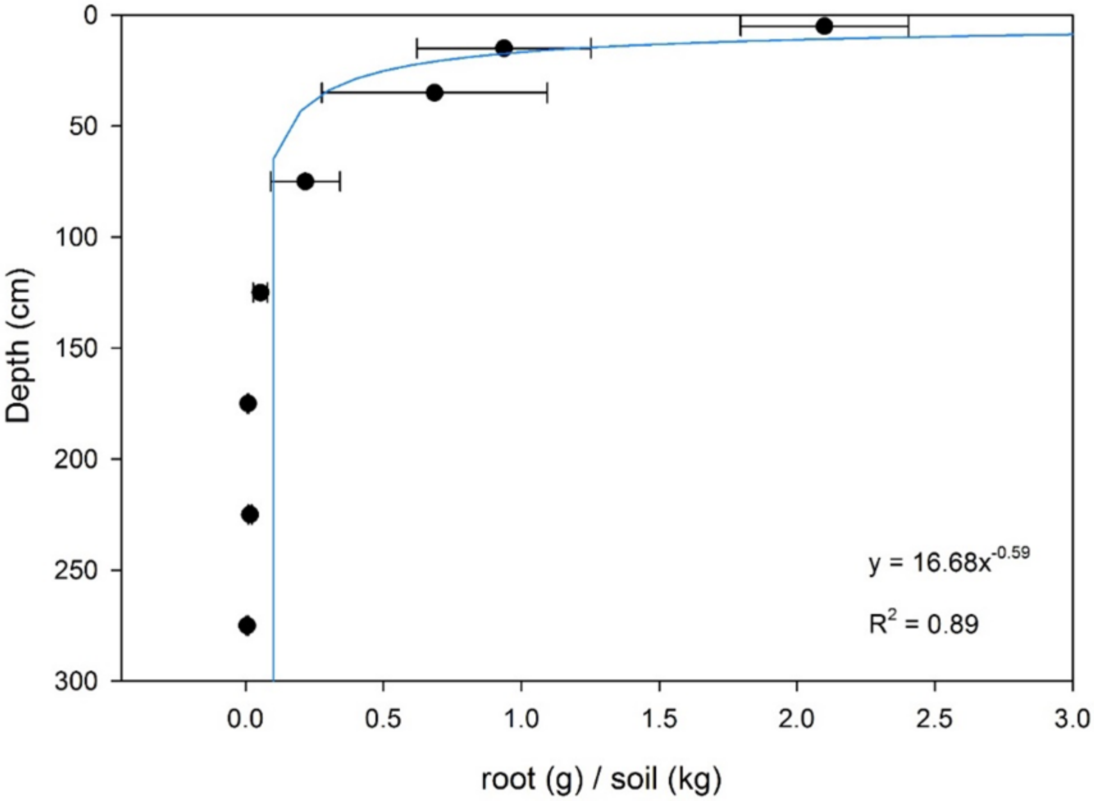

Figure 4.2. Root biomass distribution collected 4 years after initiation of a throughfall exclusion experiment in Taliaferro County, Georgia. Data presented are means with standard error (n=16). Blue line represents a power function fit to the data.

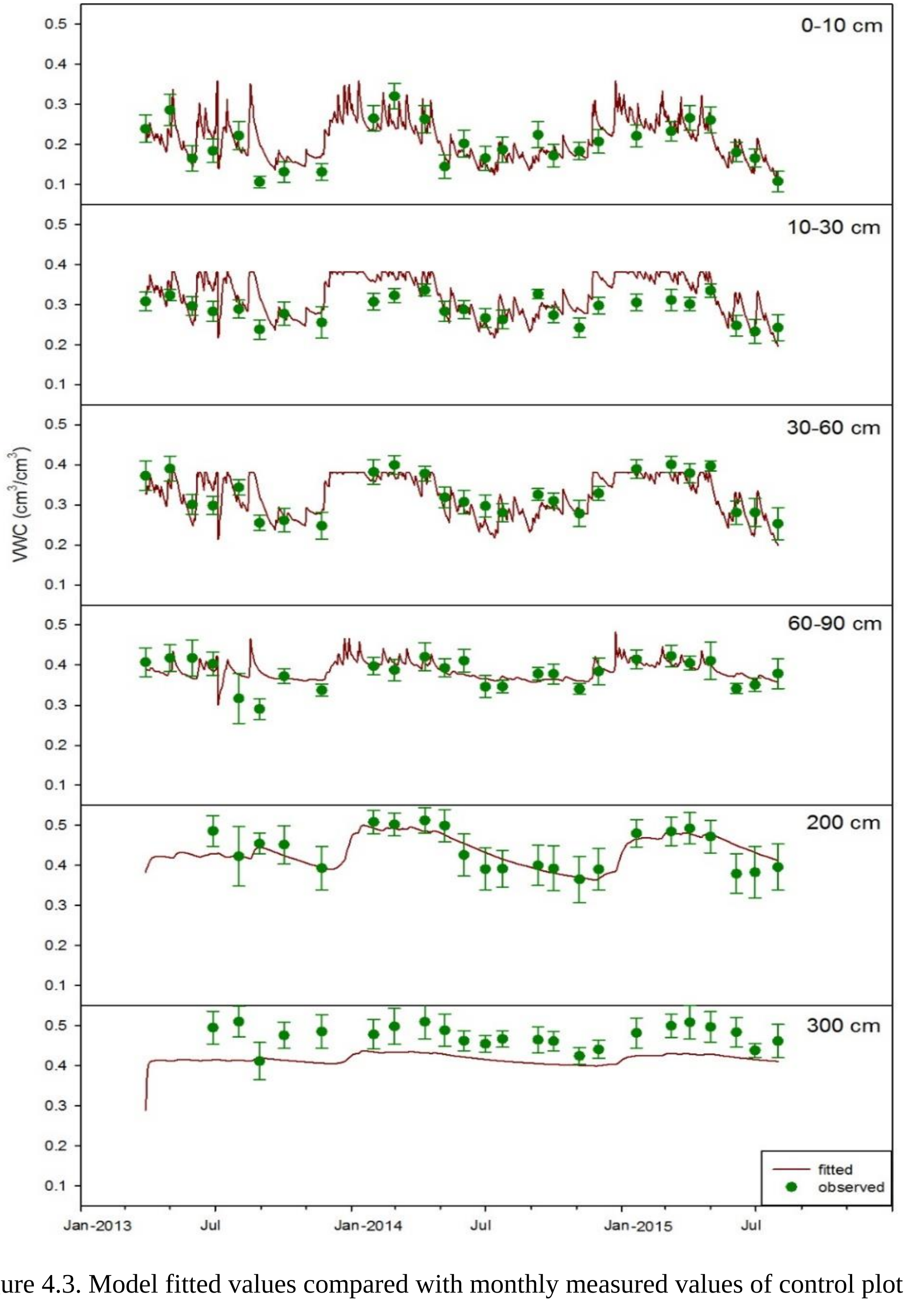

Figure 4.3. Model fitted values compared with monthly measured values of control plots used in model calibration. Model predicted values are based on the placement of observation nodes. March 29, 2013 was used as day 1.

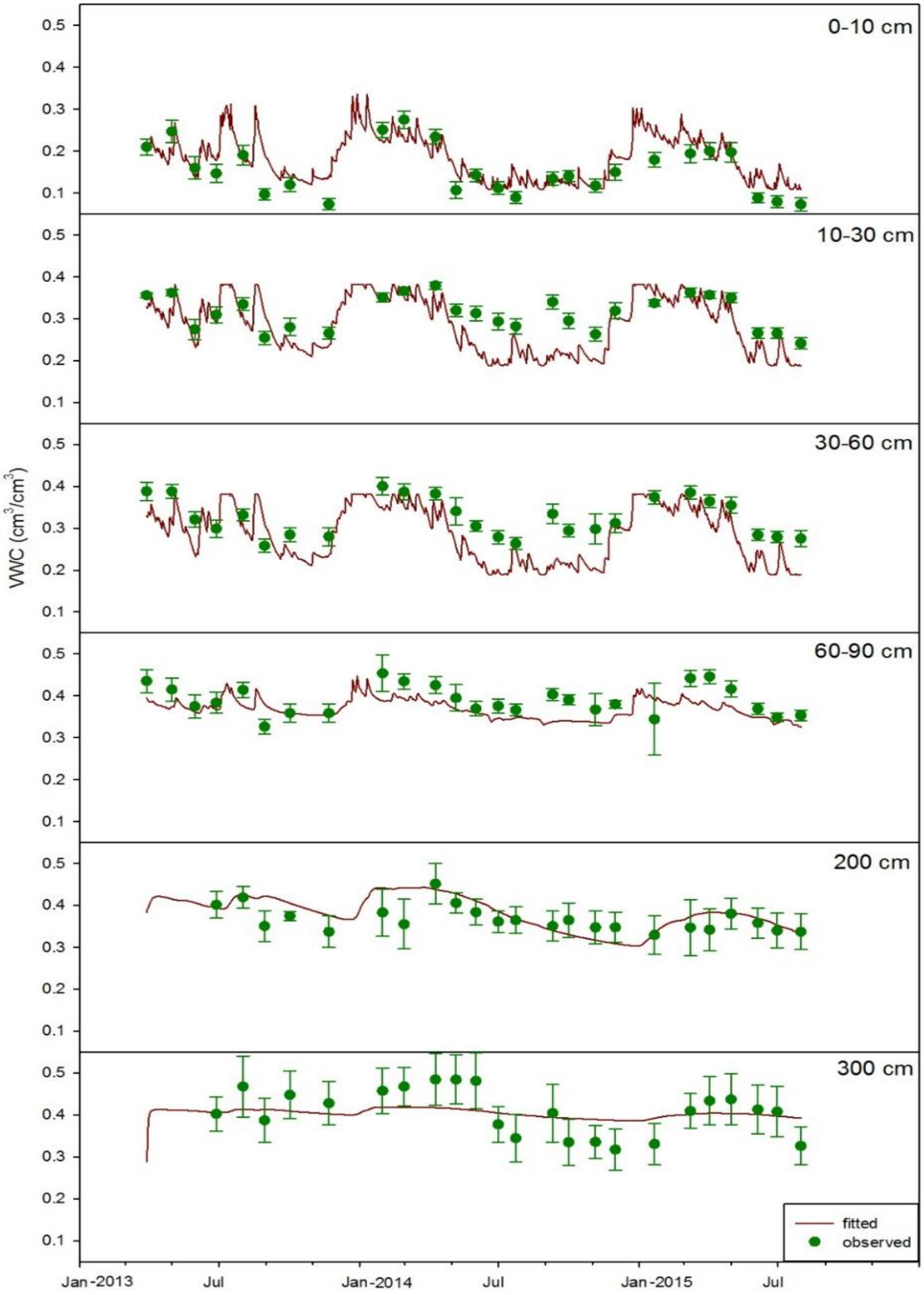

Figure 4.4. Model fitted values compared with monthly measured values of 30% throughfall reduction plots used in model validation. Model predicted values are based on the placement of observation nodes. March 29, 2013 was used as day 1.

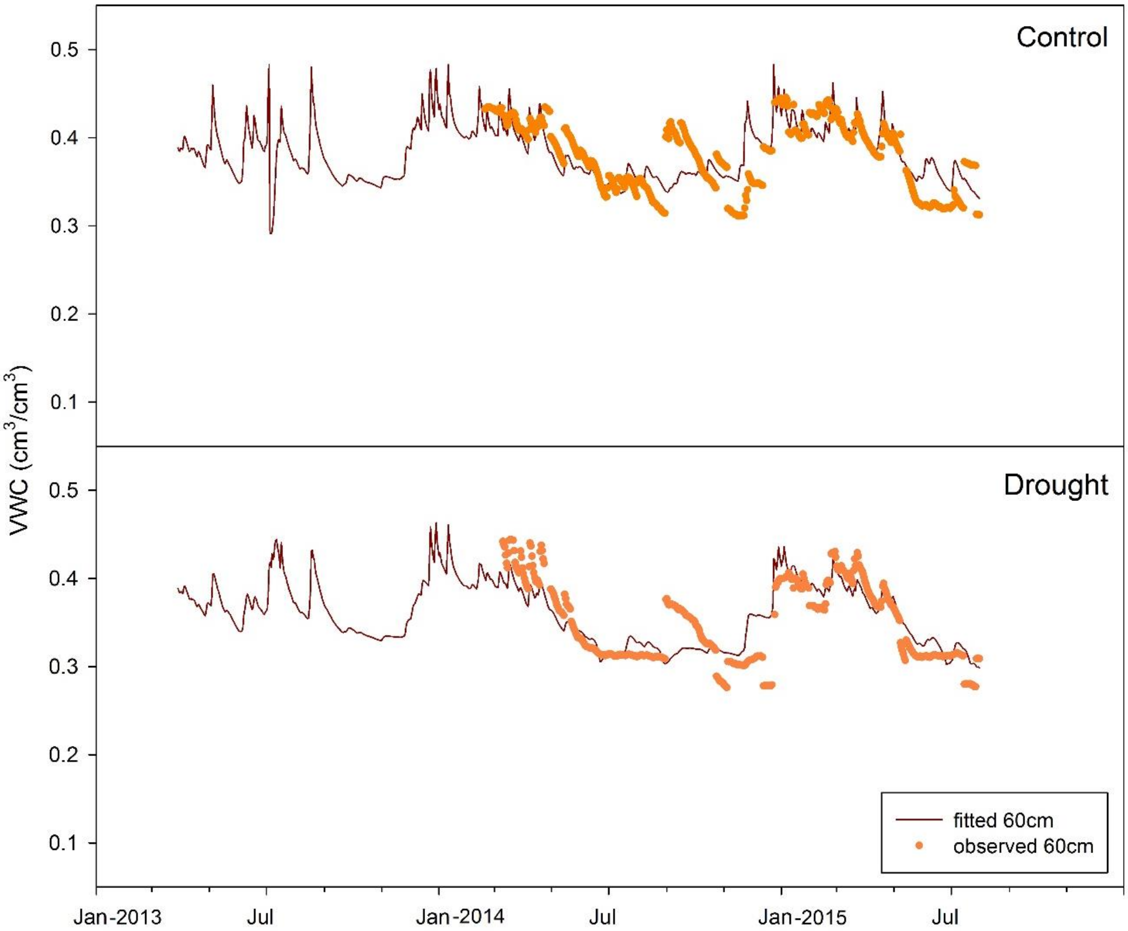

Figure 4.5. Model fitted values compared with daily measured values at 60 cm of both control and 30% throughfall reduction plots. Model predicted values are based on the placement of observation nodes. March 29, 2013 was used as day 1.

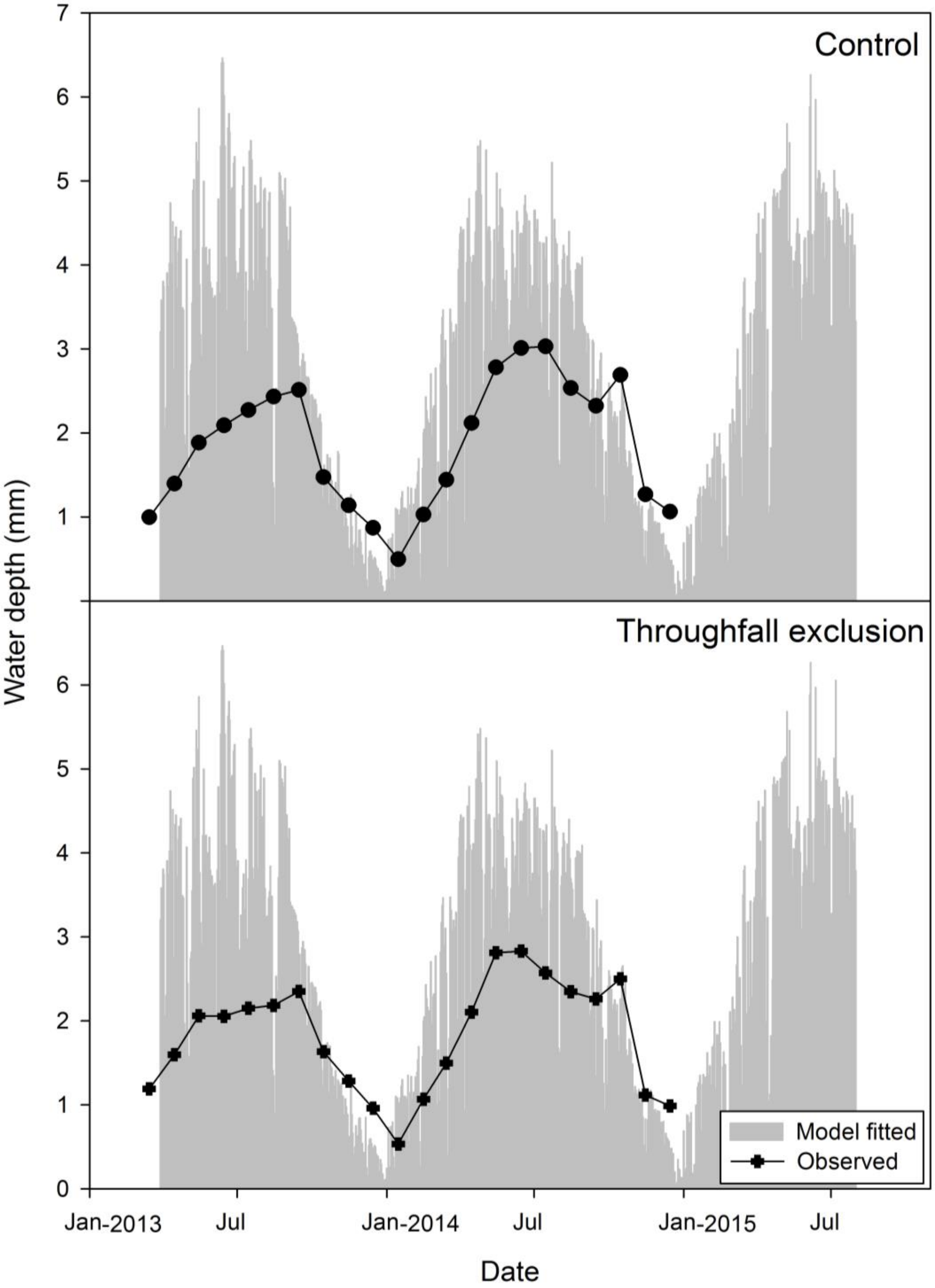

Figure 4.6. Daily model fitted ET (gray bars) and observed AET (black line) under control and 30% throughfall exclusion treatments over the period between March 2013 to July 2015.

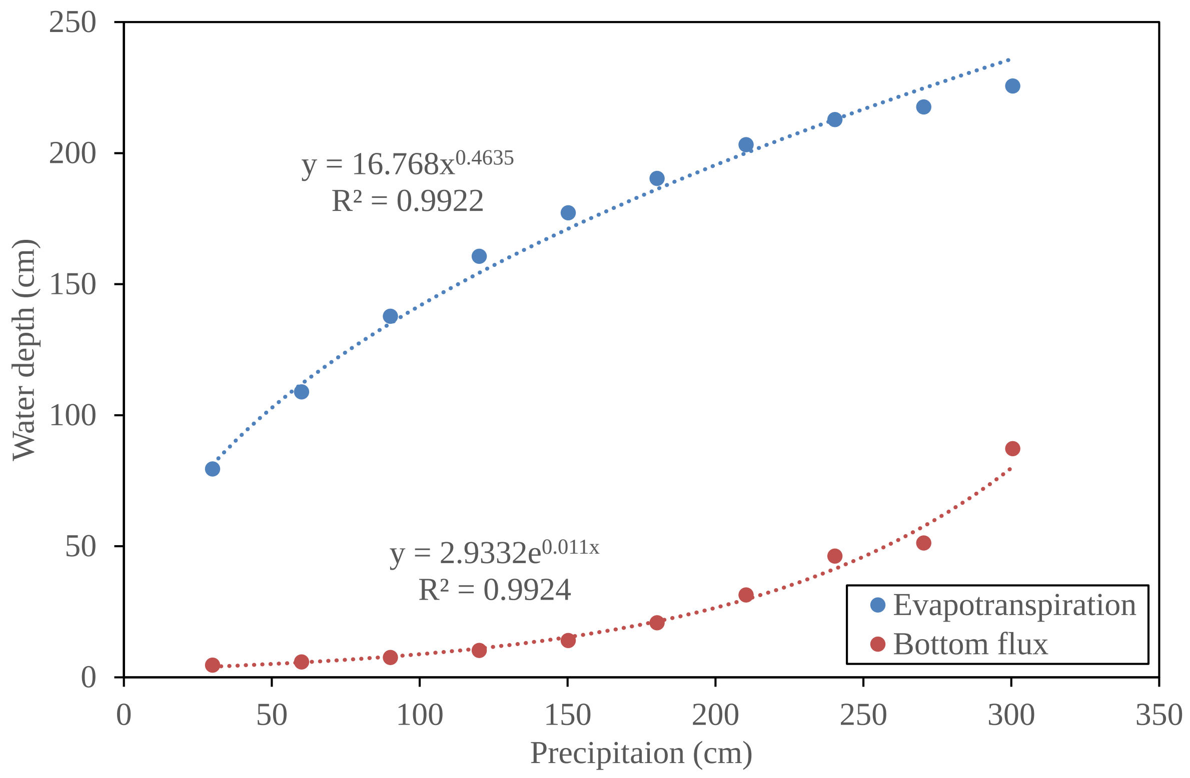

Figure 4.7. Model predicted root water uptake and water yield over the period of March 2013 to July 2015 relative to the total precipitation input over that period. Each point from right to left represents an additional 10% exclusion of PPT input from 10 to 90%. Cumulative precipitation was evenly reduced throughout the simulation period. Dotted lines are regression fits to simulated exclusions.

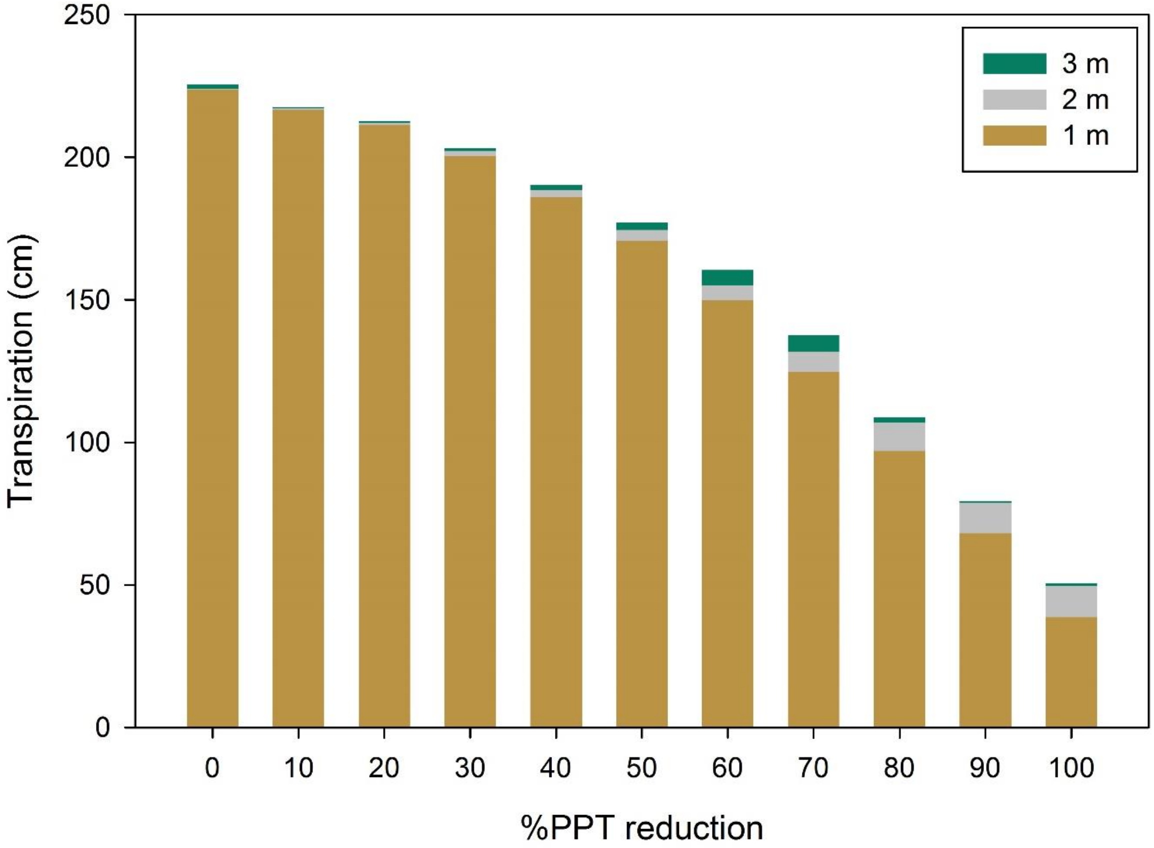

Figure 4.8. Modeled cumulative transpiration with different rooting depths in relation to evenly distributed precipitation reduction from March 2013 to July 2015. Rooting depths were either 1, 2, or 3 m.

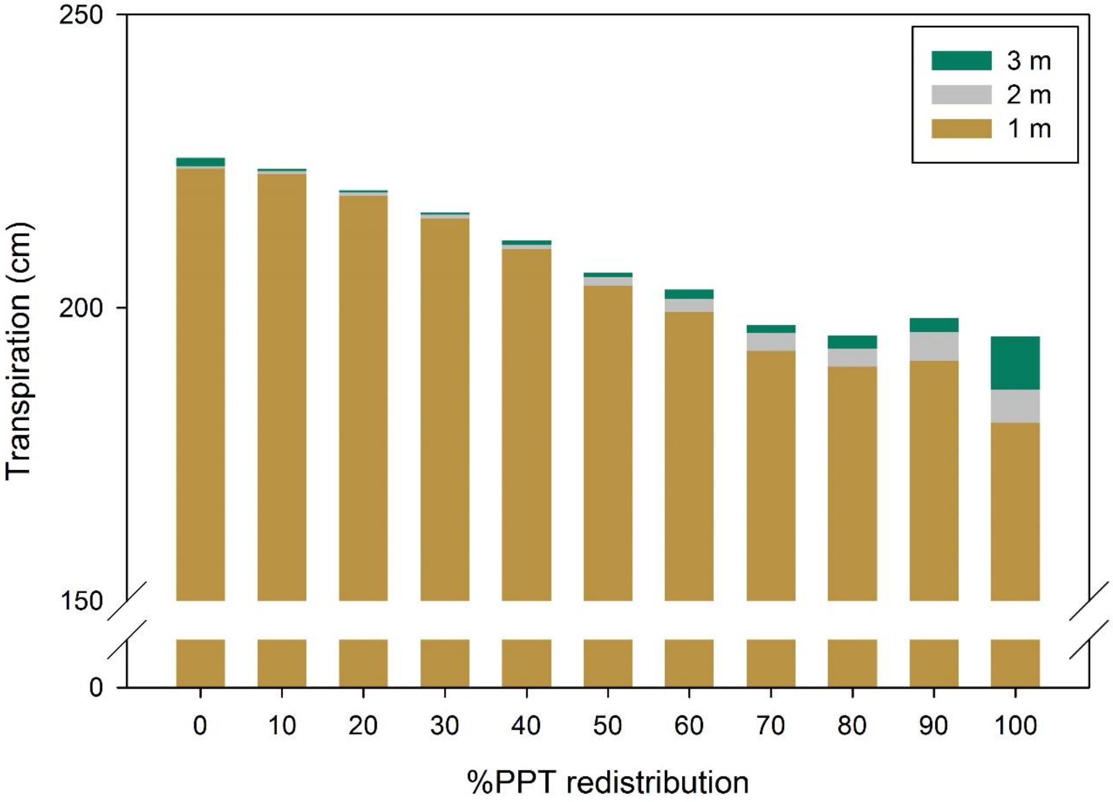

Figure 4.9. Modeled cumulative transpiration with different rooting depths in relation to seasonal precipitation redistribution from March 2013 to July 2015. Rooting depths were either 1, 2, or 3 m. The summer (June, July and August) PPT was reduced, and the winter (December, January and February) PPT were increased an equal percentage.

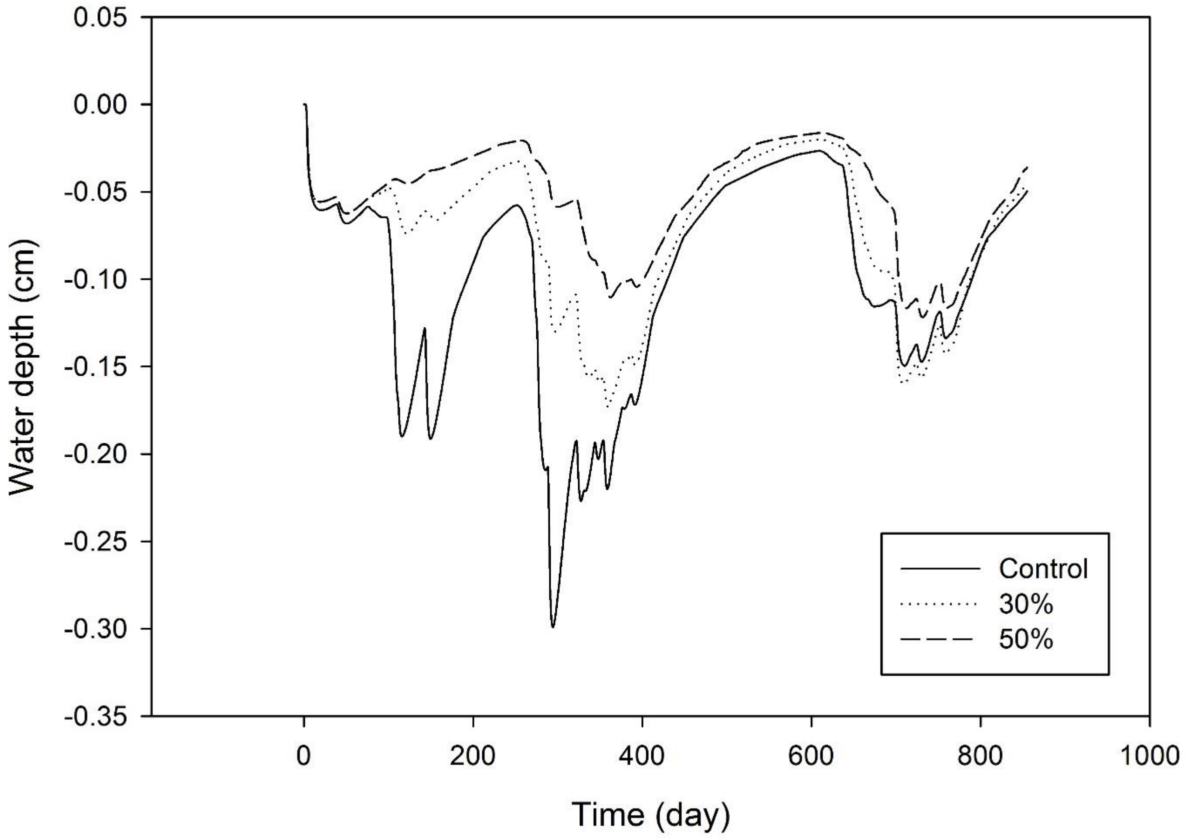

Figure 4.10. Model predicted bottom flux over the period of March 2013 to July 2015 under different seasonal drought conditions. Summer months (June, July and August) precipitation were reduced 30% or 50%, and winter months (December, January and February) precipitation were increased 30% or 50%, respectively.

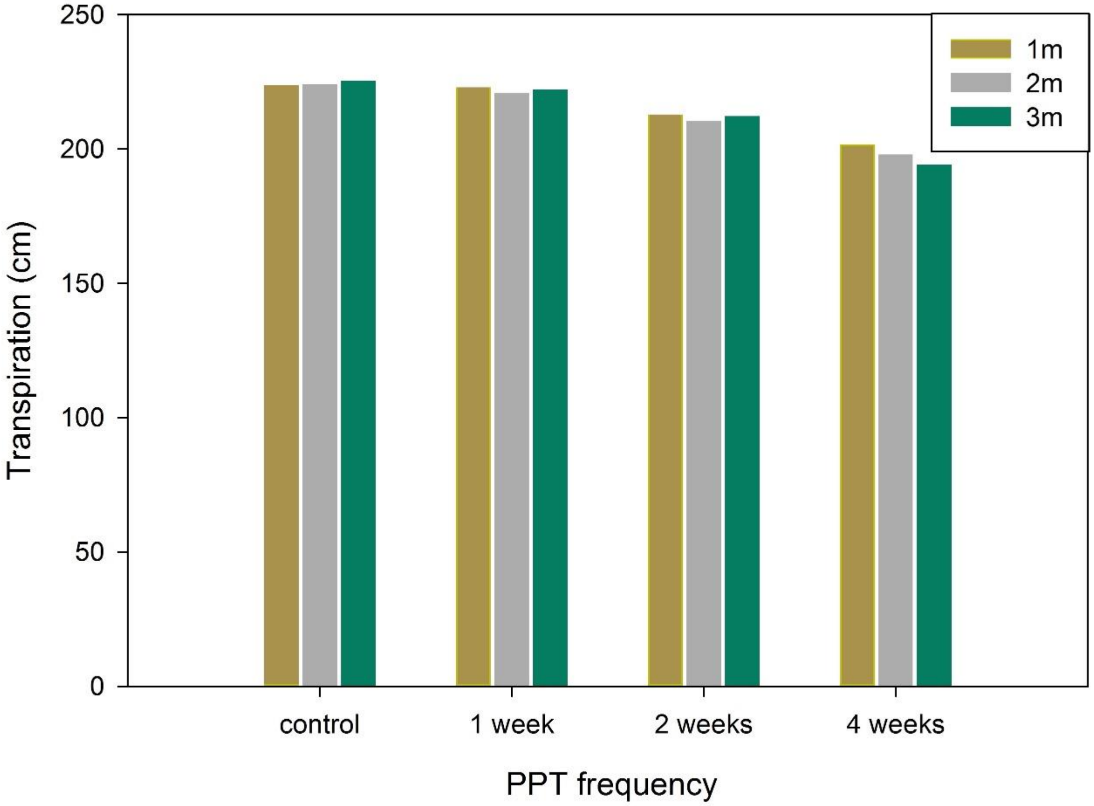

Figure 4.11 Modeled cumulative transpiration with different rooting depths in relation to different precipitation frequency from March 2013 to July 2015. Precipitation frequency was either as measured (control), or summed and applied once every week, once every two weeks, or once every four weeks. Rooting depths were either 1, 2, or 3 m.

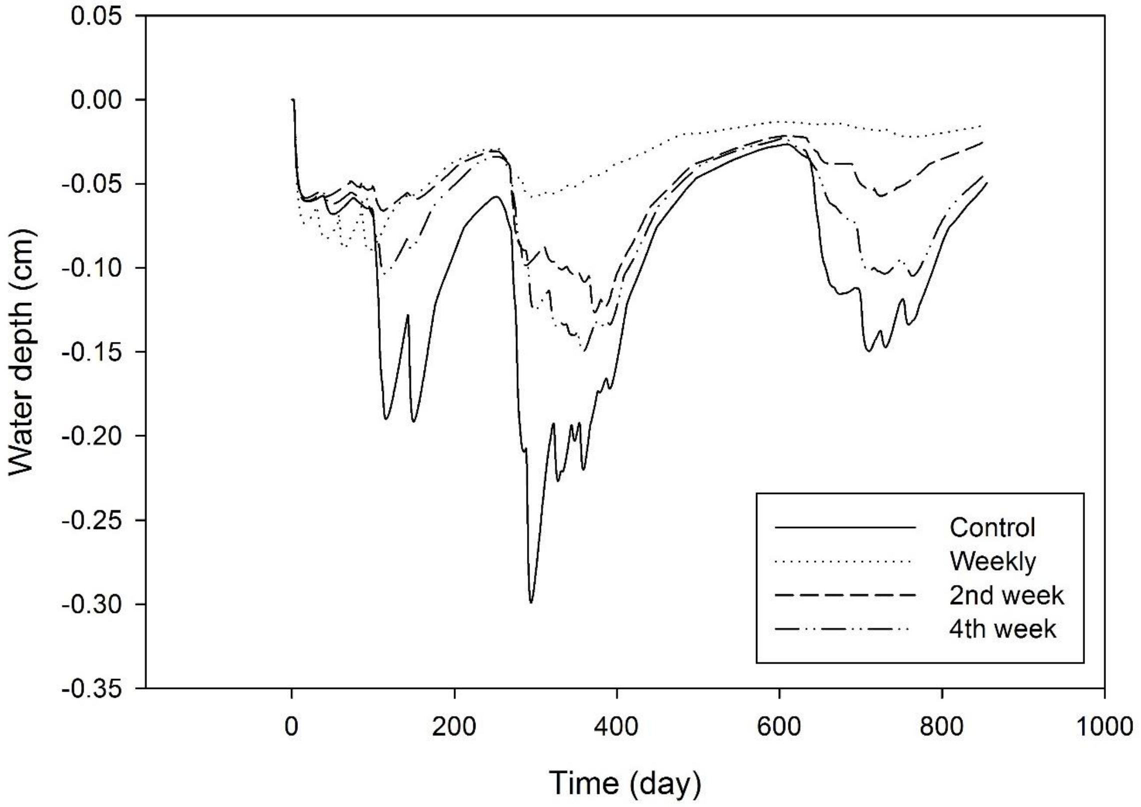

Figure 4.12. Model predicted bottom flux over the period of March 2013 to July 2015 under different precipitation frequency conditions. Precipitation frequency was either as measured (control), or summed and applied once every week, once every two weeks, or once every four weeks.

CHAPTER 5

CONCLUSION

This study investigated the possible effects of climate change on loblolly pine plantations of the Southeast U.S., specifically, change in precipitation. Three studies were individually addresses in Chapter 2, 3 and 4 of this dissertation: 1) the effect of drying-wetting cycles on deep soil carbon, 2) throughfall reduction x fertilization effect on deep soil water usage, and 3) modeling the effect of throughfall reduction on deep soil water content.

The effects of drying-wetting cycles on deep soil carbon were studied through an incubation experiment. Four soils, to the depth of three meters, from four loblolly pine plantations in Florida, Georgia, Oklahoma, and Virginia were incubated through three drying-wetting cycles. During incubations, soil CO_2 respiration was generally greatest in surface soils and declined with depth. Compared to soils that were kept constantly moist, drying-wetting cycles did not consistently stimulate more soil CO_2 respiration. Cumulative CO_2-C respiration as a proportion of total soil C, however, was higher in soils below 1 m than above. Total C and water extractable C were the best indicators for cumulative CO_2-C respiration ($p = 0.82$). Assuming that there is no other factor (i.e., new carbon inputs) affecting soil C mineralization at depth other than soil moisture cycles, this study indicates that there would be no significant change to soil CO_2 respiration in deep soils under more severe drying-wetting cycles.

Throughfall reduction x fertilization effect on deep soil water usage were tested by applying a throughfall reduction treatment (ambient versus ~30% throughfall reduction) and a fertilization treatment (no fertilization versus fertilization) in a 10-year-old loblolly pine plantation in Taliaferro county, Georgia. Soil moisture were monitored to the depth of three meters from March 2013 to July 2015. Fertilization lowered soil moisture for all depths and differences were significant at 30-60 cm (2.9%, $p<0.0001$) and 300cm (4.5%, $p<0.0001$). Throughfall reduction also lowered soil moisture for all depths and differences were significant in the surface soils (0-30 cm) (1.2-3.6%) and deep soils (below 2m) (2.6-3.6%). Fertilization significantly decreased 10-90 cm soil water when combined with the throughfall reduction treatment. Soils of all depths were rarely depleted of plant available water, with the exception of 0-10 cm mainly during growing season. Under throughfall reduction treatment, soil below 90 cm consistently accounted for more than half of the change in plant available water. Soil water storage can satisfy evapotranspirational demand in the face of increasing dryness in this clay rich Piedmont soil when considering the whole soil profile.

The throughfall exclusion experiments above suffer from not necessarily simulating natural drought because of the permanent structure that exclude an equal amount of input for every month, while droughts or specifically climate change may alter the seasonal input of precipitation or change in pattern of extreme precipitation. To address plant response to drought in both deep rooting and soil water utilization as well as soil drainage, we utilize a throughfall exclusion experiment in a *Pinus taeda* L. plantation of the southeast U.S. to calibrate and validate a hydrological model. The model was accurately calibrated using 914 days of data under ambient rainfall (R^2=0.84 and RMSE = 0.04) and validated using 30% throughfall reduction data (R^2=0.67 and RMSE = 0.04). When less precipitation was received, bottom flux decreased much faster than evapotranspiration. When precipitation was reduced more than 30%, plants relied on soil water to satisfy evapotranspirational demand. Under the scenarios of seasonal precipitation redistribution and heavy storms, both evapotranspiration and bottom flux decreased, while surface runoff increased. Although root biomass measured both before and 4 years after the treatment had no significant difference between treatment, there is additional gain in evapotranspiration with deeper root under evenly reduced precipitation and seasonal precipitation redistribution scenarios, not when precipitation frequency was adjusted. The deep soil provides an important buffer capacity when precipitation alone can’t satisfy the evapotranspirational demand.