This is to certify that the
dissertation entitled

WHOLE-PLANT RESOURCE ECONOMIES AND ASSOCIATED MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS: TOWARDS A MECHANISTIC UNDERSTANDING OF PLANT RESPONSES TO RESOURCE VARIATION

presented by

Justin Michael Kunkle

has been accepted towards fulfillment
of the requirements for the

Doctoral degree in Forestry

Major Professor's Signature

May 7, 2008

Date

WHOLE-PLANT RESOURCE ECONOMIES AND ASSOCIATED MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS: TOWARDS A MECHANISTIC UNDERSTANDING OF PLANT RESPONSES TO RESOURCE VARIATION

By

Justin Michael Kunkle

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Forestry

2008

ABSTRACT

WHOLE-PLANT RESOURCE ECONOMIES AND ASSOCIATED MORPHOLOGICAL AND PHYIOLOGICAL TRAITS: TOWARDS A MECHANISTIC UNDERSTANDING OF PLANT RESPONSES TO RESOURCE GRADIENTS

By

Justin Michael Kunkle

Differences in plant resource economies (i.e., resource-use efficiency, resource access and storage capacity) and related plant traits may underlie species specific variation in growth and survival across resource gradients. In my dissertation, I combine potted plant and field studies to explore functional traits as the basis of these mechanisms and how they relate to variation in whole-plant performance over resource and disturbance gradients.

First, with respect to soil N availability, I investigated how fine root dimensions and N concentrations vary during senescence for N fertilized and unfertilized seedlings of species that differ in soil N affinity (*Populus tremuloides* Michx, *Acer rubrum* L., *Acer saccharum* Marsh. and *Betula alleghaniensis* Britton). Senescence-related decreases in root mass per length and root length indicated substantial root mass loss among species. Mass-based root N increased from live to dead roots 10-35% among species, whereas N decreased in dead roots when values were corrected by changes in mass (−12 to −28%). My data along with re-analyzed values from the literature suggest that N resorption may occur in fine roots, which would lead to increased whole-plant N use-efficiency.

Second, I quantified interrelations of whole-plant total non-structural carbohydrates (TNC_{WP}), relative growth rates (RGR) and associated functional traits for seedlings of 36 temperate and boreal species grown in a common low-light environment.

Across species, plant traits related to surface area for above- and below-ground resource capture were strongly related to RGR, whereas proportional allocation to root mass was the strongest predictor of TNC_{WP}. Although RGR and TNC_{WP} were negatively correlated, when RGR was normalized for plant mass effects, RGR was weakly, but positively related to TNC_{WP}. Furthermore, independent of plant mass, carbon conservation traits were positively related to RGR and TNC_{WP}. In contrast to previous research, my findings suggest that in low light environments, independent of mass effects, traits that increase growth also increase TNC_{WP}.

Third, I examined the relationship of plant traits to tolerance (i.e., survival) of water deficits using a conceptual framework that classified traits into water-use efficiency (WUE) and water access (W_{access}) categories. Seedlings of eight tree species differing in soil resource affinity were transplanted across glacial landforms with differences in water holding capacity. I found that both the ability maintain positive photosynthetic rates (i.e., W_{access}) and high photosynthesis per unit water loss (i.e.,WUE) during drought enhanced seedling survival. Across species, increased W_{access} was realized via deeper rooting which was positively related to seed and seedling size. Interspecific variation in WUE was positively related to area-based leaf N (leaf N_{area}). Thus, differential expression of these traits may partly underlie interspecifc differences in growth and survival responses, which likely contribute to the observed species distribution patterns across glacial landforms in northwestern Michigan.

To my parents, brother and Miss Heidi Frei for their enduring support and encouragement

ACKNOWLEDGEMENTS

First of all, I would like to thank my parents for the incredible guidance and advice that they have provided me throughout the years. Both of my parents worked extremely hard and sacrificed many things to see me through my college years at Franklin and Marshall and I will always be grateful. In addition, my parents and brother have always encouraged and supported me in every aspect of my life, and without that I would never be where I am today. My family possesses an amazing work ethic and this is something that has been passed down through the generations and this mindset has enabled me to persevere through many of life's challenges, including my PhD program. I also would like to thank the rest of the Kunkle-Kratzer family for all of the letters of support and care packages that helped me stay motivated during the last few weeks leading up to my defense.

I cannot thank Miss Heidi Frei enough for her love and support, especially during the last few months leading up to my dissertation defense. Heidi is truly one of the most selfless people I know and she sacrificed so much to help me achieve my goals. She also introduced me to long distance running and its many rewards. In addition, she showed me that there is so much more to life than scientific research and I look forward to the future as we build a life together.

My advisor, Mike Walters has been a source of inspiration and knowledge that has helped me tremendously in my development as a scientist. His work ethic and passion in the field are truly contagious. Over the years we have spent a lot of time together in the laboratory and field and I hope that he enjoyed this time as much as I did.

Besides providing me with substantial financial support and guidance, he also allowed me the freedom to pursue many of my research interests.

My committee members, Mike Walters, David Rothstein, Rich Kobe and Bert Cregg provided guidance and scientific expertise that greatly improved my dissertation project. David was kind enough to adopt me as an honorary member of the Rothstein lab and provided me with full access to lab supplies and the C/N elemental analyzer. He also took the time to talk to me about a post-doctoral position that I was offered on the Big Island of Hawaii. I am especially grateful that all of my committee members were all willing to read my dissertation with less than a week before my defense date.

I would also like to thank my undergraduate mentor, Dr. Timothy Sipe for introducing me to the many aspects of ecological research in forested ecosystems. He provided me with a solid foundation in how to design and carry out research projects, which prepared me well for all of the challenges of a PhD project. Before working with Tim at the Harvard Forest, I didn't know how I could turn my interest in nature into a career. His dedication to students and teaching is remarkable and Franklin and Marshall College is very fortunate to have him as a faculty member.

And finally, I wanted to thank all of the organizations that provided generous financial support for my dissertation research. Michigan State University helped initiate my work with a Plant Science Fellowship, and continued their support with a Dissertation Completion Fellowship and supplemental funding through the Department of Forestry. The National Science Foundation supported me as a graduate research assistant through a research grant awarded to Mike Walters and Rich Kobe. NSF also supported me through

the GK-12 fellowship program. The Hanes Fund of the Michigan Botanical Club provided funding that helped me to expand the scope of my dissertation research.

TABLE OF CONTENTS

LIST OF TABLES

Appendix

LIST OF FIGURES

Appendix

INTRODUCTION

General Introduction

Plant ecologists have long sought the physiological mechanisms that account for the distribution of species through time and space. Several lines of research highlight the importance of resource availability in shaping spatial patterns in the distribution of tree species. For example, numerous landscape-scale studies have documented associations between the distribution of overstory tree species and variation in soil resources (nitrogen, soil water) (Zak et al. 1989, Reich et al. 1997a, Bongers et al. 1999, Wang et al. 2006, Engelbrecht et al. 2007). Among seedlings and saplings, growth and survival generally increase with increasing levels of light (Pacala et al. 1994, Kobe et al. 1995) and nitrogen availability (Walters and Reich 1997, Finzi and Canham 2000, Walters and Reich 2000), but responses are species-specific. Furthermore, spatial and temporal variation in soil water availability affect juvenile tree growth and survival (Walters and Reich 1997) and similar to nitrogen, responses differ across species (Caspersen and Kobe 2001, Engelbrecht and Kursar 2003, Engelbrecht et al. 2005, Kobe 2006). Collectively, these observations suggest that species distribution patterns may stem from differential species performance across resource gradients.

It has been hypothesized that species differences in growth capacities may underlie distribution patterns across resource gradients. For example, species composition in high resource, competitive environments may reflect rapid growth responses, whereas species with low inherent growth rates may have the ability to tolerate harsh growing conditions (Grime 1977, Chapin 1980). This hypothesis suggests that there is an unavoidable "trade-off" between rapid growth under high resources versus

survival in poor resource environments, which has been supported with experimental evidence across gradients of light (Kobe et al. 1995, Poorter and Bongers 2006, Poorter et al. 2006) and soil resources (Schreeg et al. 2005). Thus, both theory, and differential species performance ranks and distribution patterns across resource gradients imply that a single plant species cannot be a superior competitor in all resource environments (i.e., Jack of all trades is a master of none, Bradshaw 1965). So, why can't a given species be superior in all aspects? Plants allocate resources to contrasting functions (e.g., growth, support, defense, storage, resource acquisition, reproduction) and these functions are subject to opposing demands. For example, investment in a specific structure or function that leads to enhanced survival in chronically low resource environments, may limit a plant's ability to acquire carbon or capture soil resources and ultimately reduce a plant's growth potential.

To date, studies have primarily focused on plant traits that underlie growth rates, especially under optimal resource environments. For example, shade-tolerant and intolerant species differ in their leaf-level photosynthetic responses (i.e., a proxy for potential growth rates) to growth light intensity, which may provide a mechanism for species sorting across successional gradients of light availability (Bazzaz 1979). In addition, based on a plant competition model, Tilman (1988) presented predictions that relative growth rates, which are hypothesized to be influenced by a plant's proportional allocation to leaves and roots, are a major determinant of grassland successional dynamics across a soil N supply gradient. Furthermore, potted plant studies showed that allocation to leaves, leaf surface area per leaf mass and whole-plant photosynthetic rates (i.e., integration of leaf allocation and specific rates of photosynthesis) were positively

related to relative growth rates (Poorter et al. 1990, Walters et al. 1993b). Although these studies provide an integrative understanding of the linkages among growth, allocational and physiological attributes and their potential role for the success of species in high resource, competitive environments, there is a paucity of studies examining the determinants of plant survival under poor resource conditions.

Variation in traits associated with resource economies likely contribute to the growth versus survival trade-off. For example, three potential whole-plant mechanisms thought to underlie plant survival in low resource environments include enhanced access to limiting resources, storage of resources and greater use-efficiency of resources to produce biomass. My global hypothesis is that plant traits associated with resource access, storage and resource-use efficiency under low resources occur at a trade-off with growth capacity under high resources. In order to gain a greater ability to explain the mechanistic causes of differential species performance ranks across resource gradients, it is necessary to isolate which plant functional traits (e.g., biomass allocation patterns, morphological and physiological traits) underlie resource access, storage and resource-use efficiency and how they relate to growth and survival in low versus high resource environments. I have proposed an experimental framework with potted plant and field-based transplant studies that explicitly examines the effects of nitrogen (Chapter 1), light (Chapter 2) and soil water availability (Chapter 3) on whole-plant physiology/morphology, allocation programs, nutrient dynamics, species-specific growth and survival, and their interactions.

Organization of dissertation

Nutrient resorption from senescing leaves is a well-documented nutrient conservation strategy (Kobe et al. 2005), recycling ~ 50% of maximum foliar N content across a variety of perennial life-forms (Aerts 1996). Fine roots may function similarly to leaves, but evidence for root resorption is equivocal. For chapter 1, I carried out a potted plant experiment that allowed me to investigate how fine root dimensions and N concentrations change during senescence and address the degree to which these changes inform the unresolved issue of root N resoprtion for N fertilized and unfertilized seedlings of species that differ in soil N affinity. I hypothesized that species associated with sites that have low N availability (*Populus tremuloides* Michx., *Acer rubrum* L.) would exhibit greater root N conservation than species that typically occur on soils with high N status (*Acer saccharum* Marsh. and *Betula allegheniensis* Britton).

Allocation to carbohydrate storage has been proposed as a low light carbon conservation strategy that contributes to the trade-off between high resource growth potential vs. low resource survival (Kobe 1997). This notion has been partly supported by studies showing that carbohydrate storage is positively related to survival (Canham et al. 1999, Iyer 2006, Myers and Kitajima 2007, Poorter and Kitajima 2007) and negatively related to growth (Iyer 2006, Myers and Kitijima 2007, but see, Poorter and Kitijima 2007). The carbohydrate storage vs. growth association is unlikely to be manifested by a single trait (e.g., storage capacity), but rather by expressions of various morphological and physiological growth-related traits. However, interrelationships between carbohydrate storage and growth-related traits have received little attention and remain incompletely understood. In chapter 2, I investigated the functional traits underlying

variation in whole-plant carbohydrate storage and relative growth rates, and potential trait-based trade-offs between them for 36 temperate and boreal woody species (angiosperm vs. gymnosperm) that were grown in a common low-light environment.

Traits potentially enhancing young seedling survival on drought-prone sites (e.g., greater proportional mass allocation to roots, deep roots, and conservative water use) may compromise growth potential, and thus competitive ability, when water is predictably plentiful. For example, increased allocation of biomass to root systems and/or the production of deep rooted large diameter "taproots" may occur at the expense of allocation to resource harvesting structures (e.g., proportional allocation of mass to leaf and root area), which contribute to high growth capacities under optimal resource conditions (Reich et al. 1998a, Poorter 1999, Walters and Reich 2000, Comas et al. 2002). Therefore, traits that confer survival during episodic drought events may occur at a trade-off with traits enhancing growth potential when soil water is plentiful. In chapter 3, I examined the relationship of plant traits to tolerance (i.e., survival) of water deficits using a conceptual framework that classified traits into water-use efficiency (WUE) and water access (W_{access}) categories.

CHAPTER 1

MEASUREMENT BASES FOR FINE ROOT N CONCENTRATIONS: IMPLICATIONS FOR SENESCENCE-RELATED N LOSS IN TEMPERATE TREE SEEDLINGS

ABSTRACT

I investigated how fine root dimensions and nitrogen (N) concentrations vary during senescence and address the degree to which these changes inform the unresolved issue of root N resorption in perennial plants. I estimated the difference in N between live and dead fine roots (ΔN) on mass, length, and calcium (N loss:root Ca) bases for fertilized (N + Ca) and unfertilized potted seedlings of four tree species. Compared to live roots, dead roots had higher N on a mass basis, and lower N on length (−5 to −16%) and Ca (−14 to −48%) bases. These differences could be partially ascribed to changes in non-N root mass during senescence, which decreased substantially for all species (−23 to −40%). ΔN on a mass basis, corrected for root mass loss ranged from −12 to −28%. For individual seedlings, dead and live root N concentrations were positively correlated (R^2 = 0.57, $P < 0.0001$), indicating that live root N is a major determinant of senesced root N. Although leaching and microbial immobilization may partially obscure quantification of N in senesced roots, these results along with re-analyzed values from the literature suggest that N resorption may occur in fine roots to a greater degree than has previously been reported, which may have implications for whole-plant resource economies and ecosystem N cycling.

Introduction

Patterns in nitrogen (N) resorption from senescing leaves and their possible consequences for ecological properties such as whole-plant resource economies and nutrient cycling have been well described (Aerts 1996, Killingbeck 1996, Silla and Escudero 2004, Kobe et al. 2005). Fine roots (here defined as < 2 mm in diameter) may function similarly to leaves, however, the extent of N resorption from fine roots of perennial plants remains unresolved (Gordon and Jackson 2000) for several reasons: (1) root studies are methodologically challenging and labor-intensive; (2) assessing fine root death and senescence is often ambiguous and subjective (Pregitzer 2002); and (3) artifacts associated with some methodologies could confound estimates of root resorption. For example, estimating root N resorption efficiency (%) as the difference in mass-based root N concentrations between live and dead roots (Nambiar 1987, Aerts 1990, Gordon and Jackson 2000) implicitly assumes that all other non-N constituents of root mass remain static. Although never quantified for roots, resorption of non-N mass from senescing leaves underestimates actual N resorption by as much as 20% (van Heerwaarden et al. 2003). Fine roots contain mobile compounds (e.g., 2-20% non-structural carbohydrates, Pregitzer et al. 2000, Kobe, unpublished data) that if resorbed would, as for leaves, lead to underestimates of mass-based N resorption. I argue that estimated differences in mass-based N concentrations of live versus dead roots (ΔN_{mass}) are confounded by physiological (i.e., carbohydrate resportion) and dimensional (i.e., root shrinkage) changes during senescence, and thus, these estimates are likely biased.

As an alternative to mass-based expressions, I propose that fine root N concentrations based on unit root length (ΔN_{length}) and unit root calcium (ΔN_{Ca}) provide

more accurate measures of actual senescence-induced alterations in root N status. Root mass loss during senescence can be described as the product of two dimensional components: decreased mass per root length and decreased root length. Thus, ΔN_{length}, which is insensitive to shifts in non-N mass per unit root length, should always be more accurate than ΔN_{mass}, and if alterations in root length during senescence are minimal, then ΔN_{length} should closely estimate N loss from live roots. However, root length, analogous to root mass per length, could change substantially during senescence. In this circumstance, ΔN_{Ca} may better estimate changes in root N than either ΔN_{mass} or ΔN_{length} because Ca is phloem-immobile (McLaughlin and Wimmer 1999) and does not resorb during leaf (van Heerwaarden et al. 2003) and presumably root senescence. Under these conditions, Ca is likely stable as roots senesce and differences in N per unit root Ca (ΔN_{Ca}) between live and dead roots would be insensitive to non-N root mass resorption.

In this paper, I focus on quantifying senescence-related changes in root mass and N, reconciling mass-, length-, and Ca-based expressions of ΔN and discuss the possible implications of these patterns for resorption of N from fine roots. Specifically I ask: (1) Do N concentrations differ between live and dead fine roots? (2) How do ΔN estimates compare among mass, length and Ca measurement bases? (3) Do fine roots lose non-N root mass during senescence, and, if so, can this account for ΔN differences among measurement bases? (4) And, lastly, do ΔN estimates vary with species, N supply and/or live root N content? To address these questions, I quantified and analyzed fine root ΔN on mass-, length-, and Ca-bases, and differences in root length and mass per length from

live to dead roots, for 3-year old potted seedlings of four broad-leaved tree species in fertilized (N + Ca) and unfertilized treatments.

Materials and Methods

Plant Material, Growing Conditions and Experimental Design

The experiment took place at the Tree Research Center, Michigan State University, East Lansing, MI (42°40' N, 84°27' W). Seeds of *Populus tremuloides* Michx. (quaking aspen), *Acer rubrum* L. (red maple), *Acer saccharum* Marsh. (sugar maple) and *Betula alleghaniensis* Britton (yellow birch) were germinated in bench-top flats filled with potting soil (Faffard 2 mix, Agawan, MA) beneath 50% neutral density shade cloth in a temperature-controlled greenhouse (Mean daily minimum and maximum temperatures were 23.6 and 18.4°C respectively). *Populus tremuloides* was germinated in mid-May 2000, and the other species in mid-May 2001. In early-June 2001, single seedlings of each species were transplanted into plastic pots (17.15 cm width × 18.73 cm height) filled with a homogenized low fertility field soil mixture (Rubicon-Menominee, and Graycalm and Grayling sands) and placed into randomly selected positions in two outdoor hoophouses (4.6 m × 27.4 m). The field soil was collected from the top 15-20 cm of sub-organic soil with a backhoe at a forested sandy glacial outwash site in Roscommon, MI (44°12' N, 84°36' W). Hoophouses were covered with neutral density shade cloth to achieve a targeted light environment of 35% full sun. Supplemental deionized water was applied to seedlings every 3-5 days from early-June to mid-September throughout the experiment. Within each hoophouse × species group, half of the pots were fertilized with

a mixture of N delivered as 13.5 $g \cdot m^{-2}$ of $(NH_4)_2SO_4$ granules and Ca delivered as 150 $g \cdot m^{-2}$ of $CaSO_4$ powder. The fertilizer was applied during late-July 2001 and in mid-June during 2002 and 2003. Approximately 152 seedlings were allocated to each hoophouse (2) × species (4) × fertilizer combination (2).

Root Measurements

Three to five seedlings were selected at random from each hoophouse × species × fertilizer combination (total = 65 seedlings) over two weeks in late-September 2003 to sample naturally-senescing roots. Soil was removed from root systems of individual seedlings by gently rinsing with deionized water. I defined fine roots as non-woody 1^{st}, 2^{nd} and 3^{rd} order lateral roots that were < 2.0 mm in diameter. More than 80% of the total length of roots sampled (~ 1600 m) was < 0.5 mm in diameter and these distributions were similar for live and dead collections (Figure 1.1). On an individual seedling basis, I collected samples of root segments from live and dead root populations. The total number of root segments per sample was determined by the mass needed for root nutrient analyses. Classification of live versus dead roots was based on color and easily observed anatomical features. Live roots were translucent and white to tan, whereas dead roots were dark gray to black, but showed no visible signs of decay (McClaugherty et al. 1982, Steele et al. 1997) (e.g., Figure 1.2). All dead roots were physically attached to the whole-root system and were disconnected with a slight pull on individual dead root segments. Visual classification was corroborated by removing the root cortex and documenting the presence (live) or absence (dead) of an intact stele

(Spaeth and Cortes 1995) on a minimum of five randomly selected root segments per sample. If any of the selected root segments were incorrectly classified, the entire sample was rejected and a new sample was collected from the same seedling using refined selection criteria (i.e., based on a restricted range of root color).

Fine root collections were refrigerated ≤ 2 days until fresh images of root samples (5-9 images × species × fertilizer × root type combination) were acquired with a flatbed scanner at a resolution of 400 DPI (Epson Expression 1680, Nagano, Japan). Following digitization, root samples were dried at 70°C for at least 48 hours, and then weighed. Digitized images were manually edited with Adobe Photoshop 7.0 (Adobe Systems Inc., San Jose, California) with the goal to produce a black (roots) and white (background) image that faithfully captured the original root image. Edited images were analyzed for total root length with WinRhizo Pro 5.0 software (Regent Instruments, Blain, Quebec). For a subset of edited images (3-5 each for live and dead roots of each species), 1st order root length of individual roots was quantified (total n = 25 each for live and dead roots). For each respective species, average first order root length data (n = 25) were used to estimate changes in root length with senescence (i.e., root shrinkage) and was calculated as: $((length_{LR} - length_{DR})/length_{LR})) \times 100$. Root mass and total root length data from individual samples were used to estimate live and dead root mass per root length.

Dried root samples were pulverized into a fine powder with a ball mill (Kinetic Laboratory Equipment Company, Visalia, California), or, for very small samples, with a mortar and pestle. Nitrogen concentrations were measured with a CHN elemental analyzer (Carlo-Erba, Milan, Italy). For root Ca measurements, sub-samples from individual seedlings had to be aggregated over each combination of hoophouse × species

× fertilization × root status (live/dead) to obtain enough material for analysis. Approximately 30-150 mg from each aggregated root sample was microwave digested in a nitric acid-hydrogen peroxide mixture (Mars 5, CEM Corporation, Matthews, NC) and Ca concentrations were measured with Direct Current Plasma Emission Spectroscopy (DCP-AES, SMI Corporation). During microwave digestion for Ca analysis, several composite samples were lost due to equipment failure, which resulted in no replication for some treatment combinations. Ca and N concentrations were expressed on an oven-dry mass basis (Ca_{mass}, N_{mass}, $mg \cdot g^{-1}$) and N concentrations were also expressed on a root length basis (N_{length}, $\mu g \cdot cm^{-1}$). Length-based N concentrations were estimated as follows: (N_{mass} × root mass)/root length. Ca concentrations were used to express root N on a Ca-basis (e.g., average N_{mass} /aggregated Ca_{mass}; N_{Ca}, unitless).

Calculations

Change in fine root N during senescence (ΔN, %) was calculated from direct measurements of live (LR) and dead roots (DR) as $\Delta N = ([N]_{LR} - [N]_{DR})/ [N]_{LR} \times 100$, on three measurement bases: (1) per unit root mass (ΔN_{mass}); (2) per unit root length (ΔN_{length}); and (3) per unit Ca mass (ΔN_{Ca}). Note that none of these calculations explicitly accounts for non-N root mass changes between live and dead roots.

Estimating non-N root mass change (Δmass) between live and dead roots was accomplished by combining changes in two dimensional components; root mass per root length, and root length as:

$$\Delta\text{mass} = 1 - \left(\left(\left[\frac{\text{mass}_{DR}}{\text{length}_{DR}} \right] \Big/ \left[\frac{\text{mass}_{LR}}{\text{length}_{LR}} \right] \right) \times \left[\frac{\text{length}_{DR}}{\text{length}_{LR}} \right] \right) \times 100.$$

Changes in root mass per length and in 1st order root length can also be used to correct ΔN_{mass} for Δmass. First, correcting ΔN only for changes in root mass per length yields the per root length based expression of ΔN:

$$\Delta N_{length} = 1 - \left(\frac{\left[\frac{N_{DR}(mg)}{mass_{DR}(g)} \right] \times \left[\frac{mass_{DR}(g)}{length_{DR}(cm)} \right]}{\left[\frac{N_{LR}(mg)}{mass_{LR}(g)} \right] \times \left[\frac{mass_{LR}(g)}{length_{LR}(cm)} \right]} \right) \times 100 = 1 - \left(\frac{\frac{N_{DR}(mg)}{length_{DR}(cm)}}{\frac{N_{LR}(mg)}{length_{LR}(cm)}} \right) \times 100.$$

Modifying ΔN_{length} with a correction for changes in total root length during senescence yields:

$$\Delta N_{corrected} = 1 - \left(\frac{\left[\frac{N_{DR}(mg)}{length_{DR}(cm)} \right] \times \left[\frac{length_{DR}(cm)}{length_{LR}(cm)} \right]}{\left[\frac{N_{LR}(mg)}{length_{LR}(cm)} \right]} \right) \times 100.$$

Thus, $\Delta N_{corrected}$ accounts for both changes in root mass per length (i.e., ΔN_{length}) and changes in length between live and dead roots. This calculation is based on the assumption that measurements of root length changes did not include any tissue loss (e.g., belowground herbivory).

Unlike ΔN_{mass} and to a lesser extent ΔN_{length}, ΔN_{Ca} may not require a correction for mass loss because Ca is assumed to be immobile during senescence. To check the

assumption of Ca immobility, expected dead root Ca concentrations were calculated from measured live root Ca and estimates of Δmass:

$$\text{expected Ca}_{DR}\ (\text{mg}\cdot\text{g}^{-1}) = \frac{\text{measured Ca}_{LR}\ (\text{mg}\cdot\text{g}^{-1})}{\left(\left[\frac{\text{mass}_{DR}\,(\text{g})}{\text{length}_{DR}\,(\text{cm})}\right] \Big/ \left[\frac{\text{mass}_{LR}\,(\text{g})}{\text{length}_{LR}\,(\text{cm})}\right]\right) \times \left(\frac{\text{Length}_{DR}\,(\text{cm})}{\text{Length}_{LR}\,(\text{cm})}\right)}.$$

Statistical analyses

I used JMP and its general linear models procedure for ANOVA for all analyses (SAS Institute, Cary N. Carolina). Individual plants were considered experimental units for most analyses. Before main analyses, fine root N concentrations were analyzed with a model that included main effects and interactions of hoophouses (i.e., blocks) (n = 2) and root status (n = 2; live root vs. dead root). Preliminary ANOVA models indicated that hoophouse and its interactions for N_{mass} and N_{length} were not significant ($P \geq 0.22$); thus we pooled these factors in the error term for subsequent analyses (Bancroft 1964). Fine root N concentrations were analyzed with a model that included main effects and interactions of species ($n = 4$), fertilizer ($n = 2$) and root status ($n = 2$). I analyzed ΔN_{mass} and ΔN_{length} with a model that included main effects and interactions of species ($n = 4$) and fertilization treatment ($n = 2$). When main effects were found to be significant ($P \leq 0.05$) in final ANOVA models, I compared pairs of treatment means with tests of least squares significant difference (Tukey-Kramer HSD). Due to lack of replication for some treatment combinations for root Ca concentrations and the similarity of fertilized and

unfertilized N_{Ca} values within live and dead categories, I present ΔN_{Ca} data as species means without statistical comparisons.

I analyzed factors affecting dead root N with a mixed least squares linear model that included main effects and interactions of species ($n = 4$) and fertilization ($n = 2$) as nominal factors and live root N_{length} as a continuous factor. The model excludes the fertilization main effect and its interactions since $P \geq 0.25$ in the preliminary model (Bancroft 1964). In addition, we used simple linear regression to model the overall relationship between live and dead root N concentrations, and in cases of significant species effects in the mixed model, species were analyzed individually.

Results

The basis on which N concentrations were expressed strongly influenced the direction and magnitude of apparent changes in N between live and dead roots. On a mass basis, N was actually higher in dead than live roots. In contrast, N was lower in dead than live roots when expressed in terms of length, Ca or when ΔN_{mass} was corrected for changes in mass during senescence ($\Delta N_{corrected}$).

Overall, mass-based root N concentrations (N_{mass}) varied with species, fertilization, root status (live/dead) and species x root status interactions, but root status effects dominated (Table 1.1a). N_{mass} was higher in dead than live roots and in fertilized versus non-fertilized treatments. For dead roots, N_{mass} was greater for *A. saccharum* and *A. rubrum* than for *P. tremuloides* and *B. alleghaniensis*, whereas N_{mass} did not differ

among species within live roots ($P < 0.01$, Tukey HSD, Table 1.1). Averaged across species, ΔN_{mass} was 14.2% for the fertilized treatment and 27.8% for the unfertilized treatments (Table 1.2). Among species x fertilization treatments, ΔN_{mass} (Table 1.2) ranged from a 6.6% increase in dead roots for fertilized *P. tremuloides* to a 40.4% increase for unfertilized *A. rubrum*.

Length-based root N concentrations (N_{length}) varied with species and root status, but not with fertilization (Table 1.1a). Species rankings in N_{length} were similar to those for N_{mass}. In contrast to patterns for N_{mass}, ΔN_{length} values were approximately 9% lower for dead than live roots and values were unaffected by species, fertilization treatments, or their interactions (Table 1.2). Given the weak effects of fertilization on ΔN_{length} and ΔN_{length}, the lack of fertilizer interactions for N_{mass} and ΔN_{mass} and low replication for N_{Ca}, I pooled fertilizer treatments for all subsequent summaries. Like N_{length}, calcium-based root N concentrations (N_{Ca}) were greater for live roots than for dead, and species ranked similarly (Table 1.1). Values for ΔN_{Ca} were even lower than those for ΔN_{length} and indicated that, averaged among species; N_{Ca} was 30% lower for dead roots than live roots (Tables 1.1, 1.2).

Both root mass per root length and root length decreased from live to dead roots, indicating substantial root mass loss during senescence for all species (Table 1.3). Averaged among species, mean root mass per root length decreased 24% and mean 1st order root length (cm) decreased by 13%, (Table 1.3), thus total mass loss was approximately 34% (34% = 1- (0.76 x 0.87). ΔN_{mass} values corrected for Δroot mass

($\Delta N_{corrected}$, mean of species = −21.0%) were closer to ΔN_{Ca} values (mean = −30.4%) than were ΔN_{length} (mean = −9.1%) or ΔN_{mass} values (mean = 19.9%) (Tables 1.2, 1.3). Expected Ca concentrations in dead roots (Expected Ca_{DR}), calculated from live root Ca, changes in mass, and assuming stable Ca during senescence (see Methods) were similar to measured dead root Ca values for 3 of the 4 study species, although expected values were lower than measured dead root Ca in all cases (11% lower on average, Table 1.3).

Live root N_{length} and species strongly affected dead root N_{length} and their interactions were marginally significant (Figure 1.3 legend). However, a model including live root N_{length}, species, and their interactions explained only modest additional variation in dead root N_{length} (adjusted $R^2 = 0.69$) over a model with only live root N_{length} as a predictor (adjusted $R^2 = 0.57$). Within species, live N_{length} vs. dead N_{length} relationships were significant for *A. rubrum* and *P. tremuloides*, which had similar slopes and intercepts (Figure 1.3 legend). Furthermore, intercepts were not significantly different from zero for either the species pooled data set ($P = 0.16$) or for individual species ($P \geq 0.84$ in all cases). Collectively, these results indicate that: (1) live root N was the primary determinant of dead root N and (2) given a zero intercept and a linear relationship, dead root N was a constant proportion of live root N over the range of live root N examined.

Discussion

Comparing estimates of ΔN

Changes in N from live to dead roots varied markedly among measurement bases, ranging from a 20% increase for ΔN_{mass} to a 30% decrease for ΔN_{Ca} with ΔN_{length} values intermediate (11% decrease). A major factor contributing to these differences was root mass loss between live and dead roots which declined, on average, by 34%. Neither mass-based nor length-based N concentrations completely account for root mass loss as roots senesce. ΔN_{mass} values corrected for root mass loss ($\Delta N_{corrected}$) indicated a loss of approximately 21% N (Table 1.3). These values likely represent the closest approximation of actual N loss from senescing roots.

My results call into question the results of comparisons of live and dead root N made on a mass-basis and not corrected for mass-loss during senescence. To my knowledge, all other studies to date that have evaluated N in live vs. dead roots have done so on an uncorrected mass-basis. These studies have found higher dead root N (Nambiar 1987, this study), no difference (Aerts 1990, Gordon and Jackson 2000), and 10% higher N in live roots (Meier et al. 1985). If root mass changes during senescence, mass-based measures are intrinsically biased and underestimate N loss between live and dead roots.

Since Ca is phloem-immobile, root Ca concentrations between live and dead fine roots may be more stable (McLaughlin and Wimmer 1999) than either fine root mass per length or length during senescence and thus I speculated that Ca should provide a more accurate estimate of N loss than length- or mass-based estimates. In leaves, Ca moves passively in the transpiration stream and accumulates in deciduous foliage throughout the growing season, with the highest Ca concentrations in senescent leaves (Burton et al.

1993, Duchesne et al. 2001). The same mechanism may not occur in roots, but it is notable that estimates of Ca in dead roots (i.e., calculated from live root Ca concentrations and mass changes, and assuming constant Ca concentrations) slightly but consistently underestimated measured values of dead root Ca (Table 1.3). This underestimate may have occurred if root Ca increases with age, as live root samples likely contained a wide range of root ages, from recently initiated to old, whereas dead root collections were likely dominated by older roots. Thus, my assumption of constant root Ca from live to dead roots may be wrong, and may result in an overestimate of N loss when expressed on a Ca-basis. Despite this caveat, estimated Ca in dead roots was, on average, only 11% less than actual Ca in dead roots. Furthermore, ΔN corrected for Δroot mass ($\Delta N_{corrected}$) was intermediate between ΔN_{length} and ΔN_{Ca} values. Altogether, my results suggest that mass-, length- and Ca-based estimates of ΔN all have their biases, and that mass-based N loss estimates corrected for root mass loss may provide the best approximation of ΔN (mean of species = –21%, Table 1.3).

Nevertheless, corrected ΔN still has limitations given the methodology in this study. First, there are several potential sources of root length loss unrelated to shrinkage, such as herbivory, parasitism or decomposition, which could lead to overestimates of root length shrinkage, and N loss. Furthermore, estimates of root length change were made on 1^{st} order roots, but shrinkage may vary among root orders. For example, if 1^{st} order roots shrink more than the higher order roots that also were included in live and dead root samples, then length shrinkage and N loss would be overestimated. Related to this, an additional potential source of error in ΔN calculations, regardless of the basis measured, is that live and dead root samples might have contained different proportions of 1^{st}, 2^{nd}

and 3rd order roots, with different diameter distributions. Root order (Pregitzer et al. 1997) and diameter (Gordon and Jackson 2000) are related to N concentrations, thus differences in live and dead root collections could lead to differences in root N between live and dead samples that are unrelated to senescence-related ΔN. However, the diameter distributions of live and dead root samples were remarkably similar with > 85% of root length being < 0.5 mm in diameter and none over 2 mm for either live or dead root collections (Figure 1.1).

Whole plant and ecosystem implications

My data indicate that live root N concentration was a more important determinant of dead root N concentrations than species and fertilization. Species effects were significantly independent of live root N, but species effects were weaker and fertilization effects were not significant (Figure 1.3 legend, and data not shown). These results suggest that species and environmental differences in dead root N are mediated primarily by how species and environment affect live root N and less so by species-specific or environmentally induced variation in ΔN. My results for fine roots are consistent with those for leaves in a 297 species global dataset (Kobe et al. 2005).

If, as my limited data suggests, the dead root N vs. live root N relationship is linear and with an intercept of zero, then dead root N is a constant proportion of live root N at any live root N concentration. It is important to note however, that, although proportional N loss may be constant, more N on an absolute basis is lost from the dead roots of plants with high live root N. To reiterate, however, my data are limited, and conclusions about the determinants of dead root N will require experiments that test these

relationships for a larger number of species and across a greater range of environmental conditions than covered in this study.

Differences in mass-based root N between live and dead roots have been interpreted as estimates of N resorption or lack thereof (Meier et al. 1985, Nambiar 1987, Aerts 1990, Gordon and Jackson 2000). My results clearly indicate that it is erroneous to conclude negligible N resorption based on studies that have used uncorrected mass-based measures of live and dead root N. For example, using uncorrected mass-based measures from published studies, I calculated ΔN_{mass} and in 63% of the estimates, my calculations suggested that resorption did not occur (Table 1.4). In contrast, when changes in mass were accounted for (i.e., using estimates of mass loss from this study), my calculations of $\Delta N_{corrected}$ implied that resorption occurred in 15 out of 16 estimates and values indicated substantial resorption (range = −4.33 to −48.52%) (Table 1.4). Altogether, results from this study and re-analysis of data from the literature further supports the notion that previous estimates of root resorption are likely biased, depending on the extent of root mass loss.

Unlike leaves, differences in root N between live and dead roots do not directly measure N resorption because other processes, including leaching and microbial immobilization, can also contribute to changes in N. At best, ΔN may serve as a crude index of resorption. If, however, I can assume that ΔN is a crude estimate of N resorption, then the moderate resorption values suggested by my results (e.g., 21% for mass-corrected estimates) is considerably less than foliar resorption values (~ 60%, Aerts 1996, Kobe et al. 2005). For example, reported foliar resorption values for the species

included in this study are: *P. tremuloides* (43%, Killingbeck et al. 1990), *B. alleghaniensis* (61%), *A. rubrum* (71%) and *A. saccharum* (66%) (Cote et al. 2002).

Post-senescent changes in root N that are independent of resorption pose obvious challenges to accurately estimating N resorption from fine roots. Although I adhered to narrow condition criteria for selecting dead roots, senesced roots may have undergone initial stages of decomposition. During decomposition of fine root litter, N can initially decrease then increase (John et al. 2002), a pattern that might be explained by leaching (Chen et al. 2002) followed by microbial immobilization of N (Ostertag and Hobbie 1999). Unlike leaves, which lose negligible amounts of N to leaching (e.g., < 0.6 % of total leaf N, Chapin and Kedrowski 1983), roots are in direct contact with the soil solution, which likely facilitates N leaching during root death. Stress-induced loss of membrane integrity during fine root senescence has been shown to increase the leakage of N in amino acids (Huang et al. 2005). Even for live, intact healthy roots in aqueous solution N efflux can exceed influx in some conditions (Lucash et al. 2005, McFarlane and Yanai 2006) but it is unclear if this occurs for plants growing in soil (McFarlane and Yanai 2006) and it is only relevant if large amounts are being lost relative to the total amount of N in live roots.

N losses through leaching were not accounted for but would have been captured by ΔN values and ultimately would have over-estimated resorption. Like leaching, N immobilization would also be captured by ΔN estimates, but, unlike leaching, immobilization would result in underestimates of N resorption. Unfortunately, there are few data on leaching or immobilization per unit root during senescence, let alone studies

that simultaneously evaluate the contributions of leaching, immobilization, and resorption to changes in root N.

Given that previous work generally indicates that mass-based N concentrations are similar in live and dead roots (Nambiar 1987, Aerts 1990, Gordon and Jackson 2000), numerous investigations covering a broad spectrum of ecological processes have assumed that fine root N is not resorbed during senescence. These processes include: fine root N and decomposition dynamics (Dilustro et al. 2001, Ludovici and Kress 2006, Valverde-Barrantes et al. 2007); covariance of foliar and fine root nutrient concentrations (Newman and Hart 2006); whole-plant and stand-level nutrient-use efficiencies (Silla and Escudero 2004, Norby and Iversen 2006, Silla and Escudero 2006); and stand-level N cycling (Will et al. 2006). I recognize the strong contributions these and other studies have made towards understanding these processes and that progress in ecological research often requires making pragmatic assumptions about processes that are poorly quantified. By clearly showing that the assumption of no resorption from roots is erroneous, my aim is to stimulate new investigations on the N dynamics of senescing roots. I believe that such investigations will be strengthened by considering N dynamics on bases that are insensitive to mass changes that occur in roots as they senesce, as I have identified in this paper.

Table 1.1. Results from ANOVA and summary of fine root nitrogen (N) concentrations.

(a) Results of a standard least squares linear model for main effects and interactions of species (n = 4), fertilization (unfertilized, fertilized) and root status (live, dead) on mass- and length-based fine root N concentrations.

ANOVA effects	d.f.	SS	*F*	*P*	Tukey-Kramer HSD[c]
N ($mg \cdot g^{-1}$)[a]					
Species	3	133.46	10.9	< 0.0001	*Pt* (ac), *Ba* (a), *Ar* (bc), *As* (b)
Fert	1	56.69	13.89	0.0003	fertilized > unfertilized
Species X Fert	3	16.22	1.32	0.2704	
Root status	1	168.52	41.28	< 0.0001	dead > live
Species X Root status	3	52.36	4.28	0.0069	
Fert X Root status	1	3.12	0.77	0.3836	
Species X Fert X Root status	3	16.93	1.38	0.2521	
N ($mg \cdot cm^{-1}$)[b]					
Species	3	41.37	67.99	< 0.0001	*Pt* (a), *Ba* (b), *Ar* (c), *As* (c)
Fert	1	0.29	1.42	0.2400	
Species X Fert	3	0.19	0.31	0.8220	
Root status	1	1.81	8.92	0.0035	live > dead
Species X Root status	3	0.44	0.72	0.5400	
Fert X Root status	1	0.11	0.57	0.4500	
Species X Fert X Root status	3	0.74	1.22	0.3100	

Note: [a]Overall model: adjusted $R^2 = 0.44$, $P < 0.0001$; [b]Overall model: adjusted $R^2 = 0.64$, $P < 0.0001$

[c]Means among species without a common letter are significantly different ($P < 0.05$, Tukey-Kramer HSD). Species abbreviations are as follows: *P. tremuloides* (*Pt*), *B. alleghaniensis* (*Ba*), *A. rubrum* (*Ar*), A. saccharum (*As*).

(b) Mean nitrogen (N) concentrations (± one SE) in live and dead fine roots collected from unfertilized and fertilized (N + Ca) potted seedlings of four tree species as expressed on root mass (mg N·g^{-1} root), length (mg N·cm^{-1} root) and Ca bases (unitless).

	N_{mass} ($mg \cdot g^{-1}$)		N_{length} ($mg \cdot cm^{-1}$)	N_{Ca} (unitless)
Species	Unfertilized	Fertillized	Overall	Overall
P. tremuloides				
Live	12.9 ± 1.3 (6)	14.6 ± 0.9 (7)	1.4 ± 0.1 (12)	1.4 ± 0.1 (4)
Dead	13.1 ± 0.8 (7)	16.1 ± 0.6 (7)	1.3 ± 0.1 (13)	1.0 ± 0.1 (4)
B. alleghaniensis				
Live	12.8 ± 0.6 (6)	13.7 ± 0.6 (8)	2.3 ± 0.1 (14)	1.5 ± 0.1 (2)
Dead	14.3 ± 1.1 (7)	15.3 ± 0.3 (9)	1.8 ± 0.1 (16)	0.8 ± 0.1 (2)
A. rubrum				
Live	12.8 ± 0.4 (8)	13.8 ± 0.5 (8)	3.0 ± 0.1 (16)	2.1 ± 0.2 (4)
Dead	17.8 ± 0.4 (8)	17.6 ± 0.5 (7)	2.8 ± 0.1 (15)	1.4 ± 0.1 (4)
A. saccharum				
Live	13.7 ± 0.6 (8)	16.8 ± 0.8 (8)	2.8 ± 0.1 (16)	1.8 ± 0.2 (3)
Dead	17.7 ± 0.5 (9)	18.1 ± 1.3 (8)	2.6 ± 0.1 (17)	1.4 ± 0.2 (2)

Species group means were calculated from samples of individual seedlings for N_{mass} ($mg \cdot g^{-1}$) and N_{length} ($mg \cdot cm^{-1}$). Overall species means for N_{Ca} (unitless) were calculated from composite samples. Sample sizes are in parentheses.

Table 1.2. Results from ANOVA and summary of changes in fine root N (ΔN) during senescence.

(a) Results of a standard least squares linear model for main effects and interactions of species (n = 4) and fertilizer (unfertilized, fertilized) on estimates of ΔN during senescence. ΔN_{Ca} was not evaluated with ANOVA due to lack of replication for some treatments (see methods).

ANOVA effects	d.f.	SS	*F*	*P*	Tukey-Kramer HSD[c]
ΔN_{mass} (%)[a]					
Species	3	4519.78	4.99	0.0043	*Pt* (a), *Ba* (a), *Ar* (b), *As* (ab)
Fert	1	1824.64	6.05	0.0176	fertilized > unfertilized
Species X Fert	3	1100.43	1.22	0.3142	
ΔN_{length} (%)[b]					
Species	3	1137.99	0.92	0.4403	
Fert	1	17.78	0.04	0.8367	
Species X Fert	3	1833.23	1.48	0.2331	

Note: [a]Overall model: adjusted $R^2 = 0.26$, $P = 0.0023$; [b]Overall model: adjusted $R^2 = 0.005$, $P = 0.4165$ [c]Means among species without a common letter are significantly different ($P < 0.05$, Tukey-Kramer HSD). Species abbreviations are as follows: *P.tremuloides* (*Pt*), *B. alleghaniensis* (*Ba*), *A. rubrum* (Ar), *A. saccharum* (*As*).

(b) Means of ΔN (± one SE) for unfertilized and fertilized (N + Ca) potted seedlings of four tree species. Fine root ΔN estimates were expressed on root mass (mg $N \cdot g^{-1}$ root), length (μg $N \cdot cm^{-1}$ root) and Ca bases (unitless). Means of ΔN_{mass} (%) and ΔN_{length} (%) represent the mean of all individual seedlings within a species (overall) or species X fertilizer group. Species means for ΔN_{Ca} (%) represent the mean of composite samples. Sample sizes are in parentheses.

	ΔN_{mass} (%)			ΔN_{length} (%)	ΔN_{Ca} (%)
Species	Unfertilized	Fertilized	Overall	Overall	Overall
P. tremuloides	13.9 ± 8.0 (5)	6.6 ± 3.1 (6)	10.0 ± 3.9 (11)	−9.1 ± 5.5 (10)	−27.2 ± 1.8 (4)
B. alleghaniensis	14.8 ± 8.8 (6)	13.2 ± 5.4 (8)	13.9 ± 4.7 (14)	−16.1 ± 7.1 (14)	−47.6 ± 2.2 (2)
A. rubrum	40.4 ± 5.6 (8)	27.9 ± 5.2 (7)	34.6 ± 4.1 (15)	−6.3 ± 3.4 (15)	−32.4 ± 3.7 (4)
A. saccharum	33.7 ± 5.9 (8)	8.8 ± 8.6 (8)	21.3 ± 6.0 (16)	−5.0 ± 3.7 (16)	−14.4 ± 7.5 (2)

Table 1.3. Root dimensional changes, corrected change in fine root N (ΔN) during senescence and root Ca concentrations.

Species	*P. tremuloides*	*B. alleghaniensis*	*A. rubrum*	*A. saccharum*
Root dimensional changes				
$mass_{LR}$:$length_{LR}$ ($mg \cdot m^{-1}$)	10.4 ± 0.5 (12)	17.4 ± 1.3 (14)	22.9 ± 0.8 (16)	18.5 ± 0.7 (16)
$mass_{DR}$:$length_{DR}$ ($mg \cdot m^{-1}$)	8.9 ± 0.5 (13)	12.3 ± 0.7 (16)	15.9 ± 0.8 (15)	14.9 ± 0.7 (17)
Δmass:length (%)	−15.2	−28.9	−30.8	−19.5
$length_{LR}$ (mm)	1.0 ± 0.01 (25)	1.0 ± 0.01 (25)	2.1 ± 0.01 (25)	1.9 ± 0.01 (25)
$length_{DR}$ (mm)	0.8 ± 0.01 (25)	0.9 ± 0.01 (25)	1.8 ± 0.01 (25)	1.7 ± 0.01 (25)
Δroot length (%)	−19.2	−10.6	−13.7	−10.3
Δroot mass (%)[a]	−30.9	−36.8	−40.1	−22.8
Corrected N loss				
$\Delta N_{corrected}$ (%)[b]	−24.0 ± 2.7 (11)	−28.0 ± 2.9 (14)	−19.4 ± 2.4 (15)	−12.4 ± 4.3 (16)
Root Calcium				
Ca_{LR} ($mg \cdot g^{-1}$):measured	10.2 ± 0.4 (4)	8.9 ± 0.4 (2)	6.4 ± 0.6 (4)	8.3 ± 1.1 (3)
Ca_{DR} ($mg \cdot g^{-1}$):measured	14.9 ± 0.6 (4)	19.2 ± 0.4 (2)	12.5 ± 0.4 (4)	11.9 ± 2.0 (3)
Ca_{DR} ($mg \cdot g^{-1}$):expected[c]	14.8	14.0	10.7	11.5

Values of root mass:root length and $\Delta N_{corrected}$ are means of individual seedlings within species groups. Root length estimates represent the mean length of individual 1st order roots. Means of root calcium concentrations represent means of composite samples within species groups. Sample sizes are in parentheses. LR = live root; DR = dead root.

Note: [a]Δroot mass (%) = 1- (fractional change in mass per unit length × fractional change in length) × 100.

[b]Calculated from ΔN_{mass} while correcting for Δroot mass from live to dead roots.

[c]Calculated from Δroot mass while assuming no resorption of Ca.

Table 1.4. Live and dead fine root N concentrations, mass-based changes in fine root N (ΔN_{mass}) and changes in fine root N corrected for mass loss ($\Delta N_{corrected}$) for data gathered from published studies (adapted from Gordon and Jackson, 2000).

Authors	Biome	Location	Species	Treatment	Study sites
McKay and Malcolm 1988	Temperate coniferous forest	Europe	Pine in spruce/pine		
Ahlstrom et al. 1988	Temperate coniferous forest	Central Sweden	spruce & shrub	solid fertl A	pine stand
				solid fertl B	pine stand
Nambiar 1987		South Australia	pine		plantation
van Praag et al. 1988	Temperate coniferous forest	southern Belgium	beech		120-yr old stand
			spruce		35-yr old stand
McClaugherty et al. 1982	Temperate deciduous and coniferous	Massachusetts	red pine		53-yr -old plantation
			mixed hardwoods		80-yr-old stand
Meier et al. 1985	Temperate coniferous	Washington	fir		23-yr-old stand
					180-yr-old stand
Arunachalam et al. 1996	Tropical deciduous forest	north-east India	pine	understory	22-yr-old forest
				gaps	
				logged	
				soil heaps	

Table 1.4 (cont'd).

Authors	Root Type	Diameter (mm)	Depth (m) or horizon	live N (%)	dead N (%)	[a]ΔNmass (%)	[a]ΔNcorrected (%)
(McKay and Maclcolm 1988)	fine	< 2mm	0.00-0.05	1.28	1.17	−8.59	−40.24
(Ahlstrom et al. 1988)	fine	< 2	ingrowth cores buried to 30 cm	1.6	1.26	−21.25	−48.52
	fine	< 2		1.12	1.08	−3.57	−36.96
(Nambiar 1987)	fine	< 0.5	0.5	1.18	1.26	6.78	−30.19
(VanPraag et al. 1988)	fine	< 1	0.2	0.999	1.64	64.16	7.32
	fine	< 1		1.131	1.224	8.22	−29.25
(McClaugherty et al. 1982)	fine	< 0.5	forest floor	1.4	1.57	12.14	−26.69
	fine	< 0.5	0-0.15	1.3	1.28	−1.54	−35.63
	fine	< 0.5	forest floor	1.66	1.56	−6.02	−38.56
	fine	< 0.5	0-0.15	1.1	1.3	18.18	−22.74
(Meier et al. 1985)	fine	0-2.0	O horizon	0.82	1.2	46.34	−4.33
	fine	0-2.0	O horizon	0.93	0.84	−9.68	−40.95
(Arunachalam et al. 1996)	fine	< 1	0-0.1	0.82	1.06	29.27	−15.49
	fine	< 1		0.62	0.62	0.00	−34.62
	fine	< 1		0.75	0.77	2.67	−32.88
	fine	< 1		0.77	0.83	7.79	−29.53

Note: [a]see methods for calculations.

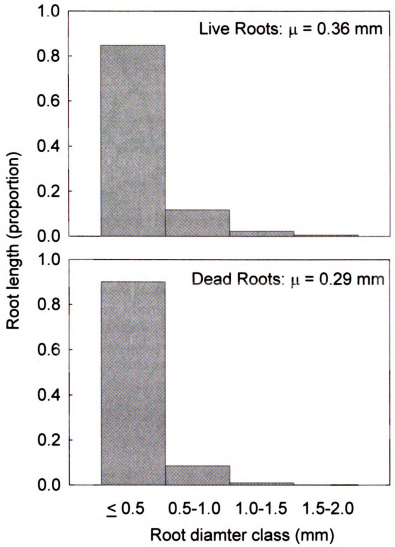


Figure 1.1. Proportion of fine root length across root diameter classes for both live and dead root categories. Root length data from individual seedlings were combined for all species and fertilizer treatments.

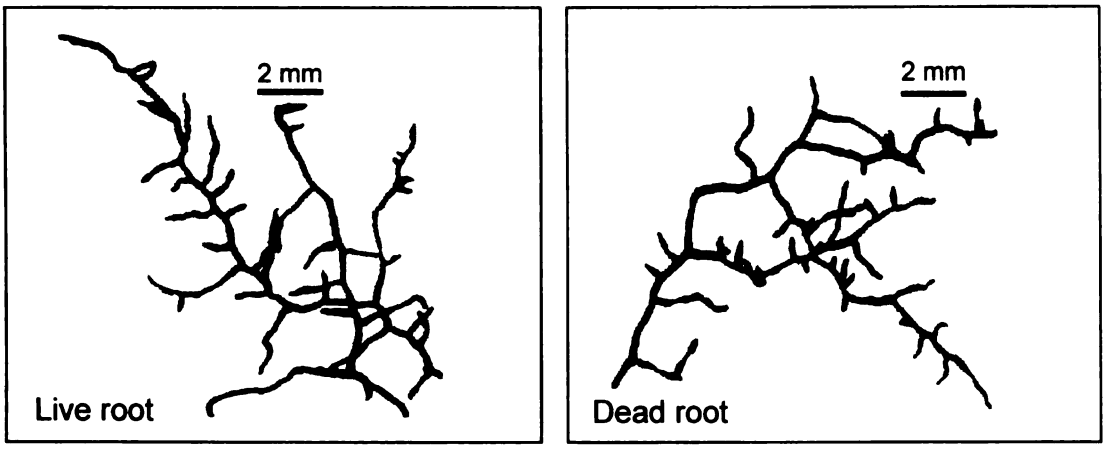


Figure 1.2. Representative examples of live and dead fine root segments for *A. saccharum*. Roots were procured from individual seedlings in late-September 2003 at the Tree Research Center, Michigan State University. Images were acquired with a flatbed scanner (Epson Expression 1680, Nagano, Japan) at a resolution of 400 DPI and later edited for inherent root color differences and shadowing with Adobe Photoshop 7.0 (Adobe Systems Inc., San Jose, California). All roots in this image are < 2.0 mm in diameter.

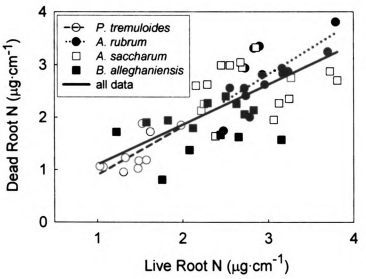


Figure 1.3. Live (LRN) versus dead (DRN) fine root N_{length} for four tree species. Data represent individual seedlings. In a mixed linear least squared model partial *P* values for LRN, species and their interaction as predictors of DRN were $P = 0.0007$, 0.0023, and 0.0614, respectively. Summary statistics for significant ($P < 0.05$) regressions are: Overall relationship, DRN = 0.332 + 0.765(LRN), $R^2 = 0.57$, $P < 0.0001$, n = 55; *P. tremuloides*, DRN = -0.025 + 0.924(LRN), $R^2 = 0.50$, $P = 0.0218$, n = 10; *A. rubrum*, DRN = -0.162 + 0.993(LRN), $R^2 = 0.51$, $P = 0.0029$, n = 15.

CHAPTER 2

PLANT TRAIT CORRELATES OF WHOLE-PLANT CARBOHYDRATE STORAGE AND RELATIVE GROWTH RATE IN TEMPERATE AND BOREAL TREE SEEDLINGS: ARE THERE TRADEOFFS?

ABSTRACT

If interspecific variation in whole-plant total non-structural carbohydrates (TNC_{WP}) is a major trait underlying trade-offs between growth vs. survival adaptive strategies, then TNC_{WP} must negatively covary with traits that enhance growth potential. I explored this hypothesis by comparing interspecific relationships of TNC_{WP}, relative growth rates (RGR), and functionally related allocational, morphological and CO_2 exchange traits for seedlings of temperate and boreal tree species grown in low light (2.8% of open sky). Consistent with their evergreen leaf habit and lack of sprouting ability, gymnosperms (n = 8) had lower TNC_{WP}, and also lower RGR, specific leaf area and root mass ratio, and greater leaf mass ratio and leaf production rates than angiosperms (n = 28). Trait interrelations also differed between groups, so I analyzed interrelations among all species and for the larger angiosperm group separately. Across all species, over three orders of magnitude, variance in seed and seedling mass were positively correlated with TNC_{WP} and negatively related to RGR. RGR and TNC_{WP} were negatively correlated but the relationship was weak and could be driven largely by covariation in plant size. In contrast, the residuals of the RGR vs. seedling mass regression correlated positively with TNC_{WP}; i.e., when plant size effects on RGR are removed, RGR is positively related to TNC_{WP}. Among physiological and morphological traits, across all species and within the

angiosperm group, leaf area ratio correlated most strongly to RGR, root mass ratio was most strongly related to TNC_{WP}, and root mass ratio and leaf area ratio were themselves negatively correlated indicating a possible necessary trade-off between leaves for productivity vs. roots for storage over all species. However, lower leaf light compensation points for photosynthesis, lower leaf production rates and lower whole-plant respiration rates contributed to greater RGR independent of plant size and/or greater TNC_{WP}, but were only weakly related to RGR. RGR independent of size was also positively related to seedling survival thus providing further support for the positive interrelations between growth-survival and carbon conservation traits in low light. In summary, under low light conditions, carbon conservation traits that increase growth independent of plant size also increase stored carbohydrates. Trade-offs between growth and storage (i.e, survival) related traits are only evident when variation in plant size is not taken into account.

Introduction

Allocation to carbohydrate storage (total nonstructural carbohydrates, TNC) has been proposed as a key plant trait that underlies perennial plant survival (Chapin et al. 1990, Kobe 1997, Machado and Reich 2006, Myers and Kitajima 2007, Poorter and Kitajima 2007). TNC may enhance survival because it can be mobilized in response to tissue loss (e.g., from fire, Kruger and Reich 1997b); herbivory (Canham et al. 1999, Myers and Kitajima 2007) and in response to resource shortfalls that limit carbon gain (e.g., drought, Busso et al. 1990, Volaire 1995); dormant seasons (Loescher et al. 1990, Kozlowski 1992); and periods of deep shade (Kobe 1997, Veneklaas and den Ouden 2005, Myers and Kitajima 2007). Long-term TNC pools can constitute as much as 45% of root mass, but are highly variable among species (range = <2%–45%) and environments (Marquis et al. 1997, Gansert and Sprick 1998, Canham et al. 1999, Newell et al. 2002, Gaucher et al. 2005, Iyer 2006, Myers and Kitajima 2007, Poorter 2007). In this paper, I explore some potential sources of interspecific variation in TNC including (1) phylogeny, (2) seed and plant size; and (3) growth vs. survival adaptive strategies. Related to (3), I investigate the popular supposition that there are necessary trade-offs between trait expressions favoring growth potential vs. storage, and that these define an axis along which species growth vs. survival (storage) adaptive strategies vary.

There could be relatively simple and general allocation based trade-offs between storage and growth related traits, such as allocation to leaves (growth) vs. roots (storage and survival), but it is possible that other traits, including ones that vary phylogenetically, may impact the form of these interrelations and as such different patterns could emerge for phylogenetically broad compared to phylogenetically narrow comparisons. For

example, general differences in the leaf habit between gymnosperm conifers (generally long-lived leaves) and winter deciduous angiosperm species could promote differences in TNC, their distribution among foliage, stems and roots, and their relationship with growth-related traits. Winter deciduous species must develop a full canopy of leaves each spring which may necessitate, compared to evergreen conifers, higher TNC reserves overall but little TNC in their ephemeral, thin and poorly defended leaves. At the other end of the comparative spectrum, TNC-growth related trait interrelations among closely related species may reveal nuanced trade-offs that could be obscured by phylogeny in comparisons of more distantly related species.

In general, seed size correlates positively with young seedling survivorship (Leishman and Westoby 1994, Saverimuttu and Westoby 1996, Walters and Reich 2000, Moles and Westoby 2004) and negatively with relative growth rates (Walters et al. 1993a, Leishman and Westoby 1994, Reich et al. 1998a, Poorter and Rose 2005). Positive survival-seed size relations have been hypothesized to occur via greater reserves, lower growth rates (dilution of reserves) and/or greater seedling size for larger seeded species and some evidence exists for all three (Green and Juniper 2004, Quero et al. 2007). Although not a test of any one of these alternative hypotheses, a logical extension is that seedlings of larger seeded species have greater TNC. There is evidence that, within species, larger seedlings have greater TNC (Lusk and Piper 2007), but little attention has been paid to interspecific relationships.

Interspecific variation in TNC has been proposed as a key trait underlying an adaptive strategy axis defined by trade-offs between high resource growth potential vs. low resource survival (Kobe et al. 1995, Schreeg et al. 2005, Poorter and Bongers 2006).

This supposition has been partially supported by studies showing that that TNC is positively related to survival (Iyer 2006, Myers and Kitajima 2007, Poorter and Kitajima 2007) and negatively associated with growth rates (Iyer 2006, Myers and Kitajima 2007, but see, Poorter and Kitajima 2007). Given these empirical results and supporting theory, simple trade-offs in the expression of morphological and physiological growth-related traits may underlie growth vs. storage/survival trade-offs (e.g., allocation to roots (storage) vs. leaves (growth)) but, to date, these interrelationships have received little attention.

The survival-growth rate relationship was been most convincingly shown for low light survival versus high light growth rate across seedlings of species that vary in a wide range of traits including seed size and phylogeny (Walters and Reich 2000). But, the shape and direction of growth-survival relations, growth-TNC relations and the traits that underlie them may depend on the sources of variation examined. For example, within species, greater light availability can lead to greater growth and survival (Kobe et al. 1995, Walters and Reich 2000) and greater growth and storage (Iyer 2006). Across species under high light, the TNC-growth relationship could be strongly negative because variation in growth and storage potentials and their underlying traits could be fully expressed. Conversely, across species under low light, the TNC-growth relationship could be less clear because the manifestation of growth and storage capacities are likely muted (e.g., Walters and Reich 1999, Portsmuth and Niinemets 2007) and traits underlying these patterns (e.g., allocation programs) may be altered in unexpected ways.

If interspecific variation in TNC is a major trait underlying trade-offs between growth vs. survival adaptive strategies, then TNC must negatively covary with traits that

enhance growth potential. If so, then what might some of these candidate traits be? High growth potential, here defined as high potential relative growth rate (RGR), requires allocation to leaves and roots with high resource acquisition capacities, which in turn requires high surface areas (as indexed by high leaf mass ratios, leaf area ratios, specific leaf areas and specific root areas (Poorter and Remkes 1990, Walters et al. 1993b)), and high metabolic potentials (as indexed by nitrogen concentrations, and respiration rates (Reich et al. 1998a, Reich et al. 1998b, Reich et al. 2003a, Tjoelker et al. 2005)). In contrast, the metabolic costs of synthesis (Poorter and Villar 1997) and maintenance (Kobe 1997) of TNC are low. Furthermore, TNC is not used for resource capture until mobilized to produce growth-related structural tissue (Chapin et al. 1990), and as such TNC storage in protected perennial organs with little chance of being consumed or damaged should be favored over storage in other areas, including those used for resource acquisition. Given these differences in growth- and storage-related traits, I hypothesize that allocation to TNC storage in roots and stems occurs at the expense of allocation to leaves and fine roots, which will lead to lower nitrogen concentrations and CO_2 exchange rates (photosynthesis and respiration).

In this paper, I quantified interrelations of whole-plant total non-structural carbohydrates (TNC_{WP}), RGR and associated morphological and physiological traits for seedlings of 36 temperate and boreal woody species that were grown in a common low light environment. I focused my comparisons of these interrelations on the following questions: (1) Does TNC_{WP} and its distribution differ between species groups of contrasting phylogenies and leaf habits (i.e., winter deciduous angiosperms vs. evergreen gymnosperms), (2) How do TNC_{WP}, RGR, seed and seedling size, and growth rates

covary?; (3) Which morphological, allocational and physiological traits are associated with TNC_{WP} and/or with RGR? Based on these comparisons can I identify trade-offs between characteristics that enhance growth vs. storage?

Materials and Methods

Study species, growing conditions and experimental design

A total of 36 temperate and boreal woody species, mostly from North America, but some with Eurasian distributions were used in this study (Table 2.1). Species differed in seed mass, taxonomic orders and leaf habit (broad-leaved, winter deciduous angiosperms and evergreen (except *Larix laricina*) gymnosperms), shade tolerance, and drought tolerance. Seeds used in the experiment were collected from the Beal Arboretum at Michigan State University (MSU), East Lansing, MI, or purchased from commercial sources (Ontario Tree Seed, Angus, ON; Lawyer Nursery, Inc., Plains, MT; Ministry of Forests, Surrey, B.C.; Sheffield's Seed Co., Inc., Locke, NY). Seeds were pre-treated and stratified according to Young and Young (1992) and germinated in bench-top trays filled with potting soil (Faffard 2 mix, Agawan, MA) underneath a 50% shade lathe house at the Tree Research Center (TRC), MSU in mid-May 2004. Over a two week interval starting in mid-June 2004, germinant seedlings were planted into individual poly-coated bleached board plant bands (7.6 cm × 7.6 cm × 25.4 cm; Zipset Plant Bands, Monarch Manufacturing, Inc., Salida CO). Plant bands in groups of 8 (large-seeded species) or 16 (small-seeded species) were inserted into milk crates (30.5 cm × 30.5 cm × 27.9 cm) and species positions within milk crates were randomly selected. Between 40 and 200 seedlings per species were planted resulting in a total of ~2275 seedlings. Seedlings were

grown in a 60/25/15% homogenized mixture of a field soil mix, silica sand and pea gravel. The field soil mix was collected from the top 15-20 cm of sub-organic soil with a backhoe at a forested sandy glacial outwash site and a moraine site in Roscommon, MI ($44^{o}12'$ N, $84^{o}36'$ W) and later combined in equal amounts. Milk crates were randomly distributed to fixed positions within a 30 m × 50 m area in the understory of a closed canopy, self-thinning, 39 year old *Pinus strobus* plantation at the TRC ($42^{o}40'$ N, $84^{o}27'$ W). The experimental area was fenced with 5 cm mesh welded wire to 1.5 m height and 1.25 cm wire mesh to 1 m height to prevent browsing by mammals. Supplemental water was only applied to seedlings during extended dry periods (i.e., more than 7 days without rain). A controlled release fertilizer (Osmocote® Plus by Scotts Fertilizer, Marysville, Ohio, USA) was applied on 13 July 2004 at the rate of 200 kg N/ha to the soil surface layer within each plant band. Canopy openness, an index of light availability, was estimated in mid-August 2004 with paired LAI-2000 plant canopy analyzers (LI-COR, Inc. Lincoln, NE). Briefly, measurements above each milk crate ($n = 232$) were obtained when the sky was uniformly overcast with one LAI-2000 unit, while an identical remote unit was placed on a tripod in a nearby clearing and simultaneously recorded open-sky values. Data from each unit were combined later to calculate canopy openness values and the mean light environment (± SE) for the experimental area was 2.81 ± 0.05 % of open-sky. Air temperature was recorded with Hobo Tidbit v2 data loggers (Onset Computer Corporation, Bourne, MA) from 30 June through 27 September 2004 and mean daily minimum, maximum and average temperatures (± SE) were 13.9 ± 0.1, 24.3 ± 0.1 and 18.4 ± 0.1^{o}C, respectively.

Measurements

Seedlings were harvested at three stages during the experiment, with harvest day varying slightly among species. Harvests, time since transplant and number of seedlings harvested were: (1) germinant harvest, ~ five seedlings (mean 5.4, range 3-9, total 194), just prior to transplant; (2) harvest 1, ~ 8 seedlings (mean 8.1, range 4-16, total 293), 49-65 days, and; (3) harvest 2, ~7 seedlings (mean 7.4, range 2-18, total 267), 85-102 days. In this report, germinant harvest mass is sometimes used as a proxy for seed mass, which can be justified since seedlings were harvested within a couple days of germination and germinant mass was strongly correlated with published values of seed size ($P < 0.0001$, $r = 0.98$, data not shown). For the germinant harvest, entire seedlings were dried. For harvests 1 and 2, seedlings were partitioned into leaves/needles, stems and roots and dried. Since most cotyledons had started to detach from seedlings by harvest 1, they were excluded from estimates of whole-plant biomass for harvests 1 and 2. Seedlings were dried in a forced air-oven at 100°C for 1 hour to quickly stop respiration and then at 70°C for 48 hours, after which the dry mass of each sample was obtained.

Leaf net photosynthesis was measured 25 August through 19 September 2004 from 8:30 to 16:00 local time with a CO_2 analyzer operating as a closed system (LI-6200, LI-COR, Inc., Lincoln, NE). The CO_2 infrared gas analyzer was calibrated daily against CO_2 standards. For angiosperm species, photosynthesis was measured on the second or third fully-expanded leaf as close to their natural orientation as was possible within either a 0.25 or 4 liter gas-exchange chamber. The small seedling size of gymnosperm species precluded photosynthesis measurements on intact seedlings. Since photosynthetic rates

of isolated foliage do not differ from whole-shoot measures for small conifer seedlings (Reich et al. 1998b), photosynthesis was measured on conifer shoots. Individual shoots (stem and needles) or multiple shoots (several individuals) were clipped along the stem and photosynthesis was measured on intact needle canopies within the 0.25 liter gas-exchange chamber. All photosynthesis measurements were expressed on a dry mass basis (nmol CO_2 g^{-1} s^{-1}). During measurements, chamber air temperature was 26.3 ± 0.1°C (mean ± SE), relative humidity was 57.4 ± 0.4% and ambient CO_2 was 372.8 ± 0.4 ppm. Prior to photosynthesis measurements, photosynthesis was induced by placing seedlings in naturally occurring sunflecks for 5 to 10 minutes. Individual seedlings were placed within a three-sided enclosure (1 m × 1 m × 2 m) that was covered on the top and three sides with black shade cloth (~5% full sun) and located within the experimental area. This structure maintained light levels that were consistently lower than 1 μmol m^{-2} s^{-1} and a small house fan was used to circulate air to maintain temperatures and CO_2 concentrations within the enclosure that were nearly identical to ambient experimental conditions. An incandescent lamp was equipped with a dimming device and placed directly above seedlings to produce photosynthetic photon flux densities (PPFD) that were < 50 μmol m^{-2} s^{-1} at leaf level. The light source was used to develop photosynthetic light response curves that consisted of 5-10 PPFD levels, starting at values slightly < 50 μmol m^{-2} s^{-1} and ending at values > 2 μmol m^{-2} s^{-1}. This particular light range was used to provide data for the estimation of leaf-level quantum yield, light compensation points and photosynthetic rates at a common PPFD (see Parameter calculations subsection for details). Two or three replicate light response curves were

obtained from randomly selected individuals for each species (overall: 10-30 points per species).

At the end of each day following photosynthesis measurements, seedlings were harvested and partitioned into leaves/needles, stems and roots to acquire: (1) biomass of seedling components; (2) images of individual leaves/needles used for gas-exchange; (3) images of whole-plant leaf/needle canopies; and (3) images of whole-plant root systems. Digitized root images were manually edited with Adobe Photoshop 7.0 (Adobe Systems Inc., San Jose, California, see Chapter 1). Leaf images were analyzed for projected leaf area with WinFolia Pro software (Regent Instruments, Blain, Quebec) for angiosperm species and WinSeedle software (Regent Instruments, Blain, Quebec) for gymnosperm species. Edited root images were analyzed for total root surface area with WinRhizo Pro 5.0 software (Regent Instruments, Blain, Quebec).

Prior to sunrise during harvest 2 (24 to 27 September 2004), seedlings randomly selected for whole-plant respiration measurements were moved to a dark room in a laboratory on the campus of MSU. Intact seedlings were harvested and root systems were rinsed with deionized water to remove soil prior to respiration measurements. Whole-plant dark respiration (R_{WP}) was measured at $25^{o}C \pm 0.03$ SE with a CO_2 analyzer operating as a closed system (LI-6200, LI-COR, Inc., Lincoln, NE). In order to obtain adequate changes in CO_2 concentrations over the course of a measurement interval, 1 to 4 intact seedlings were placed in either a 0.25 or a 4 liter gas-exchange chamber, depending on individual plant size. Seedlings were allowed to stabilize for 2-5 minutes before measurements were recorded. Between 2 and 4 replicate measurements were obtained

for each species and respiration rates were expressed on a dry mass basis (nmol CO_2 g^{-1} s^{-1}).

Total non-structural carbohydrate and nitrogen concentrations

Individual seedling tissue samples from harvest 2 were aggregated by tissue type (i.e., leaves, stems, roots) for each species. Aggregated tissue samples were pulverized into a fine powder with a ball mill (Kinetic Laboratory Equipment Company, Visalia, California) prior to TNC and N analyses. TNC was quantified using a modification of Roper et al. (1988) and Marquis et al. (1997). This procedure involved a two-stage analysis with an extraction of soluble sugars from the plant tissue followed by starch analysis of the extraction residues. Approximately 15-20 mg of each aggregated tissue sample was extracted three times at 75°C using 2ml of 80% ethanol and then centrifuged at 1900g for 5 minutes. The supernatants were collected and diluted with 6 ml of deionized water. Concentration of soluble sugars (i.e., glucose equivalents) in extracts was measured at 490 nm with a visible spectrophotometer (Spectronic 20D+, Thermo Scientific, Waltham, MA) using a phenol-sulfuric acid colorimetric assay (Dubois et al. 1956). The pellet remaining after ethanol extraction was dried and then gelatinized by autoclaving at 125°C for 10 minutes along with 2 ml of 0.1 M sodium acetate buffer, pH 4.8. After cooling, samples were incubated with ~60 units of amyloglucosidase from *Aspergillus niger* (Sigma-Aldrich, St. Louis, MO) at 55°C for 3 hours. The extract was analyzed colorimetrically for starch using a glucose-specific trinder reagent (Pointe Scientific, Inc., Canton, MI). Absorbance was measured at 505 nm with a UV

spectrophotometer (Lambda 20 scanning spectrophotometer, Perkin-Elmer, Waltham, MA). TNC concentrations (mg g^{-1} dry mass) for aggregated tissue samples were calculated as the sum of glucose equivalent measures for soluble sugars and starch. Lastly, mass-based N concentrations of aggregated tissue samples were assessed with dry combustion gas-chromatography (NA 1500 elemental analyzer, Carlo-Erba, Milan, Italy) for each species.

Parameter selection and calculations

A priori, I selected six morphological traits (leaf mass ratio, LMR; specific leaf area, SLA; leaf area ratio, LAR; stem mass ratio, SMR; root mass ratio, RMR; specific root area, SRA), two allocational traits (leaf partitioning ratio, LPR; root partitioning ratio, RPR), five CO_2 exchange traits (leaf-level photosynthesis, A_{30L}; whole-plant photosynthesis, A_{30WP}; leaf-level light compensation point, LCP; quantum yield, QY; whole-plant dark respiration rate, R_{WP}), and one physiochemical trait (whole-plant N concentration, N_{WP}) to relate to TNC_{WP} and RGR (described following and Table 2.1). Traits chosen were ones that have been theoretically and empirically related to RGR and/or TNC (Walters et al. 1993b, Reich et al. 1998b, Poorter 2001, Kobe et al. unpublished manuscript). Hereafter, to simplify presentation, this group of traits, and TNC_{WP} and RGR will be referred to collectively as functional traits.

LMR (leaf mass/total plant mass, in g g^{-1}), SMR (stem + petiole mass/total plant mass, in g g^{-1}) and RMR (root mass/total plant mass, in g g^{-1}) were calculated for both

harvest 1 and harvest 2 data. SLA (leaf area/leaf mass, in $cm^2\ g^{-1}$) was determined on plants harvested during CO_2 exchange measurements (between Harvests 1 and 2). These values were used to calculate leaf area ratio (LAR; leaf area/total plant mass, in $cm^2\ g^{-1}$), for both harvest 1 and harvest 2 mass data as LMR x SLA = LAR. Similarly, root surface area determined during gas exchange measurements was combined with biomass data from this harvest to calculate SRA (root area/root mass, $cm^2\ g^{-1}$).

In contrast to LMR and RMR, which are static descriptors of biomass fractions, the allocational traits LPR and RPR (leaf partitioning ratio, Δ leaf mass/Δ total plant mass; root partitioning ratio, Δ root mass/Δ total plant mass, respectively, in %) capture the dynamics of newly produced biomass fractions during defined growth intervals (Poorter 2001). LPR and RPR were calculated for the harvest 1 to harvest 2 interval. Since our harvest interval was from early August to late September, the negative LPR values we calculated for eight of the 36 species likely resulted from the initiation of leaf senescence in some angiosperm species or from the loss of cotyledons in conifer species. In these cases, species with negative LPR values were assigned a LPR value of 0.

The leaf-level CO_2 gas exchange vs. PPFD relationships were within the linear portion of the response curve (<2 to <50 PPFD), so they were fitted with least squares simple linear regression (JMP 4.0, SAS Institute, Cary, North Carolina, USA). The resulting species-level fits from these models ($P < 0.0001$, for all; R^2 range = 0.869 – 0.992, see Appendix, Table A.1) were used to estimate photosynthesis at a PPFD of 30 $\mu mol\ m^{-2}\ s^{-1}$, a level commonly observed in temperate forest understories (Weber et al. 1985, Sipe and Bazzaz 1995). Photosynthesis at 30 $\mu mol\ m^{-2}\ s^{-1}$ PPFD was expressed

on both a leaf mass basis (A_{30L}, nmol CO_2 (g $leaf^{-1}$) s^{-1}) and a plant mass basis (A_{30WP}, nmol CO_2 (g $whole\text{-}plant^{-1}$) s^{-1}), where $A_{WP30} = A_{30L} \times LMR$). The slope of species-level A-PPFD fits is the apparent quantum yield of photosynthesis (QY, unitless), and the Y-intercept of this fit is the leaf-level light compensation point for photosynthesis (LCP, PPFD at which net photosynthesis = 0). Since whole plant respiration rate (R_{WP}, in nmol CO_2 g^{-1} s^{-1}) was measured on whole seedlings it was calculated from whole-plant CO_2 exchange and dry mass data.

Average relative growth rate (RGR, mg g^{-1} d^{-1}) was calculated as: (*ln*[mean biomass at harvest 2) – *ln*[mean germinant biomass])/days (Evans 1972), where days ranged among species from 85-102. From TNC concentrations for leaves (TNC_{leaf}), stems (TNC_{stem}) and roots (TNC_{root}), we calculated whole-plant TNC concentrations (TNC_{WP}) as: $TNC_{WP} = (TNC_{leaf} \times LMR) + (TNC_{stem} \times SMR) + (TNC_{root} \times RMR)$. Similarly, whole-plant N concentrations (N_{WP}) were calculated as: $N_{WP} = (N_{leaf} \times LMR) + (N_{stem} \times SMR) + (N_{root} \times RMR)$. Whole-plant TNC pool distribution (%) among organs was calculated as: (organ-level TNC pool size/whole-plant TNC pool size) × 100.

Statistical analysis

All analyses were completed with JMP statistical software (SAS Institute, Cary, North Carolina, USA). For all analyses, species means were considered experimental units. Due to distribution characteristics all traits except RGR and TNC_{WP} required Log_{10}

transformation to normalize distributions in order to satisfy the assumptions of least squares methods.

Differences in functional traits, TNC_{WP}, RGR and size between angiosperm and gymnosperm groups were compared with t-tests (Table 2.1). Many of the plant traits were related to mass at the time of measurement for both angiosperm and all species data sets (Table 2.2), and, on average, gymnosperms seedlings were smaller than angiosperms (Table 2.1). These factors led me to compare gymnosperm and angiosperm groups normalized for mass by comparing partial *P*-values for taxonomic order (angiosperms, gymnosperm) in models also including mass, and presenting least squares means adjusted by mass. Based on the results of gymnosperm-angiosperm comparisons above (see Table 2.1 for results) subsequent analyses were conducted for three data sets, angiosperms (n = 28), gymnosperms (n = 8) and all data (n = 36). Data were also analyzed for *Quercus spp.*, the most well represented genus (n = 9). For the sake of brevity, analyses of groups with limited sample sizes (gymnosperm and *Quercus spp.*) are only presented when they provide unique insight to the overall analysis. To analyze differences in the distribution of TNC between gymnosperms and angiosperms, ANOVA was used to evaluate TNC as a function of order, organ type (leaves, stems, roots) and their interactions. For significant nominal effects ($P \leq 0.05$), treatment means were compared with Tukey-Kramer HSD for organ types within orders and Student's t test for orders within organ type.

TNC_{WP}, RGR, plant sizes and plant trait interrelations were first examined with Pearson correlations. Due to the potential influence of plant size on both TNC_{WP} and RGR (MacFarlane and Kobe 2006), the relationship between residual values for

regressions of RGR and TNC_{WP} vs. plant mass were generated for both all data and angiosperm data sets. Both of these residuals and raw values of RGR and TNC_{WP} were correlated with plant traits. Correlations between these residuals and plant traits can be interpreted as the correlation between TNC_{WP} or RGR with the plant trait independent of plant mass effects. I compared correlations of residuals for TNC_{WP} and RGR vs. mass for each harvest with plant traits, and patterns were similar among harvests (data not shown). For further analyses with plant traits, I used the residuals of germinant mass with RGR and the residuals of Harvest 2 mass for TNC_{WP}. Justification for this approach includes: (1) brevity, (2) residual RGR values are thus expressed as independent of germinant mass and thus independent of seed size and size at the beginning of the interval used to calculate RGR, and (3) Harvest 2 mass was the harvest at which TNC_{WP} was determined.

Based on the results of correlation analyses, I developed multiple regression models of RGR and TNC_{WP} using combinations of plant traits as predictors. Models were developed by first including the strongest bivariate predictor, then adding the variable with the second strongest bivariate predictor, and its interaction. If the added variable and its predictor did not both improve the adjusted R^2 and have a significant partial P (at $P < 0.10$) then it was removed. This process was continued iteratively until all plant traits were examined. Models were developed for RGR and TNC_{WP} both with and without mass (germinant harvest mass and harvest 2 mass, respectively) as the first added predictor so as to provide the multiple regression equivalents of correlations with

residuals of regressions of TNC_{WP} and RGR with plant mass. In addition to multiple regressions with RGR and TNC_{WP} as predictor variables, I also developed multiple regression models of RMR at harvest 2 with RMR at harvest 1 as the first added predictor. I did this because RMR was overwhelmingly the best predictor of TNC_{WP} with no other trait contributing extra explained variance, and RMR increased between harvest 1 and harvest 2. Thus, modeling increases in RMR as a function of plant traits can provide additional insight on the contribution of plant traits to increases in TNC_{WP}.

Results

Functional trait comparisons for gymnosperms and angiosperms

Among the 18 traits measured (Table 2.1), germinant mass varied the most (2,874-fold) and N_{WP} the least (two-fold). Reflecting the low light growth environment, RGR was low overall but only one species *Quercus phellos*, had negative RGR. TNC_{WP} varied 13-fold across all species but varied less within angiosperm (five-fold) and gymnosperm groups (two-fold) as the orders formed distinct groups (Student's t-test) with gymnosperms having 1/5 the TNC_{WP} of angiosperms. Compared to angiosperms, gymnosperms also had, on average, similar RGR, higher LMR and LPR, lower RMR and RPR, lower SLA and a slightly lower LAR, slightly higher SRA, lower A_{30L} and slightly lower A_{30WP}, similar QY but higher LCP, higher R_{WP} and slightly higher N_{WP}. However, gymnosperms had, on average, lower mass than angiosperms and several functional traits varied strongly with mass (Tables 2.2, 2.3) such that differences in

functional traits between angiosperms and gymnosperms could be driven by differences in mass. Normalized by covariation in mass, the general differences (but often not the magnitude of differences) between gymnosperms and angiosperms were preserved for LMR, LPR, RMR, RPR, SLA, LAR, A_{30L}, A_{30WP}, LCP, and TNC_{WP}. Particularly for LAR and A_{30WP}, the magnitude of differences at a common mass were much greater than for comparisons of raw data means between groups with angiosperms having much greater values. Differences in direction and/or significance for gymnosperm vs. angiosperm comparisons at a common mass as compared to raw data include: for gymnosperms, lower RGR, lower SRA, modestly lower QY, and no difference in R_{WP} or N_{WP}.

In a mixed model, plant order and plant organ (leaves, stems roots) had strong interacting effects on TNC ($P < 0.0001$) revealing differences in TNC distribution among organs between plant orders. For angiosperms, TNC concentrations ranked leaves < stems < roots, whereas for gymnosperms TNC concentrations were much lower and did not differ among organs (Figure 2.1a). Calculated as the product of organ-based TNC concentrations and mass fractions, TNC pool partitioning differed between plant orders for roots and leaves but not stems with angiosperms having a greater proportion of the total TNC pool in roots (> 70% vs. 35%) and gymnosperms having a greater proportion in leaves (> 50 % vs. ~7%) (Figure 2.1b).

Interrelations of plant size, TNC_{WP} and RGR

Seedling mass right after germination at the beginning of the experiment (Germinant mass) correlated strongly with mass (Final) approximately three months later at the end of the experiment (Table 2.2), a pattern explained by large variation in germinant mass combined with low RGR (Table 2.1) resulting from the low light environment in which seedlings were grown. Across all species, RGR was strongly negatively related to mass, especially germinant mass, and TNC_{WP} was positively related to mass, especially final mass which was when TNC_{WP} was determined (Table 2.2, Figure 2.2a,b). However, despite a generally strong relationship overall, angiosperms and gymnosperms had different relationships with lower RGR for a given germinant mass for gymnosperms (Table 2.1, Figure 2.2a). Despite these differences, RGR consistently declined with germinant mass for angiosperms, gymnosperms and *Quercus spp.* (Figure 2.2a). For TNC_{WP}, the inclusion of gymnosperms (i.e., all species data) strengthened the positive relationship between TNC_{WP} and final mass, but this was due to low final mass for gymnosperms as TNC_{WP} was unrelated to final mass within the gymnosperm group (Figure 2.2b). TNC_{WP} was negatively related to RGR for the angiosperm group, but the relationship was weak and could have been driven by the combination of positive size-TNC_{WP} covariation and negative size-RGR covariation (Figure 2.2c). Furthermore, TNC_{WP}-RGR correlations were insignificant for gymnosperms and strongly positive for *Quercus spp.* seedlings which varied little in size (Table 2.1, Figure 2.2c). To remove plant size effects from the relationship between RGR and TNC_{WP}, I correlated the

residuals of the germinant mass–RGR relationship with TNC_{WP} and found a positive significant relationship for all data and a positive, but insignificant ($P = 0.106$) relationship for angiosperms (Table 2.2, Figure 2.2d, inset).

Relationships of functional traits with size, RGR and TNC_{WP}

Most functional traits were strongly related to seedling size (Table 2.3). Relationships were generally a little stronger for final mass when most of the traits were measured than for germinant mass, but overall relationships were similar, likely due to the strong correlation between germinant mass and final mass (Table 2.2). Differences between correlations for all data and angiosperms are due to fundamentally different interrelations for some characteristics and/or differences in average mass between the two groups (Table 2.1 and data not shown). For angiosperms, negative relationships with mass were strong for morphological traits including biomass fraction traits (LMR, RMR), leaf morphology (SLA), and especially surface area to mass ratios (LAR, SRA). They were also negative for indices of metabolism including N_{WP} and R_{WP} and photosynthetic traits (QY, LCP, A_{30L}, A_{30WP}).

For all species, angiosperm and gymnosperm data sets, LAR was the single trait most strongly related to RGR and the form of the relationship was similar for all groups (Table 2.3, Figure 2.3a). SLA, a component of LAR, and SRA, like SLA and LAR a measure of surface area per unit mass, were also closely and positively related to RGR (and negatively related to mass). Whole plant photosynthetic rate (A_{30WP}), a physiological manifestation of LAR, was also strongly related to RGR (Table 2.3).

For all species, angiosperm and gymnosperm data sets, RMR was the single trait most strongly related to TNC_{WP} and the positive relationship was consistent for all groups (Table 2.3, Figure 2.4a). Many of the traits negatively related to size and positively related to RGR were negatively related to TNC_{WP}. Those traits that followed this pattern for both angiosperm and all species groups included LMR, SMR, RMR, SRA, RWP, and QY. LPR, RPR, and LCP were related to TNC_{WP}, but unrelated to RGR and more weakly related to mass than to TNC_{WP} (Table 2.3, Figure 2.4b,c). Thus, lower relative allocation to leaves, greater allocation to roots and maintaining positive photosynthesis at lower PPFD contributed to higher TNC_{WP}, but not to lower RGR. For both angiosperm and all data groups, RGR independent of mass (i.e., the residuals of the RGR vs. germinant mass relationship) correlated negatively with LPR and LCP and positively with RPR (Table 2.3, Figure 2.3b,c). The only variable significantly correlated with TNC_{WP} independent of whole-plant mass effects on TNC_{WP} was RMR (Table 2.3). Thus, at any given size, species with greater RMR had greater TNC_{WP}.

In multiple regressions, the only trait that contributed to explained variance in RGR over and above LAR was SRA and this was only for the all data group (Table 2.4). For models of RGR with germinant mass as the first term in the model (i.e., RGR independent of size effects), SLA was most important additional predictor for the all species data group and the addition of either LCP or LPR to SLA and germinant mass explained additional variance in RGR. For angiosperms, SLA was unimportant. Instead, LPR and LCP added to models already including germinant mass explained additional variance in RGR. For both all data and angiosperm data groups, no functional trait

explained variance in TNC_{WP} over and above that explained by RMR. RMR increased for all species from harvest 1 to harvest 2 (data not shown). Modeling harvest 2 RMR by first including harvest 1 RMR as a predictor provides insight into the factors responsible for increases in RMR (and thus TNC_{WP}). The factors that increase RMR between harvests 1 and 2 were generally the same that contributed to increased RGR independent of mass; LPR and LCP. In addition, R_{WP} explained additional variance in harvest 2 RMR for the angiosperm group. Substituting RPR for LPR in models where LPR was significant yielded similar, but slightly weaker results. Thus, TNC_{WP} increases with RMR, and RMR and RGR independent of mass increase with lower LCP and LPR, and for angiosperm RMR, lower R_{WP}.

Discussion

Angiosperm and gymnosperm seedlings differed strongly in TNC_{WP} and TNC distribution among leaves, stems and roots. TNC_{WP} was markedly higher in angiosperms than gymnosperms, which is consistent with patterns found for root TNC concentrations of four temperate species (Kobe 1997) and TNC_{WP} of three cold-temperate species (Machado and Reich 2006). Root systems dominated whole-plant TNC pools for angiosperms due to a combination of high root TNC concentrations and high RMR. In contrast, for gymnosperms a majority of the overall low whole-plant TNC pools were in leaves due to high LMR, but not higher leaf TNC concentrations as concentrations were similar among organs. Strikingly different TNC patterns for gymnosperms likely reflect

two general differences between the species representing these groups; differences in leaf habit, and differences in sprouting ability. Except for *Larix laricina*, gymnosperms were all evergreen and all angiosperms were winter deciduous. Following complete leaf senescence in the autumn and winter dormancy, angiosperms have to mobilize TNC reserves from stems and roots early in the spring in order to initiate carbon gain through new leaf production and subsequent photosynthesis (Teng et al. 1999). By contrast, the existing evergreen needle cohorts of gymnosperms are able to support early growing season photosynthetic carbon gain for later needle production obviating the need to store large amounts of TNC to develop a canopy. In this study the higher LPR of gymnosperms and the negative relationship between LPR and storage across all species indicates that gymnosperms continue to develop a leaf canopy late in the growing season at the expense of allocating carbon to TNC. Resprouting of lost aboveground stem tissue is nearly ubiquitous among angiosperms but rare among gymnosperms (Del Tredici 2001, Bond and Midgley 2003). Perhaps especially for angiosperms associated with environments with a high probability of aboveground damage or death (e.g., fire prone and herbivore modified ecosystems), there may be a selective premium placed on TNC storage, especially in roots, which would allow vigorous resprouting following aboveground tissue loss. Similar TNC_{WP} for winter deciduous *Larix laricina* and the evergreen gymnosperms is somewhat surprising, given that this species must completely replace its leaves on an annual basis, but it may reflect a low sprouting capacity which has been reported for the congener *Larix kaempferi* (Shibuya et al. 2007).

In addition to differences in TNC_{WP} between plant orders, differences in leaf habit and related traits led to fundamentally different relationships between functional

traits and RGR for gymnosperms and angiosperms. Gymnosperms had lower A_{30L} and SLA, but a higher LMR than angiosperms with the patterns in leaf traits consistent with the leaf lifespan differences between these groups (Reich et al. 1999). This resulted in gymnosperms having higher RGR at a given A_{30L} and SLA given their higher LMR and vice versa. However, because LAR integrates SLA and LMR, LAR relationships with RGR had the same form across groups. At a similar mass, despite two-fold greater LMR for gymnosperms, SLA was > three-fold greater for angiosperms resulting in greater LAR and RGR for angiosperms. Differences in LAR between similar sized first-year seedlings of angiosperms and gymnosperms may dissipate as seedlings get older as evergreen gymnosperms will continue to accrue new foliage cohorts while retaining at least one older cohort (Reich et al. 1999), whereas angiosperms will not.

Across all species, LAR was the single trait most closely related to RGR, and in combination, only SRA described additional variance in RGR. It should be noted that the strength of the relationship between LAR and RGR could be artificially inflated due to a statistical artifact because the same whole-plant mass values were used to calculate LAR (X axis) and RGR (Y axis) (Prairie and Bird 1989, but see, Berges 1997). However, this statistical difficulty does not invalidate the importance of this relationship because LAR is one of the theoretical determinants of RGR (i.e., RGR = LAR × net assimilation rate, Evans 1972). Whole-plant photosynthetic rate (A_{30WP}) a physiological manifestation of LAR (Walters et al. 1993b, Kruger and Volin 2006), was also strongly related to RGR. These functional traits and RGR were also among the most strongly negatively related to mass. Collectively, the strong negative relationship between RGR and size can be explained by the necessary decline in resource acquiring surfaces (root surface area and

leaf area) as a proportion of total mass as structural and support tissue (and storage) in stems, and higher order roots increases (Givnish 1988). It was not surprising that variation in RGR independent of size effects (i.e., residuals of RGR vs. germinant mass) was unrelated to the functional traits that were themselves strongly size dependent and strongly related to raw RGR data as there was little residual variation in these traits independent of mass. In other words, at any given mass, there was little variation in LAR to explain variation in RGR at the same given mass. Instead, light compensation point (LCP) and leaf and root partitioning ratios (LPR, RPR) which were unrelated to raw RGR values and more weakly related to mass than many other functional traits, were the most strongly related functional traits with RGR-mass residuals.

While I show that TNC_{WP} is related to mass, it was the stronger relationship between mass and RMR that drove this relationship, as RMR was the strongest single variable related to TNC_{WP} and the only trait that explained additional variation in TNC_{WP} over and above mass effects. Thus, bigger seedlings tended to have greater fractions of total mass in roots and greater TNC_{WP}, but RMR and TNC_{WP} varied independent of size. TNC_{WP}, RMR and RGR independent of mass were all associated with mostly the same set of carbon conservation traits (lower values for new leaf production, light compensation points for photosynthesis and whole plant respiration). This combined with the weak positive relationships between TNC_{WP} and RGR independent of mass (and the strong positive relationships within *Quercus spp* which varied little in initial mass) suggests that for young tree seedlings in low light; (1) growth independent of mass and TNC_{WP} are positively related, (2) carbon conservation traits

lead to greater growth independent of mass and TNC_{WP}, (3) these carbon conservation traits are not the same ones driving growth in high light (Walters et al. 1993b, Kruger and Volin 2006) and/or driving growth when differences in initial mass are not taken into account. Thus, seedlings with high storage capacity (i.e., large germinant size, high TNC_{WP}) were still "growing" and accumulating biomass, but newly acquired photosynthates were preferentially allocated to TNC in stems and roots, instead of to growth-related structural components (e.g., leaves). The particular relationships I found among TNC_{WP}, RGR and functional traits might be restricted to low light environments like the one I used (mean = 2.81 % canopy openness). Traits such as LAR have been shown to have a diminishing effect on growth as light decreases which might result in the increased importance of other traits to RGR (Walters and Reich 1999, Portsmuth and Niinemets 2007). However, even in my low light environment, when initial mass was unaccounted for, LAR was the single most important driver of RGR. Furthermore, these results suggest that indeterminate (i.e., continuous production of leaves, high LPR) vs. determinate growth patterns (low or zero LPR values later in the growing season) may distinguish species that store a little vs. a lot of TNC (Kays and Canham 1991, Kobe 1997, but see Canham et al. 1999).

A strikingly strong general result of this study is the predominant influence that seed size has on plant characteristics. While some of these relations may represent necessary allometric constraints (e.g., biomass fractions) it is also possible that strong relationships between functional traits and seed mass represent selection for combinations of traits including seed size that confer greater fitness in a given set of environmental conditions (Wright and Westoby 1999, Reich et al. 2003b). For example, large seed mass

was associated with large seedlings, with greater RMR, lower LAR and growth rates and higher TNC_{WP}. Attaining a large stature as a juvenile tree is a function of initial germinant size and growth rates and growth rate and seed size are often inversely related (Walters and Reich 2000, Green and Juniper 2004, this study). Yet, after nearly three months of growth, final mass was strongly related to germinant mass (and seed mass), with very similar rankings among species (Spearman's $\rho = 0.97$, data not shown). In another study (Chapter 3), large seeded species had larger seedlings even after over two years of growth independent of resources and that these seedlings have deeper roots and during drought have greater access to water and greater survival. Other studies show increased representation of large seeded species as aridity increases (Wright and Westoby 1999). Thus, the combination of traits large seedlings have may confer greater survival under low resource conditions and thus may be under similar selection pressure rather than merely being allometrically constrained.

My results may help to reconcile some of the equivocal data on TNC–plant size relations that have been reported in previous studies. The positive TNC_{WP}–germinant mass (and final mass) relationship I found contrasts with Myers and Kitajima (2007), who found that across a more limited number of species ($n = 7$) TNC concentrations and pool sizes in stems and roots were not correlated with seed mass for tropical tree seedlings. The positive TNC_{WP}–germinant mass association in our study may provide an explanation for the positive relationship between seed size and early seedling survival (Walters and Reich 2000), as it has been hypothesized that over the short term storage reserves from large seeds could be mobilized to sustain metabolic activity and may replace tissues that are lost to herbivores or pathogens (Leishman and Westoby 1994,

Green and Juniper 2004). However, this is merely speculation as I did not determine TNC_{WP} for young germinants and TNC_{WP} was more a function of RMR than mass. Within a narrow light range (2-5% of open sky), Lusk and Piper (2007), found that TNC_{WP} in large seedlings (400–600mm) was higher (22% of dry mass) than those of small seedlings (40-60mm, 14% of dry mass) of six broad-leaved evergreen species, but this difference was driven by light demanding taxa (*Aristotelia chilensis*, *Northofagus dombeyi*, *Eucryphia corditolia*). Based on the positive association between TNC_{WP} and growth rates in our study, it is probable that the light demanding species in Lusk and Piper (2007) had higher growth rates, which over time led to the accumulation of more TNC in larger seedlings. In a complementary study with some overlapping species and similar growing conditions (2-5% of open sky), Lusk (2004) found that two of the more light demanding species (*Aristotelia chilensis* and *Eucryphia corditolia*) sustained higher growth rates than species with higher shade tolerance early in ontogeny, but this pattern reversed in later stages of ontogeny (i.e., size × species interaction). A model of carbohydrate allocation predicts that small plant size is an outcome of allocation to TNC (Kobe, 1997) and Machado and Reich (2006) found that whole-plant and tissue-level TNC concentrations generally decreased with increasing size within three cold-temperate sapling species. However, in Machado and Reich (2006), plant mass was associated with age and saplings varied widely in age (range = 6–24 years), which may partly explain the negative relationship between TNC_{WP} and plant mass. Unlike TNC_{WP}, mass-based whole-plant and tissue-level respiration rates increased with plant size/age, presumably due to higher costs of protein turnover in older saplings (Machado and Reich 2006).

Therefore, it is possible that larger saplings in this experiment actually allocate similar or higher amounts of photosynthates to TNC, but higher respiration rates may ultimately reduce TNC concentrations.

Collectively, our observations along with empirical data from other studies imply that there is a trade-off between high storage capacity (and associated carbon conservation traits) and allocation of carbohydrates to structural components for the interception of light (i.e., leaves). It is hypothesized then that allocation to TNC enhances survival in stressful environments but likely compromises growth capacity and thus competitive ability in high resource environments. The evaluation of the TNC-survival versus growth capacity trade-off requires one important caveat and that is I did not explicitly examine this life history trade-off because I did not measure growth rates and/or competitive ability in a comparable high light treatment. However, I did find a positive relationship between survival (over the three months of the experiment) and TNC_{WP} (Figure 2.5) thereby providing additional support for the positive interrelations between growth-survival and carbon conservation traits in low light environments.

Table 2.1 Summary of seedling characteristics for angiosperm and gymnosperm species.

	seed mass (mg)	final mass (mg)	RGR ($mg\ g^{-1}\ d^{-1}$)	LMR ($g\ g^{-1}$)	SMR ($g\ g^{-1}$)
Angiosperms					
Acer negundo	21.5	174.5	20.3	0.25	0.36
Acer rubrum	5.5	127.8	31.1	0.33	0.28
Acer saccharinum	73.9	1067.9	25.2	0.25	0.35
Acer saccharum	45.7	498.6	23.7	0.25	0.21
Aesculus glabra	2796.6	3419.4	2.0	0.11	0.15
Aesculus hippocastanum	4023.7	5301.0	2.6	0.17	0.26
Ailanthus altissima	12.1	121.6	22.9	0.27	0.21
Alnus incana	2.3	26.0	25.1	0.40	0.33
Carya tomentosa	1435.1	1689.0	1.6	0.23	0.08
Catalpa speciosa	13.7	277.7	30.1	0.30	0.30
Cornus amomum	6.0	96.5	28.0	0.29	0.27
Cornus sericea	4.2	81.2	30.6	0.33	0.21
Gleditsia triacanthos	96.6	754.9	19.4	0.20	0.35
Juglans cineraea	1285.1	4592.3	12.6	0.20	0.31
Lindera benzoin	43.6	380.0	21.6	0.27	0.13
Platanus occidentalis	1.8	19.6	24.7	0.48	0.25
Quercus alba	557.0	1126.3	6.6	0.21	0.11
Quercus bicolor	2113.4	2776.9	2.9	0.27	0.20
Quercus coccinea	1079.9	2088.3	6.5	0.31	0.12
Quercus macrocarpa	732.5	1302.3	5.8	0.28	0.11
Quercus phellos	491.4	489.7	0.0	0.33	0.20
Quercus prinus	1906.9	2203.6	1.4	0.33	0.13
Quercus robur	880.8	1138.0	2.6	0.20	0.11
Quercus rubra	1863.1	2184.1	1.6	0.31	0.16
Quercus velutina	1327.9	1894.2	3.6	0.34	0.13
Rhus typhina	6.8	74.8	24.2	0.33	0.31
Robinia pseudoacacia	27.7	136.6	15.8	0.25	0.34
Ulmus americana	10.1	84.0	21.0	0.36	0.25
Mean	111.6	492.2	14.8	0.27	0.20
LS mean (for mass)			17.1	0.29	0.22
Gymnosperms					
Abies amabilis	20.4	39.3	6.5	0.49	0.20
Abies concolor	13.1	42.5	11.8	0.53	0.21
Larix laricina	1.6	13.2	21.5	0.55	0.25
Picea stichensis	1.4	9.0	18.6	0.48	0.29
Pinus nigra	13.3	59.2	15.0	0.52	0.22
Pinus ponderosa	25.0	84.1	12.1	0.57	0.22
Pinus strobus	8.7	31.6	12.9	0.58	0.25
Pseudotsuga menziesii	7.5	29.4	14.1	0.53	0.21
Mean	7.8	31.3	14.0	0.53	0.23
LS mean (for mass)			5.8	0.42	0.18
P, t-test	0.007	<0.001	0.86	<0.001	0.458
Partial P, model incl. mass			<0.001	0.001	0.268

Table 2.1 (cont'd).

	RMR ($g^{-1}\ g^{-1}$)	LPR (%)	RPR (%)	SLA ($cm^2\ g^{-1}$)	LAR ($cm^2\ g^{-1}$)	SRA ($cm^2\ g^{-1}$)
Angiosperms						
Acer negundo	0.39	0.0	101.5	431.6	148.4	567.6
Acer rubrum	0.38	9.1	50.0	365.4	154.8	373.2
Acer saccharinum	0.40	12.0	51.6	440.0	137.9	286.2
Acer saccharum	0.54	9.5	69.9	368.4	124.0	326.8
Aesculus glabra	0.74	0.0	100.3	347.4	35.5	51.3
Aesculus hippocastanum	0.57	13.1	65.1	256.6	41.7	116.6
Ailanthus altissima	0.52	9.2	80.8	657.5	193.4	422.3
Alnus incana	0.27	20.7	28.5	554.9	228.1	711.2
Carya tomentosa	0.70	0.0	0.0	376.5	91.3	100.2
Catalpa speciosa	0.40	0.0	67.0	589.5	206.8	450.7
Cornus amomum	0.44	0.0	60.7	515.4	191.6	460.8
Cornus sericea	0.45	16.0	56.5	446.7	159.1	380.4
Gleditsia triacanthos	0.45	10.0	54.4	414.4	82.2	194.6
Juglans cineraea	0.50	0.0	241.0	542.6	138.2	98.7
Lindera benzoin	0.59	16.9	71.7	525.4	164.2	409.0
Platanus occidentalis	0.28	40.2	29.8	575.7	347.0	834.9
Quercus alba	0.69	17.0	73.5	273.5	55.2	75.7
Quercus bicolor	0.54	16.2	65.4	274.9	78.8	172.7
Quercus coccinea	0.57	18.3	73.2	253.2	80.5	106.3
Quercus macrocarpa	0.62	19.1	72.1	299.1	82.0	161.2
Quercus phellos	0.47	26.5	59.2	259.2	117.7	317.7
Quercus prinus	0.53	22.9	63.0	230.4	56.6	128.7
Quercus robur	0.68	3.6	89.2	230.8	58.3	185.0
Quercus rubra	0.53	11.7	65.5	291.7	95.9	169.9
Quercus velutina	0.53	22.8	65.4	239.4	77.9	139.4
Rhus typhina	0.36	25.4	41.7	740.2	318.9	790.8
Robinia pseudoacacia	0.40	0.0	58.4	540.9	307.2	405.6
Ulmus americana	0.39	34.2	0.0	389.3	116.6	342.2
Mean	0.48	14.0	66.3	385.0	117.5	245.3
LS mean (for mass)	0.45	--------	------	423.0	141.2	313.3
Gymnosperms						
Abies amabilis	0.32	31.2	64.4	137.7	62.1	420.2
Abies concolor	0.26	60.5	0.0	150.2	81.1	475.1
Larix laricina	0.20	45.5	28.2	316.2	154.1	636.6
Picea stichensis	0.23	47.4	28.0	195.5	96.7	398.7
Pinus nigra	0.26	0.0	90.3	149.8	90.6	454.5
Pinus ponderosa	0.21	63.8	4.8	178.7	94.1	376.6
Pinus strobus	0.17	59.2	21.3	150.1	101.8	428.6
Pseudotsuga menziesii	0.26	41.0	34.1	194.4	114.4	467.1
Mean	0.23	44.0	33.9	178.0	96.4	451.8
LS mean (for mass)	0.30	--------	------	129.0	50.8	192.3
P, t-test	<0.001	<0.001	0.049	<0.001	0.037	0.031
Partial P, model incl. mass	<0.001	--------	0.799	<0.001	<0.001	<0.0001

Table 2.1 (cont'd).

	A_{30L} (nmol g^{-1} s^{-1})	A_{30WP} (nmol g^{-1} s^{-1})	LCP (μmol m^{-2} s^{-1})	QY (unitless)
Angiosperms				
Acer negundo	42.0	15.1	10.2	0.072
Acer rubrum	36.0	17.3	7.3	0.062
Acer saccharinum	38.5	13.2	5.5	0.049
Acer saccharum	56.6	22.5	3.3	0.091
Aesculus glabra	28.8	4.0	6.0	0.042
Aesculus hippocastanum	30.4	5.8	4.1	0.05
Ailanthus altissima	79.3	26.5	9.8	0.073
Alnus incana	64.5	34.9	10.3	0.079
Carya tomentosa	52.6	10.6	4.6	0.049
Catalpa speciosa	69.5	29.4	5.8	0.069
Cornus amomum	53.1	22.3	6.8	0.064
Cornus sericea	68.8	29.3	8.9	0.093
Gleditsia triacanthos	31.5	9.3	8.3	0.052
Juglans cineraea	29.9	9.8	7.4	0.040
Lindera benzoin	57.5	20.1	2.9	0.052
Platanus occidentalis	79.3	44.5	11.6	0.088
Quercus alba	23.9	6.1	7.0	0.046
Quercus bicolor	27.4	9.9	4.5	0.053
Quercus coccinea	24.9	9.4	6.4	0.051
Quercus macrocarpa	28.9	10.6	5.6	0.053
Quercus phellos	27.8	8.8	8.2	0.047
Quercus prinus	27.7	10.2	7.4	0.058
Quercus robur	18.2	5.1	7.6	0.048
Quercus rubra	29.5	12.4	6.8	0.060
Quercus velutina	29.2	12.0	4.6	0.058
Rhus typhina	94.4	45.2	9.6	0.091
Robinia pseudoacacia	36.7	16.1	11.4	0.063
Ulmus americana	65.0	24.9	9.1	0.086
Mean	40.6	14.2	6.8	0.060
LS mean (for mass)	47.0	17.7	7.3	0.064
Gymnosperms				
Abies amabilis	21.8	11.4	9.9	0.084
Abies concolor	23.0	12.0	12.4	0.085
Larix laricina	27.3	17.1	15.0	0.065
Picea stichensis	26.5	12.8	11.0	0.072
Pinus nigra	7.5	4.9	20.2	0.063
Pinus ponderosa	4.0	2.3	25.7	0.051
Pinus strobus	23.5	13.9	10.7	0.082
Pseudotsuga menziesii	12.0	6.9	17.2	0.052
Mean	15.3	8.6	14.5	0.068
LS mean (for mass)	9.2	4.0	11.4	0.053
P, t-test	<0.001	0.0642	<0.001	0.203
Partial P, model incl. mass	<0.001	<0.001	0.01	0.021

Table 2.1 (cont'd).

	R_{WP} (nmol g^{-1} s^{-1})	N_{WP} (mg g^{-1})	TNC_{WP} (mg g^{-1})
Angiosperms			
Acer negundo	16.6	26.1	121.1
Acer rubrum	10.6	23.9	129.5
Acer saccharinum	7.7	15.4	118.2
Acer saccharum	4.0	20.6	192.8
Aesculus glabra	3.5	28.3	180.7
Aesculus hippocastanum	4.6	16.4	147.1
Ailanthus altissima	5.6	24.3	130.3
Alnus incana	19.5	29.7	52.0
Carya tomentosa	4.9	27.0	163.9
Catalpa speciosa	9.8	19.8	94.5
Cornus amomum	12.3	18.2	103.9
Cornus sericea	13.9	20.4	132.3
Gleditsia triacanthos	5.3	22.6	125.3
Juglans cineraea	8.4	20.3	177.8
Lindera benzoin	8.4	21.7	165.8
Platanus occidentalis	18.7	28.3	55.7
Quercus alba	3.5	16.9	245.3
Quercus bicolor	5.9	14.9	112.6
Quercus coccinea	4.2	14.5	161.8
Quercus macrocarpa	4.6	16.5	169.7
Quercus phellos	4.8	15.0	114.1
Quercus prinus	6.8	18.0	138.2
Quercus robur	4.4	18.4	113.3
Quercus rubra	5.6	15.7	107.0
Quercus velutina	4.3	15.7	157.6
Rhus typhina	23.7	23.3	110.4
Robinia pseudoacacia	15.6	31.5	122.1
Ulmus americana	12.6	24.9	81.2
Mean	7.5	20.4	133.3
LS mean (for mass)	8.8	21.4	124.0
Gymnosperms			
Abies amabilis	14.4	26.4	37.1
Abies concolor	15.0	23.0	20.3
Larix laricina	18.0	22.9	26.0
Picea stichensis	9.7	21.3	38.2
Pinus nigra	33.0	29.3	20.0
Pinus ponderosa	16.7	30.3	19.5
Pinus strobus	11.4	28.0	18.8
Pseudotsuga menziesii	19.3	26.7	25.5
Mean	16.1	25.8	25.7
LS mean (for mass)	9.2	21.9	57.0
P, t-test	0.001	0.012	<0.001
Partial P, model incl. mass	0.84	0.788	<0.001

Table 2.2. Correlation matrices for germinant mass, final mass, relative growth rate (RGR), residuals of RGR vs. germinant mass, whole-plant total non-structural carbohydrates (TNC_{WP}) and residuals of TNC_{WP} vs. final mass. The top number is the correlation coefficient for angiosperms only and the bottom number represents the coefficient for all species. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

Germinant mass					
0.96*** 0.95***	Final mass	Angiosperms All species			
-0.92*** -0.81***	-0.77*** -0.58***	RGR			
0.00 0.00	0.28 0.32*	0.39* 0.58***	Resid. RGR vs. germ mass		
0.54** 0.64***	0.61*** 0.77***	-0.38* -0.21	0.31 0.53***	TNC_{WP}	
-0.05 -0.15	0.00 0.00	0.12 0.37*	0.18 0.44**	0.79*** 0.64***	Res. TNC_{WP} vs. final mass

Table 2.3. Correlation statistics for interrelationships between plant functional traits and germinant mass, final mass, relative growth rate (RGR), residuals of RGR vs. germinant mass, whole-plant total non-structural carbohydrates (TNC_{WP}) and residuals of TNC_{WP} vs. final mass. The top number is the correlation coefficient for angiosperms only and the bottom number represents the coefficient for all species. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

		Initial mass	Final mass	RGR	Residuals RGR vs Mass	TNC_{WP}	Residuals TNC_{WP} vs Mass
LMR	All	-0.72***	-0.78***	0.44**	-0.24	-0.83***	-0.35*
	Ang	-0.56**	-0.64***	0.58**	-0.08	-0.58***	-0.24
SMR	All	-0.59***	-0.46**	0.64***	0.29	-0.43**	-0.11
	Ang	-0.59***	-0.48**	0.65***	0.27	-0.54**	-0.31
RMR	All	0.76***	0.84***	-0.47**	-0.25	0.90***	0.38*
	Ang	0.79***	0.78***	-0.73***	-0.11	0.77***	0.37*
LPR	All	-0.39*	-0.56***	-0.03	-0.59***	-0.64***	-0.32
	Ang	-0.17	-0.30	-0.02	-0.45*	-0.29	-0.14
RPR	All	0.41*	0.50**	-0.13	0.35*	0.48**	0.15
	Ang	0.34	0.44*	-0.15	0.41*	0.40*	0.18
SLA	All	-0.17	0.07	0.57***	0.74***	0.40*	0.54***
	Ang	-0.76***	-0.68***	0.77***	0.19	-0.36	0.07
LAR	All	-0.62***	-0.52**	0.80***	0.36*	-0.21	0.30
	Ang	-0.84***	-0.82***	0.82***	0.08	-0.55**	-0.05
SRA	All	-0.89***	-0.86***	0.69***	0.00	-0.69***	-0.13
	Ang	-0.89***	-0.89***	0.77***	-0.14	-0.70***	-0.19
A_{30L}	All	-0.20	0.00	0.48**	0.55***	0.35*	0.56***
	Ang	-0.80	-0.76***	0.75***	0.03	-0.43*	0.05
A_{30WP}	All	-0.67***	-0.40*	0.68***	0.40*	0.11	0.42*
	Ang	-0.87	-0.84***	0.80***	-0.01	-0.56**	-0.05
LCP	All	-0.56***	-0.69***	0.16	-0.49**	-0.75***	-0.35*
	Ang	-0.50**	-0.58**	0.27	-0.46*	-0.58**	-0.20
QY	All	-0.71***	-0.69***	0.55***	0.04	-0.45**	0.14
	Ang	-0.78***	-0.79***	0.66***	-0.14	-0.50**	-0.02
R_{WP}	All	-0.78***	-0.79***	0.54***	-0.16	-0.75***	-0.21
	Ang	-0.80***	-0.80***	0.69***	-0.11	-0.67***	-0.24
N_{WP}	All	-0.54***	-0.59***	0.29	-0.26	-0.48**	-0.04
	Ang	-0.53**	-0.58**	0.39*	-0.26	-0.29	0.09

Table 2.4. Multiple regression models of relative growth rate, relative growth rate with initial mass as a covariate, whole-plant total non-structural carbohydrates, and root mass ratio. Models were developed by first including the strongest bivariate predictor (Table 2.1), then adding the variable with the second strongest bivariate predictor, and its interaction. Additional variables were left in the model if adjusted R^2 values and Pratt indices indicated that their inclusion explained additional variance in the predicted term.

Predicted	Predictor	Standard. b	P value	F	M. S.	Adj. R^2
All data						
RGR	LAR	-------	<0.0001	60.3	2208	0.63
RGR	LAR SRA	0.605 0.292	<0.0001 0.0300	36.3	1186	0.67
RGR	Germ. mass	-------	<0.0001	65.45		0.65
RGR	Germ. mass SLA	-0.737 0.444	<0.0001 <0.0001	93.48	1468	0.84
RGR	Germ. mass SLA LCP	-0.874 0.355 -0.218	<0.0001 <0.0001 0.0165	74.6	1007	0.86
RGR	Germ. mass SLA LPR	-0.826 0.337 -0.182	<0.0001 0.0003 0.0520	69.5	998	0.85
TNC_{WP}	RMR_{Sept}	-------	<0.0001	139	94885	0.80
RMR_{Sept}	RMR_{Aug}	-------	<0.0001	316	0.903	0.90
RMR_{Sept}	RMR_{Aug} LPR	0.809 -0.250	<0.0001 <0.0001	277	0.473	0.94
RMR_{Sept}	RMR_{Aug} LPR LCP	0.720 -0.230 -0.150	<0.0001 <0.0001 0.0076	239.00	0.319	0.95
Angiosperms						
RGR	LAR	-------	<0.0001	53.2	2221	0.66
RGR	Germ. mass	-------	<0.0001	147.1	2809	0.84
RGR	Germ. mass LCP	-1.030 -0.230	<0.0001 0.0055	101.4	1472	0.88
RGR	Germ. mass LPR	-0.953 -0.181	<0.0001 0.0156	93.14	1457	0.87
	Germ. mass LCP	-1.050 -0.212	<0.0001 0.0046	87.07	1009	0.91
TNC_{WP}	RMR_{Sept}	-------	<0.0001	38.07	27313	0.58
RMR_{Sept}	RMR_{Aug}		<0.0001	135	0.28	0.83
RMR_{Sept}	RMR_{Aug} LPR	0.880 -0.190	<0.0001 0.0132	87	0.146	0.86
RMR_{Sept}	RMR_{Aug} LPR R_{WP}	0.625 -0.180 -0.110	<0.0001 0.0062 0.0019	88	0.102	0.91
RMR_{Sept}	RMR_{Aug} LPR LCP	0.810 -0.180 -0.110	<0.0001 0.0148 0.0630	66	0.099	0.88

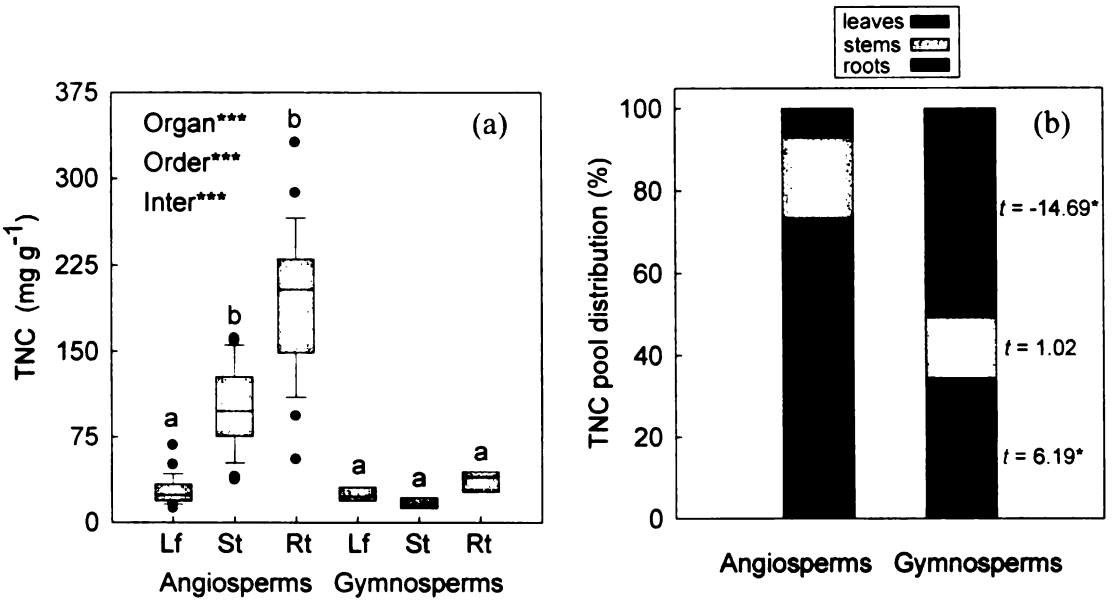


Figure 2.1. Box plots of tissue-level (Lf = leaves, St = stem, Rt = roots) non-structural carbohydrate concentrations of Angiosperms (n = 28) and Gymnosperm (n = 8) species (a). Lower and upper ends of the boxes represent the 25th and 75th percentile, lower and upper whiskers represent the 10th and 90th percentile and the horizontal lines within the boxes represent the median. Tissue-level TNC concentration means that do not share a common letter are significantly different ($P < 0.05$, Tukey-Kramer HSD). Total non-structural carbohydrate (TNC) partitioning for angiosperms and gymnosperms (b). Significant t-test statistics (* $P < 0.0001$) indicate differences between plant orders (angiosperms, gymnosperms). In TNC partitioning to specific organs (leaves, stems, roots). Results of ANOVA for TNC as a function of order, organ (leaves, stems, roots) and their interactions are indicated as: *** $P < 0.0001$.

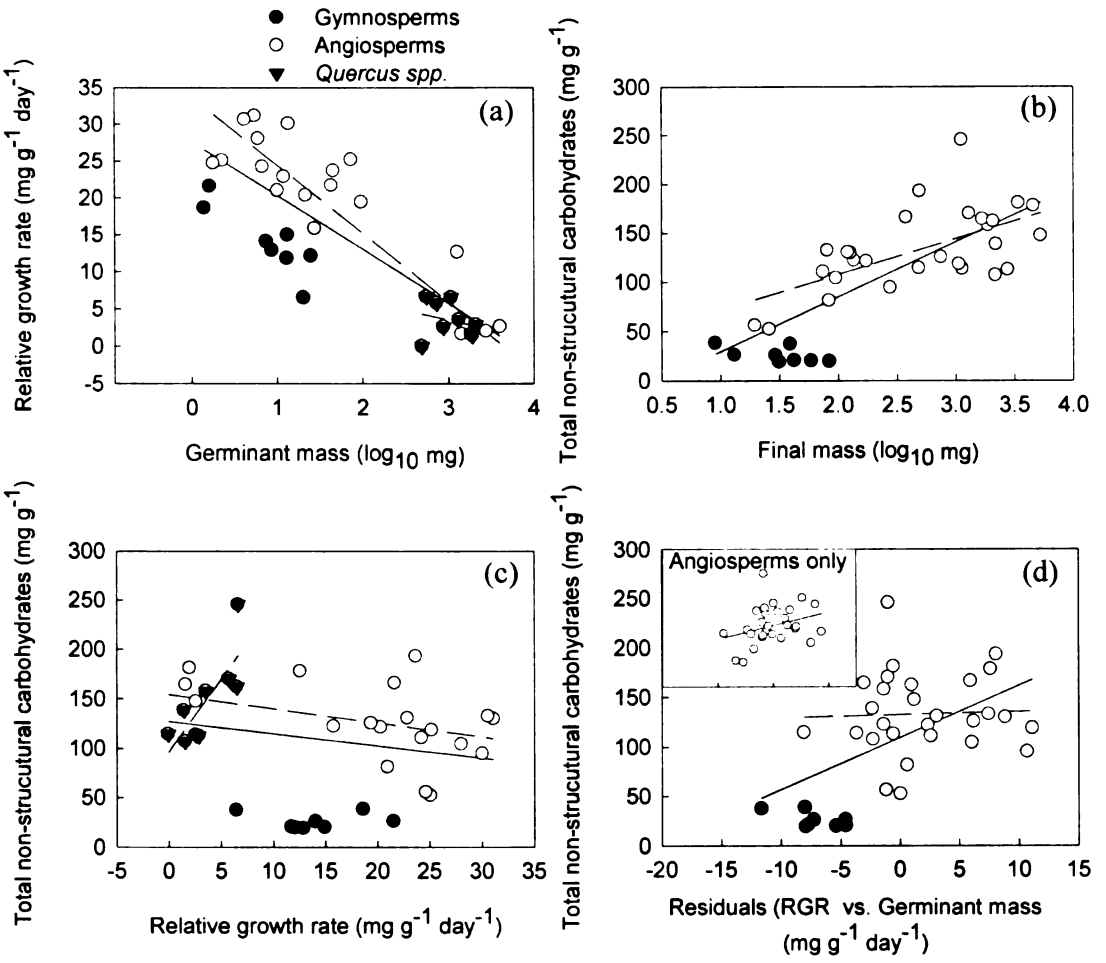


Figure 2.2. Relationships between relative growth rate and germinant mass (a), total non-structural carbohydrates and final mass (b), total non-structural carbohydrates and relative growth rate (c), and total non-structural carbohydrates and the residuals of the regression of relative growth rate vs. germinant mass (d). The inset on (d) is for the residuals of the regression of relative growth rate vs. germinant mass for angiosperms only and has the same axis scales as the larger figure panel. In the larger panels, solid lines are regression fits of all data, and hatched lines are for angiosperms, and in (a) and (c) for *Quercus spp.* Correlation statistics for these relationships are in Table 2.2.

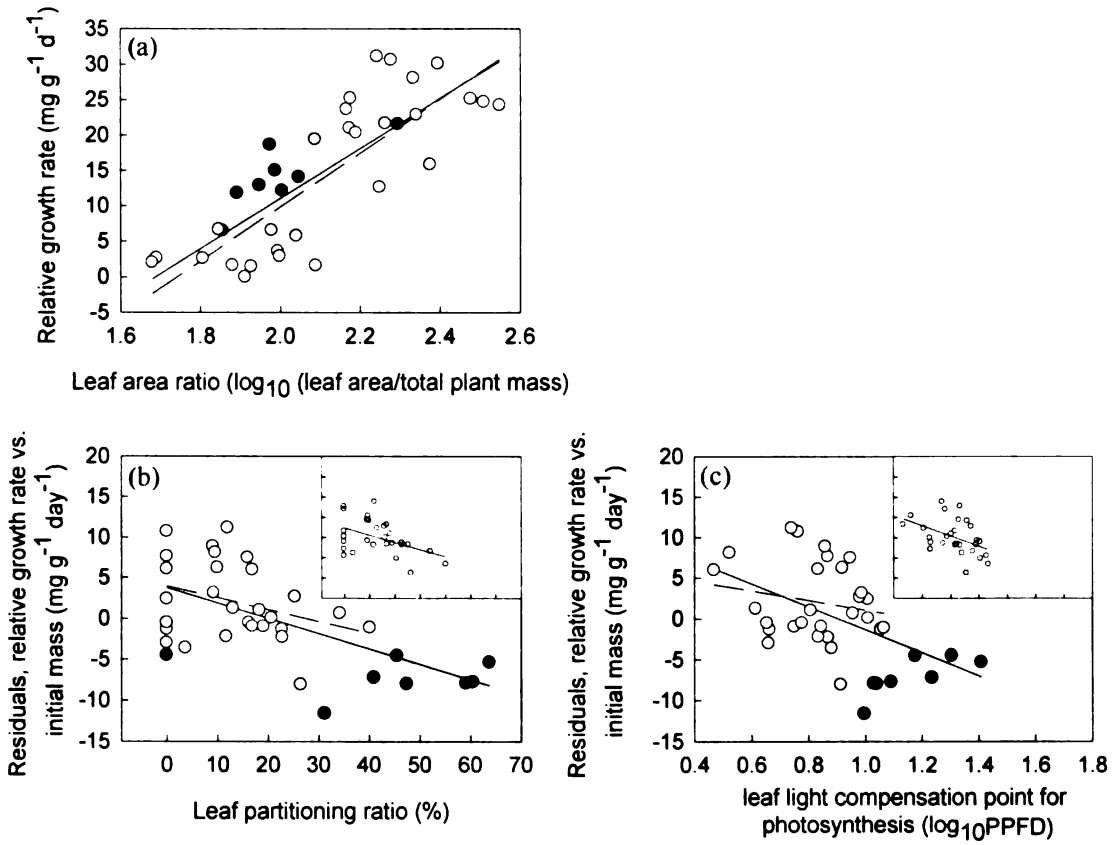


Figure 2.3. Relative growth rate vs. leaf area ratio (a), and residuals of the regression of relative growth rate vs. germinant mass vs.leaf partitioning ratio (b), and vs. leaf light compensation point (c). Corresponding correlation statistics are in Table 2.3. See Figure 2.2 legends for other details.

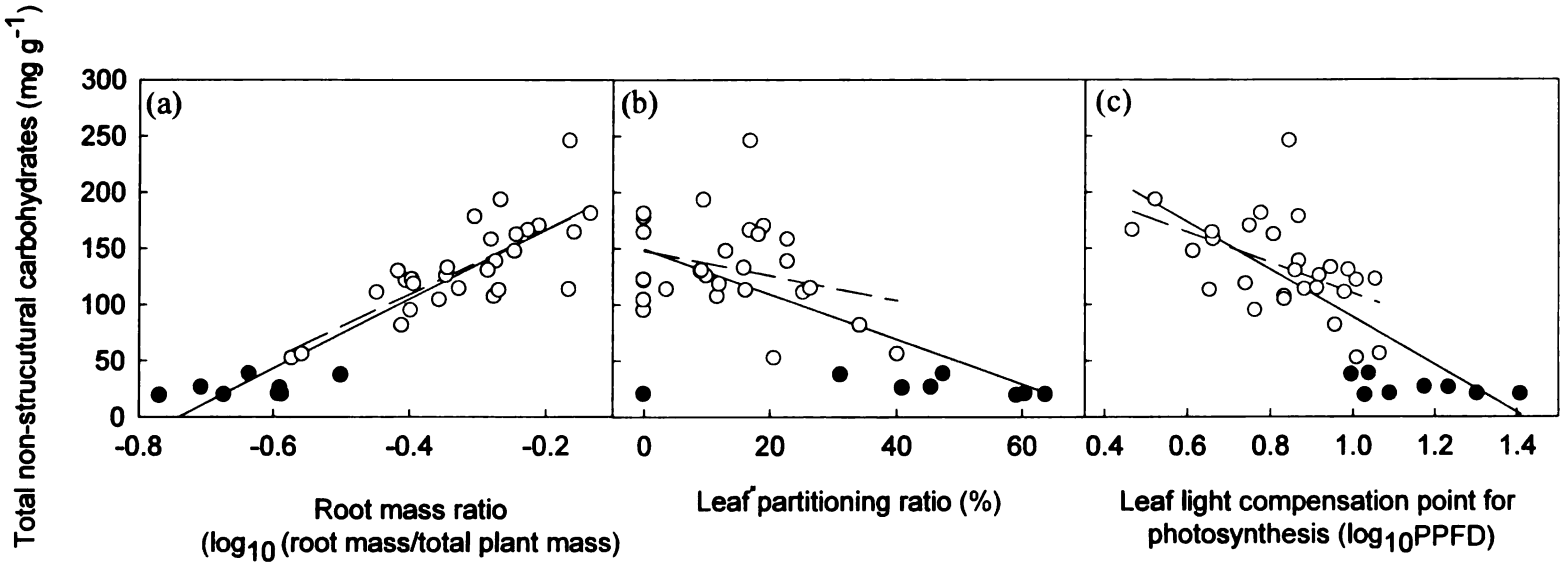


Figure 2.4. Relationships of total non-structural carbohydrates with root mass ratio (a), leaf partitioning ratio (b), and leaf-level light compensation point for photosynthesis (c). Corresponding correlation statistics are in Table 2.3. See Figure 2.2 legends for other details.

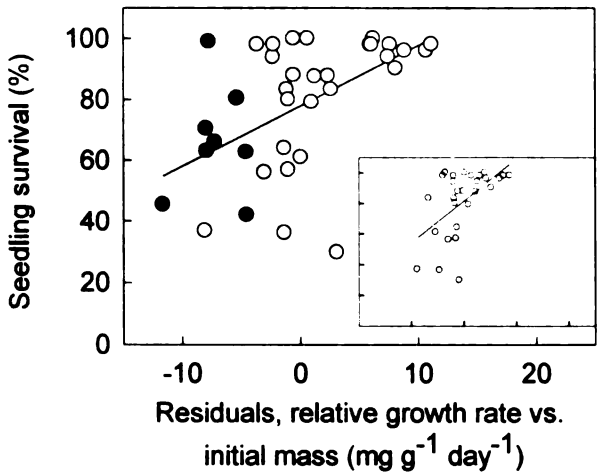


Figure 2.5. Seedling survival vs. the residuals of the regression of relative growth rate vs. germinant mass for all data (larger panel) and of seedling survival vs. the residuals of the regression of relative growth rate vs. germinant mass for angiosperms for the inset panel. Fits are for all data (larger panel) and angiosperms only (inset). Pearson correlations are $r = 0.52$, $P = 0.001$ for all data and $r = 0.55$, $P = 0.002$ for angiosperms.

CHAPTER 3

ASSOCIATION OF MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS WITH NORTHERN TEMPERATE TREE SPECIES LANDFORM AFFINITY

ABSTRACT

Greater water use efficiency (WUE) and access to water (W_{access}) may be two general adaptive mechanisms to low soil water availability. Contrasting glacial landforms with differences in water holding capacity (outwash-low, ice contact-moderate, moraine-high), and dominant vegetation, in northwestern lower Michigan provide an ideal system to develop a mechanistic understanding of the association between plant traits and plant performance. First-year seedlings of eight tree species (in order of increasing site moisture affinity, (*Quercus velutina, Quercus alba, Quercus rubra, Prunus serotina, Acer rubrum, Acer saccharum, Fraxinus americana, Betula alleghaniensis*)) were transplanted across these landforms. In their third year, leaf gas-exchange and soil moisture were measured monthly, and seedlings were completely excavated early-summer and fall to obtain growth, size and morphological characteristics. 2002 had a dry growing season with July-September precipitation of 11.2 mm vs. a 30-year average of 31.8 cm. Soil moisture decreased from moraine to outwash sites and all sites were lowest in July. The ability to maintain positive photosynthetic rates (i.e., W_{access}) and high photosynthesis per unit water loss (i.e.,WUE) during drought enhanced seedling survival. Across species, increased W_{access} was realized via deeper rooting which was positively related to seed and seedling size. Interspecific variation in WUE was positively related to area-based leaf N (leaf N_{area}). *Quercus spp*, which were generally the most xeric adapted of the species, had greater leaf N_{area}, root depth, seed and seedling size and survival on

all sites. Conversely, more mesic-associated species had lower survival, but had the highest values of traits related to surface area for resource capture and growth potential under optimal resource conditions, especially on the most mesic sites. Thus, these contrasting suites of traits may partly underlie interspecific differences in growth and survival responses, which likely contribute to the observed species distribution patterns across glacial landforms in northwestern Michigan.

Introduction

Composition of temperate forest communities depends on the species-specific responses of individual trees, particularly seedlings and saplings, to spatial and temporal variation in resource availability (Kobe 1996, Pacala et al. 1996). To date, most studies examining interspecific variation in plant growth and survival in relation to natural and experimental resource variation have mostly focused on nitrogen and light (Kobe et al. 1995, Canham et al. 1996, Walters and Reich 1997, Carlton and Bazzaz 1998, Fahey et al. 1998, Finzi and Canham 2000, Walters and Reich 2000). In contrast, much less is known about water despite the fact that tree species distribution patterns are associated with regional rainfall gradients (Swaine 1996, Bongers et al. 1999, Wang et al. 2006), regional variation in potential evpotranspiration (Gholz 1982) and species-specific differences in drought sensitivity (Engelbrecht et al. 2007). Species-specific variation in young seedlings' sensitivity to water deficits may function as an important ecological filter by controlling species composition via mortality (Haeussler et al. 1995). For example, soil water availability is an important limiting resource to juvenile tree growth and survival (Coomes and Grubb 2000, Tanner and Barberis 2007) and species vary markedly in these responses (Caspersen and Kobe 2001, Sack 2004, Engelbrecht et al. 2005, Kobe 2006, de Gouvenain et al. 2007). Suites of plant traits likely underlie these responses; however, our understanding of the physiological mechanisms and associated plant traits that govern plant performance across gradients of soil water availability is limited.

Two general mechanisms thought to underlie adaptations to low water availability are greater efficiency in using water to produce biomass (WUE) and enhanced access to water (W_{access}). Greater WUE occurs primarily by maximizing photosynthetic gain per

unit water lost through transpiration, especially in extreme xeric environments (Cowan and Farquhar 1977, Cowan 1986). Evidence for WUE as an adaptation to soil water deficits remains equivocal. Based on interpretation of carbon isotope ratios (^{13}C:^{12}C), WUE has been found to be greater in xeric than mesic habitats in some studies (Gurevitch et al. 1986, Ehleringer and Cooper 1988, Dudley 1996), but not others (Schulze et al. 1996, Schulze et al. 1998). For seedlings of four temperate tree species, using instantaneous gas-exchange measurements as an index of WUE (i.e., photosynthesis/stomatal conductance to water vapor), Ni and Pallardy (1991) found no clear trend towards increased WUE for more xeric species. Higher WUE has been found for wheat cultivars adapted to drought prone habitats (VandenBoogaard and Villar 1998). However, an annual crop completes its life cycle in a single season, placing a selective premium on rapid growth. Rapid growth is characterized by high leaf nitrogen, and high photosynthetic rates (Reich et al. 1998a, Reich et al. 1998b), resulting in greater WUE mostly as a consequence of higher photosynthetic rates drawing down intercellular CO_2 concentration rather than stomatal regulation minimizing water loss (Field et al. 1983). Furthermore, higher WUE via lower stomatal conductance could increase soil water availability to competing plants, depending on how transpiration is manifested on a whole-plant basis (Cohen 1970) and several studies demonstrated that the preemption of water (i.e., presumably through greater W_{access}) is more important than WUE to growth and survival in drought-prone environments (Bunce et al. 1977, Delucia et al. 1988, Delucia and Heckathorn 1989, Royce and Barbour 2001). Thus, empirical evidence suggests that high WUE may not be a fundamental component of drought adaptation.

Reich and Hinckley (1989) showed that greater W_{access}, as evidenced by higher pre-dawn leaf water potential, was highly correlated with daily maximum leaf conductance and presumably photosynthesis. Thus, greater W_{access} may sustain photosynthesis during drought events. Similar to the positive association between sapling survival and photosynthetic rates under waterlogged conditions (Pennington and Walters 2006), the maintenance of positive carbon balance via enhanced W_{access} could increase seedling survival during prolonged water deficits. Greater W_{access} may be realized by attaining a large size and/or through increased proportional allocation of mass to roots (root mass ratio, RMR), surface area (Givnish 1986, VandenBoogaard and Villar 1998) or rooting depth (Nepstad et al. 1994, Canadell et al. 1996, Jackson et al. 1996, Schulze et al. 1996, Jackson et al. 1999). Since water availability typically increases with soil depth during extended dry periods (Landsberg 1986), deep roots are likely the primary location of water uptake. Variation in root depth may be related to species differences in seed size (Kohyama and Grubb 1994, Guerrero-Campo and Fitter 2001) or species associated with xeric environments may produce deeper tap-roots for a given investment in root mass (Yamada et al. 2005). Although there is evidence of greater rooting depth in extreme environments (Canadell et al. 1996) and modest increases in root mass allocation in response to water limitation (Poorter and Nagel 2000), information on rooting depth patterns and root morphology of species grown together across soil moisture gradients under realistic field conditions is scant. However, one recent study showed that variation in rooting depth among first-year seedlings of five Mediterranean woody species growing in a common garden were strongly related to survival during a prolonged drought event

(Padilla and Pugnaire 2007). This finding suggests that rooting depth is an important species-level trait with potential consequences for seedling establishment in dry environments and community dynamics across gradients of soil water availability.

Traits potentially enhancing young seedling survival on drought-prone sites (e.g., greater proportional mass allocation to roots, deep roots, and conservative water use) may compromise growth potential, and thus competitive ability, when water is predictably plentiful. For example, increased allocation of biomass to root systems and/or the production of deep rooted large diameter "taproots" may occur at the expense of allocation to resource harvesting structures (e.g., proportional allocation of mass to leaf and root area), which contribute to high growth capacities under optimal resource conditions (Reich et al. 1998a, Poorter 1999, Walters and Reich 2000, Comas et al. 2002). Therefore, traits that confer survival during episodic drought events may occur at a trade-off with traits enhancing growth potential when soil water is plentiful. Quantifying the interrelationships of plant performance and specific plant traits during drought events will contribute significantly to the efforts to understand current species distribution patterns and aid in predicting the future outcome of climate change (e.g., altered precipitation regimes IPCC 2001) on landscape-level forest composition patterns.

Striking differences among dominant forest communities are apparent among contrasting glacially derived landforms in northern lower Michigan that differ in soil texture (Host et al. 1988), nitrogen availability (Zak et al. 1989) and calcium availability (Schreeg et al. 2005). For example, slow-growing oak-dominated stands on low-fertility drought-prone outwash plains are adjacent to productive mesic hardwood forests on high fertility, mesic moraines (Table 3.1). This landscape provides an ideal model system to

develop a more complete mechanistic understanding of the plant traits that underlie species-specific responses to variation in soil water availability as site differences in soil water and nutrient availability are not confounded by variation in regional climate.

In this study, eight species (*Acer rubrum, Acer saccharum, Betula alleghaniensis, Fraxinus americana, Prunus serotina, Quercus alba, Quercus velutina,* and *Quercus rubra*) differing in soil resource affinity were transplanted across six sites, two on each post-glacial landform within this regional landscape (outwash = 2, ice contact = 2, moraine = 2). One site on each of the landforms was chosen to be well-drained and the other to have an elevated water table in order to try to minimize covariation in nutrients and water availability across sites. For multiple seedling plots on each site we quantified soil resource availability (soil N and water) species-specific rooting depth, root morphology, gas-exchange, seedling water status and survival in response to natural seasonal variation in soil moisture. Specific predictions were:

H1. Across sites and gas-exchange sampling dates, at higher soil moisture, interspecific variation in leaf-level photosynthesis will be most strongly associated with leaf N status as opposed to traits associated with W_{access}.

H2. Across sites and gas-exchange sampling dates, at lower soil moisture, interspecific variation in leaf-level photosynthesis will be most strongly associated with some combination of traits that confer W_{access} (e.g., whole-plant mass, RMR, root surface area, root depth).

H2a. The association between leaf-level photosynthesis and root depth and photosynthesis during the peak of a drought will be strongest on the most xeric site and weakest on more mesic sites.

H2b. Compared to species associated with mesic sites, species associated with drought prone sites will have greater rooting depths.

H3. Following a prolonged drought event, species with the greatest survival will have greater expressions of traits associated with W_{access} and higher photosynthetic rates under low soil moisture, whereas WUE will be generally unimportant.

H3a. WUE will be strongly associated with leaf N.

H4. High allocation to traits that promote W_{access} during drought events will occur at a trade-off with traits associated with high growth potential under optimal resources (e.g., proportional allocation to leaf and root area) and this trade-off may partly underlie current overstory species distributions across this post-glacial landscape.

Materials and Methods

Research Sites and Plot Layout

This study was conducted in the Manistee National Forest (MNF), Wexford and Manistee counties, in the northern lower peninsula of Michigan (Figure 3.1). The MNF's glaciated landscape results in wide landscape scale variation in forest composition (Table 3.1) that is associated with post-glacial landform variation in soil nutrients (Nitrogen, N and Calcium, Ca) and soil water holding capacity. The forests are second growth stands that established after extensive logging around the turn of the 20th century. Mean annual

precipitation totals 81 cm (Albert 1994) and is distributed, on average, evenly throughout the year; however, year to year growing season precipitation is variable due to stochastic drought events. The MNF provides an ideal natural soil moisture gradient without the confounding effects of climate, elevation and latitude. In order to span a gradient in soil mineral nutrients and water, field sites were established in six forest stands across the glaciated landscape in the MNF, including two on outwash plains (OW, low water), two on ice contact landforms (IC, intermediate water) and two on moraines (MOR, high water). Sites were selected to achieve some variation in soil water independent of nutrients by choosing three well-drained (OW, IC, MOR) and three sub-irrigated sites (OW, IC, MOR). Sites were chosen with the aid of the ecosystem classification systems of Cleland et al. (1993) and all three well-drained sites were previously used as reference sites in the development of this system.

Based on visual estimates, seedling transplant plots were positioned across a continuous light gradient (~1-32 % open sky) within each site. However, due to species- and site-specific differences in the openness of overstory canopies (e.g., open oak canopies on xeric sites versus closed sugar maple canopies on moraine sites), the lowest light levels were not present at ice contact and outwash sites. Plots were established within five targeted light levels on the two outwash sites, six levels on the two ice contact sites and six or seven levels on moraine sites. Plots were weeded as necessary throughout the experiment to maintain consistent light levels at the seedling level, but this maintenance was minor.

Seedling plots consisted of four subplots for two separate seedling harvests, which were used to quantify species-specific morphology, rooting depth, physiology and

survivorship in relation to natural variation in aboveground and belowground resources, especially soil water availability. Plots were fenced with 2 inch welded wire to approximately 1.5 m in height and 1.25 cm wire mesh to a height of 1.0 m to prevent mammalian herbivory. Subplots were 120 cm by 140 cm with a 40 cm buffer zone between subplots and between the fence and outer subplots. Individual seedlings were randomly placed into subplots within a 7 x 8 grid system with 20 cm spacing between seedlings. Three to eight seedlings (depending on germination success) of each species (*Acer rubrum, Acer saccharum, Betula alleghaniensis, Fraxinus americana, Prunus serotina, Quercus alba, Quercus velutina,* and *Quercus rubra*) were transplanted into field plots.

Seedling establishment and transplanting

For all eight species, we obtained seed from a commercial source (Sheffield's Seed Co., Inc., Locke, NY) and all seed originated from USDA Hardiness Zone 4 or 5. Seeds were pre-treated and stratified according to Young and Young (1992) throughout late winter and early spring 2000 at MSU. Recent germinants were planted into seedling flats (individual root plugs were 12 cm deep by 5.5 cm in diameter) at the Department of Forestry's Tree Research Center (TRC), MSU. Seedlings were grown in low fertility field soil obtained from a sandy glacial outwash site in Roscommon County, MI and watered with deionized water in order to minimize nutrient carryover effects to field plots. Starting in April 2000, seedlings were initially grown in a whitewashed, temperature and humidity controlled greenhouse at the TRC and transferred in mid-May to an outdoor lathe house and grown under 25% of full sun until mid-July.

In mid-July, seedlings were transported in vans to MNF, where they were kept outdoors under moderate light conditions and watered with tap water until transplanting. Due to low germination, young naturally established germinants of *F. americana* and *P. serotina* were excavated and directly transplanted into field plots. Overall, I transplanted approximately 7600 seedlings into field plots between July 20 and October 15, 2000. Before transplanting, soil from seedling flats was gently rinsed from seedling root systems and seedlings were stored on trays with wet newspaper. Given the large scale of this transplant experiment, only enough seedlings were prepared in this manner that could be manageably planted in a single day. This process was repeated each day throughout the duration of the transplanting. To minimize the potential confounding factors associated with transplant shock, seedlings received supplemental water for approximately two weeks after initial transplant.

Resource measurements

Canopy openness (%), an index of light availability, was estimated at the top of the seedling canopy for each sublot across all six sites during late summer 2002 with paired LAI-2000 plant canopy analyzers (LI-COR, Inc. Lincoln, NE). Briefly, measurements above each subplot were obtained when the sky was uniformly overcast with one LAI-2000 unit, while an identical remote unit was placed on a tripod in a nearby clearing (< 1 km away from each site) and simultaneously recorded open-sky values. Data from each unit were combined later to calculate canopy openness values and subplot estimates were averaged to obtain plot-level means (n = 35).

To characterize landform variation in soil N availability, we measured standing extractable pools and mineralization rates in the upper 20 cm of mineral soil with *in situ* incubation of soil cores (Raison et al. 1987). Separate incubations took place over three intervals (May 16–June 12, July 9–August 13, August 20–September 18) during the 2002 growing season. Within each plot, closely spatially paired PVC cores (5.08 cm diameter) were placed in the buffer zone near each respective subplot. One core from each pair was bulked (time 0 = initials) at the plot-level, placed in polyethylene bags inside an ice-filled cooler and transported to the laboratory for analysis. The remaining core from each pair was covered with a loose fitting cap to prevent leaching and was allowed to incubate for approximately 30 days (finals). Like initial cores, incubated cores were bulked at the plot-level and transported to the laboratory for processing and analysis. In the laboratory at MSU, approximately 20 g fresh weight soil from bulked samples was sieved (4 mm sieve), homogenized and extracted with 50 ml of 2M KCl. Nitrate (NO_3^-) and ammonium (NH_4^+) in solutions were measured colorimetrically with a continuous flow ion autoanalyzer (OI Analytical, College Station, Texas, USA). Differences in NO_3^-–N and NH_4^+–N between initial and final extracts were used to calculate net rates of N–mineralization (mg g soil^{-1} d^{-1}). Calculated N mineralization rates from the three incubation intervals were averaged to estimate integrated growing season variation in soil N availability within and between sites.

To assess landform variation in soil water availability, sub-samples (20 g) of soils from bulked plot-level samples used for initial N extracts (May 16, July 9, August 13, September 18) were dried in a forced-air oven at 105°C for 48 hours to determine

gravimetric soil water (%). To determine vertical profiles in soil moisture, additional samples were collected with a bucket auger at 0-20 cm, 20-40 cm, 40-100 cm depths from each subplot on June 25, July 25 and September 9, 2002. For all samples, sub-plot values were averaged to obtain plot-level means (n = 35) for each respective depth interval.

Seedling physiology measurements

At all six sites, we measured leaf-level CO_2 and H_2O exchange at four different sampling intervals throughout the 2002 growing season. Measurement periods were: (1) June 9–25, (2) July 11–23, (3) July 24–August 8, and (4) August 12–30. For each site and measurement period, measurements were collected on a single cloudless day from 8:30 to 18:00 h local time (24 days of measurements total). Due to a variety of logistical constraints, measurement times differed slightly between sites and measurement periods, but importantly for species comparisons, measurement times did not differ between species, and species × site and species × measurement period interactions were not significant (Appendix, Tables A.2, A.3). On each measurement day, gas exchange was measured multiple times in all plots (range = 4–8) and plots were sampled in an order that would approximately distribute sampling times evenly throughout the day for each respective plot. Upon arrival at each plot, a subplot was randomly selected to start measurements and when I returned to each plot later in the day, a second subplot was selected. Sampling within plots alternated between each of the selected subplots throughout the day. Within subplots, one leaf from a seedling of each existing species was sampled for gas exchange and to the degree possible leaves were not re-sampled as

sampling was dispersed throughout the seedlings and leaves of a given species within each respective subplot over the course of the day.

I simultaneously measured leaf-level photosynthesis, stomatal conductance to water vapor and transpiration and photosynthetic photon flux density (PPFD) with two LI-COR 6400 portable infrared gas analyzers (LI-COR Inc., Lincoln, NE). Gas-exchange was measured under ambient conditions with the 2 × 3 cm leaf chamber and the LI-COR 6400 was operated as an open system. The inlet air stream was attached to a buffer volume consisting of a 20 gallon garbage bag with air containing 377.0 (± 20.1 SD) ppm of CO_2 that was attached to the LI-COR 6400 with a 2 m long (3 mm inside diameter) section of Bev-A-Line® IV plastic tubing (Thermoplastic Processes, Inc., Stirling, NJ, USA). This approach was used to minimize ambient CO_2 induced variation in photosynthesis. For measurements at each subplot, a new buffer volume of air was collected at approximately seedling level. Depending on the light environment, flow rates were adjusted in order to maximize CO_2 differentials between the reference and sample infrared gas analyzers. Measurements were collected only after stable photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) values and CO_2 differentials had been maintained for at least 10 s. For leaves that were too small to completely cover the chamber, a transparent grid system (150; 0.04 cm^2 blocks) was used to estimate the amount of leaf area that was sampled during gas-exchange measurements. Leaf area estimates were used to re-calculate gas-exchange rates. Gas-exchange was measured concurrently with volumetric soil moisture measurements. Volumetric soil moisture was measured to a depth of 20 cm with a time domain reflectrometor (TDR, Environmental

Sensors, Inc., Victoria, British Columbia) and based on variation in volumetric soil moisture between the four gas-exchange measurement periods, periods were classified into very low, low, moderate and high soil moisture categories (Appendix, Table A.4). Photosynthesis measurements provide an index of W_{access} for a given soil moisture and light availability. Water use efficiency of photosynthesis (WUE, mmol CO_2 mol^{-1} H_2O) was calculated from instantaneous gas-exchange measurements as photosynthesis/transpiration. A total of 3516 instantaneous gas-exchange measurements were made during 2002. At all six sites, for each of the measurement periods, individual gas-exchange measurements within subplots were averaged at the species-level and subplot values were averaged to determine plot-level species means.

Seedling Survivorship and Harvests

Throughout the three year experiment I monitored seedlings for survivorship at five different census dates (July and September 2001, June, August and October 2002). For a particular census interval (e.g., June-Aug 2002), species-specific seedling survival at the plot-level was calculated as: (number individuals surviving at end of interval/number individuals surviving at beginning of interval) × 100. There was a prolonged dry-period during each year seedling survival was tracked and in the year following the experiment (August 1 2001, July 25 2002, August 19 2003). Furthermore, gravimetric soil moisture during these drought events was strongly correlated (Appendix, Figure A.1) and species-specific seedling survival during a single drought event (June-Aug 2002) scaled well with survival over the entire experiment (July 2001-October 2002) (Appendix, Figure A.2).

Due to the frequent occurrence of drought events in this landscape and the strong association between subsets of seedling survival data, we believe that seedling survival over the duration of the experiment more effectively integrates species- and subplot-specific survival responses to drought than during a single census interval. Thus, hereafter, survival (%) will refer to survivorship over the entire experiment.

Within each plot, all surviving seedlings in two of four subplots were harvested June 18–30 2002 (harvest 1, n = 1559) and in the remaining two subplots from October 5–November 2002 (harvest 2, n = 1380). Pre-dawn on the mornings of harvest 1, leaf xylem water potential was determined for a sub-sample of seedlings and plots (n = 223 individual seedlings) with a pressure bomb (PMS Instruments, Corvallis OR, USA). These values provide an additional index of W_{access} as seedlings should be in equilibrium with soil water potential at this time of the day, and predawn water potentials have been found to be closely related to leaf conductance during the photoperiod (Reich and Hinckley 1989). At each harvest, seedlings were completely excavated and sandy soils enabled high recovery of fine roots. Maximum rooting depth was measured for each individual seedling with a meter stick (to the nearest 0.1 cm). Seedlings were placed in polyethylene bags inside ice-filled coolers and transported to a nearby field laboratory where they were stored in refrigerators (0–24 hours) until processed. Seedlings were gently rinsed with deionized water to remove excess soil and were partitioned into root, stem (including petioles) and leaf fractions. Plant fractions were dried in a forced air-oven at 100°C for 1 hour to quickly stop respiration and then at 70°C for 24 hours. After preliminary drying, samples were transported to MSU, dried at 70°C for another 24

hours, and then weighed. From harvest 1 primary biomass data, we calculated root mass ratio (RMR; root mass/total plant mass, in g g^{-1}).

Prior to drying at the field laboratory, images of whole-plant root systems and leaves were acquired with a flatbed scanner at resolutions of 400 and 200 DPI, respectively (Epson Expression 1680, Nagano, Japan) and archived for image analysis. Digitized root images were manually edited with Adobe Photoshop 7.0 (Adobe Systems Inc., San Jose, California) with the goal to produce a black (roots) and white (background) image that faithfully captured the original root image. Edited root and leaf images were analyzed for total surface area with WinRhizo Pro 5.0 and WinFolia Reg 2003b, respectively (Regent Instruments, Blain, Quebec). From harvest 1, primary biomass data and root and leaf surface area data were used to calculate specific root area (SRA, cm^2 g^{-1}) and leaf area ratios (LAR, cm^2 g^{-1}).

Within subplots from harvest 1, leaves from individual seedlings of each respective species were bulked and pulverized into a fine powder with a ball mill (Kinetic Laboratory Equipment Co., California). To assess plant nitrogen (N) status, sub-samples (2–4 mg) of bulked leaf samples (n = 426) were measured at MSU with dry combustion gas-chromatography (NA 1500 elemental analyzer, Carlo-Erba, Milan, Italy). Species-specific leaf N values for bulked subplots were averaged to obtain plot-level means, which were expressed on a leaf area basis (leaf N_{area}, μg cm^{-2}).

Statistical analysis

Unless noted otherwise, all statistical analyses were carried out with JMP 4.0 statistical software (SAS Institute, INC., Cary, North Carolina, USA). Gravimetric soil moisture

was first analyzed with a mixed linear model that included main effects and interactions of site (n = 6) and sampling date (n = 6) as nominal factors and canopy openness (%) as a continuous factor. Based on the significant effect of sampling date on gravimetric soil moisture (Appendix, Table A.5), linear models were also developed that included main effects and interactions of site (n = 6) and canopy openness (%) for each respective sampling date and for growing season averages. For the July 25 sampling date (i.e., the peak of the drought), vertical gravimetric soil moisture profiles were evaluated with linear models that included main effects and interactions of site (n = 6) and depth interval (n = 3; 0–20 cm, 20–40 cm, 40–100 cm). Variation in seasonal averages of N-mineralization rates was tested with models that included main effects and interactions of site (n = 6) and canopy openness (%). Analyses of soil characteristics were based on plot-level means (n =35) of canopy openness and soil resources. When main effects of site were found to be significant ($P \leq 0.05$), I compared pairs of site means with Tukey-Kramer HSD.

Plant trait values were compared among species and other sources of variation on two bases: (1) as means of seedlings at a common harvest time and (2) as estimates at a common mass based on trait–mass allometric functions. I decided to use estimates at a common mass because plant traits scaled non-proportionally with whole-plant mass (Appendix, Figure A.3) and plant mass varied among species, sites and light environments. Preliminary analyses indicated that site-specific allometric relations by species were appropriate functions for these estimates. My justifications for this decision were (1) within each site, mixed models for the main effects and interactions of species (n = 8), mass (whole-plant or root mass, depending on the trait) and canopy openness on

plant traits showed that species and mass effects dominated, whereas canopy openness and its interactions were generally unimportant (data not shown). (2) Mixed models of the main effects and interactions of mass, site (n = 6) and species on traits indicated strong mass and species effects, but also significant site main effects and interactions (Appendix, Tables A.6-A.9). Using data from individual seedlings from harvest 1 (n = 1520), standardized major axis (SMA) linear regression (after Warton et al. 2006) was used to estimate allometric relationships of whole-plant mass with root mass, rooting depth and leaf area (SMARTR, Version 2.0) and of root mass with root area for every site by species combination. SMA fitting techniques were considered appropriate, as there was error associated with both the X and Y variables. These regressions (Tables 10-33) were used to estimate RMR, root depth and LAR at a common whole-plant mass of 0.5 g and SRA at a common root mass of 0.3 g. These values were selected to maximize the degree of overlap among data. Species traits were not estimated at a common mass if regression equations were not significant ($P > 0.05$) or species were not within ± 0.1 g of the common whole-plant (0.5 g) or root mass (0.3 g). The influence of interspecific variation in seed size on whole-plant size and rooting depth patterns of transplanted seedlings was explored with linear regression. Published values of seed mass were used for these analyses (Young and Young 1992). SMA techniques were not applied to seed mass interrelationships because seed mass was estimated without associated error as a published value.

In this study, indices of W_{access} included pre-dawn water potential for a sub-sample of individual seedlings from harvest 1 (i.e., beginning of the drought event) and A_{area} during measurement periods that varied in soil moisture status. Several plant traits

were examined for their associations with W_{access} and/or WUE, including leaf N_{area}, whole-plant mass, total root area, SRA, RMR, and maximum root depth. We assessed these associations with two complementary approaches. First, Pearson's correlations were used to test for associations between pre-dawn water potential and plant characteristics at the individual seedling level. Secondly, leaf-level photosynthesis was analyzed as a function of PPFD ($\mu mol\ m^2\ s^{-1}$) with simple linear regression and as a function of PPFD in combination with plant traits with multiple linear regression. Values used for regressions were species-specific plot-level means (n = maximum of 280). These models were evaluated for each measurement period (very low, low, moderate and high soil moisture conditions) and then compared to identify plant characteristics driving plant gas-exchange responses to increases and decreases in soil moisture.

Preliminary models of WUE as functions of PPFD, leaf N_{area}, site and their interactions indicated significant site effects (Appendix, Table A.34), thus, PPFD and leaf N_{area} effects on WUE were assessed for sites separately. Models were generally weaker or not significant at higher moisture status (data not shown) so I only present data from the measurement period with very low soil moisture.

Within the three well-drained sites (OW1, IC 1, MOR 1) which tended to have lowest soil moisture during drought, canopy openness data were fitted to seedling survival data (%) with a Gompertz growth function (i.e., general form: $\theta_1 \exp[-\exp(\theta_2 - \theta_3 - \text{Log}_{10}\ \text{canopy openness})]$). The Gompertz growth function has been used previously to predict survival as a function of seedling relative growth rates (Walters and Reich 2000) and due to the strong relationship between light availability

and RGR (Walters and Reich 2000), we expected canopy openness to model survival with a similarly shaped function. Within each well-drained site, the function was solved iteratively for the best fit (i.e., minimized residual sum of squares) using the nonlinear platform within JMP. Due to an inability to fit a function to survival data at MOR 1, data from the plot with the highest light availability were excluded and the analysis was repeated. All fits were significant at $P < 0.05$. Based on model estimates of seedling survival from nonlinear model fits, species-plot residuals of light-survival functions ($SURV_{resid}$) were calculated for each plot as follows: observed species survival – overall plot-level survival estimate (for all species combined). Alternatively, species-specific survival deviations from overall plot-level average survival were calculated as: average plot-level species survival – overall average plot-level survival (for all species combined). The advantage of this approach was that unlike the calculation of $SURV_{resid}$, which excluded high light data from MOR, all data were used for estimates of survival deviations. Species-specific $SURV_{resid}$ and survival deviations represent variation in survival that was unexplained by canopy openness (i.e., removing the effects of canopy openness in seedling survival) and my goal was to account for this unexplained variance. As a result, I used linear regression to examine relationships between $SURV_{resid}$, survival deviations and size (whole-plant mass), morphological (root area, SRA, RMR, root depth) and physiological characteristics (leaf-level photosynthesis,WUE).

Results

Resource availability

Across all six landform study sites, canopy openness within seedling transplant plots ranged from 0.7 to 46 % (Table 3.2) and generally ranked as follows across landforms: OW > IC > MOR. Variation in canopy openness was greatest in MOR sites (43 and 18 fold) and lowest within OW sites (6 and 3 fold). Measures of canopy openness were highly correlated with averages of instantaneous PPFD obtained during gas-exchange measurements both within (Table 3.2) and across sites ($P < 0.0001$, $r = 0.92$, data not shown).

The 2002 growing season was marked by a prolonged drought in which July through September precipitation was approximately 1/3 of the 30-year mean (11.2 vs. 31.8 cm average, 1971-2000 period, Wellston Tippy Dam NOAA Climatic Station, Figure 3.2). Soil moisture varied markedly among sampling dates, with averages across sites ranging from a low of 5.3 % at the peak of the drought on 25 July to a high of 13.5 % on 16 May (Appendix, Table A.5, Figure 3.2). Site effects explained most of the variation in soil water (Appendix, Table A.35), whereas canopy openness effects independent of site were weak. Soil moisture varied across sites for all sample dates, but only moderately on July 9, and was generally highest at MOR sites and lowest at OW 1 (Table 3.3, Figure 3.2). Furthermore, for MOR and OW sites, but not IC sites, the well-drained site had lower soil water than the corresponding sub-irrigated site. Surprisingly, soil moisture decreased with increasing soil depth (0-20 cm = 20-40 cm > 40-100 cm) on five of the six sites for all measurement dates (height of the drought, Figure 3.3; other data not shown).

Similar to soil water, site effects explained most of the variation in average growing season N-mineralization rates (Appendix, Table A.35), and canopy openness effects independent of site were weak (canopy openness: $P > 0.1276$, Appendix, Table A.36). Among sites, N-mineralization rates varied 3–5 fold, with MOR sites generally having higher N-mineralization rates than the others (Figure 3.4).

Seedling characteristics

Averaged across species, site-level leaf N_{area} varied from 56.7 to 66.8 μg cm^{-2}, with landforms generally ranked OW = MOR > IC. In general, leaf N_{area} was highest for the *Quercus* species, intermediate for *B. alleghaniensis* and lowest among *P. serotina*, *A. rubrum*, *A. saccharum* and *F. americana* (Figure 3.5). Across all sites, intraspecific variation in leaf N_{area} was low for most species, except for *F. americana*, which varied 1.5–fold (Figure 3.5).

Among species, average whole plant mass, root surface area, RMR and root depth were highest for the three *Quercus* species, intermediate for *A. saccharrum* and *F. americana*, and lowest for *P. serotina*, *A. rubrum* and *B. alleghaniensis* across most sites (Appendix, Figures A.4-A.6; Figure 3.6). When compared at a common mass, species rankings were similar for RMR, however, patterns of root depth were the reverse of the general; root depths were actually lowest for the *Quercus* species at a common mass of 0.5 g (Figure 3.6). Across landforms, whole-plant mass and root surface area generally ranked as follows: MOR > OW > IC (Appendix, Figures A.4, A.5), whereas root depth ranked: OW > IC > MOR (Figure 3.6). Despite two years of post-germination growth,

species variation in whole-plant mass and root depth was strongly positively associated with seed size for all sites (Figure 3.7).

Across species, SRA and LAR varied 2.3−fold and 5−fold, respectively. For most sites, species values of SRA were highest for *B. alleghaniensis* and *A. rubrum*, intermediate for *F. americana*, *A. saccharum* and *P. serotina* and lowest for *Quercus* species (Appendix, Figure A.7). When species were compared at a common mass, *Quercus* species maintained the lowest SRA and LAR values and this trend was most evident at moraine sites (Appendix, Figure A.7; Figure 3.8). However, differences in SRA among the other species were more subtle than species comparisons at a common harvest, whereas differences among estimates of LAR were more pronounced. Across landforms, SRA and LAR generally ranked as follows: MOR > IC > OW.

Gas-exchange interrelationships

Throughout the 2002 growing season, A_{area} varied considerably among species, sites and measurement periods that differed in soil moisture status (Appendix, Figure A.8). A_{area} was positively related to PPFD and the slopes and the amount of variance in A_{area} explained by PPFD increased with soil water (Tables 3.4-3.6, Figure 3.9), except for the date with the highest soil water (Table 3.7). At this early growing season date leaves of *Quercus* species had not fully developed, especially within the MOR sites and this may explain the weaker relationship for this date (J. Kunkle and M. Walters, personal observation).

Models with PPFD, leaf N_{area} and their interaction explained more total variation in A_{area} than models with just PPFD and their overall effects increased as soil moisture status increased (e.g., 3% additional variance explained at very low water vs. 11% at moderate soil water), again, except for the highest, and earliest soil water sampling date (Tables 3.4-3.6, Figure 3.10). The PPFD x leaf N_{area} terms were significant for low and moderate soil water conditions (Tables 3.5, 3.6). The lack of a significant independent effect of leaf N_{area} on A_{area} at high water (Table 3.7) may be due to leaves that were not fully developed by this early season sampling period.

In comparison to PPFD and leaf N_{area}, which had the largest influence on A_{area} as soil moisture increased, variation in root depth, whole-plant mass and root surface area had the greatest effect on A_{area} on the lower soil water measurement dates. For example, at the highest soil water, root depth was not a significant predictor of A_{area} independent of PPFD (Table 3.7), whereas at moderate soil water, the interaction of PPFD and root depth was significantly related to A_{area} (Table 3.6). Under low and very low moisture levels, root depth was positively related to A_{area} and the interaction of PPFD and root depth was also significant, but only under low moisture conditions (Tables 3.4, 3.5, Figure 3.11). Notably, in comparisons of models at low and very low soil moisture, the influence of PPFD was stronger under low moisture (i.e, F-value: 99.22 vs. 47.24), whereas variation in root depth showed a greater effect on A_{area} under very low soil moisture (i.e., F-value: 21.49 vs. 13.15). In models with PPFD, whole-plant mass, root area and their interactions with PPFD showed effects similar to that for root depth on A_{area} (Tables 3.4-

3.7). Unlike whole-plant mass, root surface area or root depth, RMR was generally not a strong positive predictor of A_{area}, and especially at low soil water. SRA was a significant positive predictor of A_{area} independent of PPFD during high soil water conditions (Table 3.7), whereas under moderate and low soil moisture conditions, SRA and the interaction of PPFD and SRA were negatively associated with A_{area} (Tables 3.5, 3.6).

As root surface area and root depth displayed similar effects on A_{area} as soil moisture levels changed throughout the growing season (Table 3.4-3.7) and because they are themselves highly correlated ($P < 0.0001$, $r = 0.73$, data not shown) it is difficult to ascertain if they are independently important for W_{access}. In order to examine this issue, root area was added as a main factor to a model that included root depth and PPFD as predictors of A_{area} under very low moisture (i.e., peak of the drought). The addition of root area to the model explained almost no additional variation and the model containing only PPFD and root depth explained more variance in A_{area} than the model containing only PPFD and root area (Table 3.8). Collectively, these models indicate that root depth was more important for increasing W_{access} and maintaining photosynthesis during the peak of the drought than root surface area.

In mixed models of A_{area} that included main effects and interactions of site, PPFD and root depth, A_{area} differed across sites under very low moisture conditions ($P = 0.0036$, Appendix, Table A.37). Thus, in an effort to examine the influence of root depth on A_{area} during the peak of the drought across sites that differed in soil water status (very low moisture dataset), A_{area} was also analyzed separately within the three well-drained

sites (OW 1, IC 1, MOR 1) with models that included PPFD, root depth and their interaction. In OW 1, the driest site during the drought, A_{area} did not vary with PPFD, but A_{area} was positively and strongly related to root depth and the PPFD × root depth interaction (Table 3.9). In contrast, on IC 1 and MOR 1, sites with greater soil water, PPFD was positively related to A_{area} and explained the most variation in the overall model. In addition, in both of these sites, the PPFD × root depth term was significant and negatively associated with A_{area} (parameter estimates −2.14 and −3.19, respectively, Table 3.9). A negative interaction term indicates that A_{area} decreased more with PPFD at deeper rooting depths.

In a mixed model with PPFD, leaf N_{area}, site and their interactions, WUE differed across sites under very low moisture levels (Appendix, Table A.34) and WUE tended to be highest at OW 1 (Appendix, Figure A.9). Thus, in site-specific models for well-drained sites, leaf N_{area} was positively related to WUE and PPFD was a moderate predictor, but only for OW 1 (Figure 3.12).

Pre-dawn water potential

During the onset of the drought, root depth and pre-dawn water potential were positively correlated and this association was consistent in both well-drained ($P < 0.0001$, $r = 0.47$, data not shown) and sub-irrigated ($P < 0.0001$, $r = 0.52$, data not shown) sites and within five out of the six study sites (P range = 0.0077-0.0001, r range = 0.38-0.63, data not shown). The association between root depth and pre-dawn water potential was stronger than for whole-plant mass ($P < 0.0001$, $r = 0.45$, data not shown), root surface area

(Figure 3.13), RMR ($P = 0.72$, $r = 0.02$, data not shown), or SRA (Figure 3.13). Intraspecific variation in root depth and pre-dawn water potential were also positively associated for 5 of the study species ($P < 0.01$ for all, r = 0.46-0.65, data not shown), but not for *A. saccharum*, *F. americana* and *B. alleghaniensis* ($P > 0.05$), the most mesic species.

Seedling survival interrelationships

Across species, seedling survival was significantly associated with canopy openness ($P < 0.05$ within each site), but responses differed among sites (Figure 3.14), depending on site-level soil moisture status and variation in light availability. For example, within OW 1 the site with the lowest soil moisture status, seedling survival was similar (estimate = 36%) across plots that ranged from 11 to 16 % canopy openness and survival decreased markedly under 30 % canopy openness (estimate = 5%). In comparison to OW 1, overall seedling survival was generally higher within IC 1, which tended to have slightly higher soil moisture, but survival responses as a function of canopy openness were similar for both sites (Figure 3.14). For instance, in plots that ranged from 3 to 10% canopy openness, survival estimates were invariable (estimate = 53%) whereas survival declined appreciably under 43% canopy openness (estimate = 32%). Due to the lack of fit for the nonlinear survival function across all data within MOR 1 ($P > 0.05$), data from the plot with the highest canopy openness (46%) were excluded from the final model fit (Figure 3.14). Similar to OW 1 and IC 1, under the highest light environment at MOR 1, seedling survival decreased considerably (mean = 18%) to a level that was the same as the estimate at the lowest light level (estimate = 18%) (Figure 3.14). In contrast to the

other two well-drained sites, MOR 1 had highest overall survival and survival showed a positive relationship with canopy openness in plots that spanned from 1 to 18% of full sunlight (survival estimate range = 18–81%).

The residuals from the nonlinear survival versus canopy openness relationships ($SURV_{resid}$) were most strongly related to whole-plant mass, root surface area and root depth for all well-drained sites (Table 3.10, Figure 3.15). The amount of variation in $SURV_{resid}$ explained by these linear models and the slopes all increased from the most mesic site (MOR 1) to the most xeric site (OW 1), indicating that these traits had increasingly positive effects on seedling survival as site-level soil moisture status decreased. However, covariance among whole-plant mass, root depth and root area (Appendix, Figure A.3, and data not shown) make it difficult to determine which predictor had functional importance for survival. In an effort to tease apart the relative importance of these predictors for survival, linear models of $SURV_{resid}$ for OW 1 were developed as follows: (1) root area added as a predictor with whole-plant mass, (2) root depth added as a predictor with whole-plant mass and (3) root depth added as a predictor with root area. When root area was added as a predictor along with whole-plant mass, the model explained less variation in $SURV_{resid}$ than a model with only whole-plant mass (Table 3.11). In contrast, when root depth was added as a factor with whole-plant mass, the model explained greater variation in $SURV_{resid}$ than in a model with just whole-plant mass (Table 3.11). Furthermore, a model with root depth and root area as main factors explained 10% more variation in $SURV_{resid}$ than a model with only root area, but only 5% more variation was explained than a model with only root depth (Table 3.11).

Collectively, results from a variety of models suggest that root depth is more strongly related to seedling survival than root surface area. Leaf N_{area}, A_{area} and WUE were positively correlated to $SURV_{resid}$, but only within OW1 (Table 3.10, Figure 3.15). For seedlings at IC 1 and MOR 1, RMR was weakly and positively associated with $SURV_{resid}$ (Table 3.10, Figure 3.15). In contrast to the other morphological and physiological characteristics, across all well-drained sites, SRA showed a negative relationship with $SURV_{resid}$ (Table 3.10, Figure 3.15).

In a complementary analysis to the one using residuals of PPFD vs. survival model fits, species-specific survival deviations from plot-level averages were related to the same set of morphological and physiological traits. The advantage of this approach was that unlike the analysis for $SURV_{resid}$, all of the transplant seedling survival data could be utilized in this alternative analysis. Results for the survival deviation versus species trait interrelationships were consistent with $SURV_{resid}$ versus trait interrelationships, with the exception of leaf N_{area}, which also showed a weak relationship with survival deviation at MOR 1 (Appendix, Table A.38, Figure A.10). The striking similarity in results between both indices of seedling survival was not surprising, considering that the $SURV_{resid}$ were highly correlated with the species-specific deviations from plot-level averages of survival within all sites ($P < 0.0001$, r range = 0.96-0.99, data not shown).

Discussion

$Water_{Access}$ vs. WUE as a basis for drought tolerance

I found that both the ability to maintain positive photosynthetic rates (i.e.,increased W_{access}) during the peak of the drought and high photosynthesis per unit water loss (i.e., water use efficiency, WUE) contributed to tolerance of drought for tree seedlings common in northern temperate forests (Figure 3.16). Increased W_{access} was achieved via deeper rooting, which varied among species with seed and seedling size and not with interspecific variation in root-whole plant allometry. Interpspecific variation in WUE was positively related to area-based leaf N content (leaf N_{area}). Although direct positive relationships of survival with photosynthetic rates and WUE were only evident at the driest site at the height of the drought, several lines of indirect evidence suggest the general importance of these mechanisms.

This study demonstrates that the drivers of leaf-level photosynthesis (A_{area}) are highly dependent on soil water status and these relationships have important implications for seedling survival during extended drought events. For example, photosynthetic photon flux density (PPFD) and leaf N_{area} became increasingly important predictors of A_{area} as soil water increased (supporting H1). This should be expected under high water availability given the dependence of instantaneous photosynthetic rates on light (Bjorkman 1981), and of photosynthetic capacity on leaf N concentrations both within (Walters and Reich 1989) and across (Field and Mooney 1986, Reich et al. 1997b) species. However, at low water availability, this relationship changed somewhat. Light

and leaf N_{area} were still significant drivers of photosynthesis, but both were weaker. At lower soil water availability increased rooting depth became an increasingly important driver of A_{area}, especially on the most xeric site (supporting H2, H2a).

As expected, species associated with drought prone sites had greater rooting depths than mesic species when compared at a common harvest, which is consistent with H2b. Surprisingly, after accounting for differences in plant mass with the use of allometric approaches, mesic species actually had deeper roots than xeric species. My results conflict with those of Yamada et al. (2005), who found that within two genera (*Dryobalanops*, *Scaphium*) in Malaysian tropical forests, sandy-soil specialists (i.e., drier soils) had deeper taproots than the clay-rich-soil specialists (i.e., wetter soils). Alternatively, in my study, differences in root depth were associated with variation in seed size (Figure 3.16), a result that is consistent with shade-tolerant seedlings in a warm-temperate rainforest (Kohyama and Grubb 1994) and with more than 300 adult woody plant species from Britain and northeast Spain (Guerrero-Campo and Fitter 2001). Furthermore, other studies showed that the abundance of large seeded species increases as environments become increasingly xeric (Wright and Westoby 1999). Thus, it appears that initial root depth advantages via larger seed sizes could be preserved until later life-history stages, but this relationship should be evaluated for a broader size and age range of individuals for the same species.

I found that variation in whole-plant mass, associated differences in root depth and the maintenance of higher rates of A_{area} during the peak of the drought were all positively related to seedling survival (Figure 3.16), which is consistent with H3 that increased W_{access} and associated traits enhances survival during water shortages.

Collectively, my results may provide a physiological basis for the strong positive relationship between root depth (but not whole-plant mass) and first year seedling survival that Padilla and Pugnaire (2007) found for first-year seedlings of five Mediterranean woody species. In my study, the root depth–survival relationship was more robust than the association between A_{area} during the peak of the drought and seedling survival. This result was not surprising because A_{area} was only measured once at each site during the peak of the drought (on different days), whereas root depth, which was positively and strongly associated with A_{area}, serves as a quantitative plant trait that integrates potential carbon gain during extreme water shortages.

Interpretation of the interrelationships between root depth, W_{access} and seedling survival necessitates one key caveat. During drought events, soil water availability typically increases with root depth (Landsberg 1986, Padilla and Pugnaire 2007), but I did not observe this pattern within my study sites. This pattern appears to be in conflict with the notion that deeper roots enhance W_{access} and the positive relationships that I found between root depth and A_{area} and survival. However, the positive association between root depth and pre-dawn water potential provides compelling evidence that deep anchored roots increase the water status of seedlings during water shortages. If moisture is lower at increasing depths then how can I reconcile the greater water status of seedlings that have roots deployed within these "drier" soil strata? Soil organic matter has been shown to increase water holding capacity; however, water may be held more tightly within soil organic matter and may not be completely available to plants. Within my study system, I speculated soil organic matter decreased with increasing soil depth, a

pattern that has been documented in other systems (Don et al. 2007). If this pattern occurs, even though gravimetric soil water was lower at deeper soil strata, plant available water might have been higher than in the upper soil horizons, which had the highest levels of gravimetric soil moisture.

Within the most xeric site whole-plant mass explained 6% greater variation in seedling survival than for root depth. This suggests that whole-plant mass may be interrelated with additional unmeasured traits besides root depth that confer survival during drought events (Figure 3.16). For example, I found a strong association between whole-plant mass and whole-plant carbohydrate storage for 36 temperate and boreal woody species (Chapter 2). Carbohydrate reserves may provide a carbon source for maintenance respiration and growth during drought events when photosynthesis is severely limited. There is direct, but fragmentary evidence for the importance of carbohydrate storage for drought tolerance. For instance, several species have greater carbohydrate pools in drought, than well-watered treatments (Dina and Klikoff 1973, Busso et al. 1990, Oosthuizen and Snyman 2001) and Busso et al. (1990) demonstrated that post-drought biomass production was associated with TNC pools in cool season grasses. However, we are not aware of any studies that directly examined the importance of interspecific variation in carbohydrate storage for drought tolerance in woody plants.

Contrary to my expectations (H3), WUE during the peak of the drought was positively related to seedling survival on the most xeric site. Although stomatal conductance was reduced considerably during the peak of the drought, my results suggest that leaf N_{area} contributed to increases in WUE by enhancing photosynthetic rates and drawing down intercellular CO_2 concentrations (Field et al. 1983). Altogether, these

results imply that the physiological basis of the relationship between WUE and seedling survival stems from the maintenance of relatively high photosynthetic rates via high leaf N_{area} rather than from primarily limiting water loss.

Drought tolerance vs. competitive ability at high water availability

Collectively, my observations along with empirical data from other studies imply that there is a trade-off between traits that enhance W_{access} and characteristics that are related to surface area for the interception of light and acquisition of soil resources, which likely compromises growth capacity under optimal resource conditions (H4). These contrasting suites of traits may underlie interspecifc differences in growth and survival responses, which likely contribute to observed species distribution patterns across glacial landforms in northwestern Michigan. For example, in comparison to species associated with mesic sites, *Quercus* species had the largest seed sizes, whole-plant mass and root depths, which enhanced W_{access} (as indexed by pre-dawn water potential and A_{area}) and survival of transplanted seedlings during acute water shortages (Figure 3.16). These results suggest that *Quercus* species possess collections of traits that enable these species to persist on ice contact and outwash landforms, which tend to have lower soil water status than moraine sites. Conversely, when compared at a common harvest or a common mass, more mesic species displayed the highest values of SRA and LAR and these expressions of traits likely maximize growth rates under high resource conditions. Due to the extreme drought event during the 2002 growing season, which resulted in severe water limitations across all sites and greatly diminished growth rates (data not shown), our ability to assess the contribution of SRA and LAR to growth capacity in this experimental

framework was extremely limited. Therefore, any examination of trade-offs can be no more than speculative since this notion could not be directly evaluated with data from this field transplant study. However, empirical data from the literature and from my study in Chapter 2 allowed me to further explore this notion. For example, SRA scales well with specific root length (SRL, $P < 0.0001$, $r = 0.93$, Chapter 2, data not shown), which has been found to be positively related with mass-based N uptake rates (Reich et al. 1998b) and growth rates (Reich et al. 1998a). Numerous multi-species studies have demonstrated that LAR is the morphological trait that is most strongly related to growth, especially in moderate to high light environments (Walters et al. 1993b, Lusk et al. 1997, Reich et al. 1998a, Poorter 1999, Walters and Reich 1999). Furthermore, in combination, LAR and SRA explained more variance in growth rates than LAR alone for 36 temperate and boreal woody seedling species (Chapter 2). In this study, differences in SRA and LAR between xeric and mesic species suggest that mesic species may realize higher growth rates when soil water is plentiful. Thus, over time, higher growth potential may enable mesic species to overtop xeric species on moraine sites, which typically have higher N-mineralization rates and soil water, especially during non-drought years. Interpretation of the seedling trait data requires one important caveat. Although comparisons of plant traits at a specific common whole-plant mass (0.5 g) or a common root mass (0.3 g) were selected to maximize overlap in the masses of study species, common masses were considerably lower than the published values of seed mass for the three *Quercus* species (> 1.85 g). Thus, at a common mass, it appears that estimates of plant traits for the *Quercus* species were based on individuals that were experiencing negative carbon balance and potentially near death. As a result, estimates of *Quercus*

traits may have been biased (RMR, SRA, LAR), but the consistency in species ranks at a common mass and averages at a common harvest (Appendix, Figures A.6, A.7; Figure 3.8), which include all seedlings, suggests that biases associated with these estimates were negligible. Furthermore, although species rankings of rooting depth were reversed when compared at a common mass and a common harvest, these rankings were consistent at progressively higher common plant masses, with the exception of the species that were excluded from these analyses due to non-overlap in masses (data not shown).

If there is a trade-off between traits that enhance W_{access} and characteristics that are related to surface area for garnering resources, then why is *Q. rubra*, a species characterized by low growth capacity as a young seedling (Walters et al. 1993a), one of the dominant species on more mesic moraine landforms (Table 3.1)? The present abundance may, in part, reflect legacy effects from disturbance histories. For example, in the early 1900s, extensive logging, subsequent fires and mass dieback of competing vegetation may have played a role in the proliferation and current dominance of this basal sprouting species (Host et al. 1988), a notion that is supported by experimental evidence in mesic hardwood stands in southwestern Wisconsin (Kruger and Reich 1997a). Additionally, why is *A. saccharum*, a species characterized by low photosynthetic and growth rates (Walters et al. 1993a), the most dominant species on moraine sites (Table 3.1)? The success of *A. saccharum* suggests that additional unmeasured physiological traits may also contribute to the success of some mesic species. I speculate that these traits may be associated with low-light carbon balance because moraine sites without frequent or severe disturbances are typically dominated by low light regeneration niches (Table 3.2). In these environments, seedling success is dependent on enduring shade for

prolonged periods of time as advance regeneration in a "seedling bank" while maintaining the capacity to respond rapidly to increased light availability from canopy openings created by the death of overstory trees (Marks 1975, Canham 1985). Based on a compilation of data from unpublished studies and from the literature, leaf-level light compensation points and respiration rates, two traits likely to play an important role for tolerance to low light availability (Lusk and Del Pozo 2002), varied considerably among our study species (Table 3.12). For example, for one of the most mesic species, *A. saccharum* tended to have a relatively low light compensation point and respiration rates, whereas *Q. alba*, one of the most xeric species had the highest values. These carbon conservation traits may help *A. saccharum* to persist in the understory until eventual canopy recruitment on moraine sites. Therefore, variation in these physiological traits may also contribute to species sorting across glacial landforms.

Table 3.1. Mean species basal area across glacial landforms in Manistee National Forest, near Cadillac, MI (condensed from Host and Pregitzer 1992). Outwash has the lowest water holding capacity and rich moraines the highest.

Species	**Common name**	**Outwash (*n* = 22)**	**Ice contact (*n* = 22)**	**Rich Moraines (*n* = 8)**
Quercus velutina	Black oak	9.3	7.8	-
Quercus alba	White oak	8.4	6.3	-
Acer rubrum	Red maple	0.3	1.2	0.1
Prunus serotina	Black cherry	-	-	2.4
Quercus rubra	Red oak	1.1	7.3	4.7
Acer saccharum	Sugar maple	-	-	11.6
Fraxinus americana	White ash	-	-	2.3
Betula alleghaniensis	Yellow birch	Not reported, assoc/w mesic/hydric sites		

Table 3.2. Mean, standard deviation, ranges and Pearson's correlation for the different indices of light availability used in this study.

Site	*n*		Canopy openness (%)	PPFD (μmol m^{-2} s^{-1})	Correlation
OW-1	5	Mean (SD)	17.1 (7.6)	324.7 (282.5)	0.91**
		Range	11.3–30.4	170.4–829.2	
OW-2	5	Mean (SD)	19.3 (14.4)	180.2 (86.5)	0.85
		Range	7.7–44.0	84.1–310.5	
IC-1	6	Mean (SD)	12.2 (15.0)	172.4 (177.8)	0.88*
		Range	3.2–42.5	43.7–517.1	
IC-2	6	Mean (SD)	15.0 (12.2)	174.3 (181.4)	0.93**
		Range	3.8–36.5	35.8–506.3	
MOR-1	6	Mean (SD)	12.2 (17.5)	107.0 (155.1)	0.96**
		Range	1.1–45.6	17.7–419.5	
MOR-2	7	Mean (SD)	5.5 (4.1)	77.9 (58.8)	0.91**
		Range	0.7–12.5	12.2–186.0	

Note: *$P < 0.05$, **$P < 0.01$.

Table 3.3. Results of a standard least squares linear model for main effects of site (n = 6) on gravimetric soil moisture (%) across different sampling dates and averaged across the growing season.

	ANOVA						Site Comparison					
Date	effects	d.f.	SS	F	P	Adj. R^2	OW-1	OW-2	IC-1	IC-2	MOR-1	MOR-2
16 May	Site	5	0.43	4.61	0.0032	0.35	A	AB	AB	AB	B	B
25 June	Site	5	0.37	3.36	0.0162	0.26	A	A	A	A	A	A
9 July	Site	5	0.28	2.49	0.0544	0.18	A	A	A	A	A	A
25 July	Site	5	0.69	7.88	< 0.0001	0.50	A	BC	AB	AB	BC	C
20 August	Site	5	1.06	6.86	0.0002	0.46	A	A	A	A	AB	B
8 September	Site	5	1.89	8.49	< 0.0001	0.52	A	A	A	A	A	B
Overall Mean	Site	5	0.64	10.04	< 0.0001	0.57	A	AB	AB	AB	BC	C

Note: For each sampling date, sites without a common letter are significantly different ($P < 0.05$, Tukey-Kramer HSD).

Table 3.4. Linear relationship of leaf-level photosynthesis (A_{area}) with photosynthetic photon flux density (PPFD) at very low soil water availability (See methods and Appendix, Table A.4. for more details about soil moisture categories). Multiple linear regression models of A_{area} as a function of PPFD in combination with plant traits (leaf nitrogen, whole-plant mass, root area, root mass ratio, specific root area, root depth).

Table 3.4.

ANOVA effects	d.f.	SS	*F*	*P*	Par. Est.	Whole-model *P*	Whole-model Adj. R^2
PPFD							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	38.73	91.73	<0.0001	1.04	<0.0001	0.28
Leaf Nitrogen							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	29.74	72.66	<0.0001	0.95	<0.0001	0.31
Log_{10} leaf N ($\mu g\ cm^{-2}$)	1	4.92	12.02	0.0006	1.29		
Whole-plant mass							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	26.21	63.7	<0.0001	0.92	<0.0001	0.30
Log_{10} whole-plant mass (g)	1	4.42	10.74	0.0012	0.32		
Root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	28.01	66.67	<0.0001	0.95	<0.0001	0.29
Log_{10} root area (cm^2)	1	2.49	5.92	0.0158	0.34		
Root mass ratio							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	35.12	81.49	<0.0001	1.02	<0.0001	0.27
RMR ($g\ g^{-1}$)	1	0.05	0.12	0.7294	0.12		
Specific root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	30.86	73.54	<0.0001	0.97	<0.0001	0.29
Log_{10} SRA ($cm^2\ g^{-1}$)	1	2.58	6.14	0.0139	–0.41		
Root depth							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	18.59	47.24	<0.0001	0.81	<0.0001	0.33
Log_{10} root depth (cm)	1	8.46	21.49	<0.0001	1.03		

Note: Models exclude interaction term when $P > 0.25$ in preliminary model (Bancroft, 1964)

Table 3.5. Linear relationship of leaf-level photosynthesis (A_{area}) with photosynthetic photon flux density (PPFD) at low soil water availability (See methods and Appendix, Table A.4. for more details about soil moisture categories). Multiple linear regression models of A_{area} as a function of PPFD in combination with plant traits (leaf nitrogen, whole-plant mass, root area, root mass ratio, specific root area, root depth).

Table 3.5.

ANOVA effects	d.f.	SS	*F*	*P*	Par. Est.	Whole-model *P*	Whole-model Adj. R^2
PPFD							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	91.54	147.70	<0.0001	1.74	<0.0001	0.39
Leaf Nitrogen							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	68.88	133.22	<0.0001	1.56	<0.0001	0.49
Log_{10} leaf N ($\mu g\ cm^{-2}$)	1	13.03	25.22	<0.0001	2.11		
Log_{10} PPFD × Log_{10} leaf N	1	9.05	17.52	<0.0001	5.30		
Whole-plant mass							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	64.53	119.55	<0.0001	1.53	<0.0001	0.47
Log_{10} whole-plant mass (g)	1	13.87	25.69	<0.0001	0.54		
Log_{10} PPFD × Log_{10} WP mass	1	7.74	14.35	0.0002	1.08		
Root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	69.84	120.63	<0.0001	1.58	<0.0001	0.43
Log_{10} root area (cm^2)	1	9.20	15.89	<0.0001	0.62		
Log_{10} PPFD × Log_{10} root area	1	3.55	6.14	0.014	1.03		
Root mass ratio							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	88.99	141.28	<0.0001	1.76	<0.0001	0.38
RMR ($g\ g^{-1}$)	1	0.58	0.92	0.3396	−0.40		
Specific root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	75.03	126.98	<0.0001	1.63	<0.0001	0.42
Log_{10} SRA ($cm^2\ g^{-1}$)	1	5.42	9.17	0.0027	−0.57		
Log_{10} PPFD × Log_{10} SRA	1	5.54	9.38	0.0025	−1.49		
Root depth							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	56.18	99.22	<0.0001	1.48	<0.0001	0.44
Log_{10} root depth (cm)	1	7.45	13.15	0.0004	0.91		
Log_{10} PPFD × Log_{10} root depth	1	6.69	11.81	0.0007	2.41		

Note: Models exclude interaction term when $P > 0.25$ in preliminary model (Bancroft, 1964).

Table 3.6. Linear relationship of leaf-level photosynthesis (A_{area}) with photosynthetic photon flux density (PPFD) at moderate soil water availability (See methods and Appendix, Table A.4. for more details about soil moisture categories). Multiple linear regression models of A_{area} as a function of PPFD in combination with plant traits (leaf nitrogen, whole-plant mass, root area, root mass ratio, specific root area, root depth).

Table 3.6.

ANOVA effects	d.f.	SS	*F*	*P*	Par. Est.	Whole-model *P*	Whole-model Adj. R^2
PPFD							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	169.24	317.36	<0.0001	2.26	<0.0001	0.58
Leaf Nitrogen							
Log_{10} PPFD ($mmol\ m^{-2}\ s^{-1}$)	1	144.06	356.44	<0.0001	2.17	<0.0001	0.69
Log_{10} leaf N ($\mu g\ cm^{-2}$)	1	9.60	23.75	<0.0001	1.83		
Log_{10} PPFD × Log_{10} leaf N	1	19.03	47.08	<0.0001	7.31		
Whole-plant mass							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	158.14	352.21	<0.0001	2.28	<0.0001	0.65
Log_{10} whole-plant mass (g)	1	4.49	10.00	0.0018	0.31		
Log_{10} PPFD × Log_{10} WP mass	1	15.07	33.56	<0.0001	1.42		
Root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	162.41	338.54	<0.0001	2.30	<0.0001	0.63
Log_{10} root area (cm^2)	1	2.09	4.35	0.0382	0.30		
Log_{10} PPFD × Log_{10} root area	1	11.66	24.30	<0.0001	1.80		
Root mass ratio							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	165.33	309.08	<0.0001	2.30	<0.0001	0.58
RMR ($g\ g^{-1}$)	1	0.62	1.16	0.2822	−0.43		
Log_{10} PPFD × RMR	1	0.75	1.39	0.2392	1.16		
Specific root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	158.62	323.92	<0.0001	2.26	<0.0001	0.62
Log_{10} SRA ($cm^2\ g^{-1}$)	1	2.80	5.71	0.0177	−0.42		
Log_{10} PPFD × Log_{10} SRA	1	8.79	17.95	<0.0001	−1.85		
Root depth							
Log_{10} PPFD ($mmol\ m^{-2}\ s^{-1}$)	1	153.04	320.10	<0.0001	2.32	<0.0001	0.63
Log_{10} root depth (cm)	1	0.59	1.24	0.2676	0.26		
Log_{10} PPFD × Log_{10} root depth	1	11.63	24.32	<0.0001	2.76		

Table 3.7. Linear relationship of leaf-level photosynthesis (A_{area}) with photosynthetic photon flux density (PPFD) at high soil water availability (See methods and Appendix, Table A.4. for more details about soil moisture categories). Multiple linear regression models of A_{area} as a function of PPFD in combination with plant traits (leaf nitrogen, whole-plant mass, root area, root mass ratio, specific root area, root depth).

Table 3.7.

ANOVA effects	d.f.	SS	*F*	*P*	Par. Est.	Whole-model *P*	Whole-model Adj. R^2
PPFD							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	90.46	130.99	<0.0001	1.63	<0.0001	0.35
Leaf Nitrogen							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	89.02	128.43	<0.0001	1.67	<0.0001	0.35
Log_{10} leaf N ($\mu g\ cm^{-2}$)	1	0.19	0.28	0.5993	0.25		
Whole-plant mass							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	89.18	128.96	<0.0001	1.70	<0.0001	0.35
Log_{10} whole-plant mass (g)	1	0.58	0.84	0.3592	−0.11		
Root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	88.64	128.07	<0.0001	1.70	<0.0001	0.35
Log_{10} root area (cm^2)	1	0.44	0.63	0.4285	−0.13		
Root mass ratio							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	103.92	171.52	<0.0001	1.88	<0.0001	0.43
RMR ($g\ g^{-1}$)	1	21.53	35.53	<0.0001	−2.55		
Log_{10} PPFD × RMR	1	2.10	3.47	0.0638	−2.19		
Specific root area							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	97.84	147.78	<0.0001	1.78	<0.0001	0.38
Log_{10} SRA ($cm^2\ g^{-1}$)	1	7.83	11.83	0.0007	0.677		
Log_{10} PPFD × Log_{10} SRA	1	0.93	1.41	0.2369	0.62		
Root depth							
Log_{10} PPFD ($\mu mol\ m^{-2}\ s^{-1}$)	1	88.42	128.46	<0.0001	1.74	<0.0001	0.35
Log_{10} root depth (cm)	1	1.34	1.94	0.1649	−0.37		

Note: Models exclude interaction term when $P > 0.25$ in preliminary model (Bancroft, 1964).

Table 3.8. Multiple linear regression models of leaf-level photosynthesis (A_{area}) during very low soil moisture at OW 1 with PPFD as a covariate, root area, root depth or both root depth and root area.

Predicted					Parameter	Whole-model	
variable	Predictor	SS	*F*	*P*	Estimates	*P*	Adj. R^2
A_{area}	$\log_{10}$ PPFD	28.0	66.7	< 0.0001	0.95	< 0.0001	0.28
	Log_{10} root area	2.5	5.9	0.0158	0.34		
A_{area}	$\log_{10}$ PPFD	18.6	47.2	< 0.0001	0.81	< 0.0001	0.33
	$\log_{10}$ root depth	8.5	21.5	< 0.0001	1.03		
A_{area}	$\log_{10}$ PPFD	18.2	46.7	< 0.0001	0.80	< 0.0001	0.34
	$\log_{10}$ root depth	7.0	17.8	< 0.0001	1.44		
	$\log_{10}$ root area	1.0	2.5	0.1142	−0.33		

Table 3.9. Multiple linear regression models of leaf-level photosynthesis (A_{area}, μmol m^{-2} s^{-1}) as a function of photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}), root depth (cm) and their interaction within the three well-drained sites (OW 1, IC 1, MOR 1) during very low soil moisture conditions.

					Parameter	Whole-model	
ANOVA effects	d.f.	SS	*F*	*P*	Estimate	*P*	Adj. R^2
OW 1							
Log_{10} PPFD (μmol m^{-2} s^{-1})	1	0.17	0.35	0.5607	0.47	0.0013	0.38
Log_{10} root depth (cm)	1	6.32	12.82	0.0014	2.75		
Log_{10} PPFD × Log_{10} root depth	1	1.70	3.45	0.0744	10.46		
IC 1							
Log_{10} PPFD (μmol m^{-2} s^{-1})	1	3.42	15.03	0.0004	0.92	0.0035	0.25
Log_{10} root depth (cm)	1	0.00	0.01	0.9193	−0.04		
Log_{10} PPFD × Log_{10} root depth	1	1.33	5.84	0.0208	−2.14		
MOR 1							
Log_{10} PPFD (μmol m^{-2} s^{-1})	1	3.46	29.26	< 0.0001	0.94	< 0.0001	0.47
Log_{10} root depth (cm)	1	0.01	0.12	0.7258	0.12		
Log_{10} PPFD × Log_{10} root depth	1	1.63	13.77	0.0007	−3.19		

Table 3.10. Summary of linear regression analyses for data in Figure 3.15. In all cases, the dependent variable is residuals of survival ($SURV_{resid}$) vs. log_{10} canopy openness nonlinear functions from Figure 3.14. Definitions for abbreviations and units for independent variables are as follows: leaf nitrogen (N, μg cm^{-2}), whole-plant mass (g), root surface area (cm^2), RMR (root mass ratio, g g^{-1}), SRA (specific root area, cm^2 g^{-1}), root depth (cm), A_{area} (leaf-level photosynthesis during the peak of the drought, μmol CO_2 m^{-2} s^{-1}), WUE (water use efficiency during the peak of the drought, mmol CO_2 mol^{-1} H_2O).

	OW 1			IC 1			MOR 1		
Independent variable	*n*	Adj. R^2	Regression equation	*n*	Adj. R^2	Regression equation	*n*	Adj. R^2	Regression equation
Log_{10} leaf N	35	0.11*	y = 64.5(x) − 112.2	47	ns		36	ns	
Log_{10} whole-plant mass	34	0.65***	y = 44.8(x) + 12.1	47	0.33***	y = 33.0(x) + 12.8	36	0.13*	y = 15.6(x) + 8.8
Log_{10} root surface area	34	0.54***	y = 66.5(x) − 100.8	47	0.32***	y = 43.2(x) − 59.4	36	0.13*	y = 20.0(x) − 26.4
RMR	34	ns		47	0.16**	y = 97.7(x) − 52.9	36	0.13*	y = 47.2(x) − 20.8
Log_{10} SRA	34	0.48***	y = −74.6(x) + 153.0	47	0.20**	y = −46.0(x) + 95.1	36	0.14*	y = −25.9(x) + 59.3
Log_{10} root depth	34	0.59***	y = 98.6(x) − 117.9	47	0.20**	y = 53.4(x) − 59.1	36	0.18**	y = 44.9(x) − 44.9
A_{area}	31	0.17*	y = 11.8(x) − 14.8	40	ns		37	ns	
WUE	31	0.17*	y = 10.5(x) − 22.5	40	ns		37	ns	

Note: Significant regressions are indicated as: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.0001$). Non-signifcant regressions are indicated as ns ($P > 0.05$).

Table 3.11. Simple and multiple linear regression models of $resid_{SURV}$ for OW 1 with whole-plant mass, root area, root depth or a combination of these seedling characteristics.

Predicted variable	Predictor	SS	*F*	*P*	Parameter Estimates	Whole-model *P*	Whole-model Adj. R^2
$resid_{surv}$	log_{10} whole-plant mass	11756.9	61.9	< 0.0001	44.8	< 0.0001	0.65
$resid_{surv}$	log_{10} whole-plant mass	1904.1	9.7	0.0039	48.4	< 0.0001	0.64
	log_{10} root area	11.9	0.06	0.8068	−6.2		
$resid_{surv}$	log_{10} whole-plant mass	1718.1	9.8	0.0038	29.9	< 0.0001	0.67
	log_{10} root depth	630.7	3.6	0.0675	41.9		
$resid_{surv}$	log_{10} root area	9864.7	39.6	< 0.0001	66.5	< 0.0001	0.54
$resid_{surv}$	log_{10} root depth	10669.5	47.7	< 0.0001	98.6	< 0.0001	0.59
$resid_{surv}$	log_{10} root depth	2003.2	10.4	0.0030	62.9	< 0.0001	0.64
	log_{10} root area	1198.3	6.2	0.0181	34.1		

Table 3.12. Leaf-level light compensation points (LCP) and respiration rates (R_L) of study species from shaded understory or greenhouse conditions. Data compiled from unpublished studies and from the literature. Species values with multiple superscripts represent averages from cited studies.

Species	LCP (mmol m^{-2} s^{-1})	R_L (μmol CO_2 m^{-2} s^{-1})
Quercus velutina	4.6[e]	0.5[c]
Quercus alba	8.2[e]	0.7[h,i]
Acer rubrum	6.8[e]	0.4[b,d,e,f,h]
Prunus serotina	–	0.10[b]
Quercus rubra	7.3[e]	0.38[b,c,d,f]
Acer saccharum	3.3[e]	0.25[a,b,g,i]
Fraxinus americana	1.1[a]	0.44[a]
Betula alleghaniensis	5.1[i]	0.16[i]

Note: [a](Bazzaz and Carlton 1982), [b](Jurik et al. 1988), [c](Kloeppel et al. 1993), [d](Kubiske and Pregitzer 1996), [e](Kunkle and Walters, unpublished data), [f](Loach 1967), [g](Lusk and Reich, unpublished data), [h](Teskey and Shrestha 1985), [i](Walters and Reich, unpublished data), (–) no data.

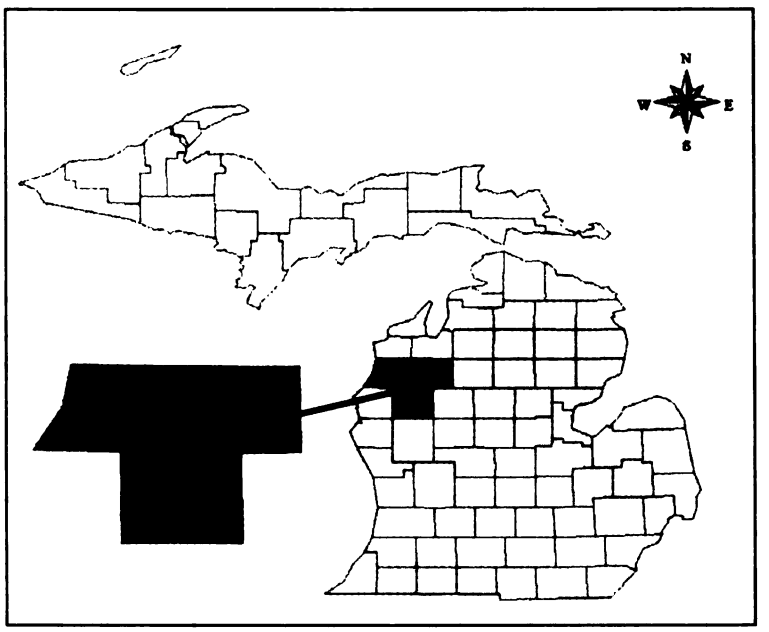


Figure 3.1. Map of study area with arrow pointing to Lake, Wexford and Manistee counties, in the northern lower peninsula of Michigan.

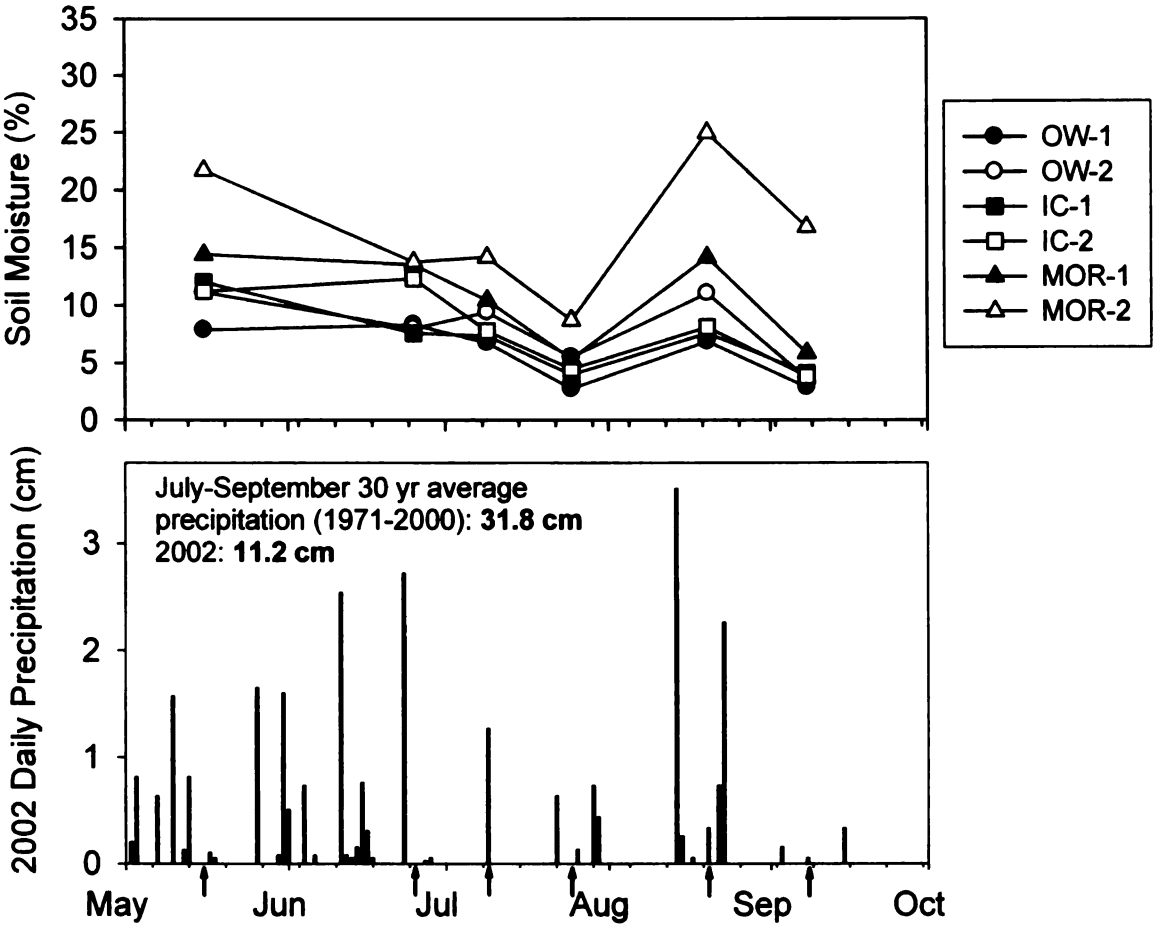


Figure 3.2. Mean gravimetric soil water availability at 0-20 cm depth for study sites located on different glacial landforms (OW = outwash, IC = ice contact, MOR = moraine) and daily precipitation from May 1 to Septmeber 15, 2002 (Wellston-Tippy Dam Weather Station). Sites followed by a 1 are well-drained, whereas sites followed by a 2 are sub-irrigated.

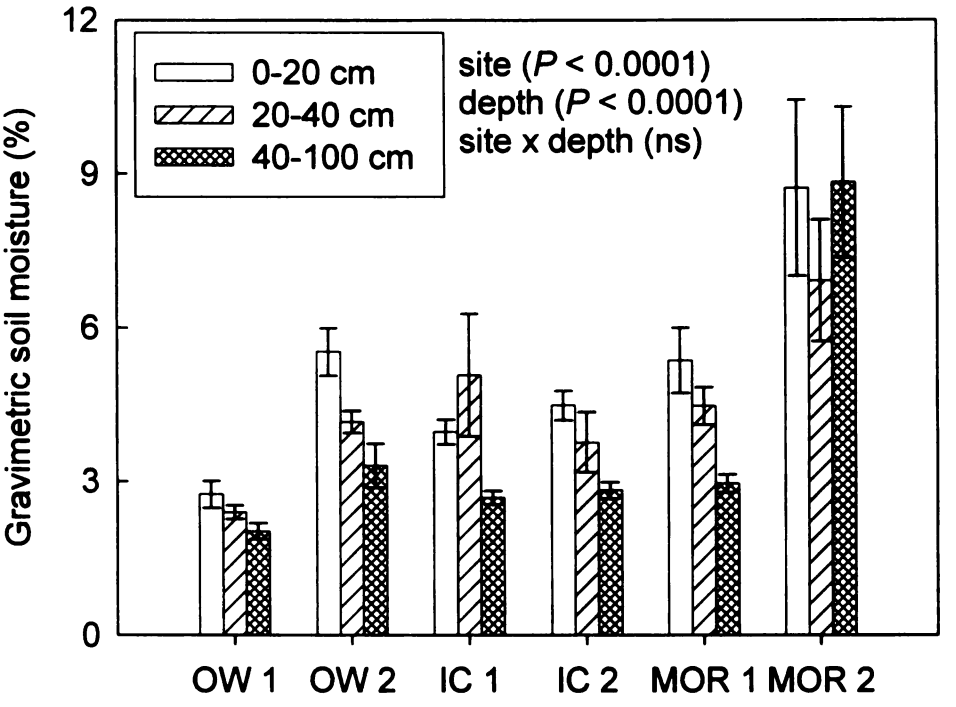


Figure 3.3. Vertical profiles (0-20 cm, 20-40 cm, 40-100 cm) of mean gravimetric soil water availability on different glacial landforms (OW = outwash, IC = ice contact, MOR = moraine) on July 25, 2002 (i.e., peak of the drought). Sites followed by a 1 are well-drained, whereas sites followed by a 2 are sub-irrigated. Results of ANOVA for soil water with site, depth and their interaction as factors.

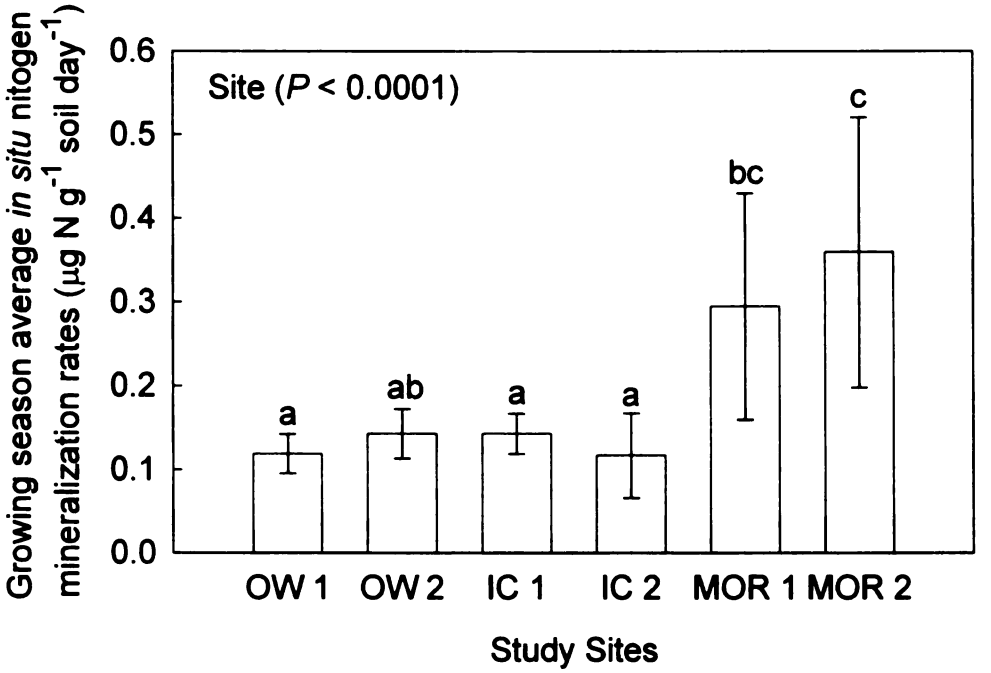


Figure 3.4. Means (± 1 SD) of *in situ* nitrogen mineralization rates across landform sites for different measurement dates and averaged across the growing season. For pairwise comparisons of sites, means followed by a different letter are significantly different at $P < 0.05$ according to Tukey HSD.

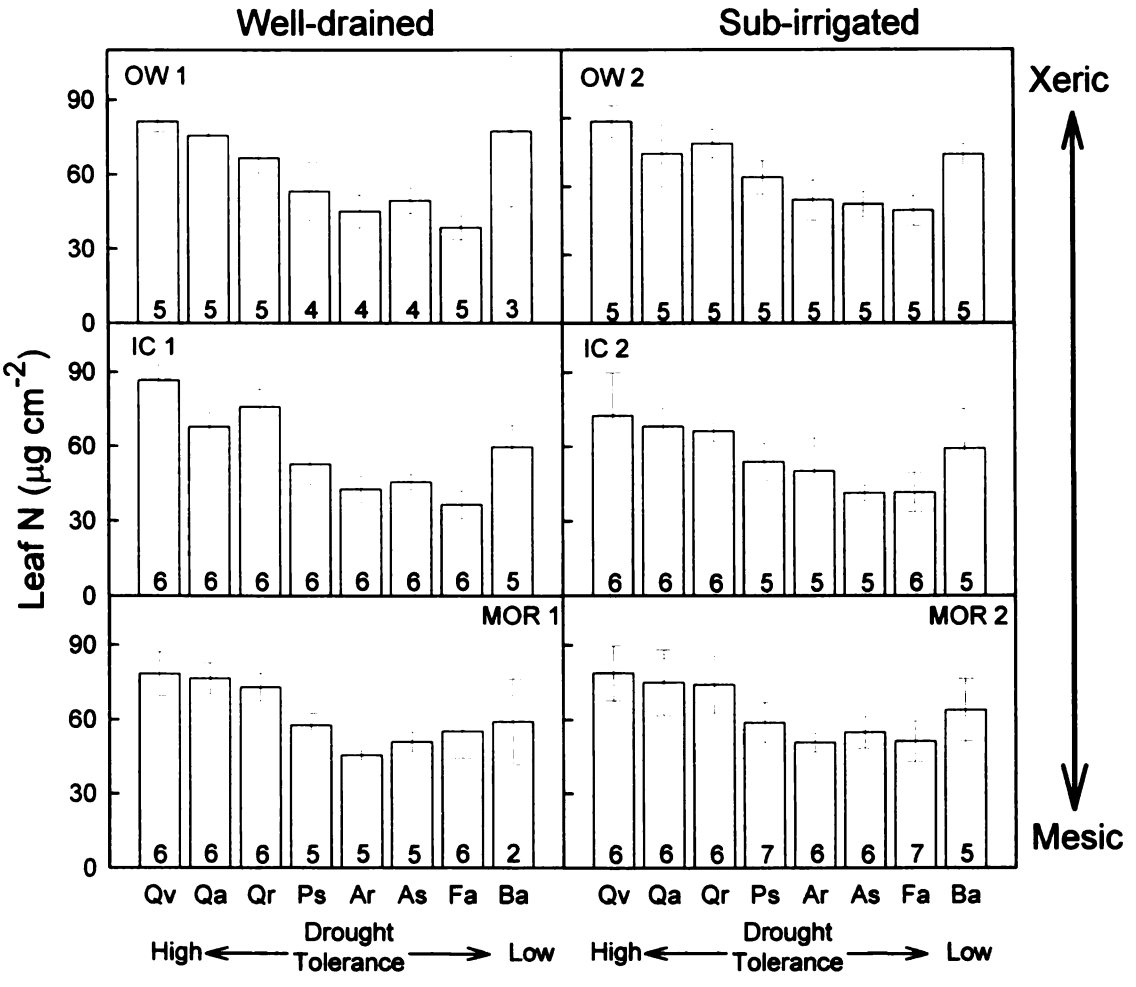


Figure 3.5. Species-level means (± SD) of leaf nitrogen content (N, μg cm^{-2}) across field sites from the June 02 seedling harvest. Numbers within or above bars denote sample sizes (number of plots) for each respective species. Sites are separated into well-drained (outwash = OW 1, ice contact = IC 1, moraine = MOR 1) and sub-irrigated categories (outwash = OW 2, ice contact = IC 2, moraine = MOR 2) (see methods for details). Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

Figure 3.6. Root depth (cm) expressed as species-level means (± SD) and as estimates at a common whole-plant mass (see materials and methods) across field sites from the June 02 seedling harvest. Numbers within or above bars denote sample sizes (i.e., number of plots) for each respective species. (n.d.) indicates that the specified common mass was beyond the range of individuals for a given species × site combination. Sites are arranged top to bottom from the most xeric site to the most mesic site. Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

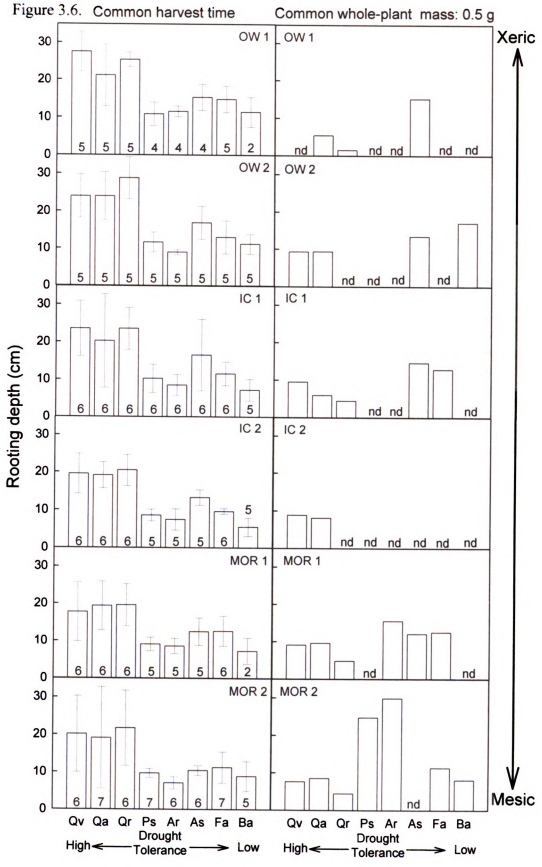


Figure 3.6. Common harvest time
Common whole-plant mass: 0.5 g
Rooting depth (cm)
OW 1
OW 2
IC 1
IC 2
MOR 1
MOR 2
Xeric
Mesic
Qv Qa Qr Ps Ar As Fa Ba
High ← Drought Tolerance → Low

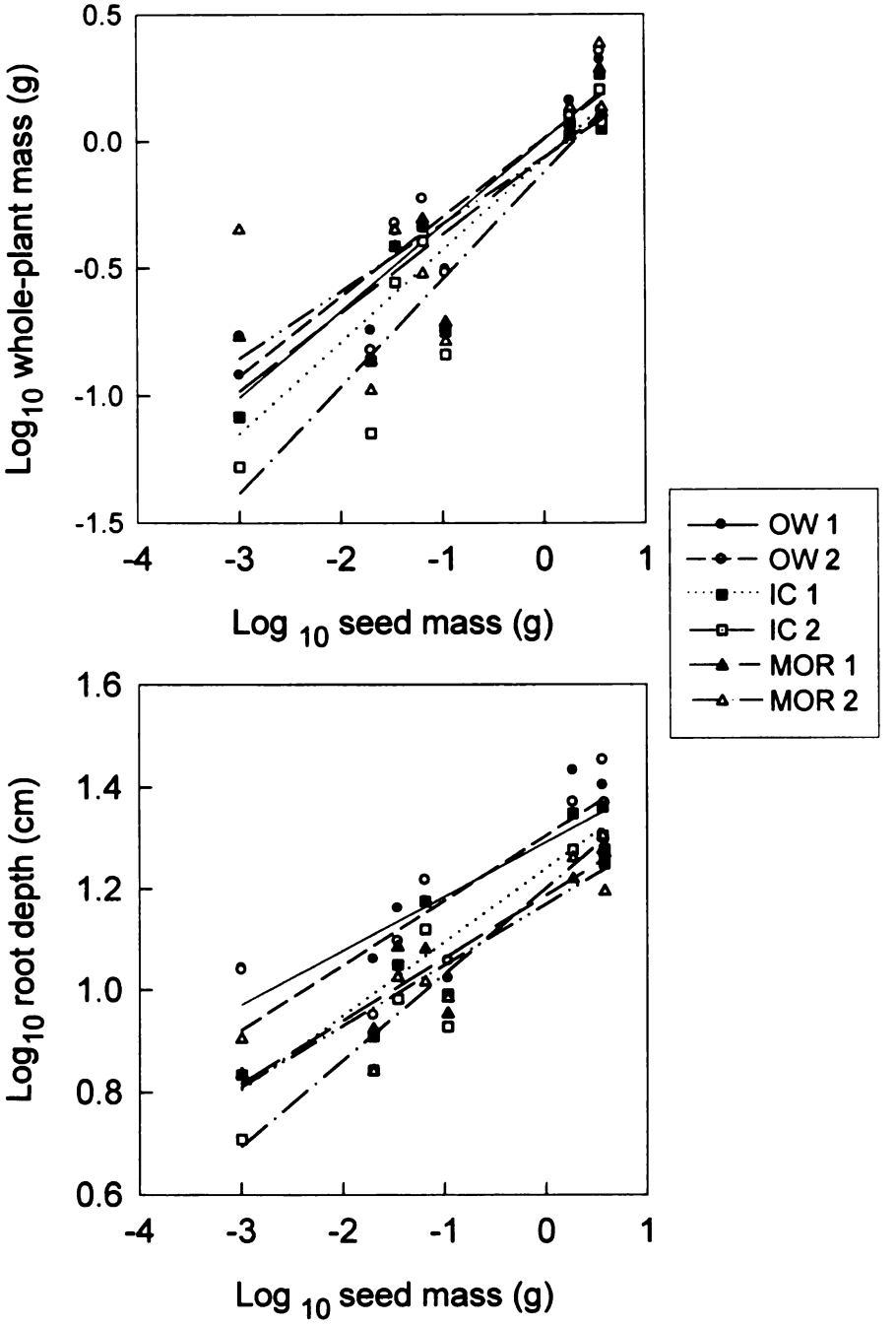


Figure 3.7. Relationships between whole plant mass, root depth and published values of seed mass. Relationships were examined within each of the study sites.

Figure 3.8. Leaf area ratio ($cm^2\ g^{-1}$) expressed as species-level means (± SD) and as estimates at a common whole-plant mass (see materials and methods) across field sites from the June 02 seedling harvest. Numbers within or above bars denote sample sizes (i.e., number of plots) for each respective species. (n.d.) indicates that the specified common mass was beyond the range of individuals for a given species × site combination. Sites are arranged top to bottom from the most xeric site to the most mesic site. Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

Figure 3.8.

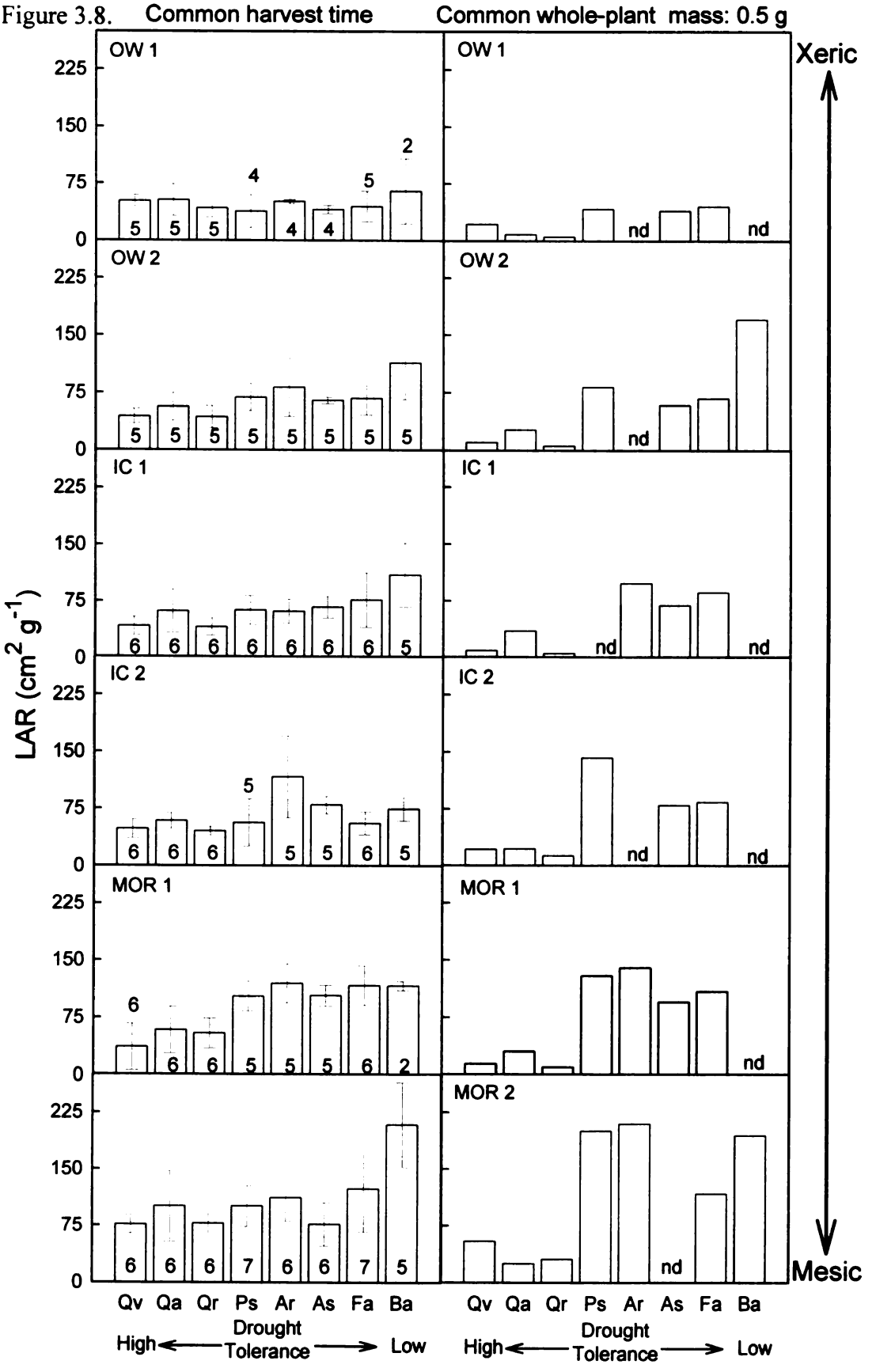

Common harvest time
Common whole-plant mass: 0.5 g
OW 1
OW 2
IC 1
IC 2
MOR 1
MOR 2
Xeric
Mesic
LAR (cm2 g-1)
225
150
75
0
nd
Qv Qa Qr Ps Ar As Fa Ba
High
Drought Tolerance
Low

Figure 3.9. Leaf-level photosynthesis (A_{area}) as a function of photosynthetic photon flux density (PPFD, mmol m^{-2} s^{-1}) for sampling periods that varied in volumetric soil water content (very low, low, moderate, high; see methods and Appendix, Table A.4 for more details). Linear regression summary statistics are provided within each respective graph panel. See Tables 3.4-3.7 for parameter estimates.

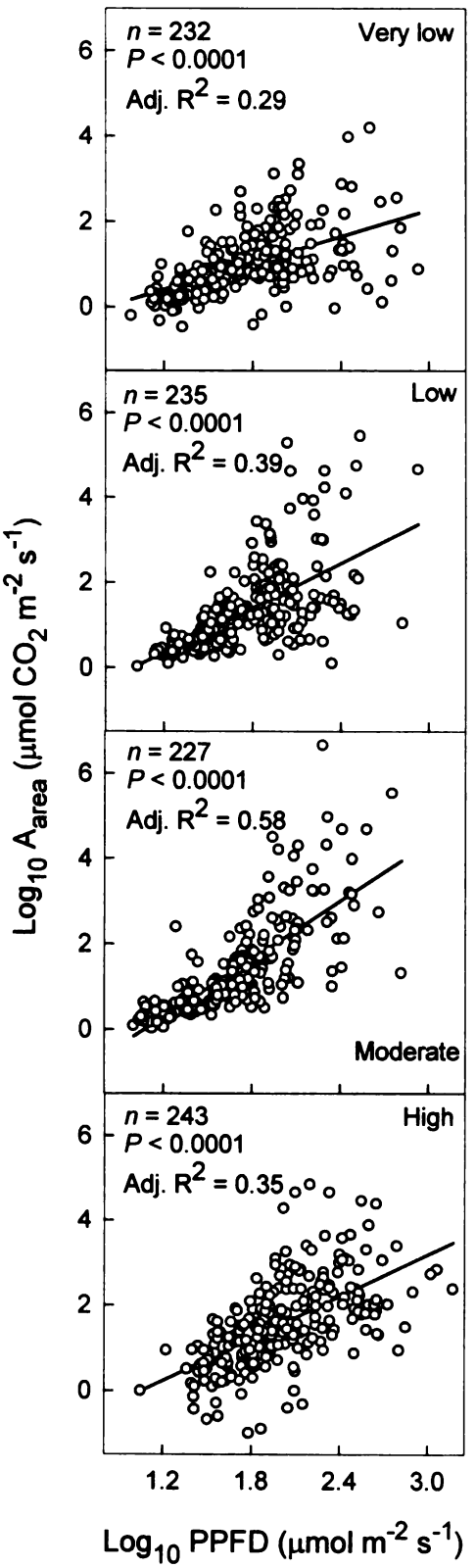

n = 232
P < 0.0001
Adj. R2 = 0.29
Very low
n = 235
P < 0.0001
Adj. R2 = 0.39
Low
n = 227
P < 0.0001
Adj. R2 = 0.58
Moderate
n = 243
P < 0.0001
Adj. R2 = 0.35
High
Log10 Aarea (μmol CO2 m-2 s-1)
Log10 PPFD (μmol m-2 s-1)
0
2
4
6
1.2
1.8
2.4
3.0

Figure 3.9.

Figure 3.10. Multiple regression model of leaf-level photosynthesis (A_{area}, μmol m^{-2} s^{-1}) in relation to photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) and leaf N_{area} (μg cm^{-2}) across all sites during (1) very low, (2) low and (3) moderate soil moisture conditions. Each datum represents a species × plot mean. Regression models are as follows: (1) very low, $A_{area} = -2.978 + 0.949 (\log_{10} PPFD) + 1.294 (\log_{10} \text{leaf } N_{area})$, adjusted $R^2 = 0.31$, $n = 227$, $P < 0.0001$; (2) low, $A_{area} = -5.176 + 1.555 (\log_{10} PPFD) + 2.115 (\log_{10} \text{leaf } N_{area}) + 5.308 (\log_{10} PPFD \times \log_{10} \text{leaf } N_{area})$, adjusted $R^2 = 0.49$, $n = 230$, $P < 0.0001$; and (3) moderate, $A_{area} = -5.999 + 2.174 (\log_{10} PPFD) + 1.833 (\log_{10} \text{leaf } N_{area}) + 7.307 (\log_{10} PPFD \times \log_{10} \text{leaf } N_{area})$, adjusted $R^2 = 0.69$, $n = 230$, $P < 0.0001$.

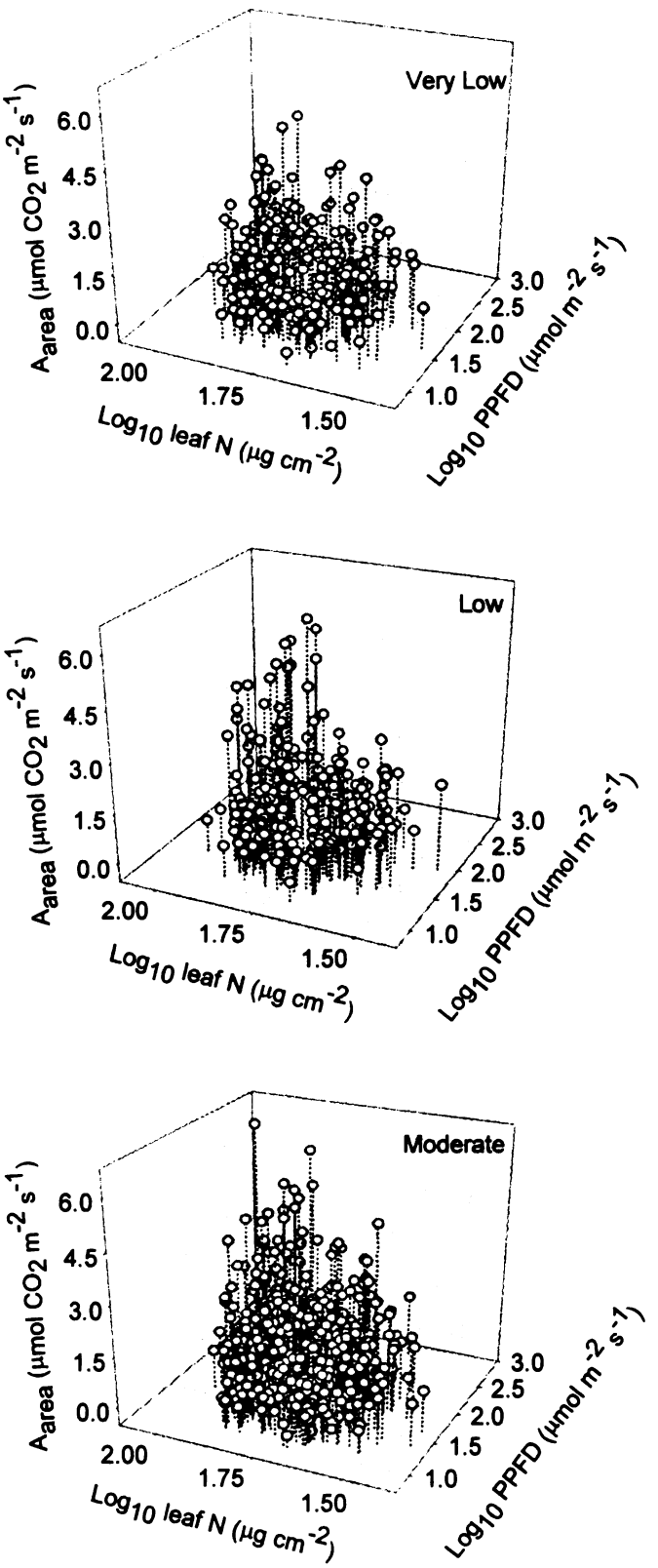

Very Low
Low
Moderate
A_{area} (µmol CO_2 m^{-2} s^{-1})
6.0
4.5
3.0
1.5
0.0
2.00
1.75
1.50
Log_{10} leaf N (µg cm^{-2})
3.0
2.5
2.0
1.5
1.0
Log_{10} PPFD (µmol m^{-2} s^{-1})

Figure 3.10.

Figure 3.11. Multiple regression model of leaf-level photosynthesis (A_{area}, μmol m^{-2} s^{-1}) in relation to photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) and root depth (cm) across all sites during (1) very low and (2) low soil moisture conditions. Each datum represents a species × plot mean. Regression models are as follows: (1) very low, $A_{area} = -1.612 + 0.81 (\log_{10} \text{PPFD}) + 1.028 (\log_{10} \text{root depth})$, adjusted $R^2 = 0.33$, $n = 227$, $P < 0.0001$; (2) low, $A_{area} = -2.380 + 1.482 (\log_{10} \text{PPFD}) + 0.911 (\log_{10} \text{root depth}) + (\log_{10} \text{PPFD} \times \log_{10} \text{root depth})$, adjusted $R^2 = 0.44$, $n = 230$, $P < 0.0001$.

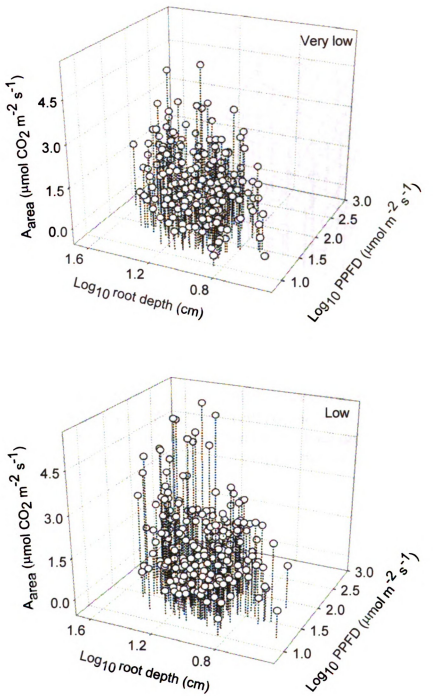

Very low
Low
A_{area} (µmol CO_2 m^{-2} s^{-1})
4.5
3.0
1.5
0.0
1.6
1.2
0.8
Log_{10} root depth (cm)
3.0
2.5
2.0
1.5
1.0
Log_{10} PPFD (µmol m^{-2} s^{-1})

Figure 3.11.

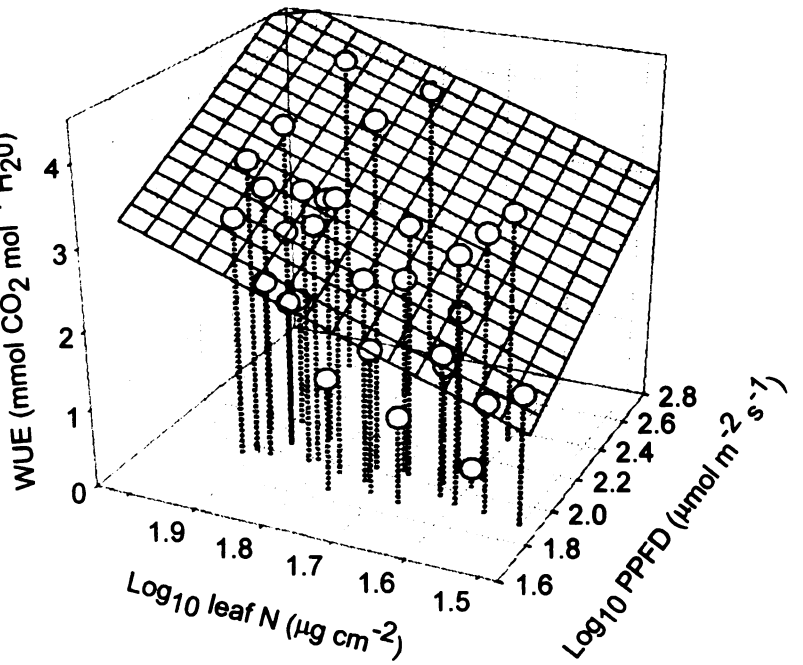


Figure 3.12. Multiple regression model of instantaneous water-use efficiency in relation to photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) and leaf N_{area} (μg cm^{-2}) at OW 1 during very low soil moisture conditions. Each datum represents a species × plot mean. Regression model: WUE = -5.75 + 1.62 (PPFD) + 2.87 (leaf N_{area}), adjusted R^2 = 0.28, n = 30, P = 0.0042.

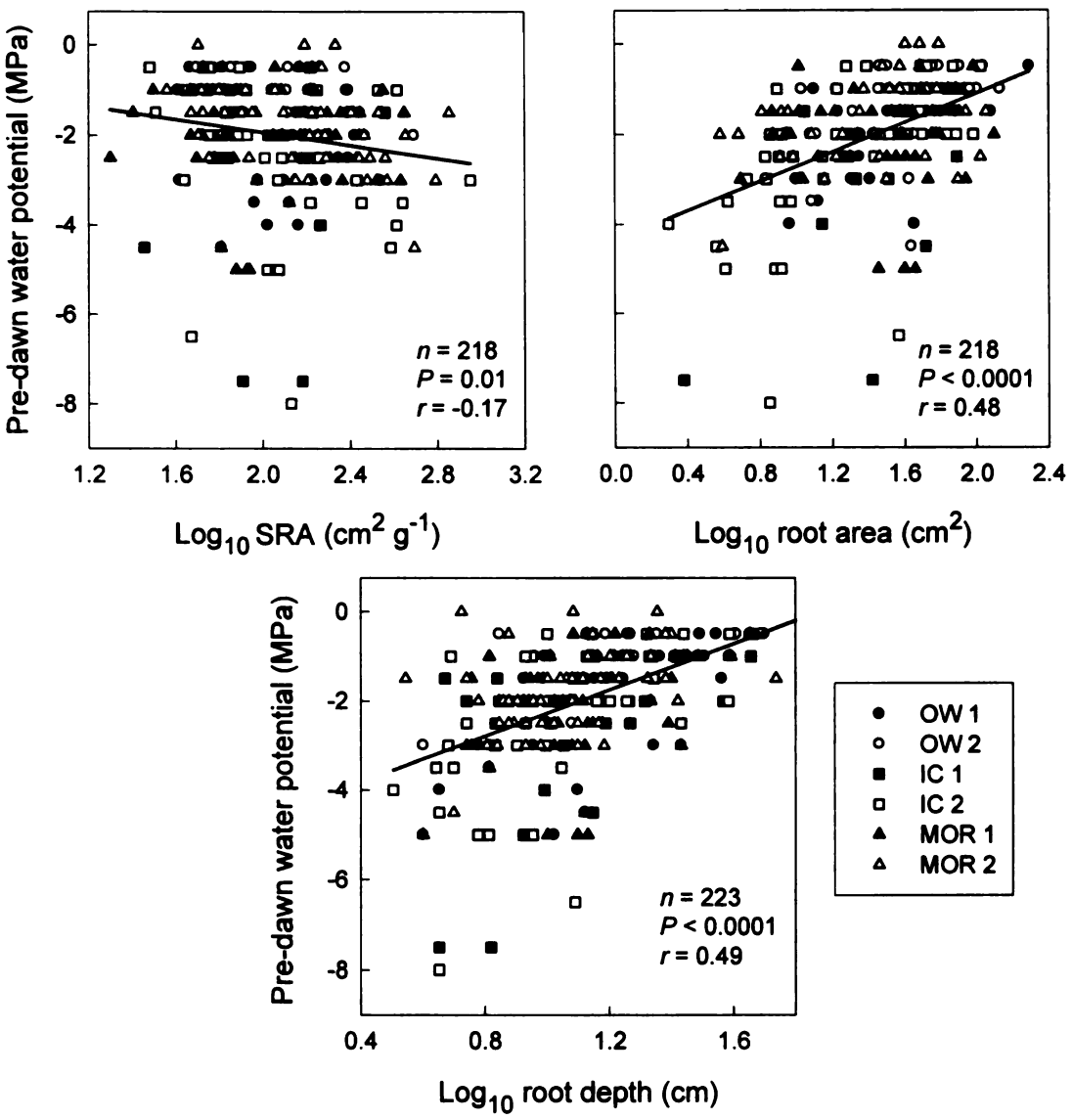


Figure 3.13. Relationships between pre-dawn water potential (MPa) and specific root area ($cm^2\ g^{-1}$), total root surface area (cm^2) and root depth (cm). Each datum represents individual seedlings of all species across all study sites. Sites followed by a 1 are well-drained, whereas sites followed by a 2 are sub-irrigated. Associated correlation statistics are provided within each graph panel.

Figure 3.14. Relationships of seedling survival (%) versus Log_{10} PPFD across all species within well-drained sites (OW 1, IC 1, MOR 1). Seedling survival was estimated as the percentage of the original seedling population (July 01) that was alive in October 02. Each datum represents a plot-level PPFD average. Data were fitted with a Gompertz function with the general form: $\theta_1 \exp[-\exp(\theta_2 - \theta_3 - Log_{10}$ canopy openness)]. Each site-specific function was solved for the best ft function (i.e., minimized residual sums of squares) iteratively using the nonlinear fit platform within JMP (SAS Institute, Cary, North Carolina). All fits were significant at $P < 0.05$.

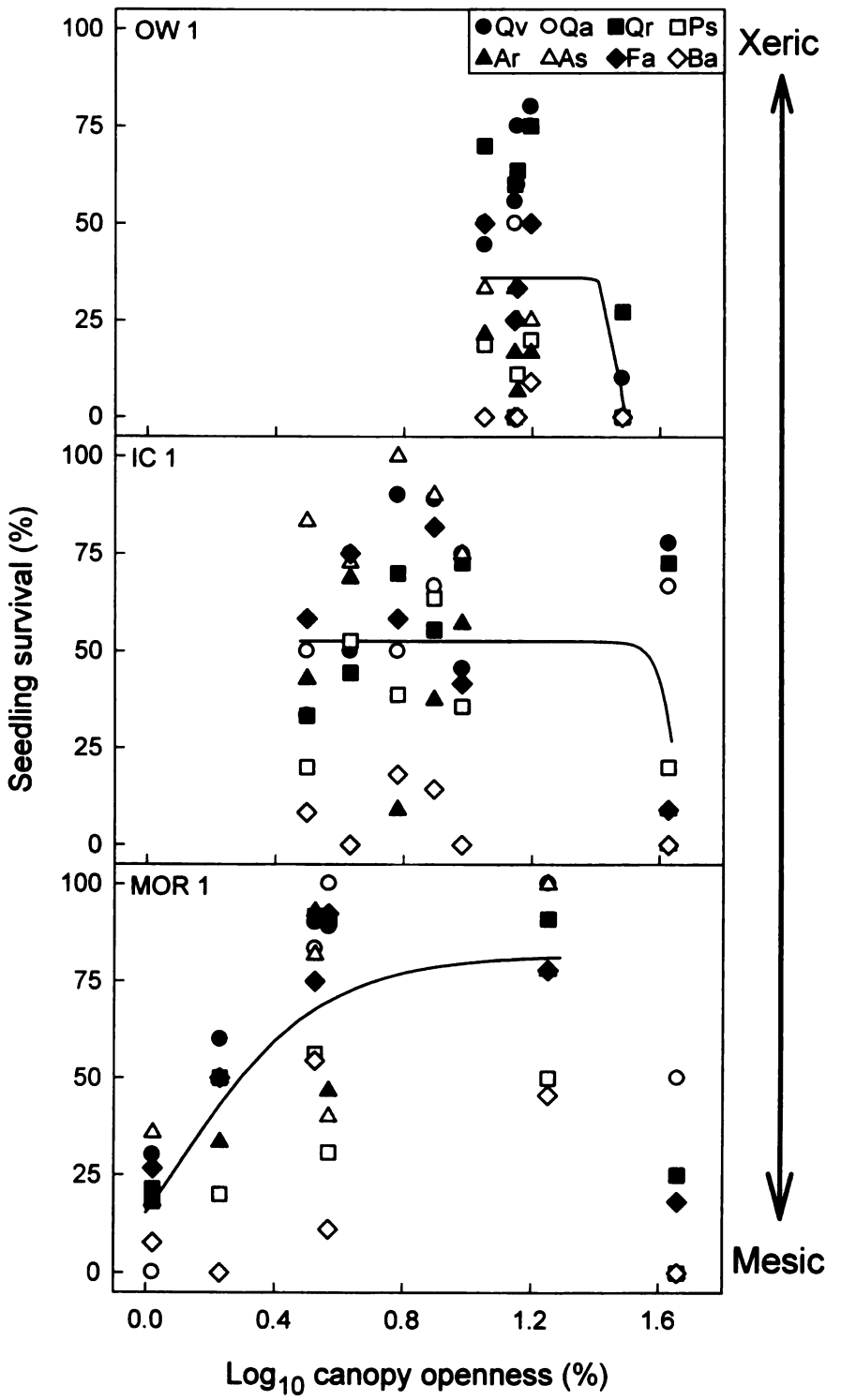

OW 1
IC 1
MOR 1
●Qv ○Qa ■Qr □Ps
▲Ar △As ◆Fa ◇Ba
Xeric
Mesic
Seedling survival (%)
Log10 canopy openness (%)
0
25
50
75
100
0.0
0.4
0.8
1.2
1.6

Figure 3.14.

Figure 3.15. Relationships of $SURV_{resid}$ (i.e., residuals of survival vs. canopy openness nonlinear functions) with leaf N_{area}, size (whole-plant mass) and morphological (root area, SRA, RMR, root depth) and physiological characteristics (leaf-level photosynthesis, A_{area}; water-use efficiency, WUE). Relationships were examined within each of the three well-drained sites (OW 1, IC 2, MOR 1). Regression equations, adjusted R^2, *P* values and *n* for these relationships are presented in Table 3.10.

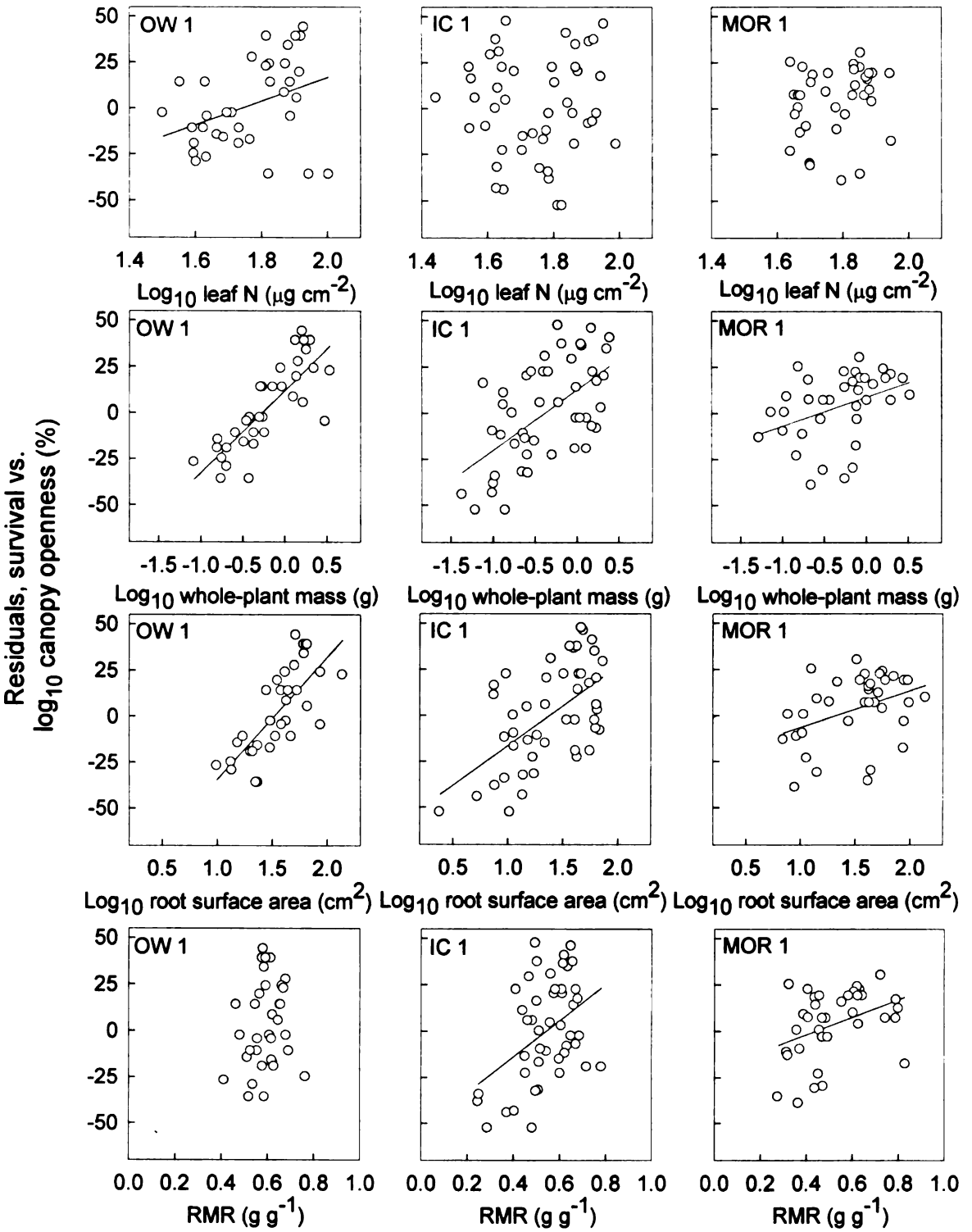

OW 1
IC 1
MOR 1
Residuals, survival vs. log10 canopy openness (%)
50
25
0
-25
-50
1.4 1.6 1.8 2.0
Log10 leaf N (μg cm-2)
-1.5 -1.0 -0.5 0.0 0.5
Log10 whole-plant mass (g)
0.5 1.0 1.5 2.0
Log10 root surface area (cm2)
0.0 0.2 0.4 0.6 0.8 1.0
RMR (g g-1)

Figure 3.15.

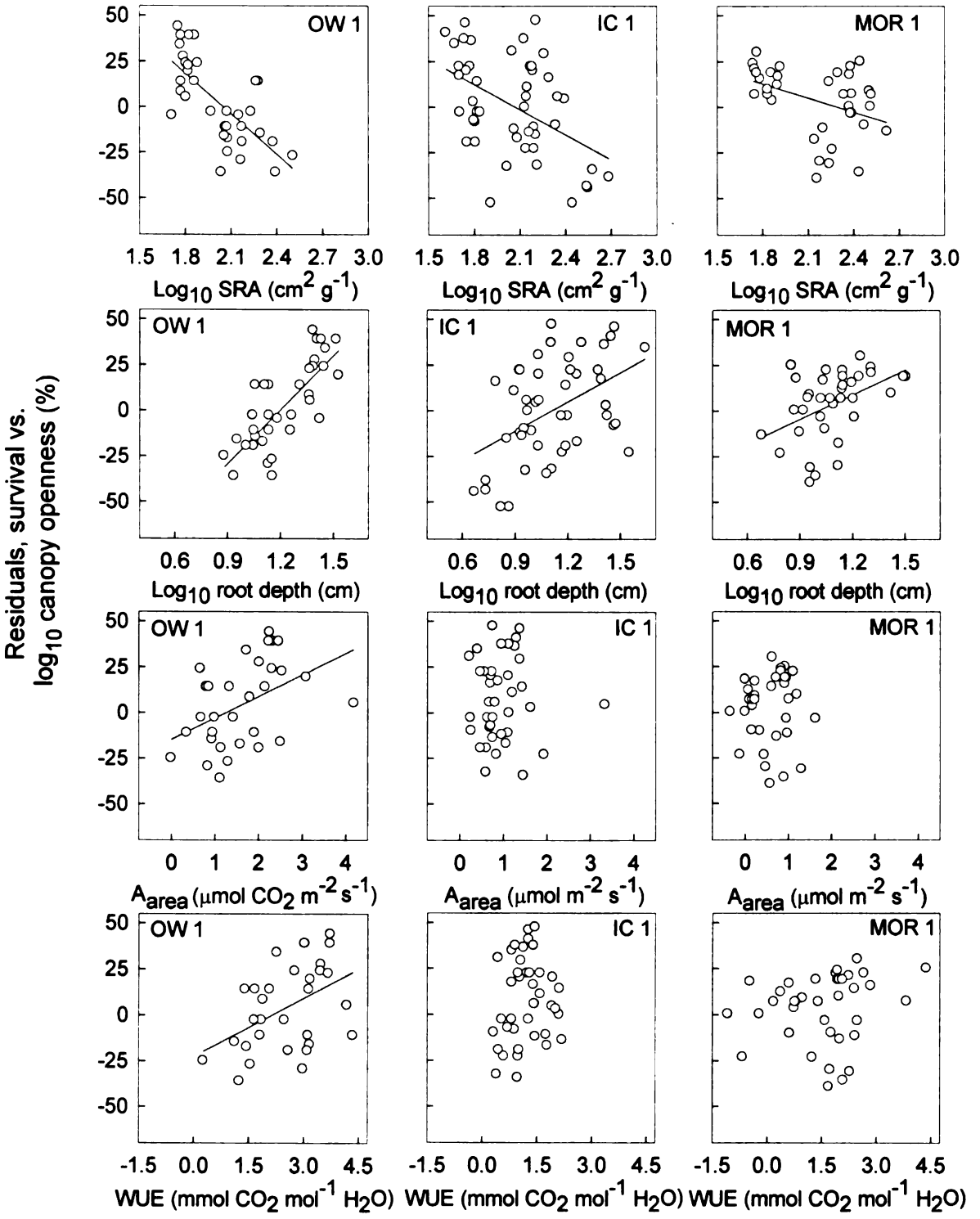


Figure 3.15 (cont'd).

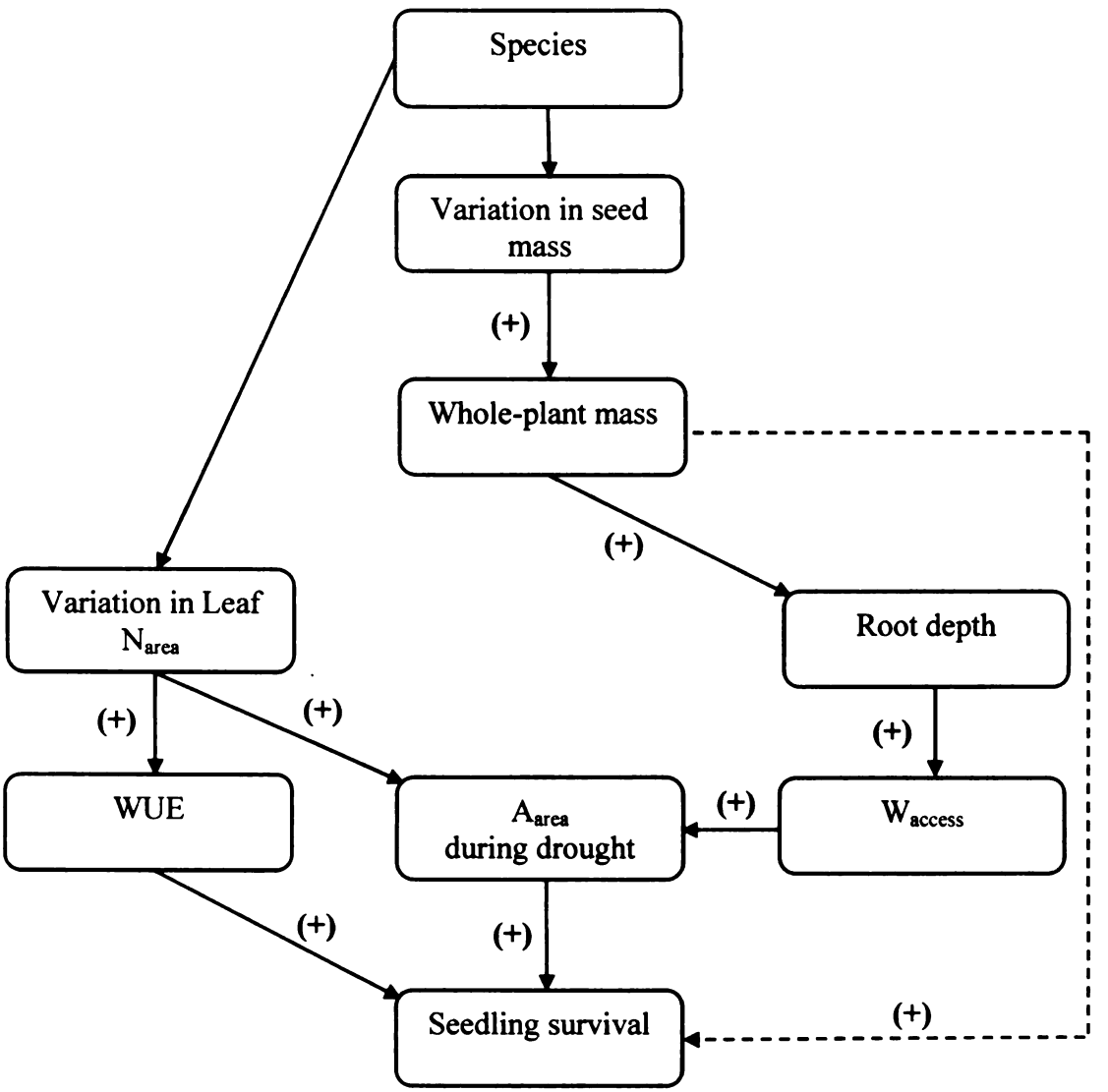


Figure 3.16. Conceptual diagram of factors influencing interspecific survival of field transplanted seedlings. Plus signs (+) indicate significance in correlation analyses or best-fit linear models. Dashed line indicates that additional, unmeasured traits that are associated with plant mass may have a positive effect on seedling survival.

APPENDIX

Table A.1. Species summary of leaf-level CO_2 gas-exchange vs. PPFD ($\mu mol\ m^{-2}\ s^{-1}$) linear regression equations and associated tests of significance and R^2 values. The resulting species-level regression equations were used to: (1) estimate photosynthesis at 30 $\mu mol\ m^{-2}\ s^{-1}$ (A_{area}); (2) quantum yield (i.e., slope = QY); and (3) light compensation point (i.e., PPFD level at which photosynthesis = 0, LCP).

Species	Regression Analyses		Estimated parameters		
	R^2	Equation	QY	LCP	A_{area}
Abies amabilis (Dougl. ex Loud.) Dougl. ex Forbes	0.94**	y = 0.084(x) – 0.837	0.084	9.93	1.69
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.	0.87**	y = 0.085(x) – 1.05	0.085	12.35	1.49
Acer negundo L.	0.94**	y = 0.072(x) – 0.731	0.072	10.22	1.41
Acer rubrum L.	0.94**	y = 0.062(x) – 0.453	0.062	7.26	1.42
Acer saccharuinum L.	0.95**	y = 0.049(x) – 0.269	0.049	5.51	1.20
Acer saccharum Marsh.	0.96**	y = 0.091(x) – 0.304	0.091	3.34	2.43
Aesculus glabra Willd.	0.97**	y = 0.042(x) – 0.252	0.042	6.00	1.01
Aesculus hippocastanum L.	0.96**	y = 0.050(x) – 0.207	0.050	4.12	1.30
Ailanthus altissima (P. Mill.) Swingle	0.92**	y = 0.073(x) – 0.709	0.073	9.76	1.47
Alnus incana (L.) Moench ssp. rugosa (Du Roi) Clausen	0.94**	y = 0.079(x) – 0.810	0.079	10.26	1.56
Carya tomentosa (Lam. ex Poir.) Nutt.	0.91**	y = 0.049(x) – 0.224	0.049	4.58	1.24
Catalpa speciosa (Warder) Warder ex Engelm.	0.95**	y = 0.069(x) – 0.399	0.069	5.81	1.66
Cornus amomum P. Mill.	0.93**	y = 0.064(x) – 0.437	0.064	6.83	1.48
Cornus sericea L.	0.98**	y = 0.093(x) – 0.825	0.093	8.86	1.97
Gleditsia triacanthos L.	0.97**	y = 0.052(x) – 0.434	0.052	8.31	1.13
Juglans cineraea L.	0.94**	y = 0.040(x) – 0.299	0.040	7.39	0.91
Larix laricina (Du Roi) K. Koch	0.98*	y = 0.065(x) – 0.978	0.065	15.00	0.98
Lindera benzoin (L.) Blume	0.97**	y = 0.052(x) – 0.152	0.052	2.94	1.40
Picea stichensis (Bong.) Carr.	0.87**	y = 0.072(x) – 0.793	0.072	10.97	1.38

Table A.1. (cont'd).

Species	Regression Analyses		Estimated parameters		
	R^2	Equation	QY	LCP	A_{area}
Pinus nigra Arnold	0.90**	y = 0.063(x) – 1.27	0.063	20.15	0.62
Pinus ponderosa Dougl. ex Laws	0.97**	y = 0.051(x) – 1.32	0.051	25.66	0.22
Pinus strobus L.	0.96**	y = 0.082(x) – 0.885	0.082	10.73	1.59
Platanus occidentalis L.	0.92**	y = 0.088(x) – 1.03	0.088	11.64	1.62
Pseudotsuga menziesii	0.98**	y = 0.052(x) – 0.902	0.052	17.21	0.67
Quercus alba L.	0.96**	y = 0.046(x) – 0.326	0.046	7.01	1.07
Quercus bicolor Willd.	0.98**	y = 0.053(x) – 0.241	0.053	4.51	1.36
Quercus coccinea Muenchh.	0.95**	y = 0.051(x) – 0.328	0.051	6.43	1.20
Quercus macrocarpa Michx.	0.97**	y = 0.053(x) – 0.297	0.053	5.63	1.28
Quercus phellos L.	0.91**	y = 0.047(x) – 0.388	0.047	8.21	1.03
Quercus prinus L.	0.99**	y = 0.058(x) – 0.433	0.058	7.41	1.32
Quercus robur L.	0.99**	y = 0.048(x) – 0.367	0.048	7.63	1.08
Quercus rubra L.	0.96**	y = 0.060(x) – 0.412	0.060	6.84	1.39
Quercus velutina Lam.	0.95**	y = 0.058(x) – 0.265	0.058	4.60	1.46
Rhus typhina L.	0.98**	y = 0.091(x) – 0.866	0.091	9.57	1.85
Robinia pseudoacacia L.	0.96**	y = 0.063(x) – 0.714	0.063	11.37	1.17
Ulmus americana L.	0.99**	y = 0.086(x) – 0.778	0.086	9.07	1.80

Note: *P < 0.001, **P < 0.0001.

Table A.2. Means, standard deviations and ranges of measurement times (0.0–24.00 h local time) across sites and measurement periods during the 2002 growing season.

Site		Measurement Periods 1 (June 9–25)	2 (July 11–23)	3 (July 24–August 8)	4 (August 12–30)
OW-1	*n*	134	122	142	102
	Mean (SD)	13.4 (2.5)	13.6 (2.1)	13.8 (2.3)	13.3 (2.3)
	Median	13.8	14.1	14.2	13
	Range	9.2–17.6	9.9–17.0	9.5–17.0	9.8–17.1
OW-2	*n*	110	114	144	148
	Mean (SD)	14.7 (2.7)	13.3 (2.1)	13.6 (2.2)	12.8 (2.4)
	Median	15.3	13.1	13.8	12.4
	Range	9.5–18.2	9.5–16.8	9.8–16.9	9.0–17.2
IC-1	*n*	169	201	126	138
	Mean (SD)	13.8 (2.2)	13.8 (1.8)	13.4 (2.1)	13.3 (2.5)
	Median	13.9	14.1	13.2	13.1
	Range	9.8–17.4	10.8–16.9	10.2–16.9	9.4–17.3
IC-2	*n*	222	134	124	111
	Mean (SD)	13.0 (2.3)	13.3 (2.2)	13.2 (2.6)	13.4 (2.3)
	Median	12.9	13.2	13.6	13.6
	Range	9.0–17.6	9.8–16.9	9.0–17.2	9.8–16.9
MOR-1	*n*	246	133	182	94
	Mean (SD)	13.5 (2.3)	13.2 (2.5)	12.8 (2.5)	14.4 (1.9)
	Median	13.7	13	12.9	14.7
	Range	9.3–17.4	9.2–17.0	8.8–16.8	11.0–17.5
MOR-2	*n*	219	104	145	109
	Mean (SD)	13.7 (2.1)	13.8 (2.5)	13.7 (2.4)	13.7 (2.1)
	Median	13.9	13.7	14.1	13.9
	Range	9.8–17.4	9.6–17.7	9.3–17.2	10.3–17.1

Table A.3. Results of a standard least squares linear model for main effects and interactions of measurement periods ($n = 4$), site ($n = 6$) and species ($n = 8$) on measurement times of leaf-level gas-exchange.

ANOVA effects	d.f.	SS	*F*	*P*
Measurement period	3	45.42	2.89	0.034
Site	5	74.88	2.86	0.014
Measurement period × Site	15	424.36	5.40	$P < 0.0001$
Species	7	3.88	0.11	0.998

Note: Overall model, $P < 0.0001$; Adjusted $R^2 = 0.022442$. Weak interactions ($P > 0.25$) were removed from the model (Bancroft, 1964).

Table A.4. Summary of soil moisture categories for gas-exchange analyses. Categories were based on variation in volumetric soil moisture which was measured concurrently with gas-exchange measurements during the 2002 growing season across seedling transplant plots.

		Volumetric soil moisture (%)				
Soil moisture category	Sampling dates	*n*	mean	SD	Min	Max
Very low	11–23 July	280	3.3	2.2	1.1	12.1
Low	24 July–8 August	280	4.2	2.4	0.9	12.4
Moderate	12–30 August	224	6.8	4.1	1.6	18.1
High	9–25 June	248	11.2	5.2	4.5	32.1

Table A.5. Results of a standard least squares mixed linear model for main effects and interactions of canopy openness (%), site (n = 6) and sampling date (n = 6) on gravimetric soil moisture (%) across seedling transplant plots.

					Whole-model	
ANOVA effects	d.f.	SS	F	P	P	Adj. R^2
site	5	2.5	19.4	< 0.0001	< 0.0001	0.64
date	5	5.5	43.4	< 0.0001		
site × date	25	1.0	1.6	0.0387		
$\log_{10}$ canopy openness (%)	1	0.1	4.0	0.0461		

Note: Models exclude interaction terms when $P > 0.25$ in preliminary model (Bancroft, 1964).

Table A.6. Results of a standard least squares mixed model for the main effects and interactions of $\log_{10}$ (whole-plant mass) (g), site ($n = 6$) and species ($n = 8$) on $\log_{10}$ (root mass) (g). The model is based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

					Whole-model	
ANOVA effects	d.f.	SS	*F*	*P*	*P*	Adj. R^2
Site	5	0.54	13.63	< 0.0001	< 0.0001	0.98
Species	7	2.33	42.02	< 0.0001		
Site × species	35	0.69	2.48	< 0.0001		
$\log_{10}$ whole-plant mass	1	66.46	8399.10	< 0.0001		
Site × $\log_{10}$ whole-plant mass	5	0.03	0.68	0.6389		
Species × $\log_{10}$ whole-plant mass	7	0.15	2.65	0.0102		
Site × species × $\log_{10}$ whole-plant mass	35	0.51	1.83	0.0024		

Table A.7. Results of a standard least squares mixed model for the main effects and interactions of $\log_{10}$ (root mass) (g), site ($n = 6$) and species ($n = 8$) on $\log_{10}$ (root area) (cm^2). The model is based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

					Whole-model	
ANOVA effects	d.f.	SS	*F*	*P*	*P*	Adj. R^2
Site	5	0.56	5.56	< 0.0001	< 0.0001	0.87
Species	7	7.70	54.41	< 0.0001		
Site × species	35	1.77	2.50	< 0.0001		
$\log_{10}$ root mass	1	47.51	2350.07	< 0.0001		
Site × $\log_{10}$ root mass	5	0.11	1.08	0.3669		
Species × $\log_{10}$ root mass	7	0.80	5.65	< 0.0001		
Site × species × $\log_{10}$ root mass	35	1.01	1.43	0.0499		

Table A.8. Results of a standard least squares mixed model for the main effects and interactions of $\log_{10}$ (whole-plant mass) (g), site ($n = 6$) and species ($n = 8$) on $\log_{10}$ (root depth) (cm). The model is based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

					Whole-model	
ANOVA effects	d.f.	SS	*F*	*P*	*P*	Adj. R^2
Site	5	0.52	3.18	0.0074	< 0.0001	0.55
Species	7	0.53	2.30	0.0250		
Site × species	35	1.87	1.63	0.0116		
$\log_{10}$ whole-plant mass	1	10.13	309.32	< 0.0001		
Site × $\log_{10}$ whole-plant mass	5	0.19	1.16	0.3259		
Species × $\log_{10}$ whole-plant mass	7	1.43	6.23	< 0.0001		
Site × species × $\log_{10}$ whole-plant mass	35	1.85	1.61	0.0135		

Table A.9. Results of a standard least squares mixed model for the main effects and interactions of $\log_{10}$ (whole-plant mass) (g), site ($n = 6$) and species ($n = 8$) on $\log_{10}$ (leaf area) (cm^2). The model is based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

					Whole-model	
ANOVA effects	d.f.	SS	*F*	*P*	*P*	Adj. R^2
Site	5	5.50	14.15	< 0.0001	< 0.0001	0.75
Species	7	15.16	27.85	< 0.0001		
Site × species	35	4.46	1.64	0.0110		
$\log_{10}$ whole-plant mass	1	102.86	1322.70	< 0.0001		
Site × $\log_{10}$ whole-plant mass	5	0.69	1.79	0.1129		
Species × $\log_{10}$ whole-plant mass	7	2.07	3.81	0.0004		
Site × species × $\log_{10}$ whole-plant mass	35	3.27	1.20	0.1971		

Table A.10. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root mass (g) for individual species and all species combined within OW 1 (well-drained outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 26)	1.095	0.945, 1.270	−0.237	−0.274, −0.200	< 0.0001	0.876
Quercus alba (*n* = 12)	0.876	0.744, 1.031	−0.202	−0.233, −0.171	< 0.0001	0.946
Quercus rubra (*n* = 45)	1.002	0.902, 1.114	−0.212	−0.246, −0.178	< 0.0001	0.882
Prunus serotina (*n* = 12)	0.949	0.766, 1.175	−0.234	−0.360, −0.107	< 0.0001	0.906
Acer rubrum (*n* = 15)	1.144	0.931, 1.406	−0.138	−0.338, 0.062	< 0.0001	0.88
Acer saccharum (*n* = 32)	1.134	1.017, 1.264	−0.149	−0.201, −0.097	< 0.0001	0.915
Fraxinus americana (*n* = 34)	1.289	1.094, 1.518	−0.188	−0.275, −0.102	< 0.0001	0.792
All species (*n* = 181)	1.069	1.038, 1.102	−0.220	−0.234, −0.205	< 0.0001	0.959

Note: Test for common slope across species: test statistic = 14.817, *P* = 0.028. Due to inadequate sample size (*n* < 6), *Betula alleghaniensis* was excluded from the analysis.

Table A.11. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root mass (g) for individual species and all species combined within OW2 (sub-irrigated outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 39)	1.008	0.915, 1.109	−0.212	−0.233, −0.190	< 0.0001	0.916
Quercus alba (*n* = 11)	1.181	0.986, 1.416	−0.225	−0.280, −0.170	< 0.0001	0.942
Quercus rubra (*n* = 41)	0.990	0.892, 1.099	−0.240	−0.280, −0.200	< 0.0001	0.897
Prunus serotina (*n* = 22)	1.087	0.910, 1.297	−0.325	−0.442, −0.208	< 0.0001	0.854
Acer rubrum (*n* = 15)	1.093	0.812, 1.473	−0.236	−0.536, 0.064	< 0.0001	0.745
Acer saccharum (*n* = 36)	1.014	0.913, 1.125	−0.246	−0.282, −0.210	< 0.0001	0.910
Fraxinus americana (*n* = 24)	1.049	0.902, 1.219	−0.329	−0.396, −0.261	< 0.0001	0.883
Betula alleghaniensis (*n* = 14)	0.742	0.614, 0.898	−0.714	−0.839, −0.589	< 0.0001	0.907
All species (*n* = 202)	1.128	1.095, 1.162	−0.263	−0.280, −0.247	< 0.0001	0.955

Note: Test for common slope across species: test statistic =12.647, $P = 0.09$. Tests for shifts in elevation between species using WALD statistic: test statistic = 72.284, $P < 0.0001$.

Table A.12. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root mass (g) for individual species and all species combined within IC 1 (well-drained ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 47)	0.946	0.868, 1.030	−0.176	−0.193, −0.159	< 0.0001	0.918
Quercus alba (*n* = 18)	1.092	0.953, 1.252	−0.214	−0.249, −0.180	< 0.0001	0.933
Quercus rubra (*n* = 49)	0.907	0.829, 0.993	−0.175	−0.199, −0.150	< 0.0001	0.906
Prunus serotina (*n* = 43)	1.141	1.002, 1.299	−0.204	−0.329, −0.079	< 0.0001	0.829
Acer rubrum (*n* = 26)	1.151	1.022,1.296	−0.145	−0.278, −0.011	< 0.0001	0.920
Acer saccharum (*n* = 52)	1.020	0.931, 1.119	−0.256	−0.299, −0.213	< 0.0001	0.895
Fraxinus americana (*n* = 45)	1.026	0.938, 1.123	−0.303	−0.351, −0.255	< 0.0001	0.913
Betula alleghaniensis (*n* = 13)	0.979	0.786, 1.219	−0.557	−0.792, −0.323	< 0.0001	0.889
All species (*n* = 293)	1.131	1.106, 1.156	−0.221	−0.236, −0.207	< 0.0001	0.964

Note: Test for common slope across species: test statistic = 17.253, *P* = 0.014.

Table A.13. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root mass (g) for individual species and all species combined within IC 2 (sub-irrigated ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 44)	1.059	0.986, 1.139	−0.194	−0.210, −0.179	< 0.0001	0.946
Quercus alba (*n* = 31)	0.960	0.823, 1.119	−0.207	−0.233, −0.181	< 0.0001	0.836
Quercus rubra (*n* = 54)	1.078	0.985, 1.181	−0.209	−0.234, −0.184	< 0.0001	0.893
Prunus serotina (*n* = 30)	0.995	0.863, 1.148	−0.363	−0.483, −0.243	< 0.0001	0.864
Acer rubrum (*n* = 17)	1.194	0.926, 1.540	−0.266	−0.629, 0.097	< 0.0001	0.782
Acer saccharum (*n* = 41)	1.345	1.213, 1.492	−0.144	−0.205, −0.083	< 0.0001	0.898
Fraxinus americana (*n* = 42)	1.100	0.970, 1.247	−0.221	−0.311, −0.132	< 0.0001	0.844
Betula alleghaniensis (*n* = 14)	1.085	0.813, 1.447	−0.340	−0.727, 0.048	< 0.0001	0.785
All species (*n* = 273)	1.175	1.153, 1.197	−0.214	−0.227,−0.200	< 0.0001	0.975

Note: Test for common slope across species: test statistic = 19.602, *P* = 0.008.

Table A.14. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root mass (g) for individual species and all species combined within MOR 1 (well-drained moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 31)	1.02	0.930, 1.113	−0.177	−0.198, −0.168	< 0.0001	0.94
Quercus alba (*n* = 19)	0.91	0.793, 1.053	−0.203	−0.239, −0.168	< 0.0001	0.92
Quercus rubra (*n* = 44)	0.99	0.901, 1.079	−0.204	−0.238, −0.171	< 0.0001	0.92
Prunus serotina (*n* = 28)	1.29	1.104, 1.503	−0.241	−0.401, −0.081	< 0.0001	0.85
Acer rubrum (*n* = 35)	1.08	0.939, 1.235	−0.351	−0.484, −0.218	< 0.0001	0.85
Acer saccharum (*n* = 28)	0.92	0.834, 1.019	−0.367	−0.401, −0.333	< 0.0001	0.94
Fraxinus americana (*n* = 46)	1.10	1.023, 1.174	−0.316	−0.354, −0.278	< 0.0001	0.95
All species (*n* = 236)	1.18	1.154, 1.213	−0.268	−0.284, −0.251	< 0.0001	0.96

Note: Test for common slope across species: test statistic = 19.6, $P = 0.004$. Due to inadequate sample size ($n < 6$), *Betula alleghaniensis* was excluded from the analysis.

Table A.15. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root mass (g) for individual species and all species combined within MOR 2 (sub-irrigated moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 42)	0.966	0.889, 1.050	−0.250	−0.273, −0.227	< 0.0001	0.931
Quercus alba (*n* = 16)	1.013	0.827, 1.241	−0.310	−0.399, −0.221	< 0.0001	0.873
Quercus rubra (*n* = 58)	0.897	0.850, 0.946	−0.243	−0.267, −0.220	< 0.0001	0.960
Prunus serotina (*n* = 61)	1.086	0.991, 1.191	−0.373	−0.458, −0.287	< 0.0001	0.874
Acer rubrum (*n* = 28)	1.110	0.963, 1.280	−0.369	−0.536, −0.202	< 0.0001	0.875
Acer saccharum (*n* = 28)	1.102	0.834, 1.456	−0.309	−0.497, −0.120	< 0.0001	0.510
Fraxinus americana (*n* = 55)	1.037	0.962, 1.118	−0.431	−0.471, −0.391	< 0.0001	0.925
Betula alleghaniensis (*n* = 30)	1.058	0.972, 1.152	−0.673	−0.725, −0.621	< 0.0001	0.952
All species (*n* = 318)	1.119	1.089, 1.151	−0.365	−0.385, −0.345	< 0.0001	0.938

Note: Test for common slope across species: test statistic = 23.522, *P* = 0.003.

Table A.16. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between root mass (g) and root area (cm^2) for individual species and all species combined within OW 1 (well-drained outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 26)	0.762	0.563, 1.032	1.758	1.700, 1.816	< 0.0001	0.465
Quercus alba (*n* = 12)	1.103	0.766, 1.587	1.818	1.709, 1.927	< 0.0001	0.721
Quercus rubra (*n* = 45)	1.584	1.236, 2.030	1.714	1.616, 1.812	< 0.0001	0.336
Prunus serotina (*n* = 12)	0.948	0.670, 1.341	2.005	1.733, 2.276	< 0.0001	0.747
Acer rubrum (*n* = 15)	1.452	0.8968, 2.352	2.654	1.851, 3.457	0.034	0.301
Acer saccharum (*n* = 32)	1.284	1.064, 1.550	2.209	2.059, 2.359	< 0.0001	0.742
Fraxinus americana (*n* = 34)	1.117	0.907, 1.374	2.283	2.119, 2.448	< 0.0001	0.663
All species (*n* = 181)	0.819	0.737, 0.909	1.876	1.821, 1.932	< 0.0001	0.491

Note: Test for common slope across species: test statistic = 16.625, *P* = 0.011. Due to inadequate sample size (*n* < 6), *Betula alleghaniensis* was excluded from the analysis.

Table A.17. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between root mass (g) and root area (cm^2) for individual species and all species combined within OW 2 (sub-irrigated outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 39)	1.118	0.882, 1.416	1.850	1.782, 1.919	< 0.0001	0.487
Quercus alba (*n* = 11)	0.716	0.493, 1.040	1.788	1.700, 1.875	0.001	0.742
Quercus rubra (*n* = 41)	1.119	0.899, 1.392	1.842	1.785, 1.899	< 0.0001	0.537
Prunus serotina (*n* = 22)	0.929	0.746, 1.158	2.100	1.901, 2.298	< 0.0001	0.774
Acer rubrum (*n* = 15)	0.941	0.715, 1.239	2.266	1.946, 2.586	< 0.0001	0.784
Acer saccharum (*n* = 34)	1.138	1.010, 1.282	2.228	2.153, 2.303	< 0.0001	0.890
Fraxinus americana (*n* = 25)	1.125	0.942, 1.345	2.376	2.226, 2.527	< 0.0001	0.828
Betula alleghaniensis (*n* = 14)	0.983	0.772, 1.253	2.519	2.196, 2.843	< 0.0001	0.849
All species (*n* = 201)	0.694	0.648, 0.743	1.929	1.895, 1.962	< 0.0001	0.762

Note: Test for common slope across species: test statistic = 9.131, $P = 0.209$. Tests for shifts in elevation between species using WALD statistic: test statistic = 224.861, $P < 0.0001$.

Table A.18. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between root mass (g) and root area (cm^2) for individual species and all species combined within IC 1 (well-drained ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 48)	0.897	0.763, 1.053	1.741	1.706, 1.776	< 0.0001	0.703
Quercus alba (*n* = 18)	0.990	0.797, 1.229	1.734	1.675, 1.794	< 0.0001	0.830
Quercus rubra (*n* = 47)	1.060	0.870, 1.293	1.729	1.686, 1.772	< 0.0001	0.558
Prunus serotina (*n* = 41)	0.996	0.848, 1.170	2.079	1.895, 2.264	< 0.0001	0.751
Acer rubrum (*n* = 26)	0.780	0.656, 0.928	2.018	1.846, 2.189	< 0.0001	0.830
Acer saccharum (*n* = 52)	1.185	1.023, 1.373	2.246	2.124, 2.368	< 0.0001	0.729
Fraxinus americana (*n* = 45)	1.108	0.980, 1.252	2.289	2.179, 2.398	< 0.0001	0.840
Betula alleghaniensis (*n* = 13)	0.846	0.510, 1.404	2.199	1.479, 2.918	0.028	0.366
All species (*n* = 290)	0.711	0.674, 0.751	1.839	1.808, 1.870	< 0.0001	0.783

Note: Test for common slope across species: test statistic = 17.552, *P* = 0.008.

Table A.19. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between root mass (g) and root area (cm^2) for individual species and all species combined within IC 2 (sub-irrigated ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 44)	0.802	0.645, 0.996	1.773	1.719, 1.826	< 0.0001	0.505
Quercus alba (*n* = 31)	1.129	0.853, 1.495	1.815	1.742, 1.889	< 0.0001	0.439
Quercus rubra (*n* = 53)	1.100	0.888, 1.363	1.802	1.751, 1.853	< 0.0001	0.410
Prunus serotina (*n* = 32)	0.963	0.800, 1.158	2.111	1.896, 2.327	< 0.0001	0.752
Acer rubrum (*n* = 17)	0.761	0.555, 1.042	2.153	1.745, 2.561	< 0.0001	0.662
Acer saccharum (*n* = 41)	1.276	1.051, 1.549	2.351	2.170, 2.532	< 0.0001	0.636
Fraxinus americana (*n* = 43)	0.916	0.722, 1.164	2.163	1.959, 2.367	< 0.0001	0.416
Betula alleghaniensis (*n* = 14)	0.953	0.692, 1.312	2.453	1.938, 2.969	< 0.0001	0.732
All species (*n* = 275)	0.646	0.612, 0.682	1.831	1.801, 1.861	< 0.0001	0.795

Note: Test for common slope across species: test statistic = 15.155, *P* = 0.038.

Table A.20. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between root mass (g) and root area (cm^2) for individual species and all species combined within MOR 1 (well-drained moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 32)	0.895	0.717, 1.118	1.803	1.738, 1.867	< 0.0001	0.638
Quercus alba (*n* = 18)	1.013	0.738, 1.392	1.779	1.700, 1.859	< 0.0001	0.630
Quercus rubra (*n* = 40)	1.162	0.988, 1.370	1.761	1.713, 1.808	< 0.0001	0.753
Prunus serotina (*n* = 27)	0.552	0.409, 0.747	1.647	1.436, 1.859	< 0.0001	0.448
Acer rubrum (*n* = 31)	0.897	0.765, 1.052	2.255	2.073, 2.437	< 0.0001	0.823
Acer saccharum (*n* = 28)	0.894	0.763, 1.047	2.194	2.104, 2.284	< 0.0001	0.845
Fraxinus americana (*n* = 43)	0.900	0.810, 1.000	2.328	2.252, 2.404	< 0.0001	0.888
All species (*n* = 224)	0.695	0.650, 0.743	1.940	1.902, 1.979	< 0.0001	0.744

Note: Test for common slope across species: test statistic = 18.638, *P* = 0.009. Due to inadequate sample size (*n* < 6), *Betula alleghaniensis* was excluded from the analysis.

Table A.21. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between root mass (g) and root area (cm^2) for individual species and all species combined within MOR 2 (sub-irrigated moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 42)	1.228	0.932, 1.618	1.823	1.699, 1.946	0.001	0.237
Quercus alba (*n* = 16)	0.913	0.680, 1.226	1.860	1.750, 1.969	< 0.0001	0.727
Quercus rubra (*n* = 58)	1.211	1.002, 1.463	1.752	1.671, 1.834	< 0.0001	0.495
Prunus serotina (*n* = 61)	0.906	0.773, 1.063	2.124	1.938, 2.310	< 0.0001	0.623
Acer rubrum (*n* = 28)	0.823	0.674, 1.005	2.208	1.955, 2.461	< 0.0001	0.751
Acer saccharum (*n* = 28)	1.104	0.910, 1.339	2.418	2.213, 2.623	< 0.0001	0.768
Fraxinus americana (*n* = 55)	0.956	0.839, 1.089	2.278	2.168, 2.388	< 0.0001	0.775
Betula alleghaniensis (*n* = 30)	0.876	0.757, 1.013	2.307	2.169, 2.446	< 0.0001	0.858
All species (*n* = 318)	0.731	0.688, 0.776	1.944	1.902, 1.987	< 0.0001	0.703

Note: Test for common slope across species: test statistic = 15.392, *P* = 0.033.

Table A.22. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root depth (cm) for individual species and all species combined within OW 1 (well-drained outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 26)	1.075	0.731, 1.579	1.226	1.116, 1.336	0.078	0.123
Quercus alba (*n* = 12)	1.407	0.859, 2.307	1.161	0.992, 1.330	0.014	0.467
Quercus rubra (*n* = 45)	1.979	1.488, 2.634	0.786	0.582, 0.990	0.023	0.114
Prunus serotina (*n* = 12)	0.740	0.396, 1.381	1.393	1.078, 1.708	0.299	0.107
Acer rubrum (*n* = 15)	−1.194	−2.091, −0.682	0.001	−0.607, 0.608	0.536	0.03
Acer saccharum (*n* = 32)	1.683	1.244, 2.275	1.687	1.462, 1.912	0.001	0.325
Fraxinus americana (*n* = 34)	2.013	1.442, 2.810	1.781	1.492, 2.070	0.055	0.111
All species (*n* = 181)	0.876	0.767, 1.000	1.299	1.237, 1.361	< 0.0001	0.183

Note: Test for common slope across species: test statistic = 15.217, *P* = 0.018. Due to inadequate sample size (*n* < 6), *Betula alleghaniensis* was excluded from the analysis.

Table A.23. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root depth (cm) for individual species and all species combined within OW 2 (sub-irrigated outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 38)	1.003	0.757, 1.330	1.273	1.202, 1.343	0.001	0.287
Quercus alba (*n* = 11)	0.907	0.548, 1.502	1.245	1.116, 1.375	0.013	0.514
Quercus rubra (*n* = 41)	0.870	0.683, 1.109	1.142	1.057, 1.226	< 0.0001	0.428
Prunus serotina (*n* = 22)	0.555	0.368, 0.838	1.362	1.215, 1.509	0.053	0.174
Acer rubrum (*n* = 15)	0.746	0.44, 1.264	1.591	1.212, 1.969	0.155	0.149
Acer saccharum (*n* = 35)	1.093	0.879, 1.359	1.458	1.374, 1.542	< 0.0001	0.616
Fraxinus americana (*n* = 24)	1.074	0.713, 1.618	1.412	1.204, 1.621	0.148	0.093
Betula alleghaniensis (*n* = 14)	0.515	0.319, 0.830	1.387	1.159, 1.615	0.019	0.377
All species (*n* = 200)	0.594	0.542, 0.652	1.316	1.287, 1.345	< 0.0001	0.561

Note: Test for common slope across species: test statistic = 15.282, *P* = 0.033.

Table A.24. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root depth (cm) for individual species and all species combined within IC 1 (well-drained ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 45)	1.058	0.805, 1.389	1.297	1.226, 1.368	0.003	0.193
Quercus alba (*n* = 18)	1.220	0.881, 1.689	1.144	1.047, 1.241	< 0.0001	0.610
Quercus rubra (*n* = 46)	1.290	0.982, 1.693	1.041	0.927, 1.156	0.004	0.178
Prunus serotina (*n* = 36)	0.945	0.671, 1.329	1.684	1.410, 1.959	0.793	0.002
Acer rubrum (*n* = 24)	0.764	0.513, 1.138	1.621	1.303, 1.938	0.068	0.143
Acer saccharum (*n* = 49)	1.107	0.871, 1.406	1.499	1.371, 1.628	< 0.0001	0.322
Fraxinus americana (*n* = 45)	0.720	0.540, 0.961	1.326	1.208, 1.444	0.04	0.094
Betula alleghaniensis (*n* = 13)	0.738	0.412, 1.323	1.578	1.078, 2.077	0.215	0.136
All species (*n* = 276)	0.618	0.565, 0.676	1.313	1.278, 1.347	< 0.0001	0.427

Note: Test for common slope across species: test statistic = 13.646, $P = 0.066$. Tests for shifts in elevation between species using WALD statistic: test statistic = 92.016, $P < 0.0001$.

Table A.25. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root depth (cm) for individual species and all species combined within IC 2 (sub-irrigated ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 44)	0.984	0.740, 1.307	1.244	1.175, 1.313	0.011	0.144
Quercus alba (*n* = 31)	0.962	0.694, 1.334	1.200	1.137, 1.264	0.006	0.233
Quercus rubra (*n* = 54)	1.054	0.805, 1.380	1.097	1.013, 1.181	0.150	0.040
Prunus serotina (*n* = 28)	0.602	0.406, 0.891	1.432	1.215, 1.648	0.837	0.002
Acer rubrum (*n* = 14)	0.703	0.408, 1.213	1.730	1.257, 2.202	0.140	0.173
Acer saccharum (*n* = 41)	1.229	0.901, 1.677	1.577	1.400, 1.754	0.154	0.051
Fraxinus americana (*n* = 41)	0.841	0.613, 1.153	1.468	1.287, 1.649	0.392	0.019
Betula alleghaniensis (*n* = 14)	0.970	0.635, 1.483	1.873	1.354, 2.393	0.004	0.517
All species (*n* = 267)	0.515	0.471, 0.562	1.273	1.244, 1.301	< 0.0001	0.462

Note: Test for common slope across species: test statistic = 10.273, $P = 0.188$. Tests for shifts in elevation between species using WALD statistic: test statistic = 92.672, $P < 0.0001$.

Table A.26. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root depth (cm) for individual species and all species combined within MOR 1 (well-drained moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 31)	0.946	0.722, 1.240	1.244	1.178, 1.309	< 0.0001	0.480
Quercus alba (*n* = 18)	0.668	0.463, 0.963	1.183	1.109, 1.256	0.001	0.502
Quercus rubra (*n* = 44)	0.977	0.743, 1.284	0.975	0.867, 1.082	0.002	0.210
Prunus serotina (*n* = 28)	−0.616	−0.909, −0.417	0.443	0.239, 0.646	0.473	0.020
Acer rubrum (*n* = 35)	0.559	0.412, 0.761	1.359	1.200, 1.519	0.004	0.224
Acer saccharum (*n* = 28)	0.705	0.519, 0.958	1.296	1.212, 1.381	< 0.0001	0.405
Fraxinus americana (*n* = 43)	0.598	0.453, 0.790	1.278	1.186, 1.369	0.002	0.203
All species (*n* = 232)	0.491	0.448, 0.538	1.228	1.202, 1.255	< 0.0001	0.507

Note: Test for common slope across species: test statistic = 13.823, *P* = 0.03. Due to inadequate sample size (*n* < 6), *Betula alleghaniensis* was excluded from the analysis.

Table A.27. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and root depth (cm) for individual species and all species combined within MOR 2 (sub-irrigated moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 42)	0.842	0.688, 1.029	1.137	1.085, 1.189	< 0.0001	0.598
Quercus alba (*n* = 16)	0.751	0.557, 1.012	1.157	1.058, 1.256	< 0.0001	0.721
Quercus rubra (*n* = 58)	0.917	0.757, 1.112	0.929	0.838, 1.020	< 0.0001	0.478
Prunus serotina (*n* = 61)	0.999	0.807, 1.238	1.694	1.508, 1.880	< 0.0001	0.317
Acer rubrum (*n* = 28)	1.040	0.729, 1.483	1.788	1.386, 2.190	0.021	0.189
Acer saccharum (*n* = 28)	−0.737	−1.085, −0.500	0.579	0.397, 0.761	0.350	0.034
Fraxinus americana (*n* = 55)	0.560	0.462, 0.678	1.223	1.167, 1.280	< 0.0001	0.512
Betula alleghaniensis (*n* = 30)	0.475	0.384, 0.587	1.050	0.990, 1.111	< 0.0001	0.695
All species (*n* = 318)	0.553	0.513, 0.597	1.202	1.173, 1.230	< 0.0001	0.524

Note: Test for common slope across species: test statistic = 39.241, *P* = 0.001.

Table A.28. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and leaf area (cm^2) for individual species and all species combined within OW 1 (well-drained outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 26)	1.757	1.265, 2.440	1.577	1.434, 1.720	0.001	0.370
Quercus alba (*n* = 12)	2.760	1.754, 4.345	1.474	1.176, 1.771	0.005	0.556
Quercus rubra (*n* = 45)	2.437	1.963, 3.027	1.169	0.991, 1.347	< 0.0001	0.496
Prunus serotina (*n* = 12)	1.400	0.917, 2.140	1.742	1.361, 2.123	0.003	0.616
Acer rubrum (*n* = 15)	1.183	0.816, 1.715	1.834	1.455, 2.214	0.001	0.598
Acer saccharum (*n* = 32)	1.339	1.061, 1.689	1.700	1.565, 1.834	< 0.0001	0.605
Fraxinus americana (*n* = 34)	1.877	1.481, 2.378	1.920	1.736, 2.105	< 0.0001	0.559
All species (*n* = 181)	1.268	1.161, 1.385	1.621	1.567, 1.675	< 0.0001	0.643

Note: Test for common slope across species: test statistic = 23.212, *P* = 0.002. Due to inadequate sample size (*n* < 6), *Betula alleghaniensis* was excluded from the analysis.

Table A.29. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and leaf area (cm^2) for individual species and all species combined within OW 2 (sub-irrigated outwash site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 39)	2.400	1.804, 3.193	1.422	1.249, 1.595	0.001	0.246
Quercus alba (*n* = 11)	1.753	1.367, 2.247	1.646	1.533, 1.759	< 0.0001	0.889
Quercus rubra (*n* = 40)	2.385	1.964, 2.896	1.097	0.912, 1.281	< 0.0001	0.646
Prunus serotina (*n* = 22)	1.325	1.051, 1.672	2.014	1.825, 2.202	< 0.0001	0.748
Acer rubrum (*n* = 15)	2.136	1.382, 3.300	2.747	1.872, 3.621	0.007	0.438
Acer saccharum (*n* = 36)	1.391	1.206, 1.605	1.886	1.818, 1.954	< 0.0001	0.831
Fraxinus americana (*n* = 24)	1.641	1.281, 2.102	2.023	1.846, 2.200	< 0.0001	0.679
Betula alleghaniensis (*n* = 14)	1.439	1.198, 1.728	2.363	2.130, 2.596	< 0.0001	0.914
All species (*n* = 201)	1.140	1.044, 1.246	1.734	1.682, 1.786	< 0.0001	0.598

Note: Test for common slope across species: test statistic = 31.950, *P* = 0.001.

Table A.30. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and leaf area (cm^2) for individual species and all species combined within IC 1 (well-drained ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 47)	2.552	2.021, 3.223	1.445	1.307, 1.582	< 0.0001	0.384
Quercus alba (*n* = 18)	1.408	0.989, 2.004	1.665	1.541, 1.789	0.001	0.537
Quercus rubra (*n* = 49)	2.453	1.977, 3.044	1.196	1.028, 1.364	< 0.0001	0.451
Prunus serotina (*n* = 42)	1.791	1.446, 2.218	2.360	2.041, 2.679	< 0.0001	0.546
Acer rubrum (*n* = 26)	1.491	1.174, 1.893	2.139	1.787, 2.490	< 0.0001	0.672
Acer saccharum (*n* = 52)	1.464	1.291, 1.660	1.975	1.89, 2.061	< 0.0001	0.802
Fraxinus americana (*n* = 44)	1.654	1.457, 1.878	2.130	2.020, 2.241	< 0.0001	0.833
Betula alleghaniensis (*n* = 13)	1.228	0.885, 1.705	2.297	1.853, 2.741	< 0.0001	0.747
All species (*n* = 291)	1.151	1.072, 1.236	1.746	1.696, 1.795	< 0.0001	0.622

Note: Test for common slope across species: test statistic = 33.497, *P* = 0.001.

Table A.31. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and leaf area (cm^2) for individual species and all species combined within IC 2 (sub-irrigated ice contact site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 42)	1.847	1.440, 2.370	1.604	1.497, 1.710	< 0.0001	0.379
Quercus alba (*n* = 31)	2.054	1.576, 2.676	1.674	1.571, 1.776	< 0.0001	0.503
Quercus rubra (*n* = 53)	1.940	1.535, 2.453	1.431	1.306, 1.556	< 0.0001	0.291
Prunus serotina (*n* = 30)	1.677	1.453, 1.936	2.357	2.153, 2.561	< 0.0001	0.861
Acer rubrum (*n* = 17)	1.142	0.768, 1.698	2.245	1.693, 2.796	0.003	0.452
Acer saccharum (*n* = 41)	1.276	1.064, 1.532	1.985	1.882, 2.088	< 0.0001	0.679
Fraxinus americana (*n* = 42)	1.694	1.341, 2.142	2.134	1.873, 2.394	< 0.0001	0.453
Betula alleghaniensis (*n* = 14)	0.959	0.688, 1.336	1.769	1.373, 2.165	< 0.0001	0.712
All species (*n* = 270)	0.997	0.935, 1.064	1.739	1.699, 1.779	< 0.0001	0.708

Note: Test for common slope across species: test statistic = 24.508, *P* = 0.003.

Table A.32. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and leaf area (cm^2) for individual species and all species combined within MOR 1 (well-drained moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 28)	2.399	1.766, 3.259	1.577	1.387, 1.767	< 0.0001	0.404
Quercus alba (*n* = 18)	1.730	1.357, 2.204	1.708	1.588, 1.829	< 0.0001	0.787
Quercus rubra (*n* = 42)	2.082	1.674, 2.59	1.338	1.158, 1.518	< 0.0001	0.526
Prunus serotina (*n* = 26)	1.240	0.971,1.584	2.183	1.941, 2.425	< 0.0001	0.656
Acer rubrum (*n* = 32)	1.152	0.960, 1.382	2.190	2.004, 2.376	< 0.0001	0.758
Acer saccharum (*n* = 26)	1.354	1.161, 1.579	2.085	2.009, 2.160	< 0.0001	0.866
Fraxinus americana (*n* = 44)	1.432	1.135, 1.807	2.166	1.995, 2.337	< 0.0001	0.432
All species (*n* = 221)	1.047	0.961, 1.141	1.894	1.841, 1.946	< 0.0001	0.583

Note: Test for common slope across species: test statistic = 30.101, *P* = 0.001. Due to inadequate sample size (*n* < 6), *Betula alleghaniensis* was excluded from the analysis.

Table A.33. Standardized major axis regression slopes (α), elevations (β), confidence intervals and associated tests of significance for log-log linear relationships between whole-plant mass (g) and leaf area (cm^2) for individual species and all species combined within MOR 2 (sub-irrigated moraine site). Analyses are based on data are from all individual seedlings that were harvested from transplant plots in June 2002.

Species	α	95% C.I.s	Log β	95% C.I.s	*P*-value	R^2
Quercus velutina (*n* = 42)	1.284	1.132, 1.455	1.820	1.773, 1.867	< 0.0001	0.845
Quercus alba (*n* = 16)	1.818	1.224, 2.699	1.641	1.310, 1.973	0.002	0.499
Quercus rubra (*n* = 58)	1.514	1.324, 1.731	1.639	1.538, 1.741	< 0.0001	0.748
Prunus serotina (*n* = 61)	1.711	1.426, 2.052	2.515	2.247, 2.783	< 0.0001	0.507
Acer rubrum (*n* = 28)	1.421	1.207, 1.674	2.448	2.202, 2.694	< 0.0001	0.834
Acer saccharum (*n* = 28)	2.029	1.376, 2.991	2.379	1.875, 2.884	0.414	0.026
Fraxinus americana (*n* = 55)	1.595	1.381, 1.842	2.247	2.128, 2.366	< 0.0001	0.725
Betula alleghaniensis (*n* = 30)	0.795	0.750, 0.842	2.227	2.201, 2.253	< 0.0001	0.978
All species (*n* = 318)	1.150	1.084, 1.219	1.986	1.942, 2.031	< 0.0001	0.721

Note: Test for common slope across species: test statistic = 93.993, *P* = 0.001.

Table A.34. Results of a standard least squares mixed model for the main effects and interactions of $\log_{10}$ (photosynthetic photon flux density, PPFD) (μmol m^{-2} s^{-1}), $\log_{10}$ (leaf N_{area}) (μg cm^{-2}) and site (n = 6) on water-use efficiency (WUE) under very low soil moisture (see methods for soil moisture classification scheme).

					Whole-model	
ANOVA effects	d.f.	SS	*F*	*P*	*P*	Adj. R^2
Site	5	52.7	16.4	<0.0001	<0.0001	0.34
Log_{10} PPFD (μmol m^{-2} s^{-1})	1	11.3	17.7	<0.0001		
Log_{10} leaf N (μg cm^{-2})	1	0.5	0.8	0.3853		
Site × $\log_{10}$ leaf N (μg cm^{-2})	5	8.5	2.7	0.0237		

Note: Weak interactions ($P > 0.25$) were removed from the model (Bancroft, 1964).

Table A.35. Results of a standard least squares mixed linear model for main effects and interactions of canopy openness (%) and site (n = 6) on gravimetric soil moisture (%) across seedling transplant plots. Models were evaluated for five different sampling dates (16 May, 25 June, 9 July, 25 July, 20 August, 8 September) and averaged across the 2002 growing season.

						Whole-model	
Date	ANOVA effects	d.f.	SS	F	P	P	Adj. R^2
16 May	Log_{10} canopy openness (%)	1	0.08	5.04	0.0328	0.0010	0.43
	Site	5	0.20	2.45	0.0582		
25 June	Log_{10} canopy openness (%)	1	0.01	0.44	0.5114	0.0281	0.24
	Site	5	0.36	3.24	0.0197		
9 July	Log_{10} canopy openness (%)	1	0.03	1.22	0.2793	0.0635	0.19
	Site	5	0.19	1.67	0.1737		
25 July	Log_{10} canopy openness (%)	1	0.01	0.81	0.3764	0.0002	0.50
	Site	5	0.54	6.11	0.0006		
20 August	Log_{10} canopy openness (%)	1	0.11	3.81	0.0611	0.0001	0.51
	Site	5	0.64	4.57	0.0036		
8 September	Log_{10} canopy openness (%)	1	0.00	0.00	0.9538	0.0002	0.51
	Site	5	1.49	6.48	0.0004		
Overall Mean	Log_{10} canopy openness (%)	1	0.02	1.73	0.1996	< 0.0001	0.58
	Site	5	0.42	6.83	0.0003		

Note: Models exclude interaction term when P > 0.25 in preliminary model (Bancroft, 1964).

Table A.36. Results of a standard least squares mixed linear model for main effects and interactions of canopy openness (%) and site (n = 6) on *in situ* nitrogen mineralization rates averaged across the 2002 growing season.

					Whole-model	
ANOVA effects	d.f.	SS	F	P	P	Adj. R^2
Log_{10} canopy openness (%)	1	0.06	2.47	0.1276	< 0.0001	0.58
Site	5	0.77	6.18	0.0006		

Note: Model excludes interaction term when $P > 0.25$ in preliminary model (Bancroft, 1964).

Table A.37. Results of a standard least squares mixed model for the main effects and interactions of $\log_{10}$ (photosynthetic photon flux density, PPFD) (μmol m^{-2} s^{-1}), $\log_{10}$ (root depth) (cm) and site ($n = 6$) on leaf-leaf photosynthesis under very low soil moisture (see methods for soil moisture classification scheme). The model is based on plot-level averages of PPFD and root depth for each respective species.

					Whole-model	
ANOVA effects	d.f.	SS	*F*	*P*	*P*	Adj. R^2
Site	5	5.43	3.63	0.0036	< 0.0001	0.49
$\log_{10}$ root depth (cm)	1	0.05	0.16	0.6884		
Site × $\log_{10}$ root depth	5	4.11	2.76	0.0196		
$\log_{10}$ PPFD (μmol m^{-2} s^{-1})	1	1.72	5.78	0.0171		
Site × $\log_{10}$ PPFD	5	5.22	3.50	0.0047		
$\log_{10}$ root depth × $\log_{10}$ PPFD	1	2.04	6.83	0.0097		
Site × $\log_{10}$ root depth × $\log_{10}$ PPFD	5	9.53	6.39	< 0.0001		

Table A.38. Summary of linear regression analyses for data in Appendix, Figure A.10. In all cases, the dependent variable is deviation in species survival from plot average survival (i.e., calculated as: species average plot survival − overall average plot survival for all species) vs. $\log_{10}$ canopy openness from Figure 3.14. Definitions for abbreviations and units for independent variables are as follows: leaf nitrogen content (N, μg cm^{-2}), whole-plant mass (g), root surface area (cm^2), RMR (root mass ratio, g g^{-1}), SRA (specific root area, cm^2 g^{-1}), root depth (cm), A_{area} (leaf-level photosynthesis during the peak of the drought, μmol CO_2 m^{-2} s^{-1}), WUE (water use efficiency during the peak of the drought, mmol CO_2 mol^{-1} H_2O).

	OW 1			IC 1			MOR 1		
Independent variable	*n*	Adj. R^2	Regression equation	*n*	Adj. R^2	Regression equation	*n*	Adj. R^2	Regression equation
Log_{10} leaf nitrogen	35	0.12*	y = 65.5(x) − 114.1	47	ns		41	0.08*	y = 60.4(x) − 34.5
Log_{10} whole-plant mass	34	0.67***	y = 44.8(x) + 12.1	47	0.33***	y = 31.9(x) + 12.4	41	0.24**	y = 20.0(x) + 9.6
Log_{10} root surface area	34	0.54***	y = 66.3(x) − 100.0	47	0.32***	y = 41.8(x) − 57.5	41	0.24**	y = 25.1(x) − 34.5
RMR	34	ns		47	0.21**	y = 107.3(x) − 58.2	41	0.25**	y = 61.7(x) − 28.5
SRA	34	0.53***	y = −76.8(x) + 157.3	47	0.23**	y = −47.5(x) + 98.2	41	0.21**	y = −30.9(x) + 69.9
Log_{10} root depth	34	0.58***	y = 96.4(x) − 115.2	47	0.19**	y = 50.8(x) − 56.2	41	0.27**	y = 52.9(x) − 54.5
A_{area}	31	0.15*	y = 11.1(x) − 14.1	40	ns		41	ns	
WUE	31	0.16*	y = 10.0(x) − 21.8	40	ns		41	ns	

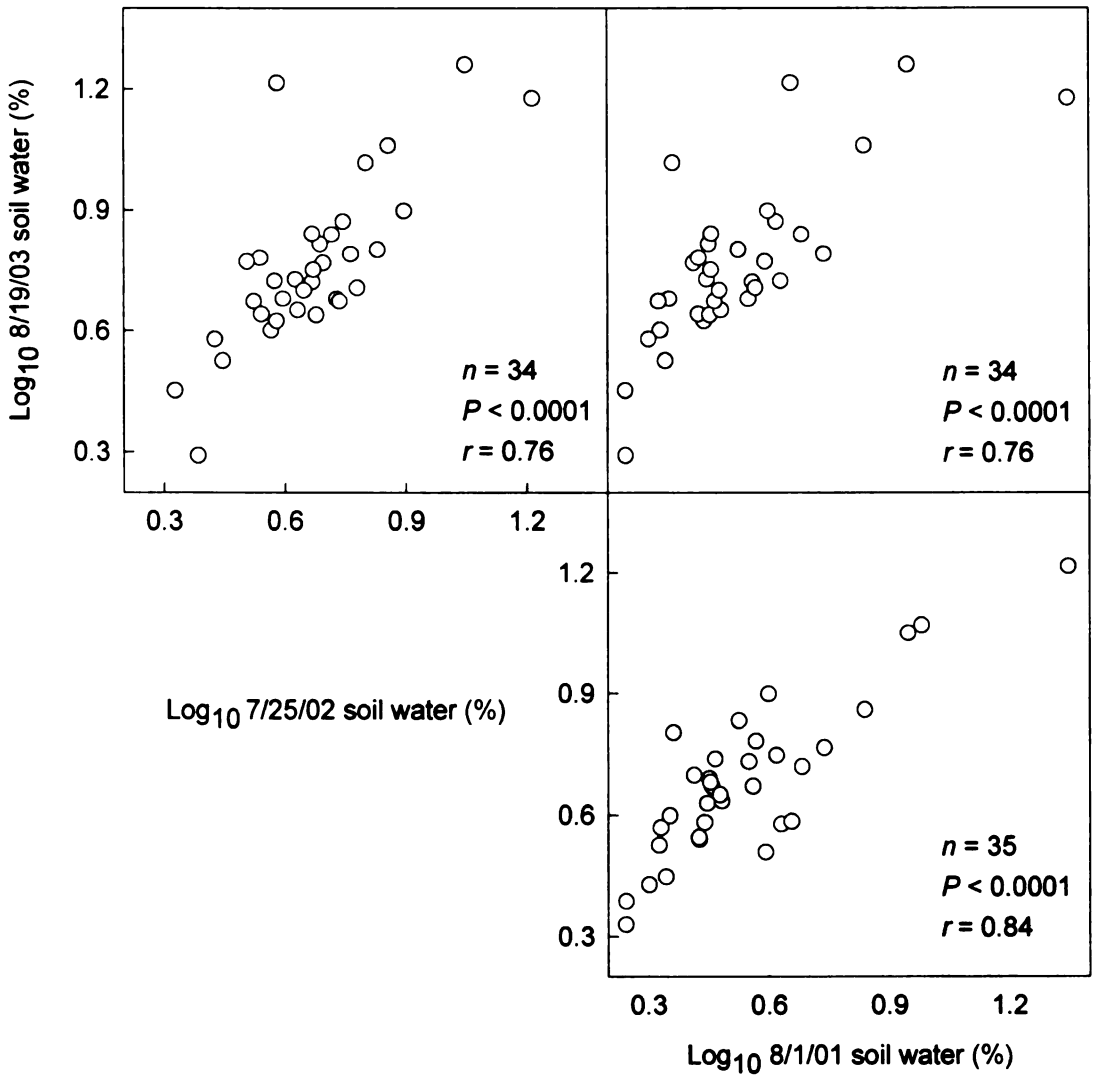


Figure A.1. Correlation matrix of gravimetric soil moisture (%) for the driest sampling date from the 2001, 2002 and 2003 growing seasons. Each datum represents a plot-level average from the seedling transplant experiment. All values were $\log_{10}$ transformed prior to analysis. Sample size, Pearson's correlation coefficients and significance of coefficients are shown in each respective panel.

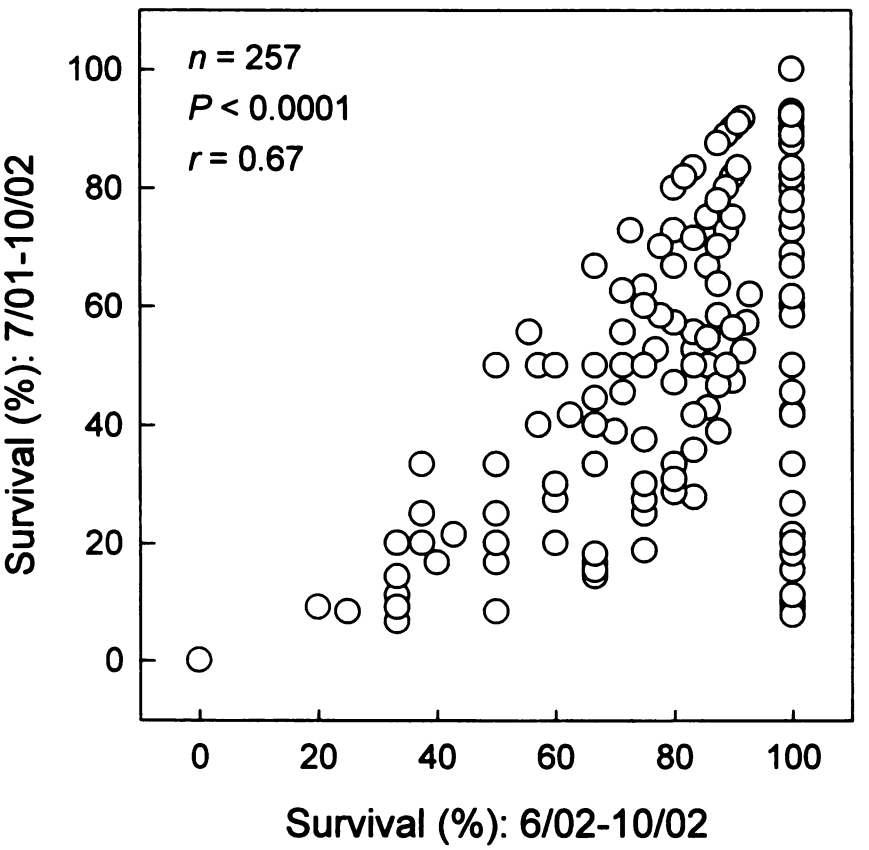


Figure A.2. Correlation between seedling survival (%) recorded after the peak of the drought in 2002 (6/02–10/02) and seedling survival (%) throughout the duration of the seedling transplant experiment (7/01–10/02). Each datum represents a species-specific average of seedling survival at the plot level. Sample size, Pearson's correlation coefficients and significance of coefficients are shown within the panel of the graph.

Figure A.3. Correlations of leaf area ratio (LAR), specific root area (SRA), root mass ratio (RMR), root depth and root surface area with total plant mass. Sample size, Pearson's correlation coefficients and significance of coefficients are shown next to each respective panel.

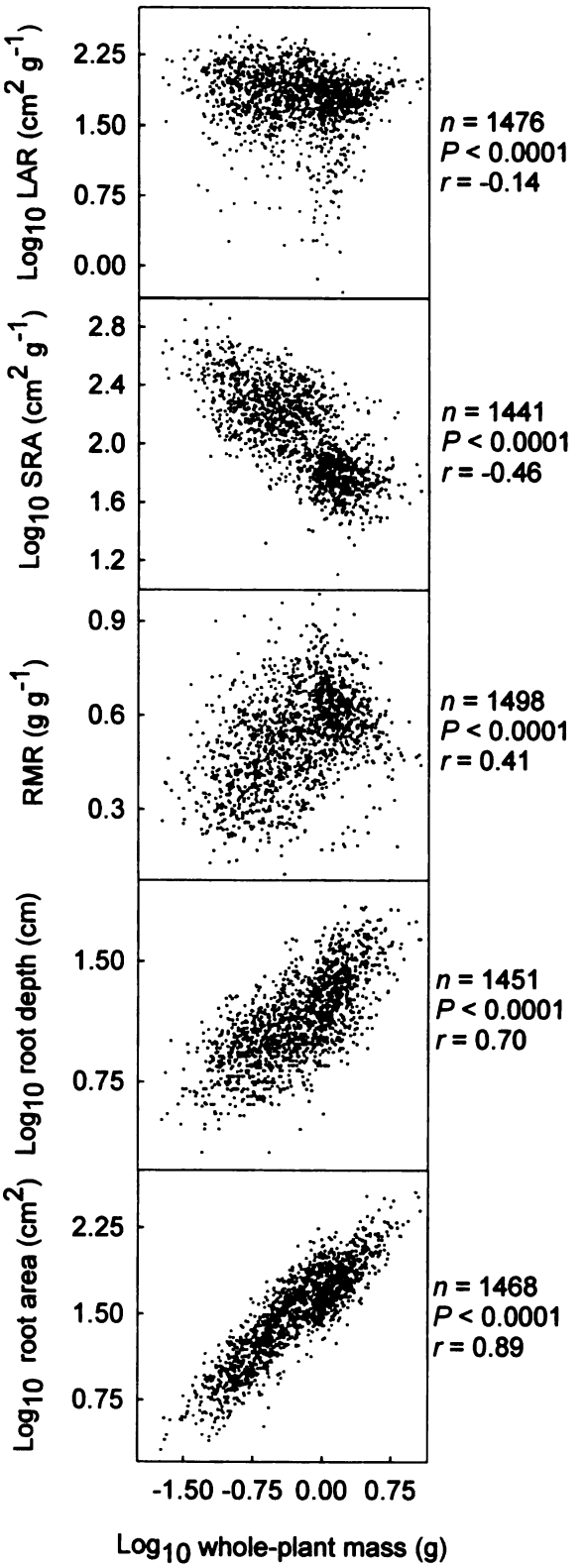

Log10 LAR (cm2 g-1)
2.25
1.50
0.75
0.00
n = 1476
P < 0.0001
r = -0.14
Log10 SRA (cm2 g-1)
2.8
2.4
2.0
1.6
1.2
n = 1441
P < 0.0001
r = -0.46
RMR (g g-1)
0.9
0.6
0.3
n = 1498
P < 0.0001
r = 0.41
Log10 root depth (cm)
1.50
0.75
n = 1451
P < 0.0001
r = 0.70
Log10 root area (cm2)
2.25
1.50
0.75
n = 1468
P < 0.0001
r = 0.89
-1.50 -0.75 0.00 0.75
Log10 whole-plant mass (g)

Figure A.3.

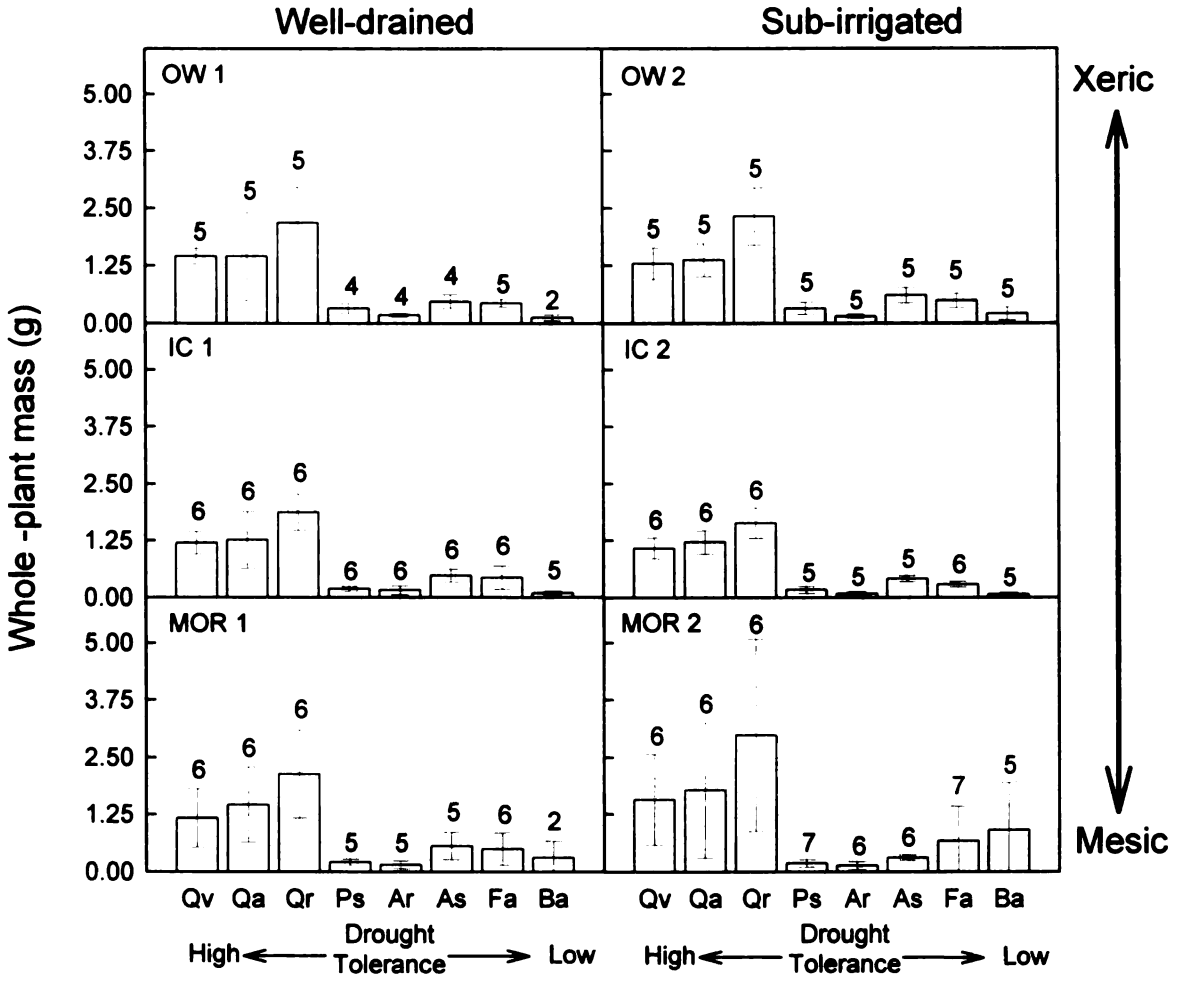


Figure A.4. Species-level means (± SD) of whole-plant mass (g) across field sites from the June 02 seedling harvest. Numbers above bars denote sample sizes (number of plots) for each respective species. Sites are separated into well-drained (outwash = OW 1, ice contact = IC 1, moraine = MOR 1) and sub-irrigated categories (outwash = OW 2, ice contact = IC 2, moraine = MOR 2) (see methods for details) and are organized top to bottom from the most xeric to the most mesic. Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

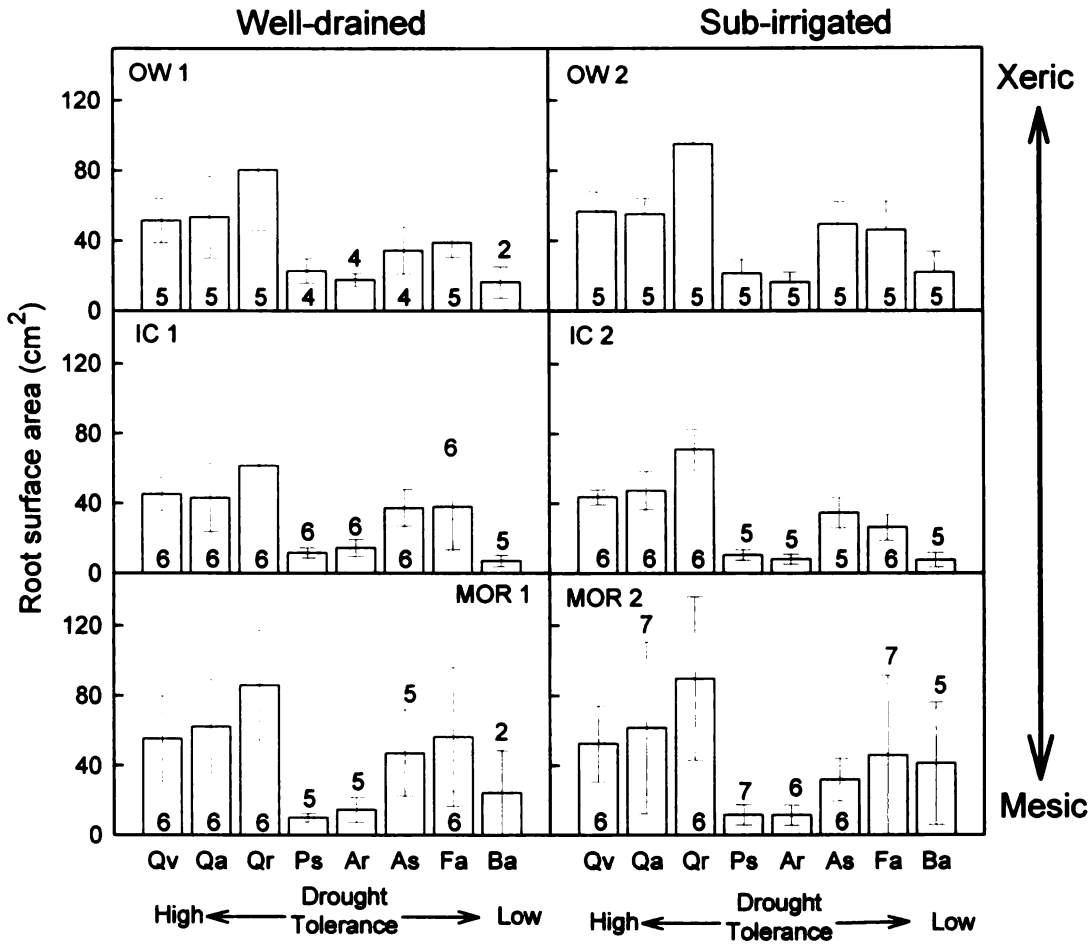


Figure A.5. Species-level means (± SD) of root surface area (cm^2) across field sites from the June 02 seedling harvest. Numbers within or above bars denote sample sizes (number of plots) for each respective species. Sites are separated into well-drained (outwash = OW 1, ice contact = IC 1, moraine = MOR 1) and sub-irrigated categories (outwash = OW 2, ice contact = IC 2, moraine = MOR 2) (see methods for details). Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

Figure A.6. Root mass ratio (g g^{-1}) expressed as species-level means (± SD) and as estimates at a common whole-plant mass (see materials and methods) across field sites from the June 02 seedling harvest. Numbers within or above bars denote sample sizes (i.e., number of plots) for each respective species. (n.d.) indicates that the specified common mass was beyond the range of individuals for a given species × site combination. Sites are arranged top to bottom from the most xeric site to the most mesic site. Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

Figure A.6. Common harvest time Common whole-plant mass: 0.5 g

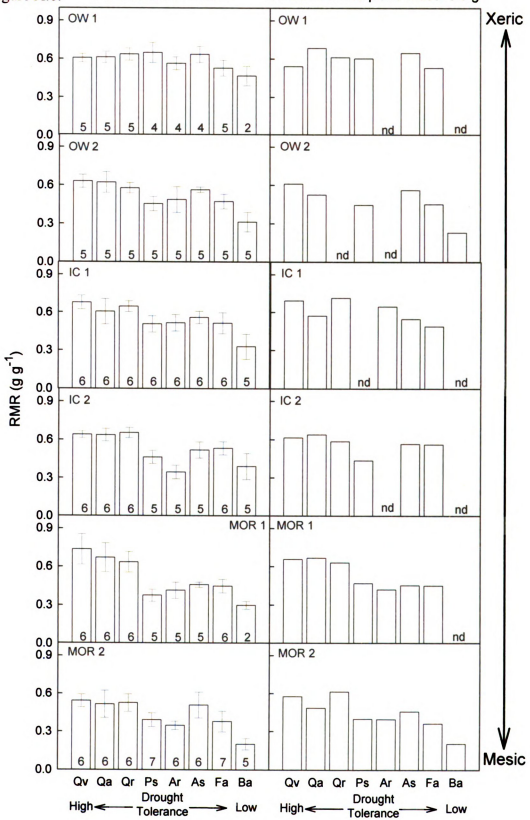
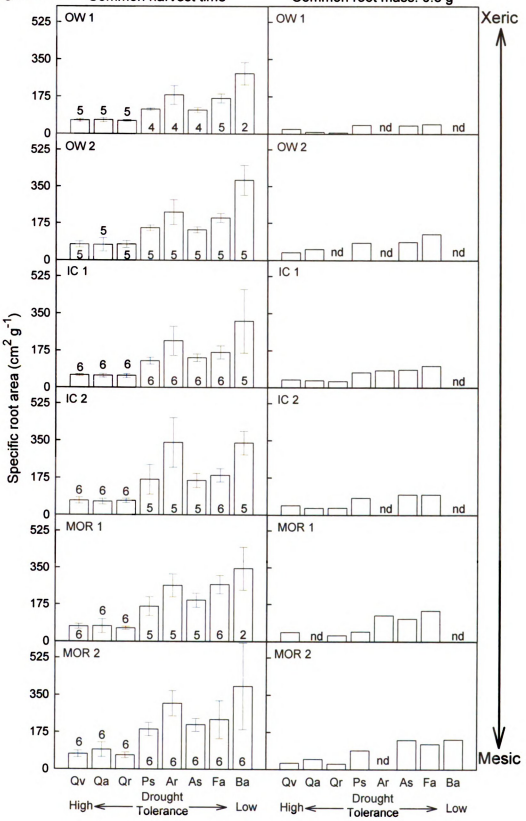


Figure A.7. Specific root area ($cm^2\ g^{-1}$) expressed as species-level means (± SD) and as estimates at a common root mass (see materials and methods) across field sites from the June 02 seedling harvest. Numbers within or above bars denote sample sizes (i.e., number of plots) for each respective species. (n.d.) indicates that the specified common mass was beyond the range of individuals for a given species × site combination. Sites are arranged top to bottom from the most xeric site to the most mesic site. Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

Figure A.7.


Common harvest time
Common root mass: 0.3 g
OW 1
OW 2
IC 1
IC 2
MOR 1
MOR 2
Xeric
Mesic
Specific root area (cm2 g-1)
525
350
175
0
nd
Qv Qa Qr Ps Ar As Fa Ba
High
Drought Tolerance
Low

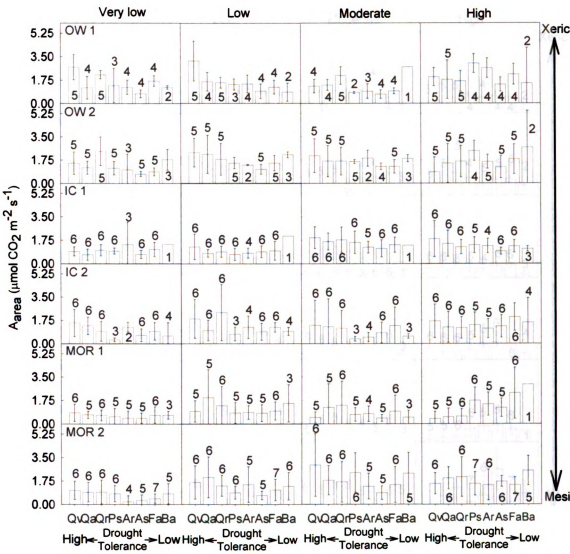


Figure A.8. Species-level means (± SD) of leaf-level photosynthesis (A_{area}) across field sites at four sampling dates that contrasted in volumetric soil moisture content (%) during the 2002 growing season (left to right, very low = 3.3%; low = 4.2%; moderate = 6.8%; high = 11.2%; and see also Appendix,Table A.4, for additional details). Numbers contained within or above bars denote sample sizes (number of plots) for each respective species. Sites are organized top to bottom from the most xeric to the most mesic (well-drained sites, outwash = OW 1; ice contact = IC 1; moraine = MOR 1; and sub-irrigated sites, outwash = OW 2; ice contact = IC 2; moraine = MOR 2) (see methods for details). Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

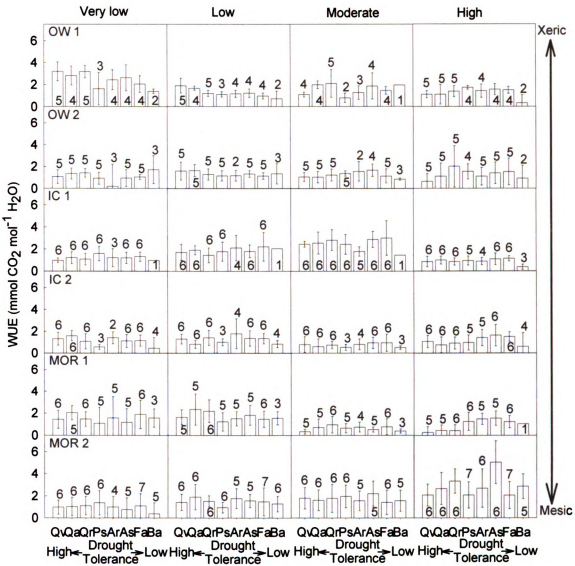


Figure A.9. Species-level means (± SD) of leaf-level water-use efficiency (WUE) across field sites (OW1, OW 2, IC 1, IC 2, MOR 1, MOR 2) at four sampling dates that contrasted in volumetric soil moisture content (%) during the 2002 growing season (left to right, very low = 3.3%; low = 4.2%; moderate = 6.8%; high = 11.2%; and see also Appendix, Table A.4 for additional details). Numbers contained within or above bars denote sample sizes (number of plots) for each respective species. Sites are organized top to bottom from the most xeric to the most mesic (well-drained sites, outwash = OW 1; ice contact = IC 1; moraine = MOR 1; and sub-irrigated sites, outwash = OW 2; ice contact = IC 2; moraine = MOR 2). Species are arranged in order of their drought tolerance. Species abbreviations are as follows: Qv = *Quercus velutina*, Qa = *Quercus alba*, Qr = *Quercus rubra*, Ps = *Prunus serotina*, Ar = *Acer rubrum*, As = *Acer saccharum*, Fa = *Fraxinus americana*, Ba = *Betula alleghaniensis*.

Figure A.10. Relationships of survival deviations (i.e., species average plot survival – overall average plot survival for all species) with leaf N_{area}, size (whole-plant mass) and morphological (root area, SRA, RMR, root depth) and physiological characteristics (leaf-level photosynthesis, A_{area}; water-use efficiency, WUE). Relationships were examined within each of the three well-drained sites (OW 1, IC 2, MOR 1). Regression equations, adjusted R^2, *P* values and n for these relationships are presented in Appendix, Table A.38.

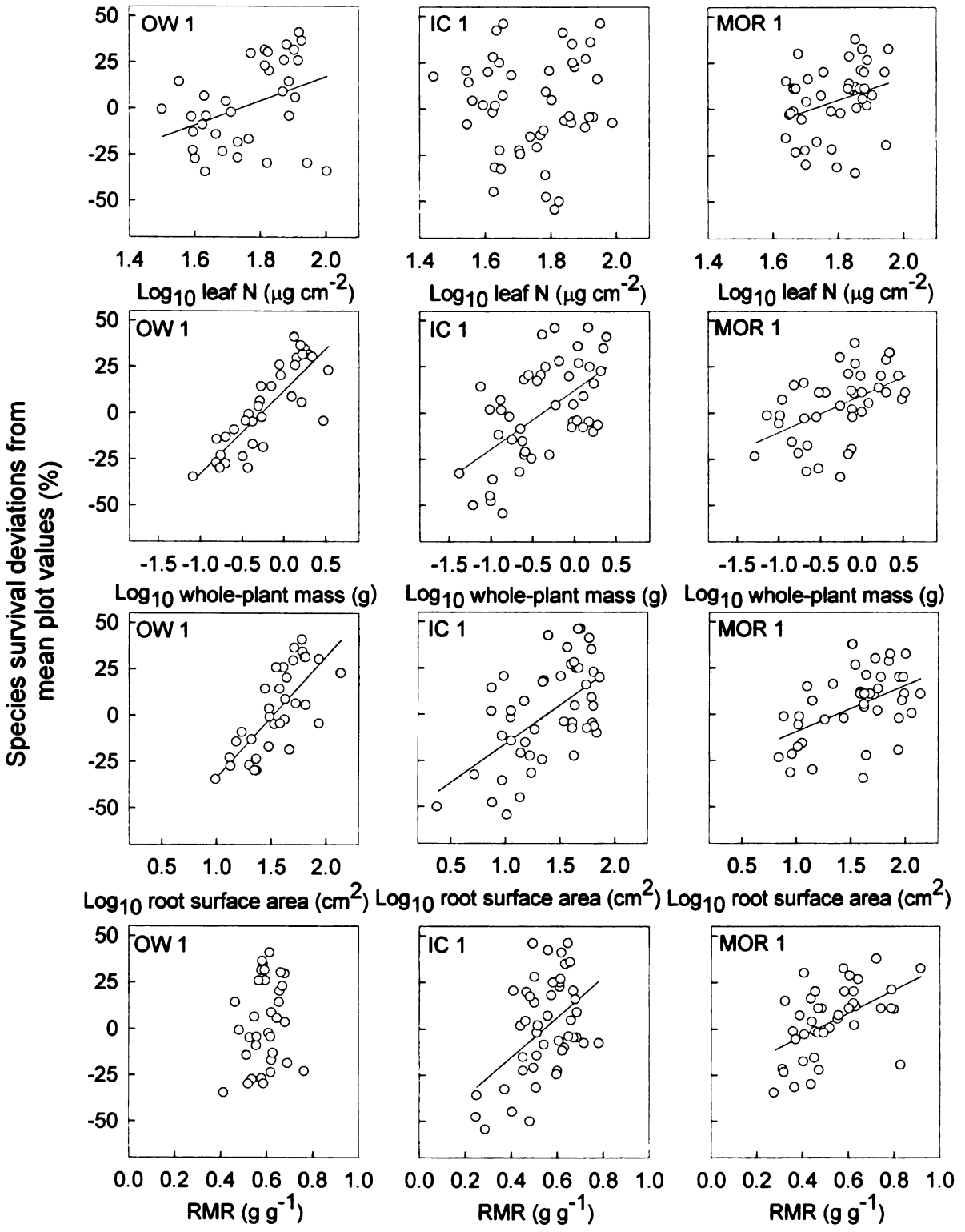

Species survival deviations from mean plot values (%)
OW 1
IC 1
MOR 1
50
25
0
-25
-50
1.4 1.6 1.8 2.0
Log10 leaf N (μg cm-2)
-1.5 -1.0 -0.5 0.0 0.5
Log10 whole-plant mass (g)
0.5 1.0 1.5 2.0
Log10 root surface area (cm2)
0.0 0.2 0.4 0.6 0.8 1.0
RMR (g g-1)

Figure A.10.

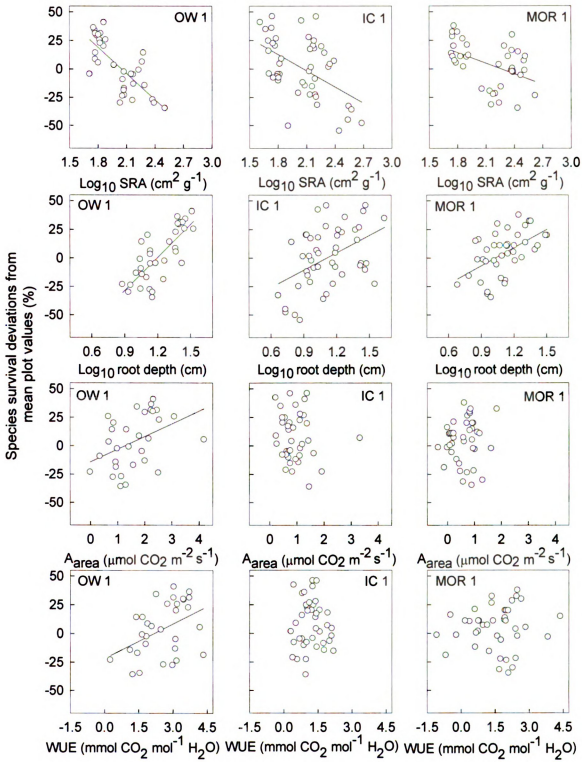


Figure A.10. (cont'd).

REFERENCES

REFERENCES

Aerts, R. 1990. Nutrient-use efficiency in evergreen and deciduous species from heathlands. Oecologia **84**:391-397.

Aerts, R. 1996. Nutrient resorption from senescing leaves of perennials: Are there general patterns? Journal of Ecology **84**:597-608.

Ahlstrom, K., H. Persson, and I. Borjesson. 1988. Fertilization in a mature scots pine (*Pinus sylvestris L.*) stand-effects on fine roots. Plant and Soil **106**:179-190.

Albert, D. A. 1994. Regional Landscape Ecosystems of Michigan, Minnesota, and Wisconsin: A working Map and Classification. U.S. Department of Agriculture, Forest Service, North Central Experiment Station, St. Paul, MN.

Arunachalam, A., H. N. Pandey, R. S. Tripathi, and K. Maithani. 1996. Fine root decomposition and nutrrient mineralization patterns in a subtropical forest following tree cutting. Forest Ecology and Management **86**:141-150.

Bancroft, T. A. 1964. Analysis and inference for incompletely specified models involving use of preliminary test(s) of significance. Biometrics **20**:427-442.

Bazzaz, F. A. 1979. Physiological ecology of plant succession. Annual Review of Ecology and Systematics **10**:351-371.

Bazzaz, F. A., and R. W. Carlton. 1982. Photosynthetic acclimation to variability in the light environment of early and late successsional plants. Oecologia **54**:313-316.

Berges, J. A. 1997. Ratios, regression statistics, and "spurious" correlations. Limnology and Oceanography **42**:1006-1007.

Bjorkman, O. 1981. Responses to different quantum flux densities. Pages 57-107 *in* O. L. Lange and P. S. Nobel, editors. Encyclopedia of Plant Physiology I. Springer, Berlin.

Bond, W. J., and J. J. Midgley. 2003. The evolutionary ecology of sprouting in woody plants. International Journal of Plant Sciences **164**:S103-S114.

Bongers, F., L. Poorter, R. Van Rompaey, and M. P. E. Parren. 1999. Distribution of twelve moist forest canopy tree species in Liberia and Cote d'Ivoire: response curves to a climatic gradient. Journal of Vegetation Science **10**:371-382.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics **13**:115-155.

Bunce, J. A., L. N. Miller, and B. F. Chabot. 1977. Competitive exploitation of soil water by 5 eastern North American tree species. Botanical Gazette **138**:168-173.

Burton, A. J., K. S. Pregitzer, and N. W. Macdonald. 1993. Foliar nutrients in sugar maple forests along a regional pollution-climate gradient. Soil Science Society of America Journal **57**:1619-1628.

Busso, C. A., J. H. Richards, and N. J. Chatterton. 1990. Nonstructural carbohydrates and spring regrowth of 2 cool-season grasses: Interaction of drought and clipping. Journal of Range Management **43**:336-343.

Canadell, J., R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia **108**:583-595.

Canham, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bulletin of the Torrey Botanical Club **112**:134-145.

Canham, C. D., A. R. Berkowitz, V. R. Kelly, G. M. Lovett, S. V. Ollinger, and J. Schnurr. 1996. Biomass allocation and multiple resource limitation in tree seedlings. Canadian Journal of Forest Research **26**:1521-1530.

Canham, C. D., R. K. Kobe, E. F. Latty, and R. L. Chazdon. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia **121**:1-11.

Carlton, G. C., and F. A. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. Ecology **79**:1305-1319.

Caspersen, J. P., and R. K. Kobe. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. Oikos **92**:160-168.

Chapin, F. S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics **11**:233-260.

Chapin, F. S., and R. A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology **64**:376-391.

Chapin, F. S., E. D. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. Annual Review of Ecology and Systematics **21**:423-447.

Chen, H., M. E. Harmon, J. Sexton, and B. Fasth. 2002. Fine-root decomposition and N dynamics in coniferous forests of the Pacific Northwest, USA. Canadian Journal of Forest Research **32**:320-331.

Cleland, D. T., J. B. Hart, G. E. Host, K. S. Pregitzer, and C. W. Ramm. 1993. Field Guide: Ecological Classification and Inventory System of the Huron-Manistee National Forests. Huron-Manistee National Forest, Cadillac, MI.

Cohen, D. 1970. Expected efficiency of water utilization in plants under different competition and selection regimes Israel Journal of Botany **19**:50-54.

Comas, L. H., T. J. Bouma, and D. M. Eissenstat. 2002. Linking root traits to potential growth rate in six temperate tree species. Oecologia **132**:34-43.

Coomes, D. A., and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecological Monographs **70**:171-207.

Cote, B., J. W. Fyles, and H. Djalilvand. 2002. Increasing N and P resorption efficiency and proficiency in northern deciduous hardwoods with decreasing foliar N and P concentrations. Annals of Forest Science **59**:275-281.

Cowan, I. R. 1986. Econmics of carbon fixation in higher plants. Pages 133-170 *in* T. J. Givnish, editor. On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, UK.

Cowan, I. R., and G. D. Farquhar. 1977. Stomata function in relation to leaf metabolism and environment. Pages 471-505 *in* D. H. Jennings, editor. Symposia of the Society for Experimental Biology. Cambridge University Press, Cambridge, UK.

de Gouvenain, R. C., R. K. Kobe, and J. A. Silander. 2007. Partitioning of understorey light and dry-season soil moisture gradients among seedlings of four rain-forest tree species in Madagascar. Journal of Tropical Ecology **23**:569-579.

Del Tredici, P. 2001. Sprouting in temperate trees: A morphological and ecological review. Botanical Review **67**:121-140.

Delucia, E. H., and S. A. Heckathorn. 1989. The effect of soil drought on water-use efficiency in a contrasting Great Basin desert and Sierran montane species Plant Cell and Environment **12**:935-940.

Delucia, E. H., W. H. Schlesinger, and W. D. Billings. 1988. Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. Ecology **69**:303-311.

Dilustro, J. J., F. P. Day, and B. G. Drake. 2001. Effects of elevated atmospheric CO_2 on root decomposition in a scrub oak ecosystem. Global Change Biology **7**:581-589.

Dina, S. J., and L. G. Klikoff. 1973. Effect of plant moisture stress on carbohydrate and nitrogen content of big sagebrush Journal of Range Management **26**:207-209.

Don, A., J. Schumache, M. Scherer-Lorenzen, T. Scholtern, and E. D. Schulze. 2007. Spatial and vertical variation of soil carbon at two grassland sites-implication for measuring soil carbon stocks. Geoderma **141**:272-282.

Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers, and F. Smith. 1956. Colorimetric method for determination of sugars and related substances. Analytical Chemistry **28**:350-356.

Duchesne, L., R. Ouimet, C. Camire, and D. Houle. 2001. Seasonal nutrient transfers by foliar resorption, leaching, and litter fall in a northern hardwood forest at Lake Clair Watershed, Quebec, Canada. Canadian Journal of Forest Research **31**:333-344.

Dudley, S. A. 1996. The response to differing selection on plant physiological traits: Evidence for local adaptation. Evolution **50**:103-110.

Ehleringer, J. R., and T. A. Cooper. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia **76**:562-566.

Engelbrecht, B. M. J., L. S. Comita, R. Condit, T. A. Kursar, M. T. Tyree, B. L. Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature **447**:80-U82.

Engelbrecht, B. M. J., and T. A. Kursar. 2003. Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia **136**:383-393.

Engelbrecht, B. M. J., T. A. Kursar, and M. T. Tyree. 2005. Drought effects on seedling survival in a tropical moist forest. Trees: Structure and Function **19**:312-321.

Evans, G. C. 1972. The Quantitative Analysis of Plant Growth. University of California Press, Berkeley, CA.

Fahey, T. J., J. J. Battles, and G. F. Wilson. 1998. Responses of early successional northern hardwood forests to changes in nutrient availability. Ecological Monographs **68**:183-212.

Field, C., J. Merino, and H. A. Mooney. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in 5 species of california evergreens. Oecologia **60**:384-389.

Field, C., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25-55 *in* T. J. Givnish, editor. On the Economy of Plant Form and Function. Cambridge University Press, Cambridge.

Finzi, A. C., and C. D. Canham. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. Forest Ecology and Management **131**:153-165.

Gansert, D., and W. Sprick. 1998. Storage and mobilization of nonstructural carbohydrates and biomass development of beech seedlings (*Fagus sylvatica* L.) under different light regimes. Trees: Structure and Function **12**:247-257.

Gaucher, C., S. Gougeon, Y. Mauffette, and C. Messier. 2005. Seasonal variation in biomass and carbohydrate partitioning of understory sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) seedlings. Tree Physiology **25**:93-100.

Gholz, H. L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology **63**:469-481.

Givnish, T. J. 1986. Biochemical constraints on crown geometry in forest herbs. Pages 525-583 *in* T. J. Givnish, editor. On the Economy of Plant Form and Function. Cambridge University Press, New York, NY.

Givnish, T. J. 1988. Adaptation to sun and shade: A whole-plant perspective. Australian Journal of Plant Physiology **15**:63-92.

Gordon, W. S., and R. B. Jackson. 2000. Nutrient concentrations in fine roots. Ecology **81**:275-280.

Green, P. T., and P. A. Juniper. 2004. Seed mass, seedling herbivory and the reserve effect in tropical rainforest seedlings. Functional Ecology **18**:539-547.

Grime, J. P. 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**:1169-1194.

Guerrero-Campo, J., and A. H. Fitter. 2001. Relationships between root characteristics and seed size in two contrasting floras. Acta Oecologica **22**:77-85.

Gurevitch, J., J. A. Teeri, and A. M. Wood. 1986. Differentiation among populations of Sedum wrightii (Crassulaceae) in response to limited water availability: Water relations, CO_2 assimilation, growth and survivorship. Oecologia **70**:198-204.

Haeussler, S., J. C. Tappeiner, and B. J. Greber. 1995. Germination, survival, and early growth of red alder seedlings in the Central Coast Range of Oregon. Canadian Journal of Forest Research **25**:1639-1651.

Host, G. E., K. S. Pregitzer, C. W. Ramm, D. P. Lusch, and D. T. Cleland. 1988. Variation in overstory biomass among glacial landforms and ecological land units in northwestern lower Michigan. Canadian Journal of Forest Research **18**:659-668.

Huang, X. M., A. N. Lakso, and D. M. Eissenstat. 2005. Interactive effects of soil temperature and moisture on Concord grape root respiration. Journal of Experimental Botany **56**:2651-2660.

IPCC. 2001. Third Assessment Report of the Intergovernmental Panel on Global Climate Change. Cambirdge University Press, New York, NY.

Iyer, M. 2006. Root carbohydrate storage in temperate and tropical forest tree seedlings: implications for species coexistence. Dissertation. Michigan State University, East Lansing.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia **108**:389-411.

Jackson, R. B., L. A. Moore, W. A. Hoffmann, W. T. Pockman, and C. R. Linder. 1999. Ecosystem rooting depth determined with caves and DNA. Proceedings of the National Academy of Sciences of the United States of America **96**:11387-11392.

John, B., H. N. Pandey, and R. S. Tripathi. 2002. Decomposition of fine roots of Pinus kesiya and turnover of organic matter, N and P of coarse and fine pine roots and herbaceous roots and rhizomes in subtropical pine forest stands of different ages. Biology and Fertility of Soils **35**:238-246.

Jurik, T. W., J. A. Weber, and D. M. Gates. 1988. Effects of temperature and light on photosynthesis of dominant tree species of a northern hardwood forest. Botanical Gazette **149**:203-208.

Kays, J. S., and C. D. Canham. 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. Forest Science **37**:524-539.

Killingbeck, K. T. 1996. Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. Ecology **77**:1716-1727.

Killingbeck, K. T., J. D. May, and S. Nyman. 1990. Foliar senescence in an aspen (*Populus tremuloides*) clone: The response of element resorption to interramet variation and timing of abscission. Canadian Journal of Forest Research **20**:1156-1164.

Kloeppel, B. D., M. D. Abrams, and M. E. Kubiske. 1993. Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. Canadian Journal of Forest Research **23**:181-189.

Kobe, R. K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecological Monographs **66**:181-201.

Kobe, R. K. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos **80**:226-233.

Kobe, R. K. 2006. Sapling growth as a function of light and landscape-level variation in soil water and foliar nitrogen in northern Michigan. Oecologia **147**:119-133.

Kobe, R. K., C. A. Lepczyk, and M. Iyer. 2005. Resorption efficiency decreases with increasing green leaf nutrients in a global data set. Ecology **86**:2780-2792.

Kobe, R. K., S. W. Pacala, J. A. Silander, and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications **5**:517-532.

Kohyama, T., and P. J. Grubb. 1994. Below- and above-ground allometries of shade-tolerant seedlings in a Japanese warm-temperate rain forest. Functional Ecology **8**:229-236.

Kozlowski, T. T. 1992. Carbohydrate sources and sinks in woody plants Botanical Review **58**:107-222.

Kruger, E. L., and P. B. Reich. 1997a. Responses of hardwood regeneration to fire in mesic forest openings. I. Post-fire community dynamics. Canadian Journal of Forest Research **27**:1822-1831.

Kruger, E. L., and P. B. Reich. 1997b. Responses of hardwood regeneration to fire in mesic forest openings. III. Whole-plant growth, biomass distribution, and nitrogen and carbohydrate relations. Canadian Journal of Forest Research **27**:1841-1850.

Kruger, E. L., and J. C. Volin. 2006. Reexamining the empirical relationship between plant growth and leaf photosynthesis. Functional Plant Biology **33**:421-429.

Kubiske, M. E., and K. S. Pregitzer. 1996. Effects of elevated CO_2 and light availability on the photosnyhtetic response of trees of contrasting shade tolerance. Tree Physiology **16**:351-358.

Landsberg, J. J. 1986. Physiological ecology of forest production. Academic Press, London, UK.

Leishman, M. R., and M. Westoby. 1994. The role of large seed size in shaded conditions: Experimental evidence. Functional Ecology **8**:205-214.

Loach, K. 1967. Shade tolerance in tree seedlings I. Leaf photosynthesis and respiration in plants raised under artificial shade New Phytologist **66**:607-621.

Loescher, W. H., T. McCamant, and J. D. Keller. 1990. Carbohydrate reserves, translocation, and storage in woody plant roots Hortscience **25**:274-281.

Lucash, M. S., J. D. Joslin, and R. D. Yanai. 2005. Temporal variation in nutrient uptake capacity by intact roots of mature loblolly pine. Plant and Soil **272**:253-262.

Ludovici, K. H., and L. W. Kress. 2006. Decomposition and nutrient release from fresh and dried pine roots under two fertilizer regimes. Canadian Journal of Forest Research **36**:105-111.

Lusk, C. H. 2004. Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. Functional Ecology **18**:820-828.

Lusk, C. H., O. Contreras, and J. Figueroa. 1997. Growth, biomass allocation and plant nitrogen concentration in Chilean temperate rainforest tree seedlings: Effects of nutrient availability. Oecologia **109**:49-58.

Lusk, C. H., and A. Del Pozo. 2002. Survival and growth of seedlings of 12 Chilean rainforest trees in two light environments: Gas exchange and biomass distribution correlates. Austral Ecology **27**:173-182.

Lusk, C. H., and F. I. Piper. 2007. Seedling size influences relationships of shade tolerance with carbohydrate-storage patterns in a temperate rainforest. Functional Ecology **21**:78-86.

MacFarlane, D. W., and R. K. Kobe. 2006. Selecting models for capturing tree-size effects on growth-resource relationships. Canadian Journal of Forest Research **36**:1695-1704.

Machado, J. L., and P. B. Reich. 2006. Dark respiration rate increases with plant size in saplings of three temperate tree species despite decreasing tissue nitrogen and nonstructural carbohydrates. Tree Physiology **26**:915-923.

Marks, P. L. 1975. Relation between extension growth and successional status of deciduous trees of northeastern United States. Bulletin of the Torrey Botanical Club **102**:172-177.

Marquis, R. J., E. A. Newell, and A. C. Villegas. 1997. Non-structural carbohydrate accumulation and use in an understorey rain-forest shrub and relevance for the impact of leaf herbivory. Functional Ecology **11**:636-643.

McClaugherty, C. A., J. D. Aber, and J. M. Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of 2 forested ecosystems. Ecology **63**:1481-1490.

McFarlane, K. J., and R. D. Yanai. 2006. Measuring nitrogen and phosphorus uptake by intact roots of mature *Acer saccharum* Marsh., *Pinus resinosa* Ait., and *Picea abies* (L.) Karst. Plant and Soil **279**:163-172.

McKay, H. M., and D. C. Maclcolm. 1988. A comparison of the fine root component of a pure and a mixed coniferous stand. Canadian Journal of Forest Research **18**:1416-1426.

McLaughlin, S. B., and R. Wimmer. 1999. Tansley Review No. 104 - Calcium physiology and terrestrial ecosystem processes. New Phytologist **142**:373-417.

Meier, C. E., C. C. Grier, and D. W. Cole. 1985. Below- and aboveground N and P use by *Abies amabilis* stands. Ecology **66**:1928-1942.

Moles, A. T., and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. Journal of Ecology **92**:372-383.

Myers, J. A., and K. Kitajima. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest Journal of Ecology **95**:383–395.

Nambiar, E. K. S. 1987. Do nutrients retranslocate from fine roots? Canadian Journal of Forest Research **17**:913-918.

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.

Newell, E. A., S. S. Mulkey, and S. J. Wright. 2002. Seasonal patterns of carbohydrate storage in four tropical tree species. Oecologia **131**:333-342.

Newman, G. S., and S. C. Hart. 2006. Nutrient covariance between forest foliage and fine roots. Forest Ecology and Management **236**:136-141.

Ni, B. R., and S. G. Pallardy. 1991. Response of gas-exchange to water stress in seedlings of woody angiosperms Tree Physiology **8**:1-9.

Norby, R. J., and C. M. Iversen. 2006. Nitrogen uptake, distribution, turnover, and efficiency of use in a CO_2-enriched sweetgum forest. Ecology **87**:5-14.

Oosthuizen, I. B., and H. A. Snyman. 2001. The influence of water stress on non-structural carbohydrate concentration in *Themeda triandra*. South African Journal of Botany **67**:53-57.

Ostertag, R., and S. E. Hobbie. 1999. Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. Oecologia **121**:564-573.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. Ecological Monographs **66**:1-43.

Pacala, S. W., C. D. Canham, J. A. Silander, and R. K. Kobe. 1994. Sapling growth as a function of resources in a north temperate forest. Canadian Journal of Forest Research **24**:2172-2183.

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.

Pennington, M. R., and M. B. Walters. 2006. The response of planted trees to vegetation zonation and soil, redox potential in created wetlands. Forest Ecology and Management **233**:1-10.

Poorter, H., and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Australian Journal of Plant Physiology **27**:595-607.

Poorter, H., and C. Remkes. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia **83**:553-559.

Poorter, H., C. Remkes, and H. Lambers. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiology **94**:621-627.

Poorter, H., and R. Villar. 1997. The fate of acquired carbon in plants: chemical composition and construction costs. Pages 37-72 *in* F. A. Bazzaz and J. Grace, editors. Plant Resource Allocation. Academic Press, London, UK.

Poorter, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. Functional Ecology **13**:396-410.

Poorter, L. 2001. Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. Functional Ecology **15**:113-123.

Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? American Naturalist **169**:433-442.

Poorter, L., and F. Bongers. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology **87**:1733-1743.

Poorter, L., L. Bongers, and F. Bongers. 2006. Architecture of 54 moist-forest tree species: Traits, trade-offs, and functional groups. Ecology **87**:1289-1301.

Poorter, L., and K. Kitajima. 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. Ecology **88**:1000-1011.

Poorter, L., and S. Rose. 2005. Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. Oecologia **142**:378-387.

Portsmuth, A., and U. Niinemets. 2007. Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. Functional Ecology **21**:61-77.

Prairie, Y. T., and D. F. Bird. 1989. Some misconceptions about the spurious correlation: Problem in the ecological literature. Oecologia **81**:285-288.

Pregitzer, K. S. 2002. Fine roots of trees: A new perspective. New Phytologist **154**:267-270.

Pregitzer, K. S., J. A. King, A. J. Burton, and S. E. Brown. 2000. Responses of tree fine roots to temperature. New Phytologist **147**:105-115.

Pregitzer, K. S., M. E. Kubiske, C. K. Yu, and R. L. Hendrick. 1997. Relationships among roof branch order, carbon, and nitrogen in four temperate species. Oecologia **111**:302-308.

Quero, J. L., R. Villar, T. Maranon, R. Zamora, and L. Poorter. 2007. Seed-mass effects in four Mediterranean *Quercus* species (Fagaceae) growing in contrasting light environments. American Journal of Botany **94**:1795-1803.

Raison, R. J., M. J. Connell, and P. K. Khanna. 1987. Methodology for studying fluxes of soil mineral-N *in situ* Soil Biology & Biochemistry **19**:521-530.

Reich, P. B., C. Buschena, M. G. Tjoelker, K. Wrage, J. Knops, D. Tilman, and J. L. Machado. 2003a. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. New Phytologist **157**:617-631.

Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: A test across six biomes. Ecology **80**:1955-1969.

Reich, P. B., D. F. Grigal, J. D. Aber, and S. T. Gower. 1997a. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology **78**:335-347.

Reich, P. B., and T. M. Hinckley. 1989. Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily diffusive conductance in 2 oak species. Functional Ecology **3**:719-726.

Reich, P. B., M. G. Tjoelker, M. B. Walters, D. W. Vanderklein, and C. Bushena. 1998a. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Functional Ecology **12**:327-338.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997b. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences of the United States of America **94**:13730-13734.

Reich, P. B., M. B. Walters, M. G. Tjoelker, D. Vanderklein, and C. Buschena. 1998b. Photosynthesis and respiration rates depend on leaf and root morphology and

nitrogen concentration in nine boreal tree species differing in relative growth rate. Functional Ecology **12**:395-405.

Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003b. The evolution of plant functional variation: Traits, spectra, and strategies. International Journal of Plant Sciences **164**:S143-S164.

Roper, T. R., J. D. Keller, W. H. Loescher, and C. R. Rom. 1988. Photosynthesis and carbohydrate partitioning in sweet cherry: Fruiting effects. Physiologia Plantarum **72**:42-47.

Royce, E. B., and M. G. Barbour. 2001. Mediterranean climate effects. I. Conifer water use across a Sierra Nevada ecotone. American Journal of Botany **88**:911-918.

Sack, L. 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? Oikos **107**:110-127.

Saverimuttu, T., and M. Westoby. 1996. Seedling longevity under deep shade in relation to seed size. Journal of Ecology **84**:681-689.

Schreeg, L. A., R. K. Kobe, and M. B. Walters. 2005. Tree seedling growth, survival, and morphology in response to landscape-level variation in soil resource availability in northern Michigan. Canadian Journal of Forest Research **35**:263-273.

Schulze, E. D., H. A. Mooney, O. E. Sala, E. Jobbagy, N. Buchmann, G. Bauer, J. Canadell, R. B. Jackson, J. Loreti, M. Oesterheld, and J. R. Ehleringer. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia **108**:503-511.

Schulze, E. D., R. J. Williams, G. D. Farquhar, W. Schulze, J. Langridge, J. M. Miller, and B. H. Walker. 1998. Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. Australian Journal of Plant Physiology **25**:413-425.

Shibuya, M., T. Yajima, M. Yoshida, and E. Sasaoka. 2007. Different biomass allocation patterns among four tree species in heavily distrubed sites on a volacanic mountain in Hokkaido, northern Japan. Ecological Research **22**:177-182.

Silla, F., and A. Escudero. 2004. Nitrogen-use efficiency: trade-offs between N productivity and mean residence time at organ, plant and population levels. Functional Ecology **18**:511-521.

Silla, F., and A. Escudero. 2006. Coupling N cycling and N productivity in relation to seasonal stress in *Quercus pyrenaica* Willd. saplings. Plant and Soil **282**:301-311.

Sipe, T. W., and F. A. Bazzaz. 1995. Gap partitioning among maples (*Acer*) in central New England: Survival and growth. Ecology **76**:1587-1602.

Spaeth, S. C., and P. M. Cortes. 1995. Root cortex death and subsequent initiation and growth of lateral roots from bare steles of chickpeas. Canadian Journal of Botany **73**:253-261.

Steele, S. J., S. T. Gower, J. G. Vogel, and J. M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiology **17**:577-587.

Swaine, M. D. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. Journal of Ecology **84**:419-428.

Tanner, E. V. J., and I. M. Barberis. 2007. Trenching increased growth, and irrigation increased survival of tree seedlings in the understorey of a semi-evergreen rain forest in Panama. Journal of Tropical Ecology **23**:257-268.

Teng, Y. W., K. Tanabe, F. Tamura, and A. Itai. 1999. Translocation of C-13-assimilates in the spring following fall assimilation of (CO_2)-C-13 by 'Nijisseiki' pear (*Pyrus pyrifolia* Nakai). Journal of the Japanese Society for Horticultural Science **68**:248-255.

Teskey, R. O., and R. B. Shrestha. 1985. A relationship between carbon dioxide, photosynthetic efficiency and shade-tolerance. Physiologia Plantarum **63**:126-132.

Tilman, D. 1988. Plant strategies and the dynamics of plant communities. Princeton University Press, Princeton, NJ.

Tjoelker, M. G., J. M. Craine, D. Wedin, P. B. Reich, and D. Tilman. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. New Phytologist **167**:493-508.

Valverde-Barrantes, O. J., J. W. Raich, and A. E. Russell. 2007. Fine-root mass, growth and nitrogen content for six tropical tree species. Plant and Soil **290**:357-370.

van Heerwaarden, L. M., S. Toet, and R. Aerts. 2003. Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. Oikos **101**:664-669.

VandenBoogaard, R., and R. Villar. 1998. Variation in growth and water-use-efficieny: a comparsion of *Aegilops* L. species and *Triticum aestivum* L. cultivars. Pages 289-308 *in* H. Lambers, H. Poorter, and M. M. I. Van Vuuren, editors. Inherent Variation in Plant Growth: Physiological Mecahnisms and Ecological Consequences. Backhuys Publishers, Leiden, Netherlands.

VanPraag, H. J., S. Sougnezremy, and F. Weissen. 1988. Root turnover in a beech and a spruce stand of the Belgian Ardennes. Plant and Soil **105**:87-103.

Veneklaas, E. J., and F. den Ouden. 2005. Dynamics of non-structural carbohydrates in two *Ficus* species after transfer to deep shade. Environmental and Experimental Botany **54**:148-154.

Volaire, F. 1995. Growth, carbohydrate reserves and drought survival strategies of contrasting *Dactylis glomerata* populations in a Mediterranean environment. Journal of Applied Ecology **32**:56-66.

Walters, M. B., E. L. Kruger, and P. B. Reich. 1993a. Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: Relationships with successional status and shade tolerance. Oecologia **94**:7-16.

Walters, M. B., E. L. Kruger, and P. B. Reich. 1993b. Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: Species, light environment and ontogenic considerations. Oecologia **96**:219-231.

Walters, M. B., and P. B. Reich. 1989. Response of *Ulmus americana* seedlings to varying nitrogen and water status. 1 Photosynthesis and growth. Tree Physiology **5**:159-172.

Walters, M. B., and P. B. Reich. 1997. Growth of *Acer saccharum* seedlings in deeply shaded understories of northern Wisconsin: Effects of nitrogen and water availability. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **27**:237-247.

Walters, M. B., and P. B. Reich. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? New Phytologist **143**:143-154.

Walters, M. B., and P. B. Reich. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology **81**:1887-1901.

Wang, X. P., Z. Y. Tang, and J. Y. Fang. 2006. Climatic control on forests and tree species distribution in the forest region of northeast China. Journal of Integrative Plant Biology **48**:778-789.

Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. Biological Reviews **81**:259-291.

Weber, J. A., T. W. Jurik, J. D. Tenhunen, and D. M. Gates. 1985. Analysis of gas-exchange in seedlings of *Acer saccharum*: Integration of field and laboratory studies. Oecologia **65**:338-347.

Will, R. E., D. Markewitz, R. L. Hendrick, D. F. Meason, T. R. Crocker, and B. E. Borders. 2006. Nitrogen and phosphorus dynamics for 13-year-old loblolly pine stands receiving complete competition control and annual N fertilizer. Forest Ecology and Management **227**:155-168.

Wright, I. J., and M. Westoby. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. Journal of Ecology **87**:85-97.

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.

Young, J. A., and C. G. Young. 1992. Seeds of woody plants in North America. Dioscorides Press, Portland, Oregon.

Zak, D. R., G. E. Host, and K. S. Pregitzer. 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern lower Michigan. Canadian Journal of Forest Research **19**:1521-1526.