A COMPARISON OF RADIATION USE EFFICIENCY BETWEEN TWO SOUTHERN APPALACHIAN FORESTS

by

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(Under the Direction of Robert O. Teskey)

ABSTRACT

We compared aboveground net primary productivity (ANPP), intercepted photosynthetically active solar radiation (IPAR), and radiation use efficiency (ε =ANPP/IPAR) between a mixed deciduous forest and a white pine (*Pinus strobus* L.) plantation in the southern Appalachian Mountains. We also examined patterns of foliage acclimation to intra-canopy light gradients, which may influence the photosynthetic radiation use efficiency (PhRUE) of forest canopies. The mixed deciduous forest had significantly greater ANPP and ε than the pine plantation. There was no significant variation in ε across the elevation gradient in either forest. Specific leaf area of foliage was acclimated to intra-canopy light gradients. Nitrogen content and A_{max} was higher in overstory trees and new pine foliage than in understory trees and one-year-old pine foliage, respectively. We found no such difference in the plasticity of SLA. Radiation use efficiency may be conservative for specific forest types across a range of environmental conditions in the southern Appalachian Mountains.

INDEX WORDS: Radiation use efficiency, Aboveground net primary productivity, Deciduous forest, *Pinus strobus* L., Specific leaf area, Photosynthesis, Light

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CHAPTER 1

INTRODUCTION

Forests have a dominant role in the terrestrial carbon cycle. They assimilate CO_2 from the atmosphere, some of which is stored for long periods of time in perennial plant parts such as stems, branches, and coarse roots. Aboveground net primary productivity (ANPP) is the difference between carbon gained through photosynthesis and carbon lost through autotrophic respiration in aboveground parts. Annual aboveground net primary productivity can be quantified by measuring total biomass production of aboveground plant parts.

Aboveground net primary productivity varies widely between different forest types, and within a single forest type growing on different sites. Nitrogen limitations cause much of the variation in ANPP that occurs in forests growing across the landscape. However, forests show more consistency in the efficiency with which they convert intercepted photosynthetically active solar radiation (IPAR, 400 – 700 nm) to biomass. This is called radiation use efficiency (ε), and is calculated as annual ANPP divided by annual IPAR. This simple ratio encompasses information about the major energy capture and metabolic processes that influence forest growth. Since ε is relatively consistent for a particular forest type, it has become a useful parameter for modeling ANPP based on the amount of IPAR by the canopy. However, the majority of studies have only considered ε for monoculture forests that are in early stages of stand development and have received intense silvicultural treatments. Very little is known about the magnitude and consistency of ε in mixed-species and mixed-age forests that exist across natural environmental gradients.

A consistent ratio of ANPP to IPAR suggests that there should be a consistent ratio of whole-canopy photosynthesis to IPAR as well. However, individual leaves show a non-linear response to increasing IPAR. We now understand that individual leaves within forest canopies acclimate to the amount of light they receive. This acclimation involves changes in the morphology of leaves that allow them to better cope with high light and water stress in the upper canopy, and with limited light availability in the lower canopy. This morphological acclimation may result in near optimal conditions for whole canopy photosynthesis, and a relatively consistent ratio of whole canopy photosynthesis to IPAR at weekly to annual time intervals.

This study was conducted at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of western North Carolina. The study sites included two adjacent 13 ha watersheds, one that contained a mature mixed-species and mixed-age deciduous forest and the other a mature eastern white pine plantation (*Pinus strobus* L.), and each covered an elevation gradient of over 200 m. The objectives were to quantify and compare ε for these two forests and to determine if mineral nitrogen availability varies considerably across the watershed, and if so, how leaf area index (LAI), ANPP, and ε respond to changing mineral nitrogen availability in these forests. This study also investigated the acclimation of foliage to intra-canopy light gradients in each forest, and attempted to determine if there are general differences in the degree of acclimation among trees that occupy different canopy heights, and between different age classes of foliage in eastern white pine.

We tested three hypotheses: 1) ε is higher for a mixed deciduous forest than for a mature eastern white pine plantation 2) increasing nitrogen availability will increase LAI and IPAR, resulting in a conservative estimate of ε at the watershed scale and 3) SLA will acclimate to intra-canopy light gradients, and the plasticity of SLA will decrease with leaf age in white pine trees, and will be greater for co-dominant trees than for intermediate and understory trees in the deciduous forest.

CHAPTER 2

LITERATURE REVIEW

General climate effects on aboveground net primary productivity

Net primary productivity (NPP) is the total amount of biomass produced by plants during a specific period of time, and is the balance between carbon gain through photosynthesis and carbon loss due to autotrophic respiration. Aboveground net primary productivity (ANPP) is the fraction of NPP that is allocated to aboveground plant parts. ANPP of forests is an important aspect of the terrestrial carbon cycle and commonly ranges from <5 to >20 Mg ha^{-1} y^{-1} for temperate forests (Reich and Bolstad 2001). The fraction of NPP allocated to ANPP may vary from 20% to 80% (Vogt 1991), and increases when water and soil nutrients are more available (Keyes and Grier 1981, Gower et al. 1992, Albaugh et al. 1998, Tateno et al. 2004).

A combination of climate and site factors affects ANPP in forests. Differences in soil water availability and temperature contribute to the variation in ANPP observed for temperate forests. Leaf area and ANPP are often positively correlated with soil water availability (Grier and Running 1977, Runyon et al. 1994, Jose and Gillespie 1997). Water stress reduces stomatal aperture in leaves, which can reduce carbon assimilation from the atmosphere, photosynthesis, and ANPP. In temperate forests, ANPP generally increases with increasing annual temperature as well (Curtis et al. 2002). Higher temperatures are associated with longer growing seasons, more optimal temperatures for photosynthesis, and increased metabolic activity of soil microbes that facilitate nutrient cycling.

Biotic and abiotic influences on nitrogen mineralization

Soil nitrogen availability limits ANPP across many temperate forests (Reich et al. 1997). Plants primarily rely on mineral forms of nitrogen, which are produced by microbes through fixation of diatomic nitrogen, mineralization of organic forms of nitrogen, and nitrification (Charley and Richards 1983). Rates of nitrogen mineralization, and the availability of mineral nitrogen in the soil, depend on soil properties and the type of inhabiting vegetation. Local vegetation influences soil nitrogen availability through the quality of organic matter shed from the plants and the rate at which it decomposes and returns nutrients to the soil. Foliage litter returned to the soil may range from 2,500 to >4,000 kg ha^{-1} y^{-1} for temperate forest types (Nadelhoffer et al. 1985). Foliage with high concentrations of labile carbohydrates has rapid rates of decomposition following abscission (Taylor et al. 1989). After these labile carbohydrates have been leached and utilized by soil microfauna, rates of decomposition are controlled by the content of recalcitrant compounds in the foliage, such as cellulose and lignin (Melillo et al. 1982, Taylor et al. 1989). Several field studies have shown topographic variation in soil nitrogen content, and net nitrogen mineralization, and have used species composition effects to explain these differences (Zak and Pregitzer 1990, Garten et al. 1994, Knoepp and Swank 1998). Gower and Son (1992) showed significant differences in net nitrogen mineralization among plantations of five different tree species grown on a similar soil in Wisconsin, USA. They attributed this result to species differences in lignin to nitrogen ratios of the foliage.

Physical soil properties, temperature, and soil moisture also influence nitrogen availability. Reich et al. (1997) included soil texture, temperature, and litterfall nitrogen in a multiple regression model that explained 81% of the variation in net nitrogen mineralization across 27 naturally regenerated forests. They showed significantly higher net nitrogen mineralization on fine textured Alfisols than on coarse textured Entisols, even among similar forest types. Major contrasts in soil chemical and physical properties across soil orders are related to water holding capacity, mineral nutrient status, and pH, all of which may influence nitrogen mineralization. Powers (1990) examined net nitrogen mineralization along a 2000 m elevation gradient in California, USA. He expressed nitrogen mineralization per unit of total soil nitrogen (*Min*N), and determined that *Min*N was positively and linearly related to average soil temperature. He also saw significant reductions in *Min*N under drought conditions. Moist and warm conditions enhance nitrogen mineralization, while drier conditions may limit the abundance and activity of important bacteria (Garten et al. 1994).

Nitrogen mineralization and ANPP

Observational field studies and manipulative experiments support the assertion that nitrogen availability is the primary resource limiting ANPP in many temperate forests. Aboveground net primary productivity is often positively correlated with net nitrogen mineralization, or indices of soil nitrogen availability, across geographic, topographic, and experimentally-induced gradients in soil fertility (Pastor et al. 1984, Nadelhoffer et al. 1985, Dalla-Tea and Jokela 1991, Gower et al. 1992, Reich et al. 1997, Balster and Marshall 2000, Tateno et al. 2004, Newman et al. 2006). Aboveground net primary productivity may increase by five fold (Dalla-Tea and Jokela 1991) and attain rates up to 25 Mg ha^{-1} y^{-1} in fertilized plantations (Samuelson et al. 2004).

There are two physiological mechanisms by which increases in soil nitrogen availability may increase photosynthetic carbon gain. First, leaf area index (LAI, m^{2}m^{-2}) increases with greater nitrogen availability, resulting in more total surface area for photosynthetic carbon gain

(Vose and Allen 1988). Second, more nitrogen uptake may result in more production of chlorophyll molecules, proteins in the electron transport chain, and the CO_2 fixing enzyme RuBP carboxylase/oxygenase (Evans 1989), which increases photosynthetic production per unit of leaf area. Evergreen conifer species appear to invest acquired soil nitrogen in the production of more foliage biomass (Vose et al. 1994), without significant increases in net photosynthetic rates (Teskey et al. 1994, Samuelson et al. 2001, Will et al. 2001, Gough et al. 2004). The magnitude of the response depends on species, stand age, and the degree of nitrogen limitation (Vose et al. 1994). For example, Martin and Jokela (2004) reported 129% and 97% increases in LAI for equal-aged stands of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) receiving a fertilizer treatment on a common site. At age 15, fertilization again increased leaf area index in the loblolly pine stands, while LAI in the slash pine stands peaked at 6-9 years of age, and was unresponsive to further application (Martin and Jokela 2004). Vose and Allen (1988) examined LAI responses to fertilization in loblolly pine plantations growing on three sites with different initial soil nitrogen status. They showed the greatest increase in LAI for the most nitrogen limited site, and no significant change in LAI on the site with highest initial soil nitrogen availability, demonstrating that the severity of nitrogen limitation affects leaf area responses to fertilization. Broadleaf deciduous trees attain higher LAI when soil nitrogen availability is improved, and some species achieve higher photosynthetic rates as well (Henderson and Jose 2005). Broadleaf deciduous trees show more rapid rates of increase in net photosynthesis with increasing leaf nitrogen content than evergreen conifer trees (Reich et al. 1995, Reich et al. 1998, Ripullone et al. 2003).

While important for photosynthetic carbon gain, nitrogen availability may also enhance ANPP by affecting patterns of biomass partitioning. Improved soil nitrogen availability typically results in higher overall NPP, and thus ANPP (Nadelhoffer et al. 1985, Gower et al. 1992, Samuelson et al. 2004). However, greater soil nitrogen availability also causes increases in biomass accumulation in aboveground parts, while decreasing carbon allocation to root biomass (Keyes and Grier 1981, Gower et al. 1992, Albaugh et al. 1998, Tateno et al. 2004). Other studies have demonstrated that fertilization accelerates stand development and ontogenetic shifts in biomass partitioning to aboveground parts (King et al. 1999, Coleman et al. 2004, Coyle and Coleman 2005).

Extrapolating the results from manipulative studies in managed plantations may be problematic because young trees in open canopies are often used and the gradients in soil fertility may be more extensive than exist under natural conditions. The relationship between soil nitrogen availability and LAI in mixed-deciduous forests is poorly understood due to the lack of relevant studies in these forests. Field studies indicate a general positive relationship between net nitrogen mineralization, or nitrogen uptake, and ANPP among mature mixed-species forests (Pastor et al. 1984, Nadelhoffer et al. 1985, Reich et al. 1997, Joshi et al. 2003, Tateno et al. 2004, Newman et al. 2006). Yet, the respective roles of leaf area expansion and photosynthesis are not well understood. In mixed deciduous forests, LAI has explained 47% (Fassnacht and Gower 1997), 62% (Bolstad et al. 2001), and 93% (Jose and Gillespie 1997) of the variation in ANPP. Bolstad et al. (2001) compiled multiple datasets from eastern deciduous forests and showed that LAI explained 39% of the variation in ANPP. Changes in species composition across experimental plots and study sites may weaken the relationship between nitrogen mineralization and both LAI and ANPP, because of differences in SLA, photosynthetic responses to increasing nitrogen uptake, and patterns of biomass accumulation associated with different species and size classes of trees. It is also likely that water and other nutrients have an equal or greater effect on LAI in some mixed deciduous forests (Fassnacht and Gower 1997, Jose and Gillespie 1997, Newman et al 2006).

Radiation use efficiency

Reich and Bolstad (2001) assembled a global dataset of ANPP values for temperate forests. They showed substantial ranges of ANPP values within stands of a single species, and in comparisons of ANPP among species. Several studies have demonstrated that the range in annual ANPP observed for monoculture forests is positively and linearly correlated to the annual amount of photosynthetically active radiation intercepted by the canopy (IPAR) (Cannell et al. 1987, Grace et al. 1987, Dalla-Tea and Jokela 1991, Will et al. 2005). For example, 90% of the variation in ANPP and annual stemwood growth of loblolly pine and slash pine plantations was explained by IPAR (Dalla-Tea and Jokela 1991, Will et al. 2005). The slope of this relationship is called radiation use efficiency (ε) (Monteith 1977).

Monteith (1977) suggested that the conversion of solar radiant energy to plant biomass should occur at a consistent level of efficiency. The simple ratio used to calculate ε (ANPP:IPAR) includes information about the major processes involved in energy capture and conversion to biomass. Aboveground net primary productivity quantifies the balance between gross photosynthetic production of carbohydrates and carbon lost through cellular respiration in aboveground plant parts. IPAR estimates the total amount of energy captured by plant canopies for photosynthesis, and accounts for the effects of total leaf area display and canopy architecture. This idea has been used to estimate ANPP for agricultural crops and monoculture forests using ground measurements of IPAR and integrated measurements of incident photosynthetically active radiation (PAR) (Cannell et al. 1987, Grace et al. 1987). More recently, ε values have been incorporated into process-based models that simulate NPP and carbon sequestration at multiple spatial scales (Landsberg and Waring 1997).

Values of ε for temperate-evergreen-conifer forests in the United States range from 0.9 g MJ^{-1} in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Pacific Northwest, to 0.2 g MJ^{-1} in ponderosa pine (*Pinus ponderosa* Dougl.) stands in Montana (Gower et al. 1999). Radiation use efficiency values of 0.46 g MJ^{-1} and 0.49 g MJ^{-1} have been reported for 21 year old slash pine and 13 year old loblolly pine stands, respectively (Gholz et al. 1991, DeLucia et al. 2002). Radiation use efficiency values can be robust for evergreen conifer species across a range in soil fertility, stand conditions, and ANPP (Dalla-Tea and Jokela 1991, Will et al. 2001, Will et al. 2005). This result is due to the consistent increase in leaf area with increasing nitrogen availability in pine forests (Vose et al. 1994), which enhances ANPP, while also increasing IPAR. In contrast, Balster and Marshall (2000) showed a curvilinear relationship between IPAR and stemwood production in fertilized stands of Douglas-fir. They suggested that stemwood production per unit of IPAR increased because of a fertilizer-induced shift in biomass accumulation in aboveground plant parts. Martin and Jokela (2004) also observed substantial fluctuations in ε in developing stands of loblolly and slash pine. They showed a variable effect of fertilization on ε during different stand-development periods, with the highest ε at 6-9 years of age (loblolly: 0.83 g MJ^{-1} and slash: 0.95 g MJ^{-1}), when ontogenetic shifts in biomass allocation to aboveground parts amplified the effect of fertilization. Some inter-annual variation in ε can be expected due to changing climate conditions, particularly when water stress limits photosynthesis. Across multiple vegetation zones in Oregon, USA, Runyon et al. (1994) estimated that 8% to >75% of IPAR was not utilized because of water and temperature related constraints on photosynthesis.

There have been few studies of ε in mixed species stands, or plantations, of broadleaf deciduous trees. Similar to pines, leaf biomass production and LAI in monocultures of broadleaf deciduous trees is positively correlated with net nitrogen mineralization, or soil nitrogen availability (Samuelson et al. 2001, Tateno et al. 2004, Henderson and Jose 2005). Allen et al. (2005) showed a positive IPAR response to fertilization and irrigation in sweetgum trees (*Liquidambar styraciflua* L.), and a consistent ε value across silvicultural treatments, with slight inter-annual variation (1.01-1.12 g MJ^{-1}). The same silvicultural treatment also increased IPAR in stands of sycamore (*Platanus occidentalis* L.). However, ANPP increased exponentially, not linearly, with IPAR for this species ($\varepsilon = 1.17$ for fertilization + irrigation treatment). If fertilization and irrigation yield greater net photosynthesis and ANPP per unit IPAR, ε values may increase across soil resource gradients in deciduous forests (Allen et al. 2005).

Ahl et al. (2004) provided evidence that ε may be higher for broadleaf deciduous trees than for evergreen conifers. Broadleaf deciduous trees may have higher net photosynthetic rates and growth efficiency (ANPP/LAI) than evergreen conifers (Gower et al. 1993), which could facilitate greater ε. However, evergreen conifers are capable of utilizing PAR throughout the entire year in some environments (Teskey et al. 1994), while deciduous trees experience a shorter growing season. Ahl et al. (2004) examined ε in two broadleaf deciduous forests that consisted primarily of one species. No studies have reported ε values for mixed deciduous forests or determined how consistent ε is across environmental gradients.

Photosynthetic radiation use efficiency: measuring canopy light gradients

The linear relationship between ANPP and IPAR is often observed in monoculture forests, even with canopies intercepting as much as 95% of the incoming PAR (Will et al. 2005). This suggests that canopy photosynthetic production should increase linearly with IPAR as well.

Yet, net photosynthesis of individual leaves is often light-saturated when exposed to PAR of one-half or two-thirds of full sunlight (Sullivan et al. 1996). Despite this condition, the ratio of canopy photosynthetic production to IPAR (PhRUE) may be fairly consistent for monoculture forest canopies. This is possible because of the arrangement of foliage and patterns of branching in trees, and acclimation of foliar morphology and physiology to intra-canopy light gradients.

Vertical profiles of light in forest canopies can be modeled using the Beer-Lambert equation, estimated using optical techniques, or measured directly. Beer's law quantifies the attenuation of solar radiation within a homogenous medium. The Beer-Lambert equation has been adapted for use in estimating relative irradiance within forest canopies (Campbell 1986). The equation predicts relative quantum flux density at canopy height h (Q_h) based on incident quantum flux density above the canopy (Q_i), cumulative LAI above height h, and an extinction coefficient (K):

$$Q_h = Q_i \exp^{(-K*LAI)}$$

The extinction coefficient is calculated as canopy silhouette area divided by canopy leaf area. Both the numerator and denominator in this ratio can be calculated by assuming that the distribution of leaf area in a plant canopy is similar to the distribution of surface area on an ellipsoid with vertical axis *a* and horizontal axis *b* (Campbell 1986). The lengths of these two axes can be modified to simulate planophile and erectophile canopies. Application of the Beer-Lambert equation in plant canopies requires the assumption that foliage is randomly dispersed throughout the canopy (Stenberg et al. 1994). This assumption is regularly violated because foliage is often clumped and distributed non-randomly within the canopies of individual trees, and entire forests. The Beer-Lambert equation has been used to estimate light attenuation and LAI in forests with varying levels of success. For example, Vose et al. (1995) measured LAI, vertical leaf area distribution, and vertical light profiles in mixed deciduous stands and calculated extinction coefficients using the Beer-Lambert equation. These extinction coefficients were used to project LAI at five test sites, and the modeled LAI values varied by -48% to +80% from LAI estimates derived from litter collection. When the data were pooled across all sites, the error ranged from 7% to15 %.

Direct measurements of PAR within canopies can be made when canopy access is possible, typically by way of scaffolding towers. Some researchers take hemispherical photographs from various canopy positions using a fish-eye lens. These photographs are used to estimate integrated quantum flux density of direct and diffuse solar radiation based on canopy gap fractions, seasonal changes in the solar zenith angle, and incident PAR measurements taken above the canopy (Niinemets et al. 2004). Others use some type of quantum sensor to take continuous or transient measurements of PAR at multiple canopy heights (Kull et al. 1999, Kull and Tulva 2002). Parker et al. (1996, 2002) devised a new method for measuring vertical light profiles in forests using a quantum sensor mounted on top of a meteorological balloon. They have successfully used this method in multiple forest types by utilizing small canopy gaps through which the balloon can ascend. They also determined that measurements of vertical PAR gradients using this method were not biased by the small canopy openings required for sampling (Parker et al. 2002).

Patterns of light penetration in the canopy vary substantially within and among forest types due to differences in crown structure and the vertical distribution of leaf area. Vose and Swank (1990) showed a 50% reduction in PAR at approximately 4 m to 7 m canopy depth in a 32 year old eastern white pine plantation. The depth decreased as the current-year foliage developed. Kull et al. (1999) reported a 67% reduction in PAR at approximately 2 m depth in a canopy dominated by two oak species. In another broadleaf-deciduous forest, average PAR decreased linearly with height in the overstory, but exponentially when data from the understory were included (Kull and Tulva 2002). Parker et al. (2002) identified three general zones of light penetration in a chronosequence of Douglas-fir-western hemlock forests: a high light/low variability zone in the upper canopy, a transitional zone with high variability, and a low light/low variability zone in the lower canopy. Total depth of the high light and transitional zones increased with forest age, concomitant with shifts in vertical leaf area distribution from the upper to lower canopy. Relative PAR reached 50% at approximately 6 m canopy depth in a 20 year old stand, compared to a 12 m depth in a 98 year old stand (Parker et al. 2002). In forests with multiple broadleaf-deciduous species, vertical patterns in leaf area distribution and PAR depend on the size and relative abundance of overstory and understory species (Vose et al. 1995).

Photosynthetic radiation use efficiency: foliar acclimation to light

Morphological and physiological characteristics of foliage change predictably with decreasing relative quantum flux within canopies of evergreen conifer and broadleaf-deciduous species. Specific leaf area increases as relative quantum flux decreases from the canopy top to bottom (Ellsworth and Reich 1993, Niinemets 1997, Bond et al. 1999, Meir et al. 2002, Marshall and Monserud 2003b, a, Niinemets et al. 2004). Both foliar nitrogen content (N_{area}) and light saturated net photosynthetic rates (A_{max}), expressed on an area basis, decrease from canopy top to bottom (Ellsworth and Reich 1993, Hollinger 1996, Kull and Niinemets 1998, Schoettle and Smith 1999, Warren and Adams 2001). Evergreen conifer species also maintain multiple age classes of foliage that experience light gradients from the terminal end of the branch inward toward the stem. There are changes in relative quantum flux across these age cohorts of foliage as well (Schoettle and Smith 1999, Warren and Adams 2001). Foliar N_{area} and A_{max} also tend to decrease along this light gradient (Schoettle and Smith 1999, Warren and Adams 2001, McGarvey et al. 2004), although a general pattern of SLA across age cohorts has not been established (Borghetti et al. 1986, Schoettle and Smith 1999, Warren and Adams 2001).

In some instances, foliar nitrogen concentrations decrease with increasing relative quantum flux due to greater structural carbohydrate content of upper canopy foliage (Niinemets 1997). However, there is typically little variation in foliage nitrogen content and A_{max} within canopies when these parameters are expressed on a mass basis (Ellsworth and Reich 1993, Palmroth and Hari 2001, Meir et al. 2002). Acclimation of specific leaf area to intra-canopy light gradients appears to moderate the changes seen in N_{area} and A_{max} within canopies. While there is a consensus that acclimation of SLA is primarily to gradients in light, it should be noted that humidity and temperature within the canopy co-vary with light, resulting in a vertical gradient in evaporative demand as well (Niinemets and Valladares 2004). Higher SLA in lower-canopy leaves enhances foliage surface area in this light limited environment, which is beneficial for light capture. Low SLA in the upper canopy may be beneficial for coping with intense light and water stress, the latter being caused by greater evaporative demand from the leaf surface, and resistance to xylem transport of water to greater canopy height. Denser leaves create a greater diffusion gradient for water loss to the atmosphere, and facilitate intra-leaf shading of chloroplasts in this high light environment (Gutschick 1999, Green and Kruger 2001, Niinemets and Valladares 2004).

Modeling analyses reveal that whole-canopy photosynthetic production may be optimized with regards to light interception when N_{area} and A_{max} change proportionally with quantum flux density within the canopy (Hirose and Werger 1987, Hollinger 1996). Also, the optimal distribution of N_{area} and A_{max} yields a consistent ratio of whole-canopy-photosynthetic production to IPAR at daily to annual time scales (Kull and Jarvis 1995, Haxeltine and Prentice 1996, Rosati et al. 2004), providing a physiological basis for the linear correlation between IPAR and ANPP. Distributions of N_{area} and A_{max} in real canopies have been shown to be only near this optimal pattern (Hollinger 1996, Bond et al. 1999, Meir et al. 2002), but still result in greater canopy photosynthesis than hypothetical canopies in which N_{area} is distributed randomly, or uniformly (Hirose and Werger 1987, Hollinger 1996).

The near-optimal acclimation of leaves to their local light environment suggests that PhRUE at the canopy scale should be relatively consistent. This idea was supported by a study in monocultures of two crop-tree species, which showed that daily canopy photosynthesis could be accurately projected based on physiological measurements of a single leaf at the canopy apex, and daily integrated PAR data (Rosati et al. 2004). This methodology has not been adapted to mixed-species forests with multiple age classes of trees. The plasticity of N_{area} and A_{max} in response to light gradients can vary by species due to their different average nitrogen concentration and net photosynthetic rates, and substantial differences in the range of SLA within their canopies (Kull and Niinemets 1998, Meir et al. 2002, Niinemets et al. 2004). Currently, no general trends in the acclimation potential of SLA have been established for shade tolerant versus shade intolerant species, although such trends would improve our understanding of whole canopy photosynthesis, and PhRUE in diverse forests.

CHAPTER 3

A COMPARISON OF RADIATION USE EFFICIENCY BETWEEN TWO SOUTHERN APPALACHIAN FORESTS[1]

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INTRODUCTION

Aboveground net primary productivity (ANPP) is the net accumulation of biomass in aboveground plant parts over a specific time period, and is an important aspect of the carbon cycle in forests. ANPP in temperate forests commonly ranges from <5 to >20 Mg ha^{-1} y^{-1} (Reich and Bolstad 2001). Within non-arid climate regions, ANPP varies widely due to species composition (Gower et al. 1993, Fassnacht and Gower 1997, Reich et al. 1997, Yuste et al. 2005) and is most often limited by nitrogen availability in the soil (Keyes and Grier 1981, Nadelhoffer et al. 1985, Vose and Allen 1988, Reich et al. 1997, Albaugh et al. 1998, Balster and Marshall 2000). With intensive management and fertilization, some plantation forests can attain rates of ANPP up to 25 Mg ha^{-1} y^{-1} (Samuelson et al. 2004).

There are two mechanisms by which increased nitrogen availability and uptake may enhance ANPP in forests. First, the photosynthetic potential of foliage is largely dependent on nitrogen content (Evans 1989). Increased nitrogen uptake from the soil can increase ANPP due to higher net photosynthetic rates in the foliage (Allen et al. 2005, Henderson and Jose 2005). Second, nitrogen enrichment causes increases in total leaf area, resulting in more surface area for photosynthetic carbon gain (Vose and Allen 1988, Albaugh et al. 1998, Samuelson et al. 2004).

Variation in soil nitrogen availability, both natural and due to silvicultural treatments, contributes to the substantial range of ANPP observed among stands of single species, or in comparisons of ANPP among species (Reich and Bolstad 2001). Several studies have demonstrated that the range in annual ANPP observed for monoculture forests is positively and linearly correlated to the annual amount of photosynthetically active radiation intercepted by the canopy (IPAR) (Cannell 1987, Grace 1987, Dalla-Tea and Jokela 1991, Will et al. 2005). The slope of this relationship is termed radiation use efficiency (ε, ANPP/IPAR) (Monteith 1977).

For example, 90% of the variation in ANPP and annual stemwood growth of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelm.) plantations was explained by IPAR (Dalla-Tea and Jokela 1991, Will et al. 2005). Radiation use efficiency can be robust for evergreen conifer species across a range in stand conditions, soil fertility, and ANPP (Dalla-Tea and Jokela 1991, Will et al. 2001, Will et al. 2005). Experiments in southern pines show that the increase in productivity obtained through soil-nitrogen amendments is driven by an increase in foliage biomass and leaf area index (LAI m^2m^{-2}) (Vose and Allen 1988, Teskey et al. 1994), not through significant increases in net photosynthetic rates (Teskey et al. 1994, Samuelson et al. 2001, Will et al. 2001, Gough et al. 2004). As a result, minimal variation in ε occurs, since leaf area expansion simultaneously increases IPAR and ANPP. While there is also a positive relationship between nitrogen availability and ANPP in deciduous and mixed species forests (Reich et al. 1997, Newman et al. 2006), it is not clear if this relationship results from consistent increases in LAI or net photosynthesis. The strength of the relationship between LAI and ANPP in mixed deciduous forests appears to vary across environments (Fassnacht and Gower 1997, Jose and Gillespie 1997, Bolstad et al. 2001). Also, there are species and functional group differences in the response of LAI (Allen et al. 2005, Henderson and Jose 2005) and net photosynthesis (Reich et al. 1995, Reich et al. 1998, Ripullone et al. 2003) to changing nitrogen availability. Fertilization can cause increases in both net photosynthesis and LAI in some deciduous species, which leads to variability in ε because of increased photosynthetic production per unit of IPAR (Allen et al. 2005). However, studies of ε in deciduous species have been mostly limited to young plantation forests. Extrapolating the results from these manipulative studies to other forests is problematic because young trees in open canopies are used, and gradients in soil fertility may be more extensive than those in unmanaged forests. Very little is known about how nitrogen availability may influence ε in forests containing multiple species and age classes of trees.

Values of ε have been reported for several species, and the differences among species are substantial (Gower et al. 1999). There have been few comparisons of ε for temperate deciduous and evergreen species growing in similar environments (Ahl et al. 2004, Allen et al. 2005, Dungan and Whitehead 2006). There are important differences in the morphology, lifespan, and photosynthetic potential of deciduous and evergreen foliage (Gower et al. 1993, Reich et al. 1995), which may result in differences in ANPP and ε. Likewise, carbon allocation to above and belowground parts may vary among species and functional groups growing on similar sites (Yuste et al. 2005), which would affect ANPP per unit of IPAR. There have been very few studies of ε in mixed-species, and mixed-aged-deciduous forests (Ahl et al. 2005), and we are aware of no studies examining ε in oak-dominated-mixed-deciduous forests in the eastern United States. Species diversity has been positively associated with productivity in forests and other plant communities (Tilman et al. 1997, Caspersen and Pacala 2001, Reich et al. 2004), and could be beneficial for ε. However, it is not known how consistent ε may be in forests with multiple species and ages of trees.

The linear relationship between ANPP and IPAR is often observed in forest canopies intercepting as much as 95% of the incoming photosynthetically active radiation (PAR) (Will et al. 2005). This suggests that there is a consistent ratio of canopy photosynthetic production to IPAR. Yet, net photosynthesis of individual leaves is often light-saturated when exposed to PAR of one-half or two-thirds of full sunlight (Sullivan et al. 1996). Despite this condition, the ratio of canopy photosynthetic production to IPAR (PhRUE) may be fairly consistent for monoculture forest canopies. This is possible because of the arrangement of foliage and patterns of branching in trees, and acclimation of foliar morphology and physiology to intra-canopy PAR gradients.

Foliar nitrogen content per unit area (N_{area}), and light saturated photosynthetic rates (A_{max}) expressed on an area basis, decrease from the top to bottom of the canopy. These changes result from the acclimation of specific leaf area (SLA, cm^2 g^{-1}) to vertical PAR gradients. Lower SLA in the upper canopy indicates leaf morphological acclimation to light, heat, and water stress, while higher SLA in the lower canopy improves light interception in the low light environment (Gutschick 1999, Green and Kruger 2001, Niinemets and Valladares 2004). Modeling analyses have shown this canopy arrangement may be close to optimal for carbon assimilation (Haxeltine and Prentice 1996, Hollinger 1996), and results in a consistent ratio of total canopy photosynthetic production to IPAR at weekly to annual time intervals (Kull and Jarvis 1995, Haxeltine and Prentice 1996, Rosati et al. 2004). The near-optimal acclimation of leaves to their local light environment suggests that PhRUE at the canopy scale should be relatively consistent. This idea was supported by a study in monocultures of two crop-tree species, which showed that daily canopy photosynthesis could be projected with reasonable accuracy based on physiological measurements of a single leaf at the canopy apex, and daily integrated PAR data (Rosati et al. 2004). Adapting this method to diverse forests would be difficult because of significant differences in acclimation potential that exist between species (Kull and Niinemets 1998, Bond et al. 1999, Meir et al. 2002, Marshall and Monserud 2003, Niinemets et al. 2004), and between age classes of foliage in evergreen trees (Schoettle and Smith 1998, Warren and Adams 2001, McGarvey et al. 2004). There may be general differences in the extent of foliage acclimation between overstory versus understory trees, because overstory trees are exposed to much larger gradients in PAR (Niinemets et al. 1999, Marshall and

Monserud 2003b). However, this idea has not been extensively tested among forest types. Eastern deciduous forests contain multiple species at co-dominant and intermediate canopy positions. These forests provide an opportunity to examine how foliar acclimation to intra-canopy light gradients varies across species, and as a function of canopy position.

We conducted a field study on two adjacent watersheds in the southern Appalachian Mountains of western North Carolina that contain contrasting forest types. There were three objectives: 1) quantify ε for a mixed deciduous forest and a 50 year old white pine plantation (*Pinus strobus* L.) 2) determine how soil nitrogen availability varies at the watershed scale, and whether this variation was correlated to LAI, IPAR, and ANPP, and 3) examine differences in PAR attenuation within the canopies of these two forests and the degree to which foliage properties are acclimated to the light gradient. We tested three hypotheses: 1) ε is greater for a mixed deciduous forest than for a mature eastern white pine plantation, based primarily on the expectation that photosynthetic potential and production efficiency are greater in the deciduous forest, and that ε is reduced during the winter months for white pine 2) increasing nitrogen availability will increase LAI, ANPP, and IPAR, resulting in a conservative estimate of ε at the watershed scale and 3) SLA will acclimate to intra-canopy light gradients, and the plasticity of SLA will decrease with leaf age in white pine trees, and will be greater for co-dominant trees than for intermediate and understory trees in the deciduous forest.

METHODS

Site description

This work was conducted at the U.S.D.A. Forest Service Coweeta Hydrologic Laboratory in Otto, North Carolina. Average annual temperature in the Coweeta basin is 13°C; average annual rainfall increases from 178 cm at lower elevation to over 250 cm at higher elevation.

Deciduous forest is the dominant land cover type in the basin and a variety of oak (*Quercus* spp.) and hickory (*Carya* spp.) species and tulip poplar (*Liriodendron tulipifera* L.) are prevalent in the upper canopy. Soils in the basin are regularly of the Inceptisol and Ultisol order.

The study site was in Watersheds 17 and 18, two adjacent 13 hectare watersheds that share a northwest aspect and range in elevation from 760 – 1021 and 726 – 993 m respectively. Two dominant soil types are common to each watershed. The Evard-Cowee complex is a very deep, well drained, fine loamy soil on slope and ridge positions and the Saunook series is a deep, well drained, fine loamy soil formed from colluvium in drainages and toe slopes (Thomas 1996, Knoepp and Swank 1997). Watershed 17 was cleared of all hardwood vegetation in 1942 and replanted with eastern white pine (*Pinus strobus* L.) in 1956 (Swank and Crossley Jr. 1988). Current basal area in WS 17 is 61 m^2 ha^{-1} and maximum canopy height is approximately 30 m. Watershed 18 contains a mixed deciduous forest that has been undisturbed since selective logging in the 1920's. The current average basal area in WS 18 is 33 m^2 ha^{-1} and maximum canopy height ranges from 30 to 40 m. There is considerable change in species assemblages across the elevation gradient. From higher to lower elevation there is a shift from the dry, chestnut oak (*Quercus prinus* L.) dominated community to a cove hardwood community with tulip poplar as the prevalent species (Elliott et al. 1999). Red oak (*Quercus rubra* L.), scarlet oak (*Quercus coccinea* Muenchh.), red maple (*Acer rubrum* L.), and pignut hickory (*Carya glabra* Mill.) are common co-dominant species throughout, while white oak (*Quercus alba* L.) occupies lower slope positions. Black birch (*Betula lenta* L.) is found at middle and lower slope positions at intermediate canopy height and sourwood (*Oxydendrum arboreum* L.), blackgum (*Nyssa sylvatica* Marsh.), rhododendron (*Rhododendron maximum* L.), and mountain laurel (*Kalmia latifolia* L.) comprise the majority of understory species.

ANPP, IPAR, and RUE

Nine 0.09 ha plots were established in each watershed and stratified in groups of three at upper, middle, and lower slope positions. During the winter of 2004/05, diameter at breast height (dbh = 1.4 m) was recorded for all trees that exceeded 5 cm dbh in each plot. In the deciduous forest, a 10 x 10 meter subplot was established within each larger plot and dbh recorded for all trees and shrubs between 2 and 5 cm diameter. The standing biomass of stems and branches was determined using allometric equations with dbh as the independent variable. Site-specific equations (McGinty 1972, Phillips 1981, Martin et al. 1998) were available for 11 prevalent deciduous species and two understory shrubs. Non-site-specific equations (Ter-Mikaelian and Korzukhin 1997) were used for striped maple (*Acer pennsylvanicum* L.), fraser magnolia (*Magnolia fraseri* Walt.), and white basswood (*Tilia heterophylla* Vent.), which accounted for less than 3% of the basal area in any plot. A regional equation (Clark III et al. 1985) was used to estimate standing green weight of white pine stems and branches. Dry weight was calculated as 41.5% of green weight (Alex Clark, unpublished data). Site-specific equations for white pine were available, but the sample trees used for their development did not include large diameter stems. The biomass projections for the regional and local equations showed close correspondence over the comparable range in dbh (Figure 1). Diameter measurements and biomass estimates were repeated in the winter of 2005/06.

Litter traps were used to collect foliage and fine litter during the 2005 calendar year. Five and ten circular litter traps (0.5 m^2) were located in each plot in the pine and deciduous forests respectively. Litter included foliage, reproductive structures, and woody debris less than 1 cm diameter. Litter was collected monthly in the pine forest and monthly beginning in June in the deciduous forest. Litter was separated into foliage and fine litter groups, dried at 65^oC, and weighed. The foliage litter collected from the pines was abscised foliage from the previous year's cohort, yet we assumed similar foliage biomass production in 2005 for the purpose of estimating this component of ANPP. Foliage litter from the deciduous forest was separated by species before being dried and weighed. Total foliage and fine litter production for entire plots was estimated using a conversion factor based on the total sample area covered by the litter traps. Aboveground net primary productivity for 2005 was estimated as the increase in standing biomass of stems and branches plus foliage and fine litter production.

Intercepted photosynthetically active radiation (IPAR) was measured using the SunScan Canopy Analysis System (Delta-T Devices Ltd., Cambridge, UK). Three parallel 20 m transects were centrally located in each plot to minimize the effect of PAR interception by trees outside the plot. Sixteen or eighteen measurements of below-canopy PAR were made along each transect resulting in 50 measurements per plot. Incident PAR was measured in a clearing between the two forests prior to sampling, then below canopy PAR was rapidly measured in three plots, followed by another measurement in the clearing to account for any change in incident PAR during sampling. This process was repeated between 12:00 and 16:00 h until all plots were sampled. Each below-canopy PAR measurement was converted to a percent of incident PAR, and these percentages averaged for each plot. To determine if changing solar-zenith angle affected IPAR measurements, IPAR was measured hourly in one plot from 12:00 to 17:00 h on July 25 for the pine plantation and August 2 for the deciduous forest. Across a range in zenith angle from 15^o to 52^o the IPAR measurements varied less than 2 %, and no trend was apparent.

Intercepted radiation was measured four times from May until September of 2005. A linear rate of change in percent-daily IPAR was assumed between sampling dates. A growing season value of percent, and total IPAR, was estimated for the deciduous forest. The growing season ranged from April 21 – October 14 because these dates corresponded to observations of initial leaf development and leaf senescence made on multiple deciduous species from a nearby tower (Brian Kloeppel, unpublished data). The last IPAR measurement of the season was taken on September 6, and daily-percent IPAR for each plot was assumed to remain at this level until October 14, at which time substantial leaf abscission began.

We estimated growing season IPAR for the pine plantation using the same dates established for the deciduous forests. We also estimated annual IPAR since some carbon assimilation is expected during the winter months for this forest. Measurements of IPAR taken with the SunScan at sampling dates in early March and late October were much higher than would be expected, and probably unreliable. This was likely due to the combined effects of solar declination angle and the complex terrain, which may have resulted in substantial IPAR by stems, branches, and trees outside of the plots. Therefore, we assumed that daily-percent IPAR declined linearly after the final sampling date in September until December 31, reaching the same value of percent IPAR as was measured on the first sampling date in May, and we assumed that daily-percent IPAR from January to May 2005 was consistent at this level. This assumption was supported by the temporal patterns of leaf abscission we observed from foliage litter collection.

Incident PAR data for 2005 were available from two climate stations in the Coweeta basin. Total solar radiation from January 1 – May 20 was measured at a climate station approximately one kilometer from the study site. Total solar radiation was converted to PAR by multiplying by 0.5. From May 21 – December 31 PAR was measured at a climate station adjacent to WS 17. Daily values of cumulative-incident PAR were multiplied by daily interpolated values of percent interception. The daily values of absolute PAR interception were summed for the growing season in each forest, and for the entire year in the pine plantation. Radiation use efficiency (ANPP/IPAR) was calculated for each plot using growing-season estimates of IPAR for both forests, and an annual estimate of IPAR for the pine plantation.

Leaf area index

Leaf area index (m^2/m^2) was estimated for each plot using foliage litter biomass and species-specific estimates of specific leaf area (SLA). Hardwood litter was separated into seven species groups that comprised over 90% of foliage biomass. Twenty leaves from each species were hydrated, pressed overnight, and their area measured using the LI-3100 Area Meter (LI-COR, Lincoln, NE). These leaves were dried at 65°C and weighed to the nearest milligram.

Twenty fascicles were selected from the pine litter to determine SLA. The length of each fascicle was measured to the nearest millimeter, and the ventral-side width was measured on three needles to the nearest 0.1mm using a micrometer. An average ventral-side width for each fascicle was calculated from these measurements. Assuming the cross section of a fascicle is circular, we estimated the circumference of each fascicle using the average width of the ventral side as the radius. The rectangular area of ventral and exterior sides of all needles was calculated and added to derive total fascicle area. Projected area was calculated by dividing total fascicle area by π (Grace 1987). Fascicles were dried at 65° and weighed to the nearest milligram. Specific leaf area is reported in cm^2/g.

Soil nitrogen availability

We used the UNIBEST PST-1 resin capsules (Unibest International Corporation, Pasco, WA) to develop indices of soil nitrogen availability in each plot. The mixed resin contained strongly acidic and strongly basic exchange sites with H^+ and OH^- as counterions. The resins were used for multiple *in situ* sampling periods by recharging the resin's counterions with H^+ and Cl^-. This was accomplished by shaking the capsules in 2 M HCl for 20 hours prior to each deployment.

Six resin capsules were buried at random locations within each plot at 5 cm soil depth, which is in the A horizon, and near the average depth of transition between the A and AB/BA horizons (Knoepp and Swank 1997). The resin capsules were collected at approximately six week intervals and stored in a moist cool container until returned to the laboratory. Each capsule was rinsed with deionized water until all visible soil matter was removed from the surface, then shaken in 40 mL of 2 M KCl for 20 hours. The resins were deployed for three sampling periods of approximately six weeks during the 2005 growing season from April 21 - September 19.

The mineral nitrogen concentration of the KCl extracts was measured by colorimetric flow injection analysis using the FS 3000 (OI Analytical, College Station, TX). Nitrate/nitrite and ammonium concentrations were determined using the cadmium reduction and alkaline phenate methods, respectively (U.S. Environmental Protection Agency, 1983a, 1983b). The total mass of each form of available nitrogen was determined for each 40 mL extract, added, and reported as total-available-mineral nitrogen per unit mass of resin (μg/g). An average index value of available nitrogen was calculated from the six resin capsules in each plot for each sampling period, and these were added to obtain a growing season index value for each plot.

Light saturated net photosynthesis, leaf nitrogen content, and SLA

Light-saturated-net photosynthesis (A_{max}), leaf nitrogen content, and SLA were measured on leaves collected along vertical transects within the canopies of each forest. We hired an arborist to climb trees and clip small branches from which leaf samples were collected and measured. Four sample areas were chosen in each forest and sampling was conducted in August and September of the 2005 growing season. In the deciduous forest, points for canopy sampling were chosen based on the presence of a common canopy dominant and intermediate species that could be accessed along the same vertical transect (Table 1). Given the more homogenous canopy structure of the white pine plantation, sample points in that stand were selected in areas where measurements of vertical PAR gradients with a meteorological balloon and light sensor could be made along the same profile (described below).

The arborist was able to access almost any point in the canopy, which allowed us to sample closely along the visualized vertical profiles, and to focus sample collection on the south-facing side of the canopy. The maximum canopy height and the height from which each branch was clipped were measured using an ultrasonic measuring device (Vertex III-360, Haglof Inc, Madison, Mississippi). Clipped branches were dropped to the ground where they were immediately cut again underwater in glass jars. At least two small branches, or a larger branch with at least one bifurcation, were collected at each height. We sampled at regular height intervals from top to bottom of the canopy of each tree, typically at three to five meter intervals, yielding three or four sample heights per tree. Six to twelve leaves were sampled from each canopy height in deciduous trees, while three fascicles from the current and previous year's cohort were sampled at each height in white pine trees. Whenever possible, we sampled the outermost branches of the crown at each height. On-site measurements of A_{max} were done immediately for ring-porous and semi-ring-porous species (*Quercus* spp. and *C. glabra*), and following the collection of all samples for other species. A_{max} was measured with the LI-6400 Portable Photosynthesis System (LI-COR, Lincoln, NE). All measurements were taken at 1200 μmol m^{-2} PAR, 375 μmol mol^{-1} CO_2 in the air stream, and near ambient humidity. Leaves and fascicles were placed in plastic bags and stored on ice before returning to the lab. Specific leaf area of leaves and fascicles was calculated as described previously. Specific leaf area and area-based estimates of A_{max} and nitrogen content are expressed for one sided area for deciduous leaves and projected-area (total area/3.14) for pine fascicles. Estimates of SLA based on total area can be calculated for pine foliage by multiplying by 3.14, and by multiplying by 2 for deciduous foliage. Estimates of A_{max} and N_{area} based on total area can be calculated by dividing by 3.14 for pine foliage, and by dividing by 2 for deciduous foliage. Dried foliage samples were mixed in a ball-mill grinder and analyzed for total nitrogen using the NC 2100 CNS Soil Analyzer (CE Instruments Ltd., Wigan, UK).

Intra-canopy vertical PAR gradients

We used a cosine corrected PAR sensor (LI-190SB, LI-COR, Lincoln, NE) mounted on top of a spherical meteorological balloon (Scientific Sales Inc., Lawrenceville, NJ) to measure photosynthetically active radiation (400-700 nm) along the same vertical transects from which foliage samples were collected. The balloon was approximately four feet in diameter when fully inflated, and strong monofilament line was used as a tether. We used stranded 28 AWG hook-up wire to connect the light sensor to a LI-1000 datalogger (LI-COR, Lincoln, NE). The wire and tether were connected with tape at one meter intervals along their length. Errors in PAR measurements occur when the cosine corrected light sensor is not level at its base. To limit this measurement error, the light sensor was capped with a table-tennis ball made of cellulose, which served as a diffuser. Field tests showed that <5% variation occurred when the PAR sensor with diffuser was held at 90^{o} from upright, although the sensor was only slightly tilted during actual measurements. The diffuser also reduced light penetration to the sensor. To correct this error, the sensor with diffuser was placed on a platform with another open LI-190SB PAR sensor, and one minute averages of incident PAR were measured from 10:00 to 16:00 h on a single day. The difference between sensors was plotted against the value of PAR measured by the sensor with diffuser, and the regression equation was used to correct each measurement ($R^2 = 0.97$).

All sampling was done between 12:00 and 15:00 h under clear sky conditions. Sampling began at a 2 m height and continued at 1 m intervals until reaching the top of the canopy. At each height twelve instantaneous measurements were taken at approximately three second intervals. Average PAR at each height was calculated from these twelve measurements, and percent of incident PAR at each height was calculated relative to the average PAR value at the top of the canopy. Measuring the vertical PAR profile at each sample area took approximately 45 minutes.

Data Analysis

We used ANOVA and a two-factor nested design to test for significant effects of forest type (n = 2), and slope position within each forest type (n = 3), on ANPP, IPAR, ε, mineral-nitrogen availability, and LAI (Kutner et al. 2005). Forest type and slope position were both fixed effects. Scatter plots and least-squares-linear regression were used to examine relationships between soil-nitrogen availability, LAI, IPAR, and ANPP, and between relative PAR and leaf characteristics. We used t-tests to compare the averages for foliage characteristics between overstory and intermediate tree species, and between one year old and new fascicles in the white pine trees.

RESULTS

Intercepted photosynthetically active radiation

As leaf development began in late April, average IPAR ranged from 66 to 71% across slope positions in the deciduous forest (Figure 2). At the beginning of June, average IPAR at all slope positions had increased to >90%, and decreased from 97% at upper slope positions to 93%

at lower slope positions. IPAR increased by 1 to 4% throughout the remainder of the growing season, which was likely due to further expansion of total LAI. .

Prior to the expansion of the current year's foliage, average IPAR was already 91% in the white pine plantation, and increased slightly from 90% at upper slope positions to 93% at lower slope positions. Eastern white pine carries two age cohorts of foliage during the growing season, and retains the current year's foliage throughout the winter, while shedding the one-year-old cohort. New foliage begins developing during late April or early May, and can continue growing into August (Vose and Swank 1990, Maier and Teskey 1992). There was a gradual increase in IPAR throughout the growing season until needle abscission began in late September. During peak leaf area display in early September, average IPAR in the white pine plantation was 97%.

Average IPAR in the middle of the growing season (c. the July 23 measurement date) was 95% (SE = 0.3%) and 96% (SE = 1.0%) for all plots in the white pine and deciduous forests respectively. There was no significant difference in total-growing-season IPAR between the two forest types (p = 0.13, d.f. = 1), or across slope positions within each forest (p = 0.77, d.f. = 4).

Aboveground biomass and ANPP

Basal area in the white pine plantation was nearly double that in the deciduous forest, yet total stem and branch biomass was significantly greater in the deciduous forest (312.54 Mg ha^{-1}) than in the white pine plantation (271.12 Mg ha^{-1}, p = 0.03, d.f. = 1). There was a significant effect of slope position on standing biomass in the deciduous forest (p = 0.03, d.f. = 2) due to significantly greater standing biomass at the upper slope position (369.63 Mg ha^{-1}) than at the lower slope (272.78 Mg ha^{-1}, Tukey's HSD test, $\alpha = 0.05$).

Average ANPP was significantly greater in the deciduous forest (11,464 kg ha^{-1} y^{-1}) than in the white pine plantation (9,963 kg ha^{-1} y^{-1}, p = 0.04, d.f. = 1), but did not vary significantly across slope positions within either forest (p = 0.23, d.f. = 4) (Figure 3). Although statistically insignificant, there was a trend of decreasing average ANPP from the upper slope to lower slope positions in the deciduous forest (12,812 to 10,816 kg ha^{-1} y^{-1}). The average total and average fraction of ANPP in stems and branches tended to decrease from upper to lower slope positions in the deciduous forest. Total and fractional NPP of foliage biomass showed the opposite trend, tending to increase from upper to lower slope positions in both forests (Figure 4).

We used pooled data from all nine plots in each forest to examine NPP, and total standing biomass, of stems and branches of trees grouped in 5 cm diameter classes. Stem and branch production, biomass, and total number of stems were normally distributed in the white pine plantation (Figure 5.). In the deciduous forest, the distributions of stem and branch production and biomass were negatively skewed across diameter classes due to the influence of trees with dbh greater than 60 cm. The distribution of trees among diameter classes was positively skewed in the deciduous forest. Diameter classes 1 – 7 for white pine generally showed less proportional stem and branch production than proportional stem and branch biomass. Diameter classes 8 – 12 showed the opposite trend. These general patterns were not evident in the deciduous forest.

Radiation use efficiency

Radiation use efficiency was significantly greater in the deciduous forest than in the white pine plantation (Figure 6). The difference was significant when we compared ε for the deciduous forest (1.25 g MJ^{-1}, SE = 0.06) to both the growing season (1.06 g MJ^{-1}, SE = 0.04), and annual estimates (0.61 g MJ^{-1}, SE = 0.02) of ε for the white pine plantation (p = 0.02 and <0.001 respectively, d.f. = 1). There was no significant change in ε among slope positions (p = 0.25, d.f. = 4), indicating that ε was conservative across the watershed for each forest. There was an insignificant regression relationship between IPAR and ANPP in both forests, likely due to the small range of IPAR among plots. Although statistically insignificant, ε decreased consistently from upper to lower slope positions in the hardwood forest (1.37 to 1.12 g MJ^{-1}).

Soil nitrogen availability, LAI, and ANPP

Mineral nitrogen availability, measured near the interface of the A and AB/BA horizons, was significantly greater in the white pine plantation than in the deciduous forest throughout the 2005 growing season ($p < 0.0001$, d.f. = 1), but did not vary significantly among slope positions within either forest ($p = 0.23$, d.f. = 4) (Figure 7). Mineral nitrogen availability showed little seasonal variation in the deciduous forest, although each sampling period was approximately six weeks, and seasonal variation may have occurred within this time period. In contrast, mineral nitrogen availability increased during each successive sampling period in the white pine plantation. Both NH_4 and NO_3 were more available in the white pine plantation than the deciduous forest. The growing-season-average accumulation of NH_4 and NO_3 by the resin capsules was 77.2 and 262.7 $\mu g\ g^{-1}$ in the white pine plantation, and 47.4 and 28.1 $\mu g\ g^{-1}$ in the deciduous forest. Nitrate availability was 7 to 16 times higher in the pine plantation than the deciduous forest during the second and third sampling periods. Nitrate was 2 to 6 times more abundant than NH_4 in the pine plantation among sampling periods, whereas average NH_4 availability was 1.5 to 2 times greater than NO_3 across sampling periods in the deciduous forest.

There was no significant difference in LAI between forests ($p = 0.93$, d.f. = 1) or among slope positions within either forest ($p = 0.57$, d.f. = 4). Leaf area index ranged from 5.1 to 6.1 among plots in the pine plantation, and from 4.8 to 7.4 in the deciduous forest. Collectively we saw no significant differences in mineral nitrogen availability, LAI, or ANPP associated with slope position. Because of the narrow range of the data, no significant regression relationships were found between these variables in the pine plantation. Aboveground net primary productivity ranged from 7,997 kg ha^{-1} y^{-1} to 14,140 kg ha^{-1} y^{-1} among plots in the hardwood forest, but was not significantly related to mineral nitrogen availability or LAI.

Intra-canopy PAR gradients

There was consistently high radiation near the top of the canopy, then a zone of rapid PAR attenuation in which measurements were highly variable, followed by consistently low levels of PAR in the understory (Figure 8). In the pine plantation, both the pattern of PAR attenuation and the average canopy height (32 m) were similar among the four sample points. There was a gradual decline in PAR in the upper canopy of the pine plantation, followed by more rapid attenuation to the base of the live crown. Among the four sampling points there was a 10 to 19% decrease in PAR at 5 m canopy depth, and a 76 to 93% reduction in PAR at 10 m canopy depth.

There were marked differences in PAR attenuation among sample points in the deciduous forest. Total canopy height ranged from 28 m to 40 m among sample points, and the canopies of intermediate and understory trees commonly existed at less than 10 m from the ground. Due to the broader vertical distribution of leaf area, the transitional zone from high to low light was much broader and more variable than in the pine plantation. Among the four sampling points, there was 7 to 79% reduction in PAR at 5 m canopy depth, and a 25 to 95% reduction in PAR at 10 m canopy depth. Figure nine shows a comparison between relative PAR and relative canopy height for the pooled data from each forest. There was more rapid reduction in PAR in the upper 20% of the deciduous forest canopy. Beyond this depth the rate of decline in average PAR was more rapid in the pine canopy.

A_{max}, nitrogen content, and specific leaf area response to light

Among all deciduous species, A_{max} was positively correlated with leaf nitrogen content when both were expressed on an area basis, but no relationship existed when both were expressed on a mass basis (Figure 10). This result was consistent for individual species, and for all the species pooled. The positive relationship between A_{max} and leaf nitrogen content was present, but weaker in white pine, and there were equally strong relationships between mass and area based estimates.

Among all species, specific leaf area consistently increased as relative PAR decreased from the canopy top to bottom (Figure 11). Species was a major source of variation in this relationship in the deciduous forest, since specific leaf area varied widely among species at similar canopy height (see Appendix 1). Age class of foliage was a source of variation in the pine plantation, since there were different relationships between age classes, and because of higher SLA in the current-year foliage than in the one year old cohort (Figure 12).

There was no relationship between N_{mass} and SLA among deciduous species, and a very weak relationship for white pine ($R^2 = 0.13$). Also, there was no significant relationship between N_{mass} and relative PAR in either forest type, indicating that acclimation of SLA to intra-canopy light gradients was causing the differences in N_{area} we observed in the canopy (Figure 13). Similarly, there was no significant relationship between A_{max} expressed on a mass basis and SLA, or relative PAR, among all deciduous species, suggesting a similar influence of specific leaf area on area-based A_{max} (Figure 14). In the pine plantation, SLA increased and area-based A_{max} decreased with canopy depth and declining relative PAR (Figure 11 and Appendix 1). However, when all data were pooled there was not an inverse relationship between SLA and area-based A_{max} as seen among deciduous species. The expected inverse relationship was not seen because average SLA and area-based A_{max} were both higher in current-year foliage (68.62 $cm^2\ g^{-1}$ and 9.80 $\mu mol\ m^{-2}\ s^{-1}$) than in one-year-old foliage (61.35 $cm^2\ g^{-1}$ and 8.04 $\mu mol\ m^{-2}\ s^{-1}$). Hence, one-year-old foliage in the middle or lower canopy sometimes had a similar SLA to new foliage at the top of the canopy, but had lower area-based A_{max}.

We tested for general differences in SLA, the range of SLA, A_{max}, and foliar nitrogen content between overstory and understory trees in the deciduous forest, and between age classes of foliage in the white pine plantation. Understory trees had significantly higher SLA, and lower area-based A_{max} and N_{area}, which is similar to the trends seen in individual tree crowns. There was no significant difference in N_{mass}, and a small but significant increase in mass-based A_{max} in understory trees. New needles had higher SLA and A_{max} than one-year-old needles, both on a mass and area basis. Nitrogen content did not change significantly between age classes. While SLA varied considerably among species, we found no statistically significant differences in the range of SLA acclimation to intra-canopy PAR gradients between overstory and understory trees, or between age classes of foliage on white pine trees.

DISCUSSION

Aboveground net primary productivity and ε

Aboveground net primary productivity in the deciduous forest was 10 to 91% greater than ANPP for five deciduous forests located along an 8° latitudinal gradient in the United States (Curtis et al. 2002), and 42% higher than ANPP reported for 14 deciduous forests in Wisconsin and Minnesota (Reich et al. 1997). Higher annual temperature and precipitation are two important environmental variables contributing to the difference in ANPP between southern Appalachian forests and similar forests at higher latitudes (Curtis et al. 2002). Average ANPP in this study was approximately 25% greater than reported by Bolstad et al. (2001) for 16 study sites at Coweeta Lab. However, the Bolstad et al. study included sites at higher elevation, which had lower ANPP. Also, their ANPP estimates were for a ten year period (1986-1995) that included severe drought conditions from 1986-1988 (Kloeppel et al. 2003). Each of these factors probably contributed to the lower average ANPP they reported.

Aboveground net primary productivity for the white pine plantation was 48% higher than ANPP reported for a similar age white pine forest (Nadelhoffer et al. 1985), and similar to a 28-year-old white pine plantation (Gower et al. 1993), which were both in Wisconsin. This study was conducted near the southern extent of the range of eastern white pine, where the maximum growth rates for this species occur (Balmer and Williston 1983).

Radiation use efficiency for the deciduous forest was 34 to 44% greater than that reported for a northern hardwood forest (mainly *Acer saccharum* Marsh), and 47 to 60% higher than a trembling aspen forest (*Populus tremuloides* Michx) (Ahl et al. 2004). Most other studies of ε in deciduous species have been limited to young monocultures that had not yet reached canopy closure (Cannell et al. 1987, Green et al. 2001, Allen et al. 2005). To our knowledge, the present study has been the first to examine ε in an oak-dominated mixed deciduous forest. The average annual ε value for the white pine plantation (0.61 g MJ^{-1}) was at the high end of the range of values reported for five evergreen conifer forests in the United States (0.2 to 0.5 g MJ^{-1}, Gower et al. 1999), but lower than those reported for some evergreen conifer forests in the Pacific Northwest (0.18 to 0.92 g MJ^{-1}, Runyon et al. 1994).

Comparison of ε and ANPP between the two forest types

Radiation use efficiency was significantly greater in the deciduous forest than either the growing season or annual estimate of ε for the white pine plantation, which supports our first hypothesis. There were corresponding differences in ANPP and growing-season ε between the two forests (15 and 18% higher in the deciduous forest), while ε for the deciduous forest was 105% greater than the annual estimate for the white pine plantation. LAI, IPAR, and soil nitrogen availability are often positively correlated with ANPP. However, mineral nitrogen availability was greater in the white pine plantation, and growing season LAI and IPAR were not significantly different between the two forests. Since these forests were growing in a similar environment, differences in species composition and age are the most likely factors causing the differences in ε and ANPP we observed.

Greater ε in the deciduous forest was probably a result of the greater photosynthetic capacity of the foliage. Maximum rate of net photosynthesis (A_{max}), specific leaf area, and foliar nitrogen content tend to be positively correlated with one another, and inversely related to foliage longevity (Gower et al. 1993, Reich et al. 1999). These foliage characteristics may also be positively related to production efficiency (ANPP/LAI) (Gower et al. 1993). The deciduous species we studied had 30 to 60% greater foliar nitrogen concentrations, 65 to 264% greater SLA, and 50 to 133% greater mass-based A_{max} than foliage from white pine trees. Thus, potential carbon gain per unit IPAR was greater in the deciduous forest. Although the white pine trees continued to intercept incident PAR throughout the winter months, this additional energy capture did not result in higher ANPP than in the deciduous forest. Much of IPAR during the winter months was probably underutilized because of environmental constraints on photosynthesis (Runyon et al. 1994).

The more productive deciduous foliage supported significantly greater ε in this comparison. However, we did not measure below-ground net primary productivity (BNPP), and this conclusion may be inaccurate if total NPP were considered. At coarse spatial scales, the fraction of NPP allocated belowground may be similar among forest types (Mokany et al. 2006).

Yet, the fraction of NPP allocated to roots varies substantially along soil resource gradients and between vegetation types at smaller spatial scales (Keyes and Grier 1981, Davis et al. 2004, Tateno et al. 2004). For example, Yuste et al. (2005) compared NPP for mature *Quercus robur* L. and *Pinus sylvestris* L. forests growing on a similar site and reported that fine root production was a larger fraction of total NPP in the pine forest, although total belowground biomass and BNPP were similar between the two forests, and NPP was more than twice as high in the deciduous forest. McGinty (1976) compared total biomass allocation between an 18-year-old white pine plantation and a deciduous forest that was in an earlier stage of development in the Coweeta basin. Root biomass and the belowground fraction of total biomass were 15 and 40% greater in the white pine plantation, but total biomass was 23% greater in the deciduous forest. These studies provide some evidence that BNPP, or the fraction of NPP in roots may be greater for pine species than deciduous species growing on similar sites, but in neither case did this result in greater overall NPP or biomass accumulation in the pine forests.

Aboveground net primary productivity and ε vary due to ontogenetic growth patterns in young plantations (Martin and Jokela 2004), while age-related declines in forest productivity are commonly observed after canopy closure. We suspect that age-related constraints on ANPP were more inhibiting in the white pine plantation than the deciduous forest, in part because of differences in physiology between the two functional groups. One hypothesis for age-related decline in forest growth is that taller trees experience more difficulty in transporting water from the soil to the canopy, which could reduce stomatal aperture and carbon gain (Yoder et al. 1994, Ryan and Yoder 1997). Broadleaf deciduous trees can attain higher rates of sapflow and transfer more water to the canopy than evergreen conifers (Catovsky et al. 2002). Hence, hydraulic limitations to carbon gain may be more detrimental for the white pine plantation. Although hydraulic limitation to carbon gain occurs in many species, it does not appear to completely explain age-related declines in stand growth (Ryan et al. 2006).

Binkley (2004) provided supporting evidence for a second hypothesis, which suggests that a subset of trees achieve greater resource use, and resource use efficiency, while resource use and growth of the remaining trees is reduced. This results in a decrease in overall stand growth. This type of age-related restraint on ANPP would likely be more inhibiting in plantations than in mixed forests. White pine is a long lived species and attains maximum volume growth at 60 to 70 years in naturally occurring stands (Burns and Honkala 1990). However, even-age monocultures of white pine reach peak volume growth at 15 to 25 years in the southern Appalachian Mountains, and the rate of volume growth continuously declines following canopy closure (Burns and Honkala 1990).

Age-related decline due to competition for resources could be partially offset in the mixed-deciduous forest due to complementary resource use. Complementary resource use in plant communities has been identified as one important mechanism underlying the positive relationship between species diversity and productivity (Tilman et al. 1997, Reich et al. 2004, Hooper et al. 2005), and may become more important in plant communities over extended periods of time (Caspersen and Pacala 2001, Tilman et al. 2001, van Ruijven and Berendse 2005). Complementary resource use in forests may improve productivity when coexisting species have different spatial and temporal patterns of resource use, thus reducing direct competition. In this case, we suspect that complementary light use supported greater ANPP and ε in the deciduous forest. Except for the largest trees, proportional stem and branch production was dispersed evenly among several diameter classes in the deciduous forest, and the majority of trees were included in the smaller diameter classes (Figure 5). Intermediate and understory species require less light to initiate photosynthesis (Sullivan et al. 1996). In contrast, a substantial amount of self-thinning was occurring in the white pine plantation. The proportion of total ANPP was consistently lower than the proportion of total biomass in the smallest seven diameter classes in the pine plantation. Carbon gain per unit of IPAR was probably greater in shade-tolerant deciduous species than in suppressed white pine individuals that were showing evidence of declining health.

Comparison of ε among slope positions within each watershed

We expected mineral nitrogen availability to be the primary soil resource limiting LAI and ANPP in these forests. However, we saw no significant differences in mineral nitrogen availability, LAI, or ANPP at different slope positions within either watershed. Knoepp and Swank (1998) determined that the inhabiting vegetation may have a more important influence on annual nitrogen mineralization than elevation in the southern Appalachians. Micro-topographical features may be associated with changes in nitrogen mineralization (Garten et al. 1994), although these fluctuations may not be critical when considering variation in LAI and ANPP at the watershed scale. We also hypothesized that ε would be a conservative parameter at the watershed scale for each forest, since we expected the primary growth response to increasing nitrogen availability to be an increase in LAI. Our data indicate that ε is conservative at the watershed scale for each of these forests, but we saw no significant relationships between mineral nitrogen availability and LAI, or ANPP. This was likely due to the small range of the data.

Although statistically insignificant, there was a slight decrease in ANPP and ε from upper to lower slope positions in the hardwood forest. This change was apparently unrelated to mineral nitrogen availability, but may have been due to changes in environmental variables along the elevation gradient we did not measure, such as soil pH and other nutrients, temperature, or incident radiation. There are other conceivable sources of variation in ε that might occur in mixed-deciduous forests. For example, species differences in A_{max} and foliar nitrogen content (Green et al. 2003), foliar photosynthesis to respiration ratios (Vose and Bolstad 1999), canopy architecture and leaf angle distribution (Green et al. 2001), sapwood volume and respiration (Chapman and Gower 1991), and leaf longevity (Gower et al. 1993, Reich et al. 1999) could all affect ANPP per unit IPAR. Also, ontogenetic effects on ANPP (Coyle and Coleman 2005) and ε (Martin and Jokela 2004) could become important when there is substantial variation in age structure among forests. Thus, it is fairly remarkable that ε did not vary significantly within a 13 hectare watershed in which considerable fluctuations in species composition occurred along the elevation gradient. This finding warrants further studies of ε in mixed deciduous forests to determine how ε responds to broader environmental gradients and associated changes in plant communities and ANPP.

Foliar Acclimation to Intra-Canopy PAR Gradients

We measured vertical PAR gradients and corresponding changes in foliage characteristics for white pine and seven hardwood species (four co-dominant and three intermediate species). The vertical gradients in PAR we measured in each forest were generally similar to those described by Parker et al. (2002). There was a zone with high and consistent levels of PAR in the upper canopy, a transitional zone that was highly variable at middle canopy heights, and a zone with consistently low levels of PAR in the lower canopy. The transition zone was broader and much more variable in the deciduous forest, which had a more vertically stratified canopy and heterogeneity in crown structure among different species of trees. It should also be noted that IPAR increased by only 7% from May until September in the white pine canopy, while LAI approximately doubled. Such a large investment in leaf biomass does not seem beneficial considering the minimal added gain in energy capture. However, IPAR by branches may have been partly responsible for such a high level of total IPAR prior to the full expansion of the new foliage.

Specific leaf area increased, while N_{area} and area-based A_{max} decreased from canopy top to bottom among all species, canopy classes, and age cohorts of foliage. This is consistent with the majority of studies reporting similar data for broadleaf deciduous and evergreen conifer species (Ellsworth and Reich 1993, Hollinger 1996, Kull and Niinemets 1998, Bond et al. 1999, Warren and Adams 2001, Meir et al. 2002, Niinemets et al. 2004). We determined that vertical variation in N_{area} and area-based A_{max} was caused by acclimation of SLA to intra-canopy PAR gradients, which is in agreement with the third hypothesis, and the findings of other studies (Ellsworth and Reich 1993, Meir et al. 2002, Palmroth and Hari 2001). The coefficient of determination for relationships between relative PAR and these three foliage characteristics were lower in this study than in others (e.g. Niinemets et al. 2004). We attribute this to the fact that we included multiple deciduous species in the regression analysis, and both age cohorts of needles in the regression analysis for white pine. The poorer R^2 values we obtained were also probably due to the fact that we could not measure directly above the sample leaves, or estimate integrated PAR at the leaf surface over an extended period of time.

In a study of two crop-tree species (*Prunus dulcis* (Mill) and *Juglans regia* L.), Rosati et al. (2004) showed that daily canopy photosynthesis could be accurately projected based on physiological measurements of a single leaf at the canopy apex, and daily integrated PAR data. The implication of this result is that foliar acclimation to intra-canopy PAR gradients results in a consistent level of photosynthetic radiation use efficiency (PhRUE) for most leaves within the canopy. However, the plasticity of foliage characteristics in response to PAR gradients has been shown to vary among species (Bond et al. 1999, Meir et al. 2002) and age cohorts of foliage (Schoettle and Smith 1998). The plasticity of SLA within the tree canopy varied among deciduous species in this study. We hypothesized that co-dominant species would show greater plasticity of SLA, since they are exposed to sharper gradients in PAR attenuation. For the same reason, we expected less variation in SLA from canopy top to bottom in 1-year-old foliage of white pine. While we showed general differences in several foliage characteristics among canopy classes of trees and age cohorts of foliage, we did not find significant differences in the plasticity of SLA. The plasticity of SLA in response to PAR gradients may be species specific, although we cannot rigorously test this assertion with these data since we only measured single individuals of each deciduous species. Our data provide further support of the hypothesis that foliage morphology acclimates to intra-canopy PAR gradients, although the comparable range in SLA among understory and overstory trees is unexpected, considering the consistently lower levels of PAR that occur deep in the canopy. Acclimation of SLA to a gradient in PAR may have occurred early in leaf development for these individuals (Niinemets et al. 2004), perhaps prior to full leaf area display by overstory trees. Differences in SLA and A_{max} between current and one-year-old white pine foliage were statistically significant, but were small, and may be less important than seasonal patterns of photosynthesis and leaf phenology for understanding PhRUE of the canopy.

In conclusion, we found that a mixed deciduous forest in the southern Appalachian Mountains had significantly higher ε than a white pine plantation growing on a similar site. We attribute this difference to greater photosynthetic production per unit IPAR in deciduous foliage during the growing season. Carbon gain during the winter for white pine was apparently not great enough to yield higher ANPP than in the more efficient deciduous forest. We reasoned that age-related effects on carbon gain and resource competition may be more detrimental for ANPP and ε in the white pine plantation than the mixed deciduous forest. Our data indicate that ε may be conservative for each of these forests at the spatial scale we examined, since mineral nitrogen availability and LAI showed little variation along the elevation gradient. Future studies of ε in mixed deciduous forests should test for variability associated with broader gradients in species composition, elevation, aspect, and latitude.

Table 1. Description of species sampled at each vertical transect in the deciduous forest.

Sample point	Canopy co-dominant species	Intermediate/understory species
1	*Quercus prinus*	*Acer rubrum* and *Oxydendrum. arboreum*
2	*Liriodendron tulipifera*	*Betula lenta*
3	*Quercus rubra*	*Betula lenta*
4	*Carya glabra*	*Oxydendrum arboreum*

Table 2. Averages of six parameters for overstory and understory trees in the deciduous forest, and by age class of foliage in the white pine forest. Values are averages of individual leaf and fascicle measurements for foliage that is included in each category. All area-based estimates were calculated using one-sided area of deciduous leaves and projected-area of fascicles (total area/3.14). Different letters indicate significant differences between the two factors of interest in each forest type (t-test, $\alpha = 0.05$).

	SLA (cm^2 g^{-1})	**Range of SLA**	**A_{max} (μmol m^{-2} s^{-1})**	**A_{max} (μmol g^{-1} s^{-1})**	**N%**	**N_{area} (g m^{-2})**
Deciduous						
Overstory	141.09a	73.38a	8.13a	0.10a	2.07a	1.53a
Understory	218.86b	62.75a	5.71b	0.12b	2.04a	0.95b
Pine						
New	68.58a	60.18a	9.80a	0.065a	1.47a	2.23a
Old	61.32b	37.31a	8.04b	0.049b	1.38a	2.26a

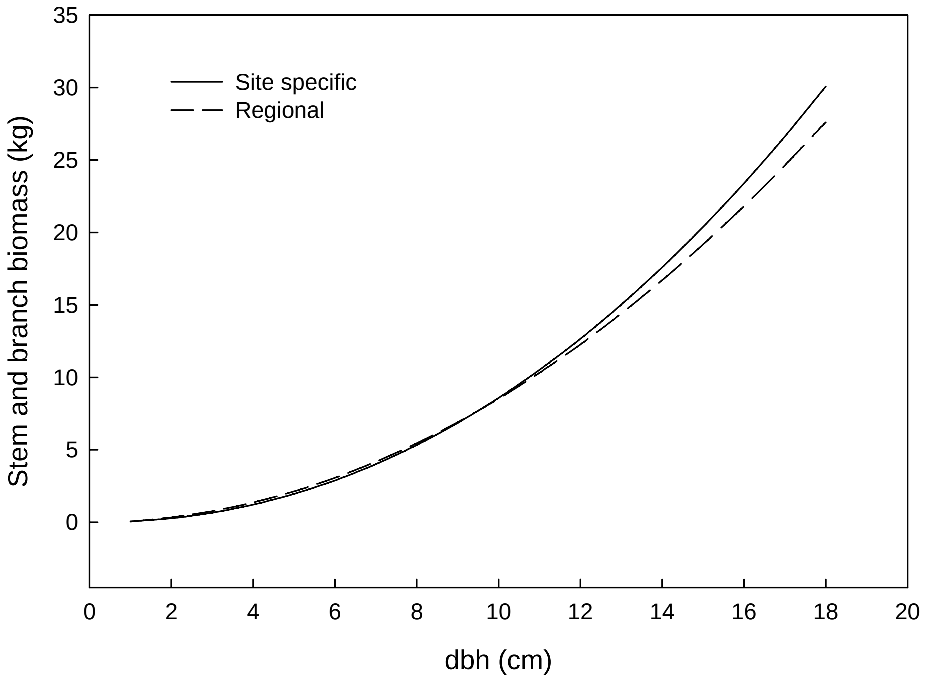

Figure 1. Comparison of a site specific and regional allometric equation for stem and branch biomass of eastern white pine. The regional equation, which was used in this study, included sample trees with maximum diameters up to 61 cm.

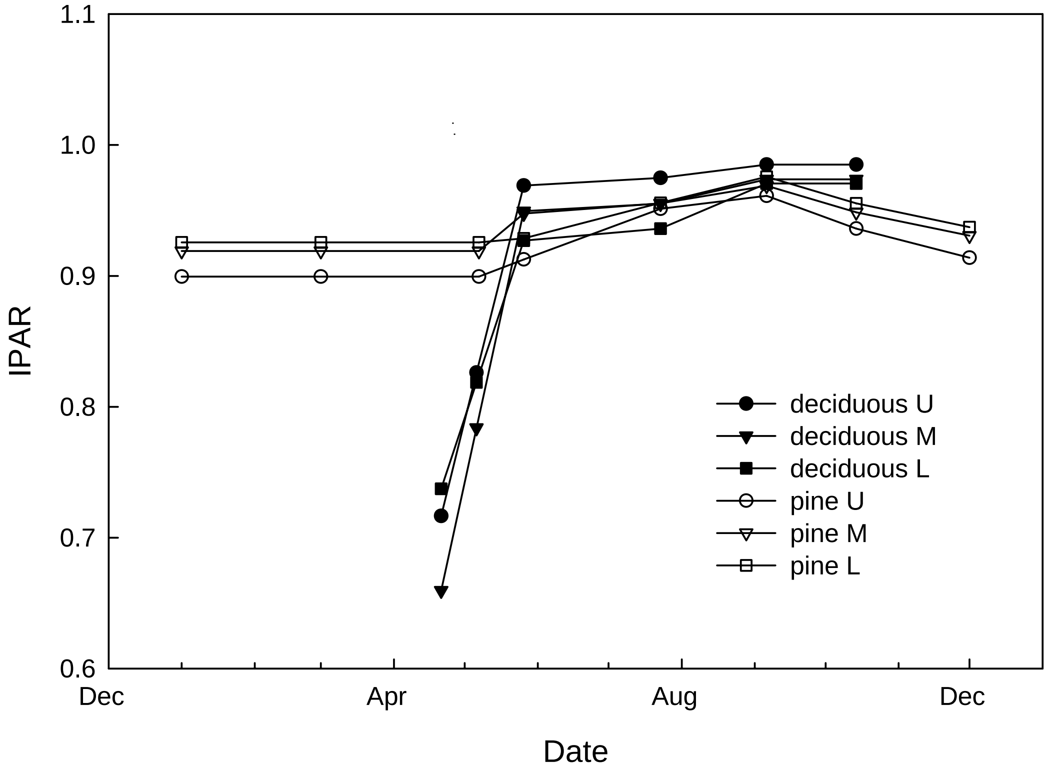

Figure 2. Annual and seasonal patterns of IPAR among slope positions within each forest. Data points are the average percent IPAR for the three plots at each slope position (U = upper slope, M = middle slope, L = lower slope). Measurements with the Sunscan System were taken four times from May 6 to September 6, 2005. Daily percent IPAR was assumed to change linearly between sampling dates. Values for the remainder of the growing season, and year, were estimated as described in the methods.

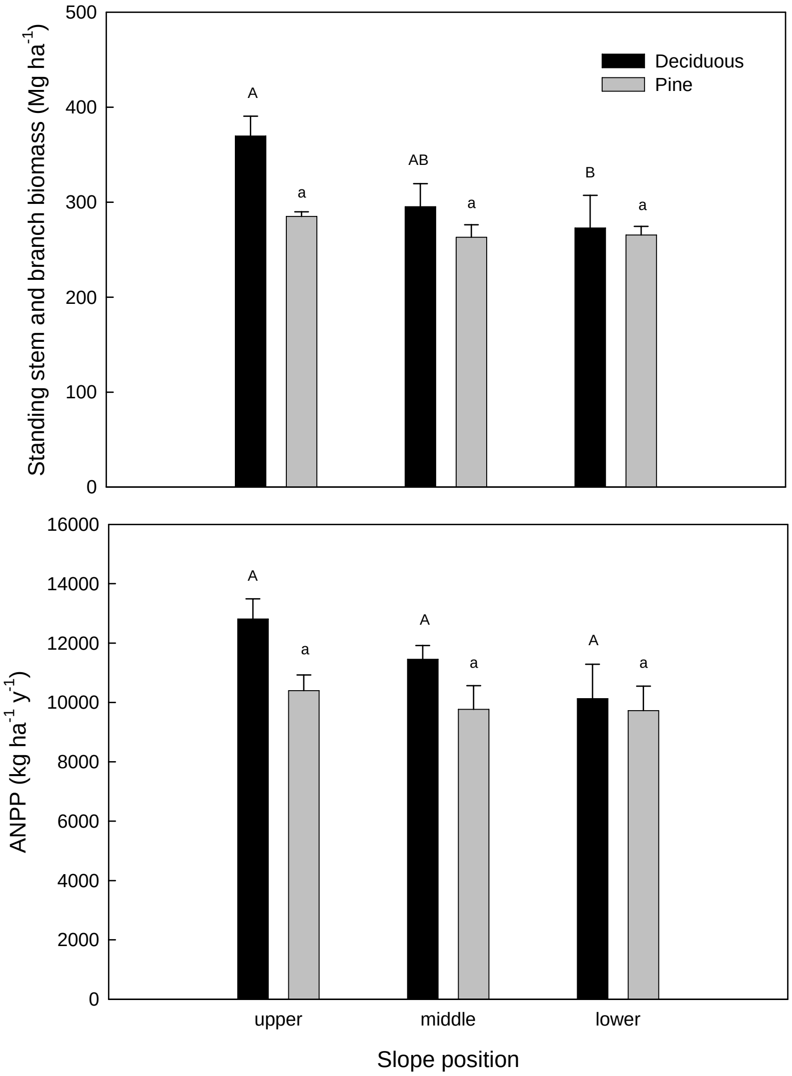

Figure 3. Comparison of total aboveground biomass and ANPP between the two forests, and between slope positions within each forest. Error bars are plus and minus one standard error. Different upper case letters indicate statistically significant differences between slope positions within the deciduous forest; lower case letters indicate significant differences between slope positions in the white pine plantation ($\alpha = 0.05$).

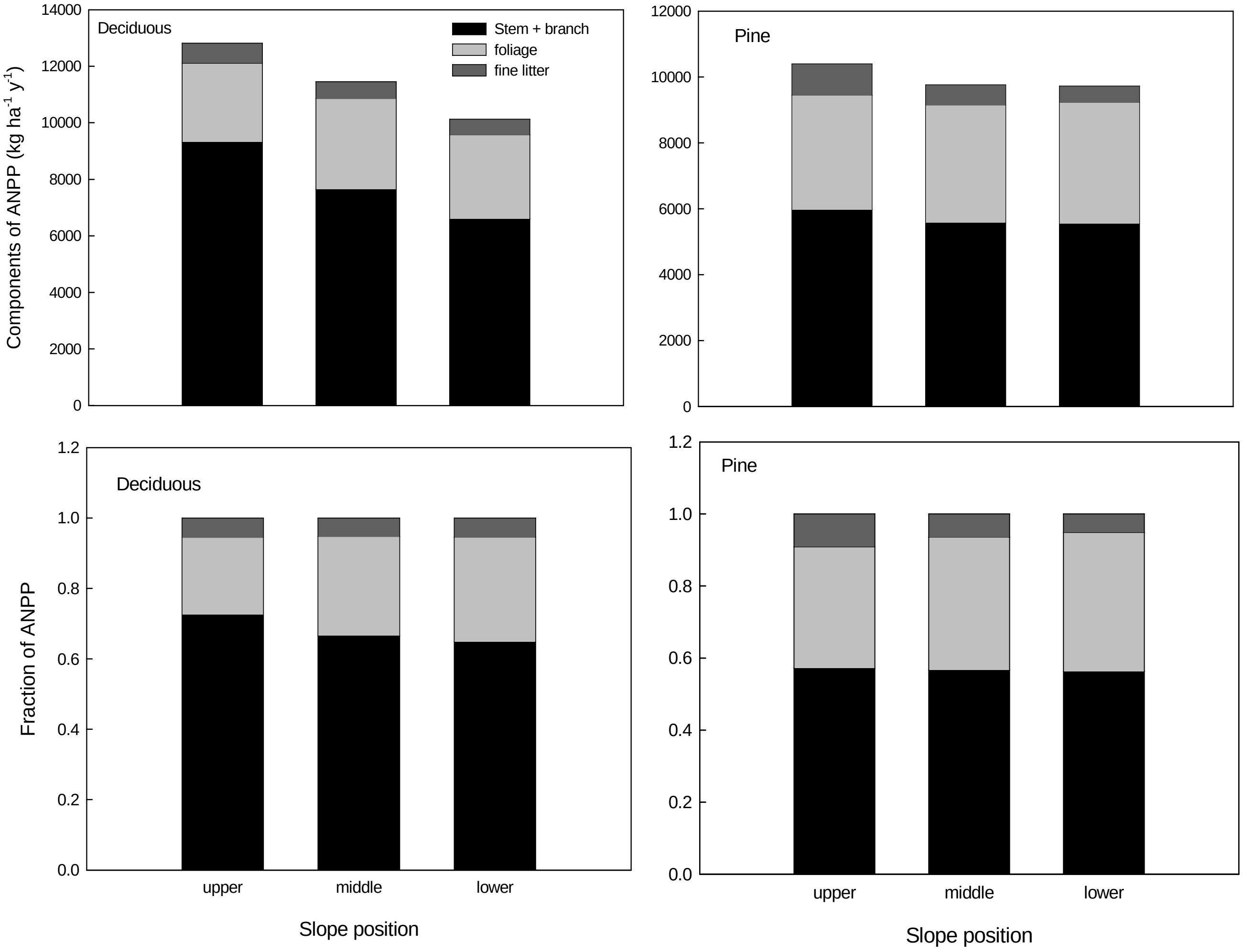

Figure 4. Comparison of total, and the percent of total ANPP in stems and branches, foliage, and fine litter biomass between the deciduous forest and the white pine plantation, and between slope positions within each forest.

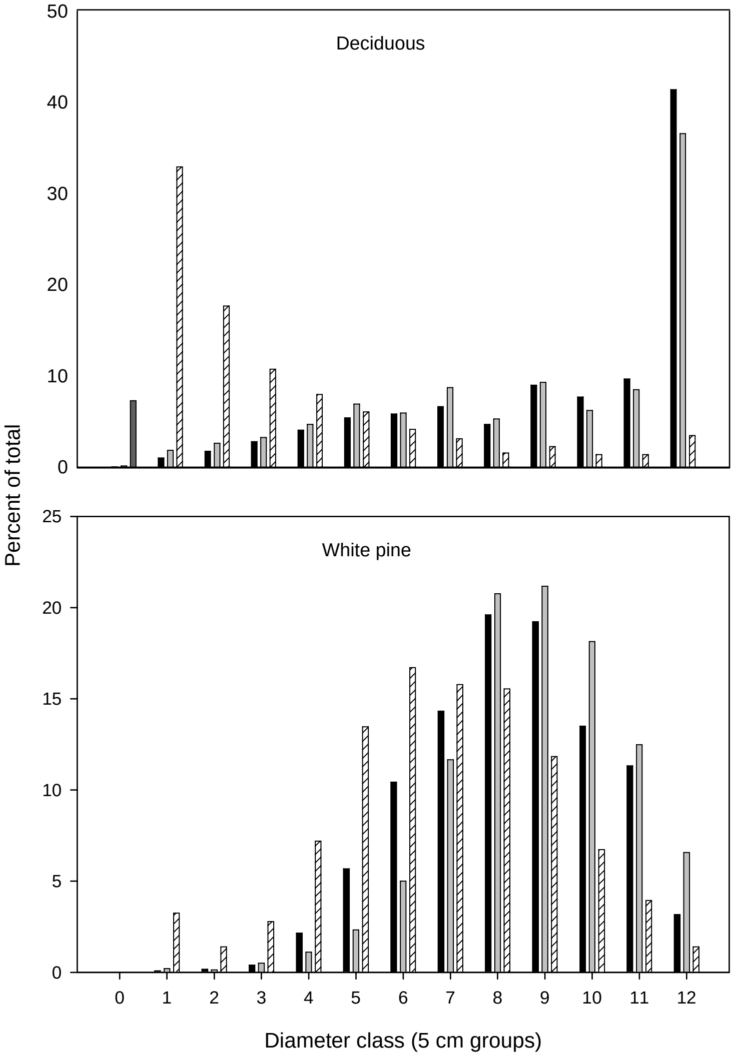

Figure 5. The percentage of total stem and branch biomass and production, and the total number of stems in each diameter class for the deciduous forest and white pine plantation. Diameter classes represent 5 cm intervals in diameter at breast height. The data include all trees sampled from nine plots in the deciduous forest (n = 577) and the white pine plantation (n = 431). Black bars represent stem and branch biomass, grey bars represent stem and branch production, and dashed bars represent the proportion of the total number of stems in each diameter class.

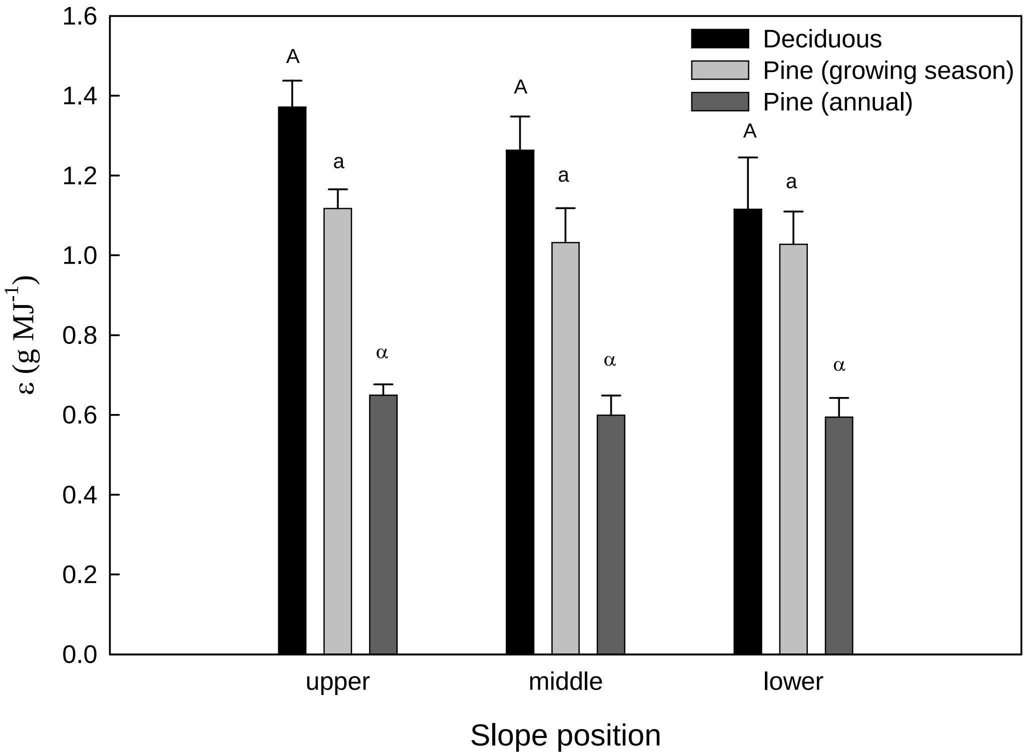

Figure 6. Comparison of ε between the deciduous forest and white pine plantation, and among slope positions within each forest. Error bars are plus and minus one standard error. Upper case and lower case letters and symbols indicate there were no statistically significant differences among slope positions within either forest. The growing season estimate of ε for white pine was calculated based on IPAR from April 21 to October 14, 2005, as was the estimate for the deciduous forest. The annual estimate of ε for white pine was calculated using an annual estimate of IPAR.

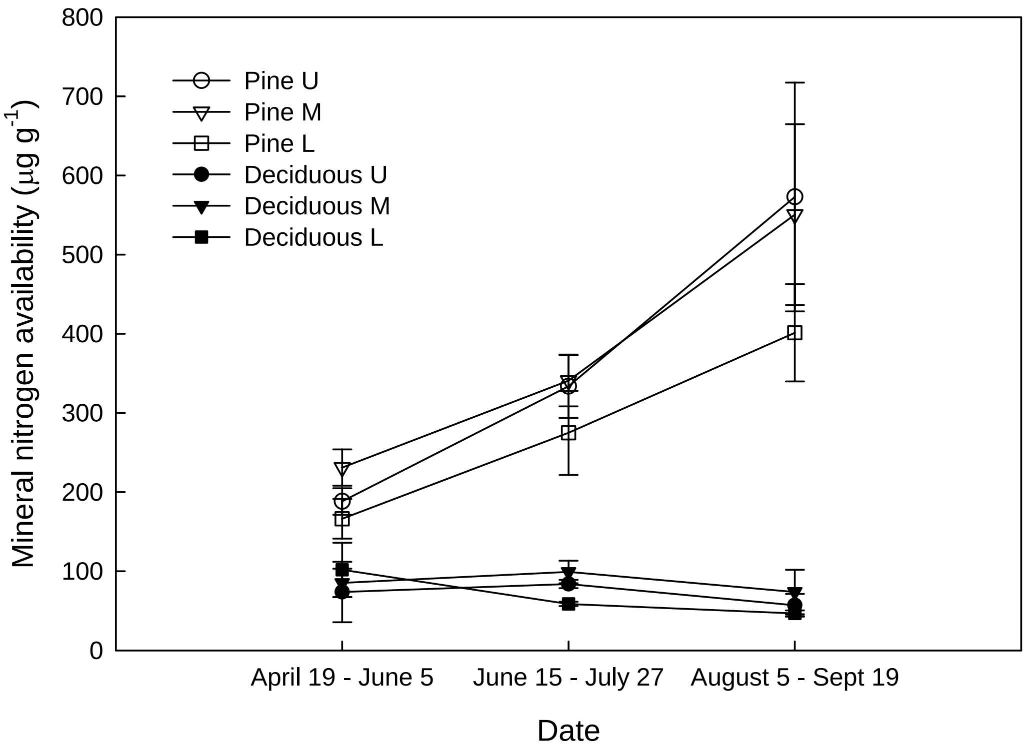

Figure 7. Seasonal changes in mineral nitrogen availability in each forest. Data points are averages of the three plots at each slope position (U = upper, M = middle, L = lower) with standard error bars. Values on the y-axis are micrograms of NH_4 and NO_3 per gram of resin. The x-axis shows the beginning and ending date of each sampling period during 2005. Mineral nitrogen availability was significantly higher in the white pine plantation than the deciduous forest for the entire growing season. There were no significant differences in mineral nitrogen availability between slope positions within either forest.

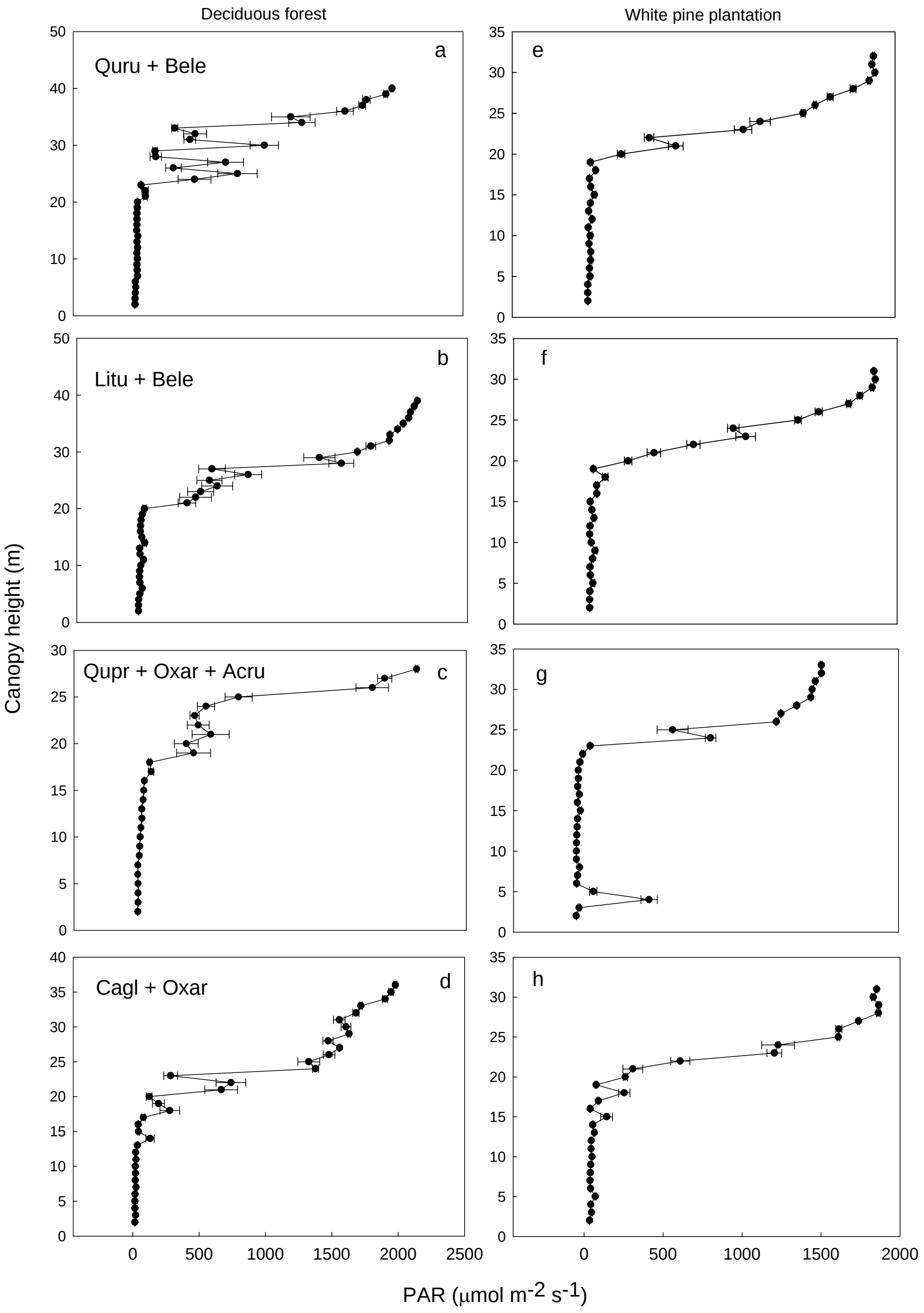

Figure 8. Patterns of attenuation of photosynthetically active radiation (PAR) at four sampling points within the deciduous forest (a – d) and white pine plantation (e – h). Data points are the average of 12 measurements taken at each canopy height, with standard error bars. Each graph for the deciduous forest (a – d) lists species codes for trees that were sampled along that vertical transect (Acru = *Acer rubrum*, Bele = *Betula lenta*, Cagl = *Carya glabra*, Litu = *Liriodendron tulipifera*, Oxar = *Oxydendrum arboreum*, Qupr = *Quercus prinus*, Quru = *Quercus rubra*). Total canopy height (y – axis) varied among sample points in the deciduous forest, but was similar in the white pine plantation.

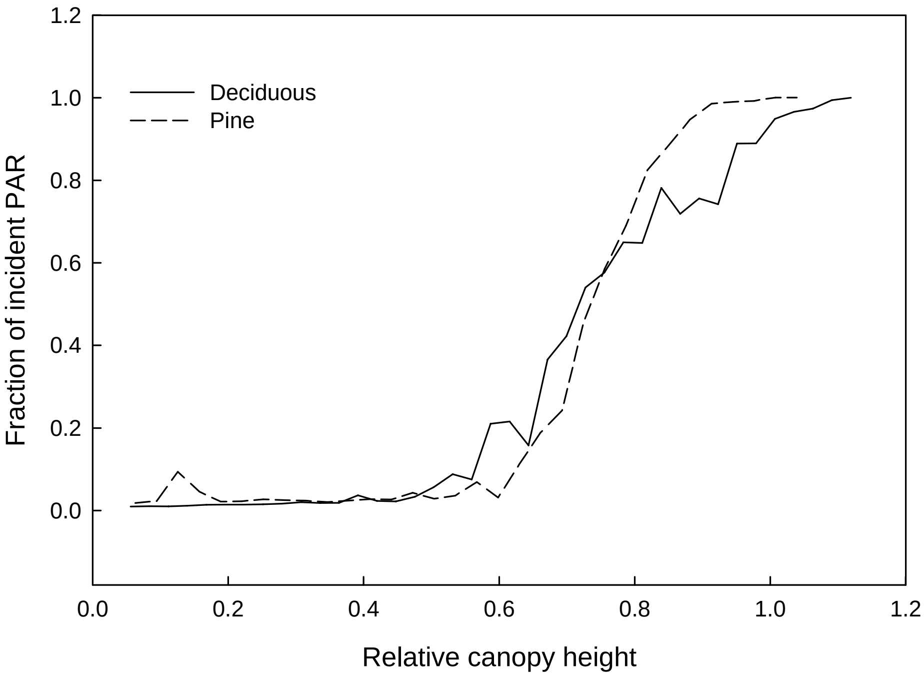

Figure 9. Comparison of PAR attenuation in the canopies of the deciduous forest and the white pine plantation. At each sampling point (n = 4 in each forest) twelve measurements were taken at 1 m height intervals from 2 m height to the top of the canopy. The lines represent the average of all 48 measurements taken at each 1 m interval in each forest. PAR is expressed as a fraction of average incident PAR at the average total canopy height (deciduous = 35.8 m, pine = 31.8 m). Height is expressed as a fraction of average total canopy height.

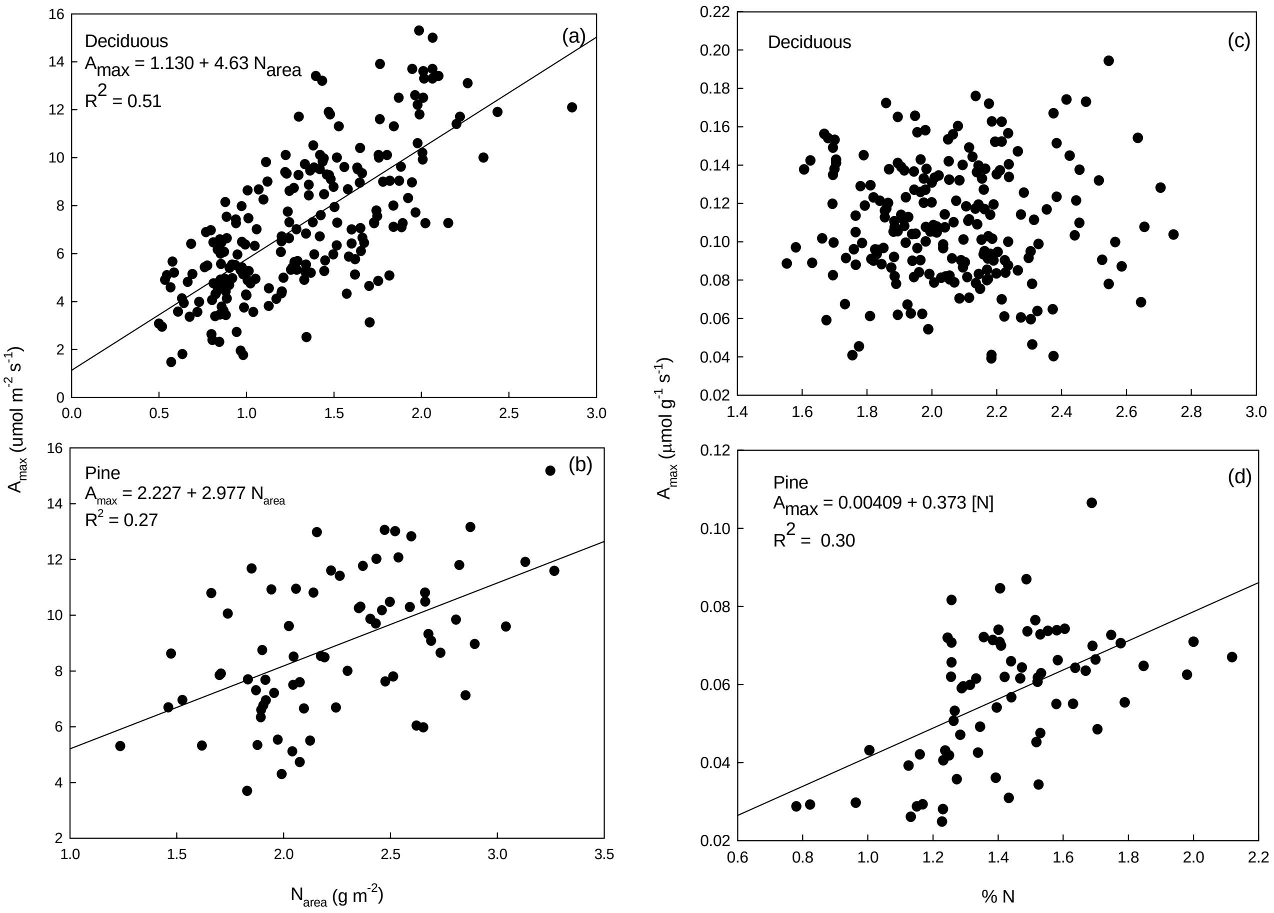

Figure 10. Relationship between nitrogen content and light saturated photosynthesis (A_{max}), expressed on an area (a and b) and mass basis (c and d), for deciduous species and white pine. Data points are individual leaf and fascicle measurements. Area-based estimates were calculated using one-sided area of deciduous foliage and projected area of pine fascicles (total area/3.14).

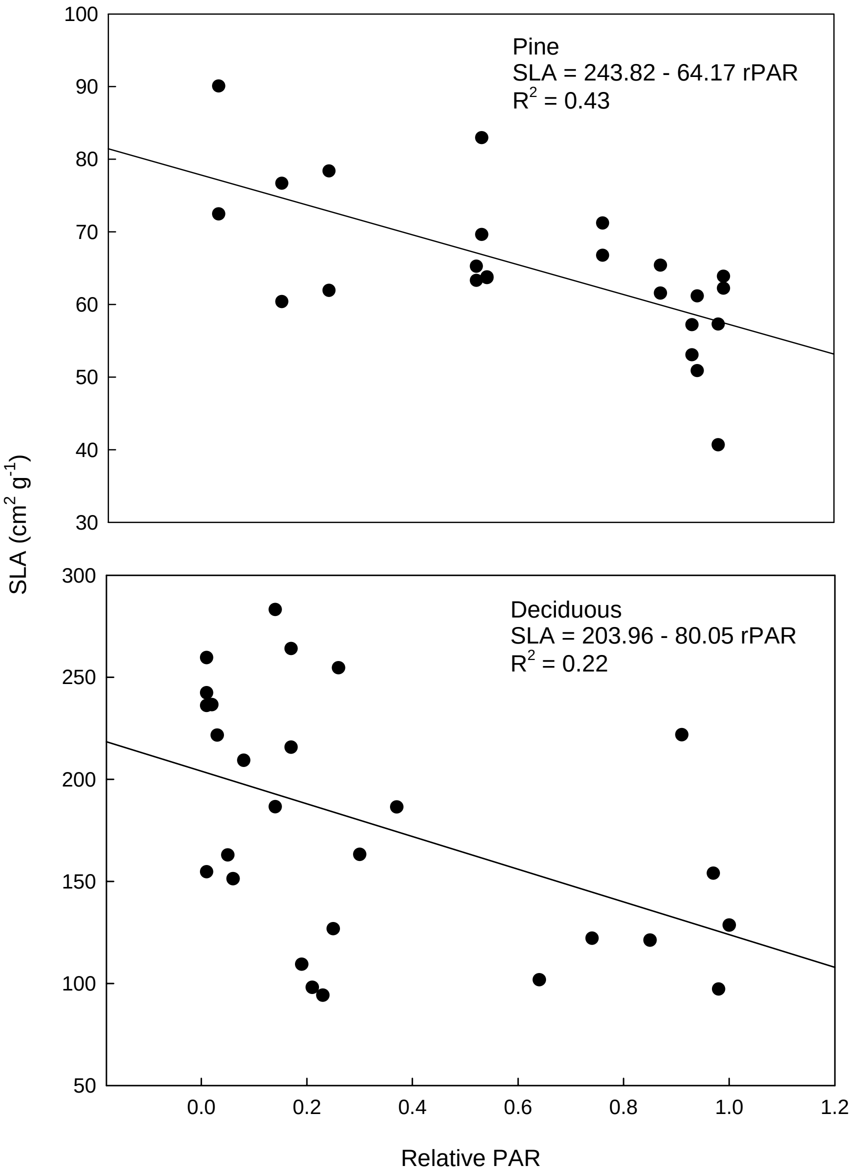

Figure 11. Relationship between relative photosynthetically active radiation (PAR) and specific leaf area (SLA) measured along vertical transects within the canopies of deciduous and white pine trees. Data points are averages of all leaves or fascicles sampled at a particular height within each tree crown. Relative PAR was calculated based on incident PAR measured above the canopy at each sampling point. SLA was calculated based on one-sided area of deciduous foliage and projected area of pine fascicles (total area/3.14).

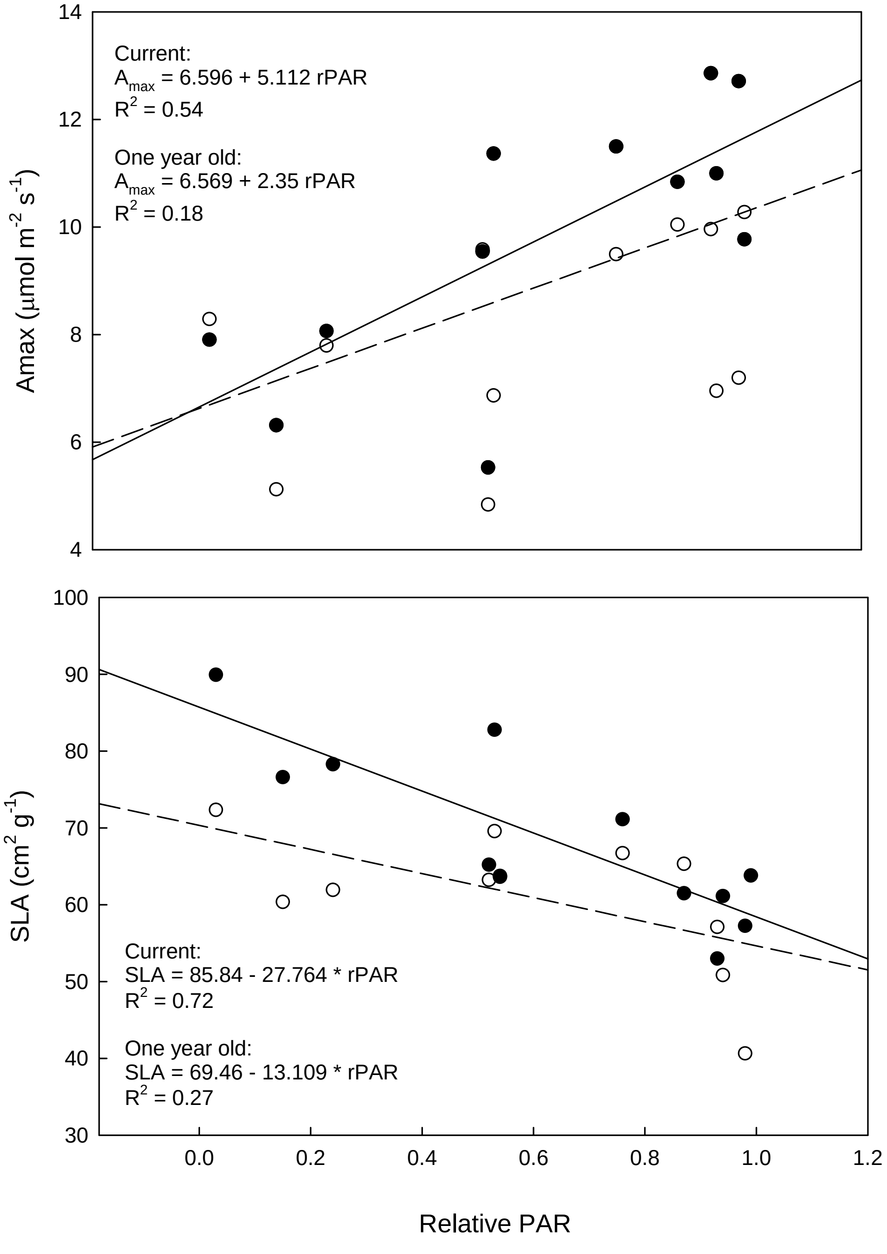

Figure 12. Relationship between relative photosynthetically active radiation (PAR) and both specific leaf area (SLA) and area-based light saturated photosynthesis (A_{max}) for current and one-year-old fascicles in white pine trees. Filled symbols and solid lines are for current year fascicles, while open symbols and dashed lines are for one-year-old fascicles. Data points are averages of 3 fascicles sampled from each cohort at each canopy height. SLA and area-based A_{max} were calculated using projected area (total area/3.14).

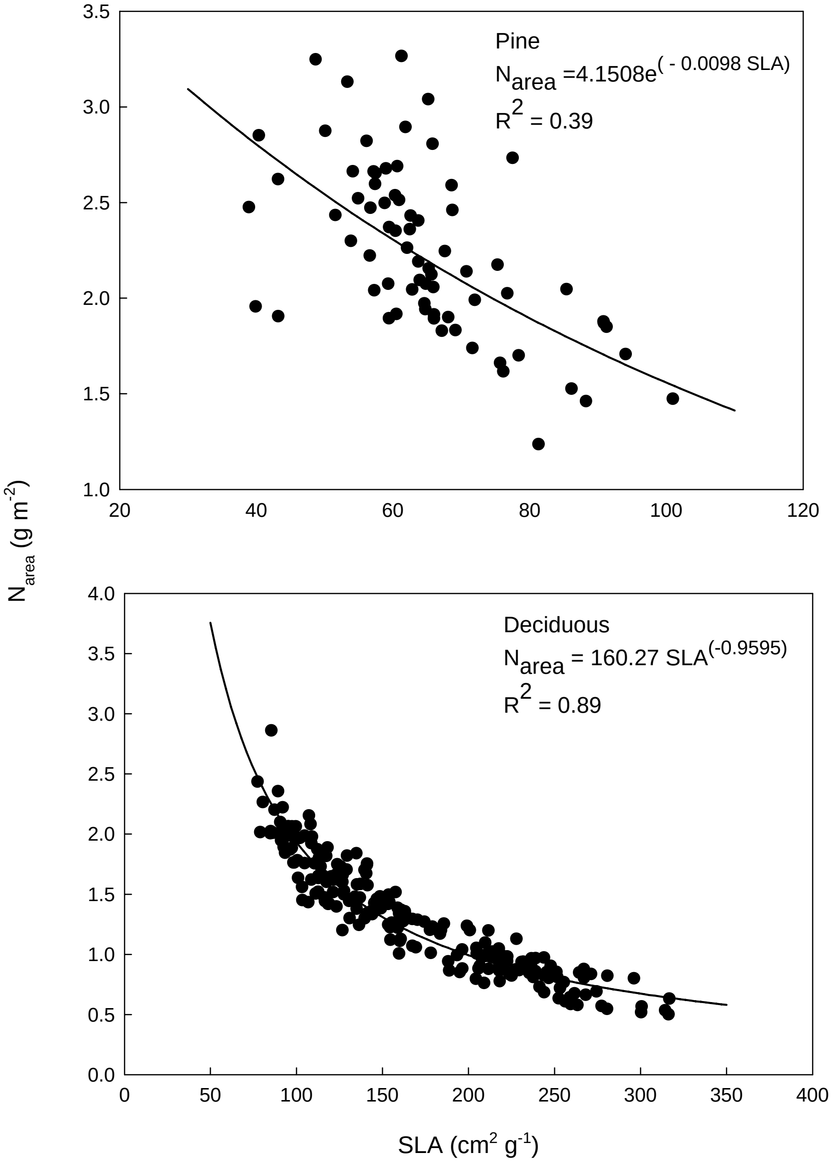

Figure 13. Relationship between specific leaf area (SLA) and nitrogen content (N_{area}) for foliage from deciduous and white pine trees. Data points are individual leaf and fascicle measurements. N_{area} was calculated based on one-sided area for deciduous foliage and projected area (total area/3.14) for pine fascicles.

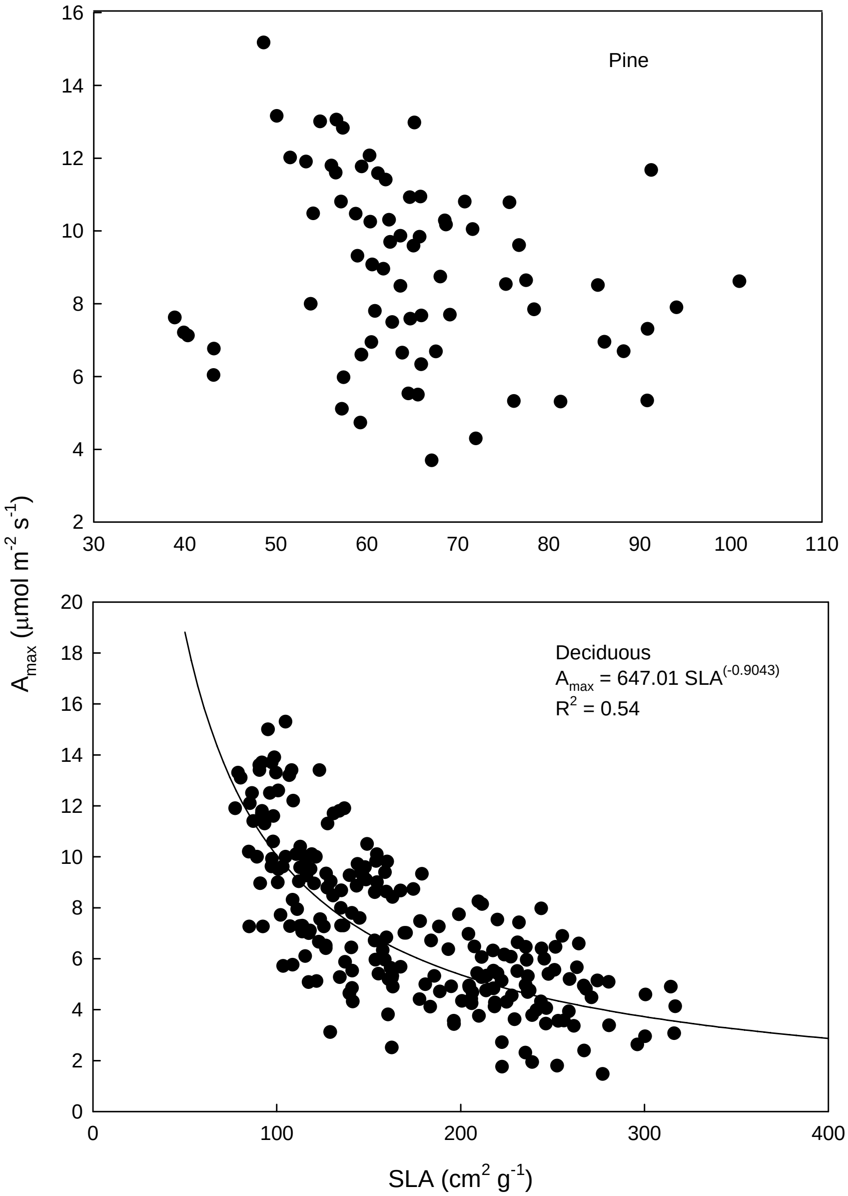

Figure 14. Relationship between specific leaf area (SLA) and area-based light saturated photosynthesis (A_{max}) for foliage from deciduous and white pine trees. Data points are individual leaf and fascicle measurements. A_{max} was calculated based on one-sided area for deciduous foliage and projected area (total area/3.14) for pine fascicles.

CHAPTER 4

CONCLUSION

Our data indicated that forests in the southern Appalachian Mountains can attain higher aboveground net primary productivity (ANPP) and radiation use efficiency (ε) than similar forest types found throughout North America, which reflects the favorable climatic conditions for forest growth in this region. This paired watershed study allowed us to test for effects of forest type on ANPP and ε, since important variables such as temperature, precipitation, and soil type were similar between the two forests. The mixed deciduous forest had significantly higher standing biomass, ANPP, and ε than the white pine plantation. We suggest that these differences were influenced in part by the greater photosynthetic capacity of deciduous species, especially the *Quercus* species which were prevalent throughout the deciduous forest. Evidence for greater photosynthetic capacity in deciduous species included their higher specific leaf area (SLA), mass-based maximum photosynthetic rates (A_{max}), and foliar nitrogen concentration. Although white pine was capable of assimilating carbon during the winter, when the deciduous trees are leafless, this did not result in greater ANPP. Leaf area index (LAI), intercepted photosynthetically active radiation (IPAR), and nitrogen mineralization are often positively correlated with ANPP, but LAI and IPAR were not significantly different during the growing season between forests, and mineral nitrogen availability was greater in the white pine plantation. Thus, greater ε in the deciduous forest seemed to be a result of greater photosynthetic capacity, and this distinction was the primary factor causing a difference in ANPP between the two forests.

We expected that LAI would vary in correspondence with any fluctuations in mineral nitrogen availability, and that ε would be conservative, since LAI has a similar influence on both IPAR and ANPP. However, we saw no significant variation in mineral nitrogen availability across an elevation gradient within either forest, and determined that ε was conservative for each forest at the watershed scale. Hence, ε could be a useful parameter for modeling ANPP in each of these forests. We identified several possible sources of variation in ε for mixed deciduous forests, some of which may have influenced the variation we saw among individual plots. Future studies should address questions about how ε responds to broader environmental gradients, and the associated changes in community composition and ANPP.

We showed that SLA of leaves and fascicles acclimates to intra-canopy gradients in PAR in each of these forests, and there were corresponding changes in area-based estimates of A_{max} and nitrogen content. This acclimation is thought to have an important influence on the photosynthetic radiation use efficiency (PhRUE) of canopies, although the relationship is not well understood in canopies with multiple species, or multiple age cohorts of foliage on individuals of a single species. Specific leaf area was generally lower in overstory than in understory trees in the deciduous forest, which resulted in higher area-based A_{max} and nitrogen content. In white pine trees, new fascicles had higher SLA than one-year-old fascicles, but also had higher area- and mass-based A_{max}. We expected there to be general differences in the extent to which SLA varied within overstory versus understory trees, and between age cohorts of foliage, since these groups experience consistently different light gradients. Such a generality could be useful for understanding PhRUE, especially in mixed-species forests. However, the plasticity of SLA did not vary significantly between age cohorts of white pine foliage, and appears to be species specific among the deciduous trees.

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APPENDIX

Appendix 1. Averages of specific leaf area (SLA), light saturated photosynthesis (A_{max}), and nitrogen content at different canopy heights for deciduous species and white pine. At each canopy height within each white pine tree, the first row of data is for new fascicles, and the second row is for one-year-old fascicles. SLA and area-based estimates of A_{max} and nitrogen content were calculated using one-sided area of deciduous foliage and projected area of pine fascicles (total area/3.14). Species codes were used to identify deciduous species (Acru = *Acer rubrum*, Bele = *Betula lenta*, Cagl = *Carya glabra*, Litu = *Liriodendron tulipifera*, Oxar = *Oxydendrum arboreum*, Qupr = *Quercus prinus*, Quru = *Quercus rubra*).

	Canopy location	**Canopy height (m)**	**Relative PAR (pooled data)**	**n**	**SLA (cm^2 g^{-1})**	**A_{max} (umol m^{-2} s^{-1})**	**A_{max} (umol g^{-1} s^{-1})**	**N%**	**N_{area} (g m^{-2})**
White pine									
1	top	29.8	0.99	3	62.22	9.77	0.06	1.37	2.23
		29.8	0.99	3	63.87	10.27	0.07	1.86	2.92
	mid	25	0.69	3	61.53	10.83	0.07	1.50	2.45
		25	0.69	3	65.39	10.04	0.06	1.74	2.67
	low	22.6	0.37	3	65.24	9.55	0.06	1.54	2.36
		22.6	0.37	3	63.29	9.58	0.06	1.80	2.83
2	top	28.5	0.97	3	53.04	12.88	0.07	1.48	2.83
		28.5	0.97	3	57.19	9.95	0.06	1.41	2.48
	mid	24.2	0.6	3	82.96	5.53	0.05	1.48	1.79
		24.2	0.6	3	69.63	4.84	0.03	1.28	1.85
	low	20.3	0.14	3	90.01	7.91	0.07	1.68	1.88
		20.3	0.14	3	72.45	8.29	0.06	1.46	2.01
3	top	28.2	0.95	3	61.16	10.99	0.07	1.50	2.45
		28.2	0.95	3	50.88	6.94	0.04	1.18	2.45
	mid	25.1	0.71	3	71.19	11.50	0.08	1.49	2.14
		25.1	0.71	3	66.77	9.48	0.06	1.29	1.95
	low	21.9	0.23	3	78.67	8.07	0.06	1.52	2.04
		21.9	0.23	3	61.93	7.79	0.05	1.29	2.10
4	top	28.7	0.97	3	57.27	12.72	0.07	1.44	2.51
		28.7	0.97	3	40.66	7.19	0.03	0.86	2.10
	mid	23.3	0.5	3	63.69	11.37	0.07	1.44	2.35
		23.3	0.5	3	63.79	6.88	0.04	1.21	1.92
	low	20	0.11	3	76.67	6.31	0.05	1.15	1.54
		20	0.11	3	60.37	5.12	0.03	1.22	2.04
Overstory									
Litu	top	39	0.99	12	128.52	6.97	0.09	2.13	1.69
	mid	36.3	0.95	12	153.91	5.11	0.08	2.39	1.59
	low	33.7	0.847	12	221.76	4.61	0.10	2.37	1.08

	lowest	24.9	0.4164	8	254.63	4.26	0.10	2.26	0.91
Qupr	top	23	0.16	10	98.00	10.66	0.10	1.90	1.97
	mid	19.8	0.08	10	109.36	11.75	0.13	2.05	1.89
	low	17.3	0.03	10	151.20	8.71	0.13	2.13	1.42
Cagl	top	35.2	0.9	10	97.21	10.95	0.10	1.91	1.99
	mid	32	0.76	9	121.15	8.65	0.10	1.92	1.59
	low	28	0.65	9	122.08	8.86	0.11	1.83	1.52
	lowest	21.9	0.21	8	186.38	5.90	0.11	1.75	0.94
Quru	top	34.2	0.89	8	101.74	9.71	0.10	2.13	2.14
	mid	31.3	0.73	8	94.11	11.77	0.11	1.99	2.13
	low	25.6	0.49	8	126.79	7.16	0.09	2.03	1.61
Intermediate									
Bele	top	12.7	0.01	5	154.64	9.72	0.15	2.14	1.38
	mid	9.6	0.01	5	242.39	6.63	0.16	2.09	0.86
	low	7.9	0.01	5	259.58	6.09	0.16	2.43	0.94
Oxar	top	17.9	0.04	8	162.86	6.20	0.10	2.14	1.32
	mid	14.1	0.03	6	221.57	3.83	0.08	2.09	0.94
Acru	top	11	0.02	5	236.49	5.65	0.13	2.11	0.89
	low	6.5	0.01	6	236.12	4.37	0.10	2.00	0.85
Oxar	top	23	0.16	7	186.56	5.51	0.10	2.01	1.09
	mid	20.4	0.14	8	264.06	4.00	0.11	1.72	0.66
	low	18.1	0.05	8	283.15	3.88	0.11	1.72	0.61
Bele	top	30.7	0.74	6	163.20	7.81	0.13	2.14	1.31
	mid	28.3	0.64	6	209.30	6.71	0.14	1.97	0.94
	low	23.7	0.28	6	215.73	5.71	0.12	2.15	1.00