Forest Ecology and Management 257 (2009) 1034–1042

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Radiation use efficiency in adjacent hardwood and pine forests in the southern Appalachians

Luke Pangle[a,*], James M. Vose[b], Robert O. Teskey[a]

[a] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, United States
[b] Coweeta Hydrologic Laboratory, USDA Forest Service, 3160 Coweeta Lab Road, Otto, NC 28763, United States

ARTICLE INFO

Article history:
Received 21 July 2008
Received in revised form 4 November 2008
Accepted 6 November 2008

Keywords:
Radiation use efficiency
Aboveground net primary productivity
Deciduous forest
Pinus strobus L

ABSTRACT

The efficiency with which trees convert photosynthetically active radiation (PAR) to biomass has been shown to be consistent within stands of an individual species, which is useful for estimating biomass production and carbon accumulation. However, radiation use efficiency (ε) has rarely been measured in mixed-species forests, and it is unclear how species diversity may affect the consistency of ε, particularly across environmental gradients. 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 50-year-old white pine (*Pinus strobus* L.) plantation in the southern Appalachian Mountains. Average ANPP was similar in the deciduous forest (11.5 Mg ha^{-1} y^{-1}) and pine plantation (10.2 Mg ha^{-1} y^{-1}), while ε was significantly greater in the deciduous forest (1.25 g MJ^{-1}) than in the white pine plantation (0.63 g MJ^{-1}). Our results demonstrate that late-secondary hardwood forests can attain similar ANPP as mature *P. strobus* plantations in the southern Appalachians, despite substantially less annual IPAR and mineral-nitrogen availability, suggesting greater resource-use efficiency and potential for long-term carbon accumulation in biomass. Along a 260 m elevation gradient within each forest there was not significant variation in ε. Radiation use efficiency may be stable for specific forest types across a range of environmental conditions in the southern Appalachian Mountains, and thus useful for generating estimates of ANPP at the scale of individual watersheds.

1. Introduction

Aboveground net primary productivity (ANPP) is the difference between carbon gained in aboveground plant parts through photosynthesis, and the carbon lost by aboveground plant parts through autotrophic respiration. In forests, ANPP is often estimated by measuring the accumulation of biomass in aboveground plant parts during a specific period of time. Aboveground net primary productivity in temperate forests generally ranges from <5 to >20 Mg ha^{-1} y^{-1} (Reich and Bolstad, 2001), although some plantation forests can attain rates of ANPP up to 25 Mg ha^{-1} y^{-1} with intensive management and fertilization (Samuelson et al., 2004). 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 soil-nitrogen availability (Keyes and Grier, 1981; Nadelhoffer et al., 1985; Vose and Allen, 1988; Reich et al., 1997; Balster and Marshall, 2000).

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 (*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). The slope of the ANPP vs. IPAR relationship was initially termed radiation use efficiency (ε = ANPP/IPAR) by Monteith (1977), while contemporary forest growth models commonly define ε as total net primary productivity per unit IPAR (ε = NPP/IPAR), accounting for both above- and belowground net primary productivity (BNPP) (Landsberg and Waring, 1997).

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 different species (Reich and Bolstad, 2001). Experiments in pine plantations have shown that the increase in

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* Corresponding author. Current address: 1661 SW 49th Street, Apt. 125, Corvallis, OR 97333, United States. Tel.: +1 706 224 8073.
E-mail address: lukepangle@gmail.com (L. Pangle).

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doi:10.1016/j.foreco.2008.11.004

productivity obtained through soil-nitrogen amendments was driven by an increase in foliage biomass and leaf area index (LAI $m^2\,m^{-2}$) (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 occurred, since leaf area expansion simultaneously caused increases in 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), LAI cannot be clearly identified as the sole cause of this relationship, since both net photosynthetic rates and LAI in broad-leaf deciduous trees have a positive response to increasing soil-nitrogen availability (Allen et al., 2005; Henderson and Jose, 2005). Further, the strength of the relationship between LAI and ANPP varies among broad-leaf deciduous species (Allen et al., 2005; Henderson and Jose, 2005), and among different environments for mixed-species deciduous forests (Fassnacht and Gower, 1997; Jose and Gillespie, 1997; Bolstad et al., 2001).

Studies of ε in deciduous species have been mostly limited to young monoculture 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 were often more extensive than those in unmanaged forests. Other forms of light use efficiency have also been calculated for some older deciduous forests and mixed-species forests using eddy covariance (Desai et al., 2008), or derived from models of gross primary productivity (Turner et al., 2003; Nightingale et al., 2007). In these studies, light use efficiency was calculated as the quotient of gross primary productivity and IPAR, or gross ecosystem productivity and IPAR. In almost all instances, IPAR has been indirectly estimated, for example, from total incoming PAR using the Beer–Lambert Law (Desai et al., 2008). Due to different methodologies and calculations of primary productivity, these estimates of light use efficiency are not directly comparable with ε calculated in this study.

Although the ε parameter has proven useful in forest growth models (e.g. Landsberg and Waring, 1997), some key unknowns remain. First, the magnitude of ε for many mixed-species forests, and its variability across environmental gradients, has not been determined. Second, 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.

We conducted a field study on two adjacent watersheds in the southern Appalachian Mountains of western North Carolina that contain contrasting forest types. Our objectives were: (1) to quantify ε for a mixed age and species deciduous forest and an adjacent 50-year-old white pine plantation (*Pinus strobus* L.) and (2) to determine how soil-nitrogen availability varies at the watershed scale, and whether this variation was correlated to LAI, IPAR, and ANPP. We tested two hypotheses: (1) ε is greater for a mixed deciduous forest than for a mature eastern white pine plantation, based primarily on the expectations that photosynthetic potential and production efficiency are greater in the deciduous forest, and that ε is reduced during the winter months for white pine, and (2) increasing nitrogen availability will increase LAI, ANPP, and IPAR, resulting in a stable estimate of ε at the watershed scale.

2. Methods

2.1. Site description

This work was conducted at the U.S.D.A. Forest Service Coweeta Hydrologic Laboratory in Otto, North Carolina, USA. Coweeta Hydrologic Laboratory includes 2185 ha within the southern Appalachian Mountains, with an elevation range of 679–1592 m. Average annual temperature in the Coweeta basin is 13 °C; average annual rainfall increases from 1780 mm at lower elevation to over 2500 mm 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. Most soils in the basin are Inceptisols or Ultisols.

The study site was in watersheds (WS) 17 and 18, two adjacent 13 ha watersheds that share a northwest aspect and range in elevation from 760 to 1021 and 726 to 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 found on slope and ridge positions and the Saunook series is a deep, well drained, fine loamy soil with colluvial input found in drainages and toe slopes (Thomas, 1996; Knoepp and Swank, 1997). Watershed 17 was cleared of all hardwood vegetation in 1942 and planted with eastern white pine in 1956 (Swank and Crossley, 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 1920s. The current average basal area in WS 18 is 33 $m^2\,ha^{-1}$ and maximum canopy height ranges from 30 to 40 m. Within WS 18 there is considerable variation in species assemblages across topographic gradients. From higher to lower elevations, and from xeric to mesic aspects, there is a shift from the dry, *Quercus prinus* L. dominated community to a cove hardwood community with *L. tulipifera* L. as the prevalent species (Elliott et al., 1999). *Quercus rubra* L., *Quercus coccinea* Muenchh., *Acer rubrum* L., and *Carya glabra* Mill. are common co-dominant species throughout. *Betula lenta* L. is found at middle and lower slope positions at intermediate canopy height and *Oxydendrum arboreum* L., *Nyssa sylvatica* Marsh., *Rhododendron maximum* L., and *Kalmia latifolia* L. comprise the majority of understory species.

2.2. ANPP

Nine 0.09 ha plots were established in each watershed, and distributed 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 above ground) was recorded for all trees that exceeded 5 cm dbh in each plot. In the deciduous forest, a 10 m × 10 m 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 were available for 11 common deciduous species, two understory shrubs, and for eastern white pine (McGinty, 1972; Phillips, 1981; Martin et al., 1998; Kloeppel et al., in preparation). 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. 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 circular litter traps (0.5 m^2) were located in each plot in the pine forest, and ten traps were located in the deciduous forest plots. Litter included foliage, reproductive structures, and woody debris less than 1 cm in 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 °C, and weighed. The foliage litter collected from the pines was abscised foliage from the previous year's cohort, and we assumed similar foliage biomass production in 2005 for the purpose of estimating this component of ANPP. 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.

2.3. IPAR

The percent of incident PAR intercepted by the canopies of each forest type 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. A total of fifty measurements of below-canopy PAR were made along the three transects in each 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° to 52° the IPAR measurements varied less than 2%, and no trend was apparent.

Intercepted PAR measurements at each plot were taken four times from May until September of 2005. A linear rate of change in percent-daily IPAR was assumed between sampling dates.

In the deciduous forest, total incident PAR and the fraction intercepted by the canopy were calculated for the entire growing season. The growing season ranged from April 21 to October 14, as 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 first and last IPAR measurements of the season were taken on May 6 and September 6, respectively. Daily percent IPAR values for the period of April 21 through May 5 were interpolated assuming the same linear rate of change that occurred between direct measurements on May 6 and May 25. Similarly, following the final direct measurement on September 6, percent IPAR for each plot was assumed to remain constant until October 14, at which time substantial leaf abscission began.

In the white pine plantation, total incident PAR and the fraction intercepted by the canopy were calculated for the entire calendar year of 2005, since it is clear that evergreen conifers in the southern Appalachians remain physiologically active throughout the winter and spring periods (Ford and Vose, 2007). In fact, Catovsky et al. (2002) estimated that one-third of annual carbon gain in *Tsuga canadensis* L. occurred during the leafless period for deciduous trees in an even colder climate than our study site. 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 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 pattern of leaf abscission we observed from foliage litter collection, as 84% of annual litterfall was collected from September through December, while only 5% of annual litterfall was collected from January through April.

2.4. Radiation use efficiency

Incident PAR data for 2005 were available from two climate stations in the Coweeta basin. Total solar radiation from January 1 to May 20 was measured at a climate station approximately 1 km from the study site. Total solar radiation was converted to PAR by multiplying by 0.5. From May 21 to 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 the deciduous forest, and for the entire year in the pine plantation. Radiation use efficiency (defined as ε = ANPP/IPAR) was calculated for each plot using the six-month estimate (4/21/05–10/14/05) of IPAR for the deciduous forest, and an annual estimate of IPAR for the pine plantation.

2.5. 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 one-sided 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 0.1 mm 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 values are based on one-sided (deciduous) and projected (white pine) area (cm^2/g).

2.6. Mineral-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 h 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 h. The resins were deployed for three sampling periods of approximately six weeks during the 2005 growing season from April 21 to 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, 1983). 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.

2.7. 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 among soil-nitrogen availability, LAI, IPAR, and ANPP.

3. Results

3.1. Aboveground biomass and ANPP

Average stem and branch biomass was similar in the deciduous forest (312.54 Mg ha^{-1}) and pine plantation (308 Mg ha^{-1}), although basal area was nearly twice as great in the pine plantation. This is attributable to greater wood density in deciduous hardwood species. There was a significant effect of slope position on standing biomass in the deciduous forest ($p = 0.03$, d.f. = 2). Standing biomass at the upper slope position (369.63 Mg ha^{-1}) was 35% greater than the lower slope position (272.78 Mg ha^{-1}, Tukey's HSD test, $\alpha = 0.05$) (Fig. 1).

Average ANPP was 13% greater in the deciduous forest (11.46 Mg ha^{-1} y^{-1}) than in the white pine plantation (10.15 Mg ha^{-1} y^{-1}); however, this difference was not statistically significant ($p = 0.06$, d.f. = 1). ANPP did not vary significantly across slope positions within either forest ($p = 0.25$, d.f. = 4) (Fig. 1), although there was a trend of decreasing average ANPP from the upper slope to lower slope positions in the deciduous forest (12.81–10.82 Mg ha^{-1} y^{-1}).

We 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 (Fig. 2). Stem and branch production, biomass, and total number of stems were normally distributed in the white pine plantation. In the deciduous forest, the distribution of stem and branch production and biomass was skewed because the trees with dbh $>$ 60 cm (diameter class 12, Fig. 2) represented an overwhelming proportion of forest biomass and stem and branch NPP. 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 patterns were not evident in the deciduous forest.

3.2. Intercepted photosynthetically active radiation and LAI

Leaf expansion began in late April in the deciduous forest, and by May 6 average IPAR ranged from 78 to 83% across slope positions in the deciduous forest (Fig. 3). In early June, average IPAR at all slope positions had increased to $>$90%, ranging from 97% at upper slope positions to 93% at lower slope positions. IPAR increased by 1–4% throughout the remainder of the growing season, which was likely due to further leaf expansion.

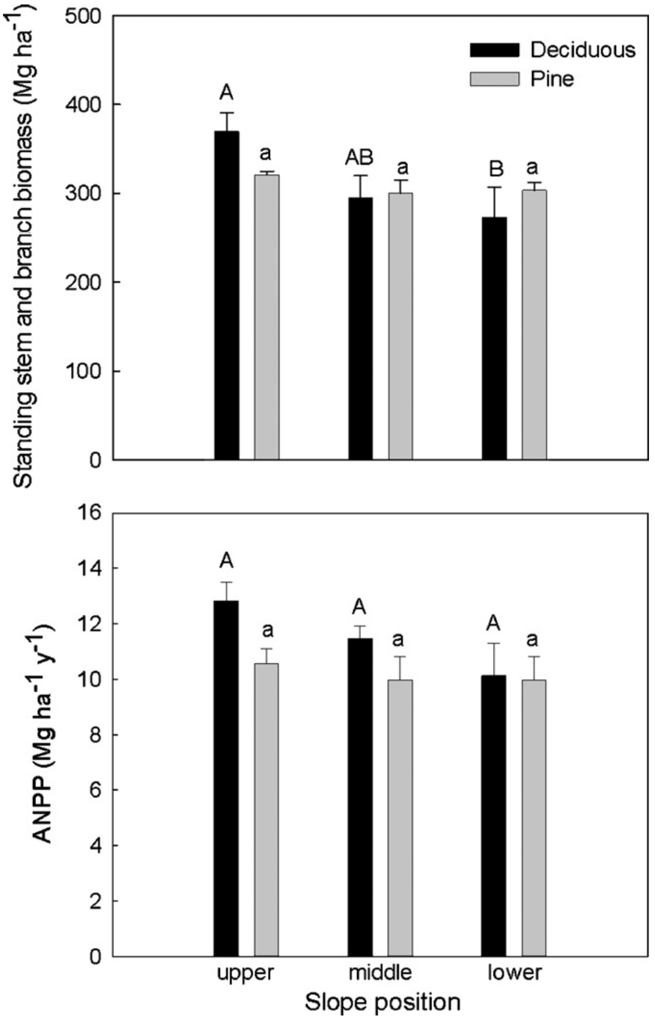

Fig. 1. Comparison of total aboveground biomass and ANPP between the deciduous forest and the white pine plantation, and between slope positions within each forest. Error bars are plus and minus one standard error. Different upper case letters indicate statistically significant differences between slope positions within the deciduous forest; lower case letters indicate significant differences between slope positions in the white pine plantation ($\alpha = 0.05$).

From January through April, prior to the expansion of the current year's foliage, average IPAR was already 91% in the white pine plantation, ranging 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 the white pine and deciduous forests, respectively. There were no significant differences in IPAR across slope positions within either forest ($p = 0.77$, d.f. = 4). There was also 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

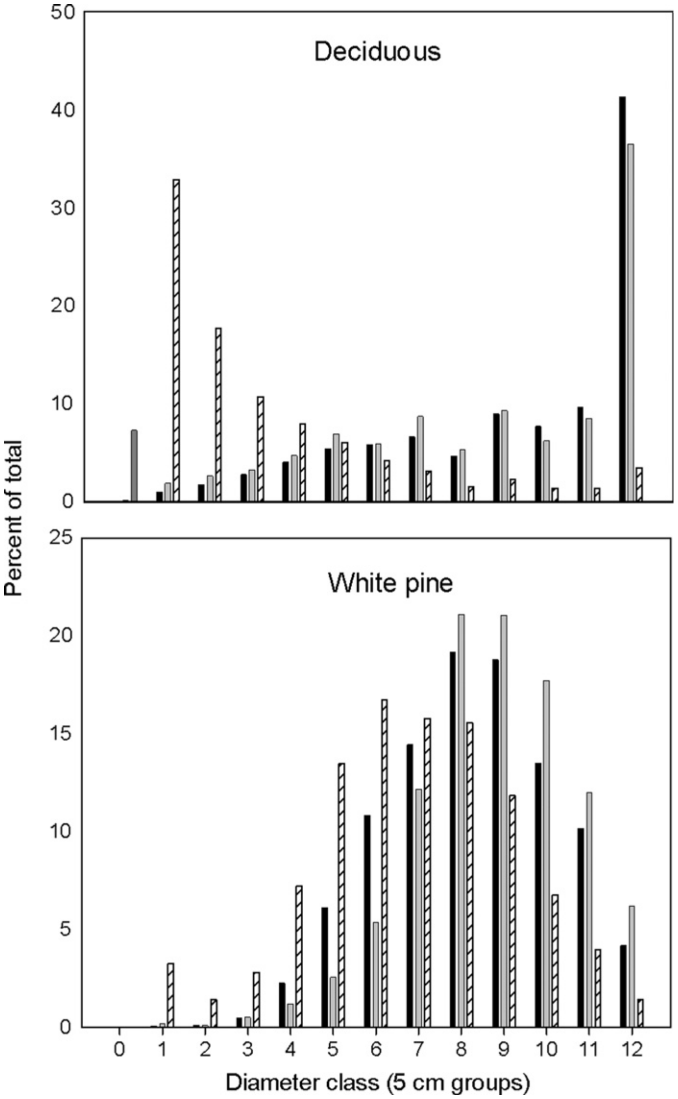

Fig. 2. The percentage of total stem and branch biomass and production, and the total number of stems in each diameter class for the deciduous forest and white pine plantation. Diameter classes represent 5 cm intervals in diameter at breast height. The data include all trees sampled from nine plots in both the deciduous forest ($n = 577$) and the white pine plantation ($n = 431$). Black bars represent the proportion of stem and branch biomass, grey bars represent the proportion of stem and branch production, and dashed bars represent the proportion of the total number of stems included in the comparison.

5.1 to 6.1 among plots in the pine plantation, and from 4.8 to 7.4 in the deciduous forest.

3.3. Radiation use efficiency

Radiation use efficiency was significantly greater in the deciduous forest (1.25 g MJ^{-1}, SE = 0.06) than in the white pine plantation (0.63 g MJ^{-1}, SE = 0.02; $p < 0.001$, d.f. = 1) (Fig. 4). There was no significant change in ε among slope positions ($p = 0.26$, d.f. = 4), indicating that ε was remarkably stable across the watershed for each forest type. Due to the small range of IPAR among plots, there was no linear relationship between IPAR and ANPP in either forest.

3.4. Mineral-nitrogen availability and ANPP

Mineral-nitrogen availability 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 it did not vary among slope positions within either forest ($p = 0.23$, d.f. = 4) (Table 1). Both NH_4 and NO_3 were more available in the white pine plantation than the deciduous forest. Nitrate was 2–6 times more abundant than NH_4 in the pine plantation among sampling periods, whereas average NH_4 availability was 1.5–2 times greater than NO_3 across sampling periods in the deciduous forest. We found no significant relationships between mineral-nitrogen availability and ANPP associated with slope position in either the pine plantation or the hardwood forest, most likely because of the narrow range of the data within each watershed.

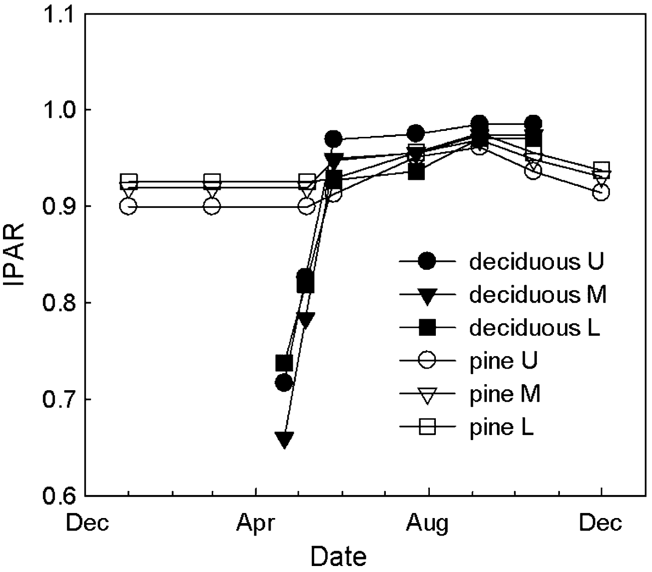

Fig. 3. Patterns of IPAR among slope positions within each forest. Data points are the average percent IPAR for the three plots at each slope position (U = upper slope, M = middle slope, L = lower slope). Measurements with the SunScan System were taken four times from May 6 to September 6, 2005. Daily 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.

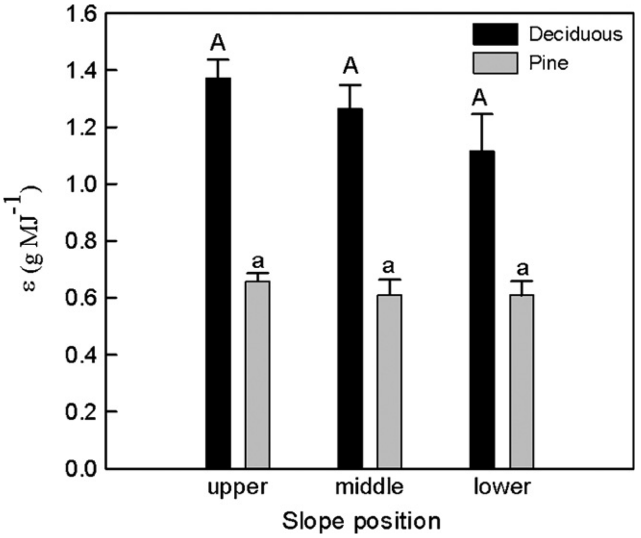

Fig. 4. Comparison of ε between the deciduous forest and white pine plantation, and among slope positions within each forest. Error bars are plus and minus one standard error. Upper case and lower case letters indicate there were no statistically significant differences among slope positions within either forest. The growing season estimate of ε for the deciduous forest was calculated based on IPAR from April 21 to October 14, 2005. The estimate of ε for white pine was calculated using an annual estimate of IPAR.

Table 1
Seasonal changes in mineral-nitrogen availability in the white pine plantation (WS 17) and deciduous forest (WS 18).

	Sample period			Seasonal total
	April 19–June 5	June 15–July 27	Aug 5–Sept 19	
Watershed 17				
Upper	188.88 (16.79)	333.56 (40.01)	572.81 (144.53)	1094.55 (196.78)
Middle	231.06 (22.85)	340.62 (32.37)	550.48 (114.23)	1122.17 (130.52)
Lower	166.25 (25.02)	274.77 (53.07)	401.28 (61.47)	842.31 (79.59)
Watershed 18				
Upper	73.72 (38.19)	83.79 (5.34)	56.94 (14.32)	214.45 (32.21)
Middle	85.22 (17.91)	99.07 (14.12)	73.71 (28.02)	257.99 (49.02)
Lower	101.82 (34.17)	58.55 (2.75)	46.83 (3.57)	207.20 (35.55)

Data represent the average index value for the three plots at each slope position with standard errors in parenthesis. Values are micrograms of NH_4 and NO_3 per gram of resin. Mineral-nitrogen availability was significantly higher in the white pine plantation than the deciduous forest for the entire growing season, and during each individual sample period. There were no significant differences in mineral-nitrogen availability between slope positions within either forest.

4. Discussion

4.1. Aboveground net primary productivity

Aboveground net primary productivity in the Coweeta deciduous forest was 10–91% greater than ANPP in five deciduous forests located along a 10° latitudinal gradient in the United States (Curtis et al., 2002), and 42% greater 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 also approximately 25% greater than reported by Bolstad et al. (2001) for 16 study sites at Coweeta. However, the Bolstad et al. (2001) study included sites with lower ANPP at higher elevations, and their ANPP estimate spanned a 10-year period (1986–1995) that included a severe drought period (1986–1988) (Kloeppel et al., 2003). Aboveground net primary productivity for the white pine plantation was 21% greater than ANPP reported for a similar age white pine forest (Nadelhoffer et al., 1985), and comparable to a 28-year-old white pine plantation (Gower et al., 1993) in the upper midwest.

4.2. Radiation use efficiency

Radiation use efficiency for the deciduous forest (1.25 g MJ^{-1}) in this study was 30–60% greater than that reported for other mixed hardwood forests in the upper midwest (Ahl et al., 2004). 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 and Kruger, 2001; Allen et al., 2005). The average annual ε for the white pine plantation (0.63 g MJ^{-1}) was higher than the range of values reported for five evergreen conifer forests in several regions of the U.S. (e.g. 0.2–0.5 g MJ^{-1}, Gower et al., 1999), but lower than maximum values reported for some evergreen conifer forests in the Pacific Northwest (0.18–0.92 g MJ^{-1}, Runyon et al., 1994).

Interannual variability in environmental variables can influence ANPP and radiation use efficiency (Runyon et al., 1994; Ahl et al., 2004; Rosati et al., 2004). For example, ε varied by 7–17% among years for five Wisconsin forest types, although it was not clear which environmental variables were driving this change (Ahl et al., 2004). During our study, annual precipitation was 207 cm, which was 18% greater than the previous 20 year average (175 cm). Hence, our estimates of ε may be near the maximum expected for these two forests at their current stage of stand development.

4.3. Comparison of ε and ANPP between forest types

Radiation use efficiency was 98% greater in the deciduous forest than the white pine plantation, supporting our first hypothesis, and demonstrating a contrast similar to that shown by Ahl et al. (2004). The white pine trees continued to intercept incident PAR throughout the winter months, and this additional energy capture did not result in higher ANPP than in the deciduous forest. Evergreen conifer species in the southern Appalachians maintain physiological activity throughout the winter months (Ford and Vose, 2007), although photosynthesis is expected to be reduced due to environmental constraints (Runyon et al., 1994). This additional annual carbon gain during the winter and spring was apparently not enough to exceed the carbon gained by deciduous trees during a more abbreviated growing season. In addition, in the autumn and winter the white pine trees only carried one age class of foliage, but IPAR was still over 90% across the watershed. This suggests that during the growing season, when the trees carry two foliage age classes, there may be substantial self-shading within the canopy, reducing the efficiency of canopy photosynthetic carbon gain.

The greater photosynthetic capacity of the foliage of the deciduous species may explain the greater ε in the deciduous forest. Mass-based rates 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 30–60% greater foliar nitrogen concentrations and 65–264% greater SLA than white pine (Pangle, 2006). Peak growing season foliage biomass was 20% greater in the white pine plantation (3.58 Mg ha^{-1}) than the deciduous forest (2.99 Mg ha^{-1}), but ($A_{\max}$) was 50–133% greater for deciduous species than for white pine (Pangle, 2006). Thus, potential carbon gain per unit IPAR was greater in the deciduous forest.

Although the deciduous forest had significantly greater ε in this comparison, we did not measure belowground net primary productivity, and this conclusion may be inaccurate if total NPP were considered. 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 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.

Average ANPP for a similar white pine plantation (WS1) at Coweeta was 13.52 Mg ha^{-1} y^{-1} from ages 10 to 15 (Swank and Schreuder, 1973), which is 33% greater than ANPP for the 50-year-old plantation in this study. This difference existed although LAI was similar between the younger plantation and the one in this study. Hence, age-related decline in ANPP is occurring in this plantation, along with substantial self-thinning. Radiation use efficiency also probably peaked early in stand development, and declined after canopy closure, as has been shown in other plantation forests (Martin and Jokela, 2004). Similar historical data are not available for the mixed deciduous forest, which was selectively logged in the 1920s, and still contains several individual trees greater than 100 years old. Hydraulic limitations on photosynthesis may limit carbon gain in taller and older trees, but this reduction in photosynthesis probably does not solely account for age-related reductions in ANPP in even-aged forests (Ryan et al., 2006). There is also no indication that photosynthesis in evergreen conifers would experience greater hydraulic limitations than in broadleaf deciduous trees, or vice versa.

Binkley (2004) and Binkley et al. (2006) introduced a conceptual model of resource-use efficiency to explain age-related decline in forest productivity. Their conceptual model emphasizes four gradual phases of forest development, each phase demonstrating a relative degree of dominance in resource use by particular cohorts of trees. The second through fourth phases of the model would occur after canopy closure, and are associated with continual declines in ANPP. Quantifying resource acquisition for individual trees is very difficult (e.g. total nitrogen uptake or PAR interception), yet comparing total biomass to total annual biomass increment gained among different size classes of trees may serve as a proxy for a direct comparison of resource-use efficiency, and help distinguish the degree of dominance in resource-use efficiency occurring in a forest (Binkley, 2004).

In this study, the largest trees in the white pine plantation consistently accounted for a greater proportion of stem and branch biomass production in the stand than they did for standing stem and branch biomass, and the opposite pattern was observed for smaller size classes of trees. However, these differences were small compared to those seen in other stands (Binkley et al., 2002, 2006), which suggests a transition between the second and third stages of stand development in the Binkley et al. (2006) model. In the deciduous forest the distribution of stem and branch biomass and production was heavily skewed due to the effect of trees larger than 60 cm in diameter (diameter class 12, Fig. 2). The distributions of biomass and biomass production in this forest are analogous with phase three in the conceptual model, when dominance in resource-use efficiency by larger trees is reduced, and the ratio of biomass to biomass production among all size classes of trees approaches 1:1. Obviously, though, total resource use is still dominated by the largest trees, despite the declining efficiency of their resource use. Hence, the mixed deciduous forest is older, has access to less mineral nitrogen, and demonstrates patterns in resource use associated with a later stage of the age-related productivity model (Binkley et al., 2006) than the white pine plantation, but maintains similar ANPP as the white pine plantation. Species diversity may explain this difference. Forests with greater species diversity are shown to maintain greater ANPP over long time periods (Caspersen and Pacala, 2001), perhaps due to commonly cited mechanisms such as complementarity in resource use. Thus far, the resource-use dominance model (Binkley et al., 2006) has been tested with data from plantations and forests with relatively low diversity, and it is not clear how the interacting effects of species diversity and age-related trends in resource-use dominance in forests may influence their long-term productivity.

4.4. Mineral-nitrogen availability, LAI, and ε

We found that mineral-nitrogen availability was significantly greater in the white pine plantation, even though ANPP was slightly less than in the deciduous forest. These results are consistent with Montagnini et al. (1989) who found that a nearby white pine plantation at Coweeta had substantially greater mineralization and nitrification rates than two late-secondary deciduous forests. The pine and hardwood watersheds in this study were adjacent to each other with similar slopes, aspects and soils, so the large difference in nitrogen availability was surprising considering the more recalcitrant, and less nutrient-rich pine litter. However, other work conducted on these watersheds has shown that concentrations of base cations, total carbon, and total nitrogen are all greater in the white pine plantation than in the deciduous forest, and may be more stable over time despite continuing sequestration into plant biomass (Knoepp and Swank, 1994; Knoepp and Swank, 1997). Prior land use could have influenced these results. All native vegetation on the pine watershed was cut in 1942, and all plant material was left on site. Furthermore, all regenerating vegetation was cut every 1–2 years until white pine was planted in 1956 (Swank and Crossley, 1988). This massive input of plant matter may have had long lasting impacts on soil carbon and nutrient pools (Knoepp and Swank, 1994), and subsequent nitrogen mineralization and nitrification rates. This effect may have been enhanced by the regeneration of the nitrogen fixing species black locust (*Robinia pseudoacacia* L.), which is an early successional species in the southern Appalachians and can increase long-term mineral-nitrogen availability (Boring and Swank, 1984; Montagnini et al., 1989).

Oak-dominated deciduous forests in the southern Appalachian Mountains have relatively low rates of nitrogen mineralization and nitrification (Garten et al., 1994; Knoepp and Swank, 1998) when compared to similar forest types from other regions (Zak and Pregitzer, 1990), and long-term analyses of stream chemistry indicate that watersheds with this cover type are conservative of inorganic nitrogen, resulting in low rates of discharge into streams (Swank and Vose, 1997). Hence, we predicted that mineral-nitrogen availability would be well correlated with LAI and ANPP, as has been demonstrated for other temperate forests (Reich et al., 1997). However, there were no significant relationships between mineral-nitrogen availability and LAI or ANPP within, or between, forest types. Within watersheds this may have been partially due to the small range in the data. However, the lack of relationships between nitrogen availability and ANPP or LAI between watersheds was surprising based on previous studies (Reich et al., 1997), and may indicate different nitrogen use efficiency or uptake capacity in pines and deciduous hardwoods.

5. Conclusion

We found that along a 260 m elevation gradient within either a mixed deciduous forest or a white pine plantation there was not significant variation in mineral-nitrogen availability, ANPP, LAI or ε. ANPP and LAI were also similar across the two forest types. However, the mixed deciduous forest showed much greater ε than the white pine plantation. We attribute this difference to greater photosynthetic production per unit IPAR in deciduous foliage during the growing season, which could not be compensated by carbon gain during the winter and spring in the white pine plantation, or by the substantially greater availability of mineral nitrogen. Age-related decline in ANPP was important in this comparison. The white pine plantation and deciduous forest appear to show age-related trends in resource-use dominance and ANPP that are consistent with those seen in other forests, although our data raise additional questions about the interacting effects of species diversity and stand structure on age-related patterns in resource-use efficiency and ANPP in forests. Future studies should examine ε across broader gradients in species composition, elevation, aspect, and latitude, to determine if the parameter is useful for predicting ANPP and carbon storage in diverse forests at spatial scales greater than first-order watersheds.

Acknowledgements

We would like to thank Ron Hendrick for providing a critical review of an earlier version of the manuscript. Patrick Bussell provided extensive assistance in the analytical chemistry laboratory which was greatly appreciated. Also, thanks to Mary Anne McGuire, Jason Nedlo, Bruno Furtado, Aaron Joslin, Nina Wurzburger, and Mike Murphy for aiding in a variety of ways. This research was supported by the UGA/USDA Forest Service Cooperative Agreement number SRS04CA11330140129.

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