Forest Productivity, Leaf Area, and Terrain in Southern Appalachian Deciduous Forests

Paul V. Bolstad, James M. Vose, and Steven G. McNulty

ABSTRACT. Leaf area index (LAI) is an important structural characteristic of forest ecosystems which has been shown to be strongly related to forest mass and energy cycles and forest productivity. LAI is more easily measured than forest productivity, and so a strong relationship between LAI and productivity would be a valuable tool in forest management. While a linear relationship has been observed between LAI and forest productivity, most of these data have been collected in needle-leaved evergreen stands. The generality and consistency of the relationship between LAI and productivity has not been as well established for deciduous forests.

Leaf area index (LAI) and aboveground net primary production (ANPP) were measured on 16 forest stands in the southern Appalachian Mountains. These stands span a range of elevation, slope position, temperature, and moisture regimes. LAI averaged 5.8 $m^2\ m^{-2}$ and ranged from 2.7 to 8.2. ANPP averaged 9.2 Mg $ha^{-1}\ yr^{-1}$ and ranged from 5.2 to II.8 Mg $ha^{-1}\ yr^{-1}$.

LAI and ANPP decreased significantly from cove to ridge sites, and ANPP decreases significantly from low to high elevation ($P < 0.05$, linear regression slope). Elevation-related differences in ANPP do not appear to be due to changes in precipitation, leaf nitrogen content, or site N mineralization rates.

Linear ANPP-LAI equations fit to the data measured in this study were significant ($P < 0.05$). These relationships were not significantly different ($P > 0.1$) from linear relationships based on data reported in most other studies of ANPP and LAI in eastern deciduous forests of North America. However, the slope of a linear regression model based on North American eastern deciduous forests was significantly different ($P < 0.05$) from one based on data collected in temperate deciduous forests for the rest of the globe. The differences were slight over the range of observed data, however, and the difference may be due to a narrower range of data for North American deciduous forests. For. Sci. 47(3):419–427.

Key Words: ANPP, LAI, precipitation, temperature, elevation.

ABOVEGROUND NET PRIMARY PRODUCTION (ANPP) and leaf area (LAI, one-sided m^2 leaf per m^2 ground area) are common, related measures of forest site productivity and structure. Studies in single-species, even-age forests have shown that LAI and ANPP covary (Gholz et al. 1994), and these results are supported by studies across a broader range of species and growth forms (Fassnacht and Gower 1997). There are many reasons for tight linkage between ANPP and LAI. including an overall increase in annual net photosynthesis with higher leaf areas, and interactions between leaf area, productivity, and moisture and temperature gradients (Leith 1975, p. 182-201, Gholz 1982, Raich and Nadelhoffer 1989, Röhrig 199 1, Gholz et al. 1994, Fassnacht and Gower 1997). While a linear relationship has been observed between LAI and forest productivity, most of these data have been collected in needle-leaved evergreen

Paul V. Bolstad. Department of Forest Resources, University of Minnesota, 1530 Cleveland Ave. N., St. Paul, MN 55108—E-Mail: pbolstad@forestry.umn.edu. James M. Vose, Coweeta Hydrologic Lab, USDA Forest Service. 3160 Coweeta Lab Rd., Otto, North Carolina 28763. Steven G. McNulty, Southern Forest Experiment Station, USDA Forest Service, 1509 Varsity Dr.. Raleigh, NC 27606.

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stands (Gholz et al. 1994). The generality and consistency of the relationship between LAI and productivity has not been established for deciduous forest types.

Strong, quantified ANPP-LAI relationships in the southern Appalachian Mountains would facilitate estimates of ANPP via measurements of LAI. Unfortunately, few studies have reported quantitative relationships between LAI and ANPP in deciduous broad-leaved forests of eastern North America. It is often easier, quicker, and less expensive to measure LAI than ANPP (Bolstad and Gower 1990, Gower and Norman 1991), and so equations relating ANPP to LAI could be used to estimate ANPP. Previous work has shown linear relationships between LAI and ANPP (Hedman and Binkley 1988, Fassnacht and Gower 1997); however, the generality of the specific linear relationships has not been established.

Forest structure and productivity are strongly influenced by terrain position (ridge to cove) and elevation in the southern Appalachians. Previous work in a subregion has identified topography as a main determinant of productivity and forest type (Smalley 1984). Site quality has been related to slope, elevation, and topographic position for some vegetation types in the southern Appalachians (Carmean 1970, Meiners et al. 1984, McNab 1989, 1993). However, these relationships have most often been developed using some index of productivity (e.g., site index). Very few studies have measured forest productivity, structure, and quantitative topographic indices at the same sites.

This article describes a study of the relationships among terrain position, elevation, ANPP, and LAI at 16 forest stands in the southern Appalachian Mountains. Our specific objectives were to (I) expand the number of eastern deciduous forest sites for which ANPP and LAI measurements have been reported, (2) report quantitative relationships between LAI, ANPP, elevation, and terrain position in the southern Appalachian Mountains, and (3) determine if NPP to LAI relationships in southern Appalachian deciduous forests are similar to those for deciduous forests in eastern North America and the world.

Methods

Study Sites

Sixteen study sites were located within the boundaries of the USDA Forest Service Coweeta Hydrologic Laboratory in western North Carolina, 35°3′N, 83°15′W (Table 1). The study area had moderate to steep slopes, well-developed drainage patterns, and many small basins. Soils were derived from the well-weathered remains of gneisses, sandstones, and granites (Hatcher 1988).

Climate in the study area has been classified as moist, warm temperate, with average January and July temperatures of 3.3 and 21.6°C at 650 m elevation (Swift et al. 1988, p. 35-55). Precipitation during the past 60 yr has averaged near 1800 mm annually at 700 m, and precipitation increases with

Table 1. Stand environmental characteristics and species composition. Columns do not necessarily sum to 100% due to rounding error.

	Site number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Elevation (m)	1.082	1,300	847	908	1,001	1.095	1.303	1.330	1.096	1.550	1.190	975	838	844	972	864
Terrain shape (deg.)	-4.5	13.1	-16.7	-7.6	6.8	-3.7	2.9	25.1	-1.5	16.6	10.6	2.1	-14.5	-5.8	6.1	0.0
Basal area (m^2 ha^{-1})	54.1	35.1	29.3	27.6	30.1	25.3	31.3	23.3	28.7	24.6	37.6	36.7	39.6	32.3	35.8	30.2
Wood volume (m^3 ha^{-1})	857	552	572	473	448	345	499	319	417	330	620	626	636	500	476	432
LAI (m^2 m^{-1})	6.9	5.4	5.4	6.7	6.0	5.2	4.7	4.5	7.2	2.7	4.1	5.2	8.2	6.0	7.4	6.5
ANPP (Mg ha^{-1} yr $^{-1}$)	11.8	9.8	9.6	9.8	9.2	8.1	8.1	7.5	8.3	5.2	8.4	11.2	11.6	9.8	9.3	9.8
Species	(percent of plot total basal area)															
Aesculus octandra	0	2	0	0	0	0	3	5	8	5	1	0	0	0	0	0
Acer pensylvanicum	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0
A. saccharum	0	1	0	0	0	0	0	16	0	1	0	0	0	0	0	0
A. rubrum	12	26	15	12	3	36	29	32	41	2	19	10	5	13	1	1
Betula spp.	0	13	9	0	0	2	4	4	3	0	0	1	0	0	0	1
Carya spp.	21	0	0	25	17	18	0	0	5	0	31	16	0	9	14	0
Cornus florida	0	0	1	0	0	0	0	0	0	0	0	1	1	2	0	0
Liriodendron tulipifera	12	0	2	5	0	5	0	0	2	0	2	19	0	7	0	0
Magnolia fraseri	0	0	3	0	0	0	0	0	5	0	0	0	0	0	0	0
Nyssa sylvatica	2	0	1	6	0	0	0	0	4	0	0	5	5	4	1	5
Oxydendron arboreum	3	0	3	11	3	0	0	0	5	0	7	0	7	3	4	4
Pinus spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	7
Quercus alba	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Q. coccinea	0	4	0	2	3	0	13	0	0	0	2	0	5	0	8	4
Q. prinus	10	41	57	23	44	12	30	29	20	0	15	31	64	26	53	57
Q. rubra	30	4	8	5	0	7	11	12	4	90	10	17	12	20	5	0
Q. velutina	9	7	0	11	31	7	11	0	0	0	7	0	0	18	14	12
Rohinia psuedoacacia	0	2	0	0	0	4	0	0	0	0	6	0	1	0	0	0
Tsuga spp.	1	0	0	0	0	9	0	0	1	0	0	0	0	0	0	1

elevation (Swift et al. 1988, p. 35–55). Temperature decreases with elevation. and there are predictable changes in temperature related to terrain shape (Bolstad et al. 1998a).

Because forest community composition may change with landscape position (Whittaker 1956. Elliott and Hewitt 1997, Bolstad et al. 1998b, Elliot et al. 1999), the study area was stratified by terrain position (ridge, sideslope. and cove) and elevation (low, < 1050 m, and high ≥ 1050 m). Sites were randomly located within each of the six unique landform strata (two elevations by three terrain positions). Sites were in uneven-aged mixed deciduous hardwood stands without human disturbance since the mid- 1920s. Sites were selected to be free of major natural disturbance in the previous IO yr (no windthrow, treefalls, or major canopy gaps), and all sites had relatively continuous, closed canopies. As is common in the region, most study stands contained substantial *Quercus prinus, Acer rubrum*, or other *Quercus* components, with *Catya* and *Liriodendron tulipifera* dominating in some instances. Understory cover varied from near zero to near 70%, and consisted of both herbaceous and woody taxa. *Rhododendron* spp. were the most common woody understory taxa at cove sites and *Kalmia* spp. were the most common on ridge sites, with overlapping mixtures at intermediate terrain positions.

Site locations were determined using a Global Positioning System (GPS) receiver, applying methods developed in the southern Appalachians to estimate location to within the nearest 5 m (Deckert and Bolstad 1996). Elevations were determined both from the GPS readings and from intersecting GPS locations with 1:24,000 scale-based digital elevation models.

Environmental Parameters

Previously collected data and models were used to estimate environmental parameters at each site. Hourly data from five climate stations were used to estimate plot average temperatures, humidity, and insolation for the period 1986-1995 (Bolstad et al. 1998a). Average precipitation was determined from station measurements and interpolation diagrams developed from a dense network of rainfall gauges (Swift et al. 1988, p. 35–55). An index of local terrain shape was calculated based on the DEM for each GPS-determined plot center, using an annular ring with a 75 m radius (McNab 1989). McNab's terrain shape index averages the slope to the eight cardinal and subcardinal compass points, uphill slopes negative and downhill slopes positive. Terrain shape values varied between -25 (cove) to +25 (ridge) in the study area.

Field and Laboratory Measurements

Allometry.—All trees ≥ 20 cm were measured on a circular 0.1 ha plot at each site. Diameter at breast height (dbh. 1.3 m) was measured using a steel diameter tape, and height was measured with a hypsometer. All trees ≥ 2.5 cm dbh were measured on a randomly selected 0.0125 ha subplot of the 0.1 ha plot. All trees ≥ 20 cm had at least one increment core to IO yr prior to the measurement date. Two increment cores were extracted at right angles and averaged on approximately 15% of the sampled trees. All trees between 2.5 and 20 cm were cored on each 0.0125 ha subplot. Ten-year growth was measured using a magnifier and micrometer. Growth was subtracted from current diameter to estimate the diameter 10 yr earlier. Preliminary estimates indicated height/diameter relationships were quite strong at individual sites. so tree heights corresponding to 10 yr earlier were estimated by fitting site-specific height/diameter equations with current data. and applying these to previous diameters. Stem diameters and heights were then used to calculate aboveground woody biomass (stem, branch, and twig) for each tree currently and at 10 yr prior, using locally and regionally developed allometric equations (Clark and Schoender 1985. Martin et al. 1998) and site-specific wood density measurements. Mortality within the past 10 yr was assessed, but sites lacked recent windthrow or standing dead trees.

Understory (plants < 5 m height, < 2.5 cm diameter) woody production was determined by counting stems taller than 50 cm in the 0.0125 ha subplot randomly selected from each plot. *Kalmia* and *Rhododendron* accounted for more than 90% of the understory woody stems. Mean per-stem biomass growth rates for understory *Kalmia* and *Rhododendron* reported by McGinty (1972) were multiplied by stem number on each plot. These two species averaged less than 3% of production across all plots. Production from plants < 50 cm tall was not measured, typically less than one-half of 1% of total ANPP in closed-canopy forests in the study area (Monk et al. 1970, McGinty 1972).

Leaf Biomass and Leaf Area Measurements.-Five 4600 cm^2 litter baskets were randomly located within each plot. Litterfall was collected approximately monthly during Fall 1995 and 1996 and twice during the rest of each year. Litter was sorted by tissue type (leaf, wood, reproductive), and by species or closely related species groups. Leaves were dried at 70°C for 48 hr and weighed. Leaf biomass per unit area was estimated by summing leaf biomass within each basket, dividing by basket area, and averaging across baskets. Leaf area was determined for each taxa using locally derived specific leaf areas (SLA) for each species or species group. SLA was determined on a subsample of leaves collected on each plot. Leaves were soaked in water for 24 hr, and then placed in a leaf press for 1 hr. Individual one-sided leaf area was measured to the nearest 0.01 m using a CID-25 1 leaf area meter (CID Inc., Vancouver, WA). redried at 70°C, and weighed to the nearest 0.001 g. Tests indicated areas from rehydrated leaves differed from fresh leaves by less than 2%. and differences were unbiased. Stand leaf areas were calculated from specific leaf area and litter basket collections.

Statistical Analyses

ANPP over a 10 yr interval was calculated for each plot by summing litterfall biomass and estimated woody biomass growth. Average litterfall biomass for 1995 and 1996 was assumed representative of litterfall for the entire 10 yr period. Temperature and precipitation for both the 2 yr and IO yr periods were near long-term averages. Long-term subcanopy light-transmission measurements (unreported) indicate leaf area at nearby plots in the Coweeta Basin were similar over the 2 yr measurement period to LAIs over the past 8 yr.

ANPP, LAI, and stand structural variables were regressed against each other and against terrain shape, elevation, and estimated environmental parameters. Single-variable linear regression and hyperbolic nonlinear regression models were fit using SAS software, version 6.12 (SAS Institute 1996). Regression diagnostics were calculated, including R^2, Cook's D, and residual plots, and model significance calculated based on appropriate sums of squares. Models were considered significant ($P < 0.05$) or weakly significant ($P < 0.1$) based on t-tests of regression slope or higher order parameters.

Results and Discussion

Stand Structure

Mean height and diameter changed with elevation and terrain shape. Mean height decreased with elevation and from cove to ridges ($P < 0.05$, linear regression between height and elevation, terrain). Mean diameter decreased weakly with terrain shape ($P < 0.1$). but did not change with elevation. Basal areas were similar across both elevation and terrain (Table I), indicating more, smaller trees were found on ridge sites relative to cove sites, but there were no trends in stem density with elevation.

Species differences are not a likely cause of differences between height or other measured stand variables. Species composition was quite variable, and no trends were observed on these plots (Table 1). Two species, ***A. rubrum*** and Q. ***prinus,*** occurred at all sites. The most common species was one of these two at 12 of 16 sites, with a high frequency of occurrence at three of the remaining four sites. ***Quercus rubra, Q. velutina,*** and ***Catya*** spp. were dominant at individual sites, but were also common across a range of sites.

Leaf Area Index

LAI varied from 2.7 to 8.2 m^{-2} m^{-2}, within the range reported for other eastern deciduous forest stands (Hutchison et al. 1986, Hedman and Binkley 1988, Bolstad and Gower 1990, Vose et al. 1995, Fassnacht and Gower 1997, Sullivan et al. 1996). LAI decreased significantly with both elevation and terrain shape ($P < 0.01$, Figures 1, 2).

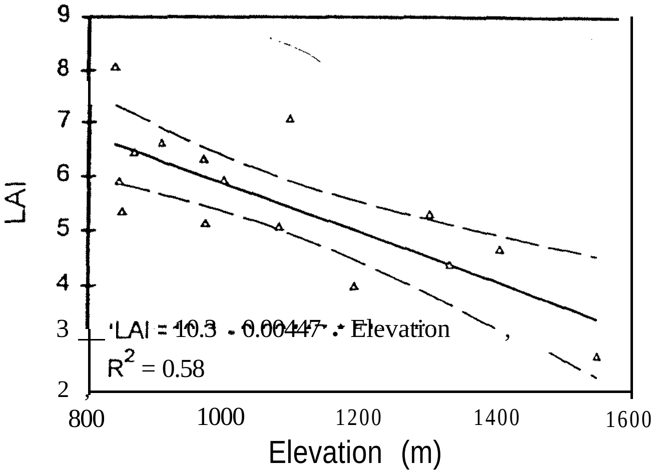

Figure 1. Leaf area index (LAI) vs. elevation for 16 deciduous broad-leaved study stands in the southern Appalachians. Linear regression was significant ($P < 0.01$). 95% confidence limits shown.

Reduced LAI at ridge sites is not likely due to a higher disturbance frequency or changes in species composition. Higher disturbance frequency may reduce LAI temporarily, until the canopy regrows to closed-canopy values. However, we selected our sites to be free of recent disturbance, so this was unlikely to be a cause of cove to ridge reductions in leaf area. Species composition may affect LAI because of interspecific differences in shade tolerance, but as noted earlier, we observed no clear patterns in species composition.

Two other factors potentially related to LAI, water and N availability, have been previously studied in the Coweeta Basin. This previous work has indicated there are no differences in N mineralization rates between ridge and cove sites (Knoepp and Swank, 1997, 1998), although one nearby study reported significant decreasing trends in N mineralization from cove to ridge sites (Garten et al. 1994). Leaf N concentrations show no trends from ridge to cove in this and other studies in the study area (Mitchell et al. 1999). Soil moisture has been shown to decline substantially from cove to ridge locations, especially at low elevations during periods of dry weather (Helvey and Patric 1988), suggesting soil moisture may be one cause of patterns in LAI.

Reduction in LAI with elevation is more difficult to interpret. While soil water and nutrient availability have been shown to limit LAI in other studies (Grier and Running 1977, Aber et al. 1982), there is not strong evidence that nutrients and soil N limit LAI here. Precipitation was higher, temperatures lower, evapotranspiration lower, and N-mineralization rates were higher at higher elevations relative to lower elevations in our study area (Swift et al. 1988, p. 35–55, Knoepp and Swank 1997). Although we did not measure N-mineralization rates and precipitation at our study sites, results reported by Swift et al. (1988, p. 35–55) and Knoepp and Swank (1997) involved plots coincident or adjacent to our study sites. The results from previous studies strongly suggest precipitation and N availability are not the main factors driving elevation-related changes in LAI at Coweeta.

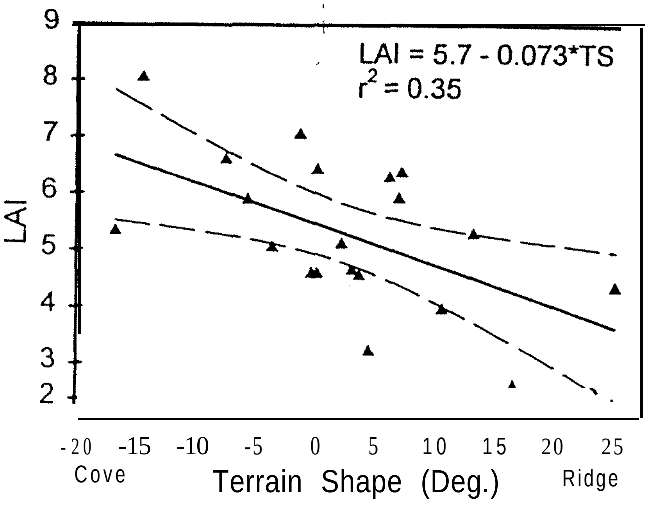

Figure 2. Leaf area index (LAI) vs. terrain shape for 16 deciduous broad-leaved study stands in the southern Appalachians. Linear regression was significant ($P < 0.01$), 95% confidence limits shown.

ANPP

Measured ANPP values averaged 9.2 Mg^{-1} ha^{-1} yr (Table 1), within the range reported for eastern deciduous forest types (Monk et al. 1970, Botkin et al. 1972, Whittaker et al. 1974, Day and Monk 1977, Crow 1978, Fownes 1985, Hedman and Binkley 1988, Host et al. 1988, Chapman and Gower 1991, Fassnacht and Gower 1997). Mean ANPP measured here was slightly higher than the 8.4 Mg^{-1} ha^{-1} yr reported by Day and Monk (1977). and near the average of 10 to 12 Mg^{-1} ha^{-1} yr for well-stocked, mesic southern Appalachian forests reported by Whittaker (1966).

Our average ANPP estimates were notably lower than the mean 15.7 Mg^{-1} ha^{-1} yr reported by Hedman and Binkley (1988) for Piedmont forests in North Carolina. Hedman and Binkley (1988) reported very high ANPP when compared to deciduous forests worldwide. ANPP values greater than 15 Mg^{-1} ha^{-1} yr are rare in deciduous forests, as Rörhig (1988) reported. ANPP was below 14.4 Mg^{-1} ha^{-1} yr for approximately 90% of temperate deciduous forests in a worldwide survey.

Our range of productivities was substantially lower than the range reported by Whittaker in southern Appalachian forests (1966). Our lowest productivity (5.2 Mg^{-1} ha^{-1} yr) was similar to the 6 to 7 Mg^{-1} ha^{-1} yr reported for higher elevation deciduous sites (Whittaker, 1966). However, our most productive site accumulated 11.7 Mg^{-1} ha^{-1} yr, and cove sites averaged 10.5 Mg^{-1} ha-t yr. This was less than one-half the 24.1 Mg^{-1} ha^{-1} yr for the most productive site reported by Whittaker (1966). He noted high productivities occurred in "unstable" stands, fully stocked with young, fast-growing trees. He estimated "typical" ANPP at 10 to 12 Mg^{-1} ha^{-1} yr for cove forests. This is near the upper range of production reported by Fassnacht and Gower (1997), and Fownes (1985).

ANPP decreased as elevation increased, from an average of 10.2 Mg^{-1} ha^{-1} yr at 900 m to 6.8 Mg^{-1} ha^{-1} yr above 1300 m. This relationship was highly significant ($P < 0.01$, Figure 3), and may have been caused by multiple factors. Prior studies have shown strong global trends of decreasing ANPP with decreasing mean annual temperatures (Leith 1975, p. 182-201). The pattern in ANPP may have been caused by both shorter growing seasons and lower temperatures during the growing season. However, the reduction in ANPP observed in this study was more than proportional to the decrease in growing season length. ANPP was reduced by over 30% across our elevation gradient, while the growing season decreased approximately 15% from low to high elevation. Mean growing season temperature also decreased with elevation, and ANPP increased significantly with mean annual temperature (Figure 4).

Soil N availability has been shown to strongly influence ANPP (Aber and Melillo 1991, p. 161–169). Low N availability often results in reduced leaf N content, and maximum photosynthetic rates are typically lower at lower leaf N concentrations (Ellsworth and Reich 1992). However, previous studies at and near these sites are mixed. Studies at locations intermixed with our sites show nitrogen mineralization rates were similar across most elevations, and highest for northern hardwood forest types, typically found at higher elevations in the southern Appalachians (Knoepp and Swank 1997, 1998). However, studies approximately 60 km west with similar forest types reported strong decreases in N mineralization and N availability from coves to ridges (Garten et al., 1994). Further studies are warranted to resolve these contradictory observations.

There was no relationship between ANPP and precipitation (linear regression, $P > 0.1$). Precipitation increased from low to high elevation over the study area (Swift et al. 1988, p. 35–55), and temperature decreased from low to high elevation.. Thus, temperature and precipitation trends were confounded across the broad elevation gradient of this study.

ANPP decreased significantly ($P < 0.05$) from cove sites to ridge sites (Figure 5). Previous work at these and nearby sites indicate lower soil moisture is common at ridgetop sites (Helvey et al. 1972, Yeakley et al. 1994), and this may be the cause of lower ridgetop ANPP. While most regions in the Southern Appalachian Mountains receive adequate summer rainfall, dry conditions late in the growing season regularly

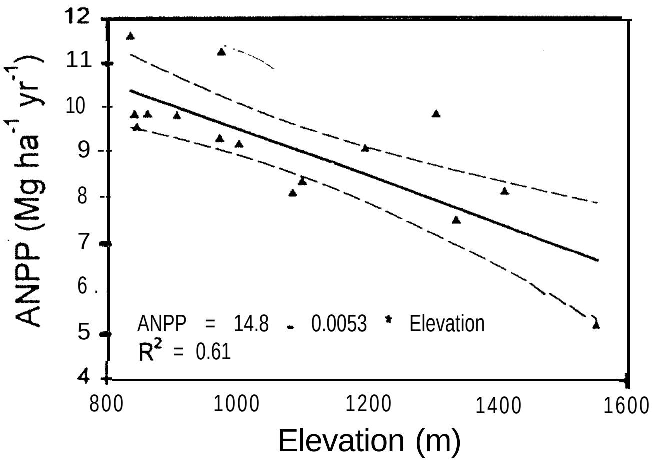

Figure 3. Relationship between ANPP and elevation for 16 deciduous broad-leaved study stands. All stands were without significant disturbance for at least the previous 70 yr. Linear regression (solid line) was significant ($P < 0.01$), 95% confidence limits shown.

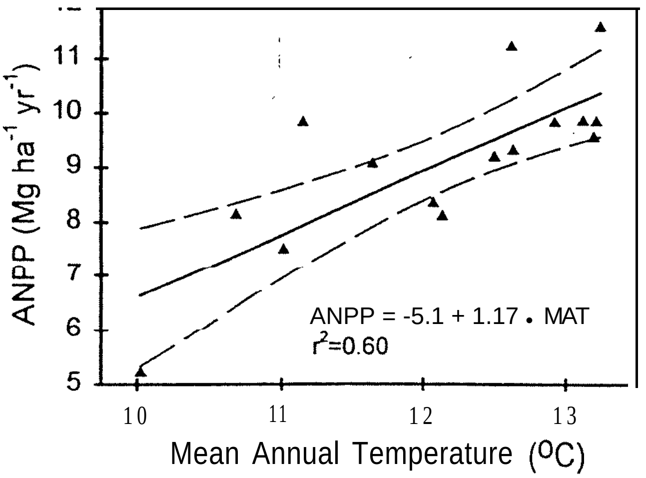

Figure 4. Relationship between ANPP and mean annual air temperature. Air temperature was derived from a network of five temperature stations located adjacent to the study sites, across the full elevation range. Linear regression was significant ($P < 0.01$). 95% confidence limits shown.

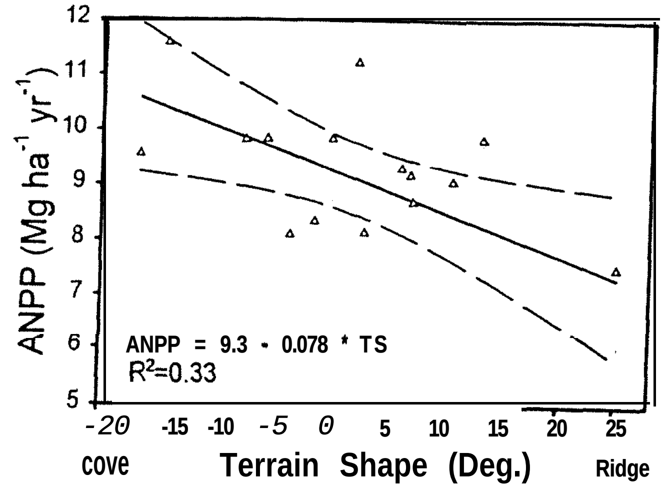

Figure 5. ANPP vs. terrain shape (McNab 1989) for 16 deciduous broadleaved study stands in the southern Appalachians. Concave (cove) sites have low terrain shape values, convex (ridge) sites have higher terrain shape values. The slope of the regression line was significant ($P < 0.01$), 95% confidence limits shown.

occur on ridge locations, most frequently at lower elevations. Dry ridge soils are common by mid-August in many years and occur earlier in the season during periodic droughts. One significant drought was observed in the 10 yr prior to our measurements. Higher drought-caused mortality rates have been documented on ridge and upper, south-facing sites (Smith 1991, Clinton et al. 1993). Reduced soil moisture, even in nondrought years, may have led to significant reductions in ANPP on these sites.

ANPP to LAI Relationships

ANPP and LAI were significantly related in our study (P c 0.01, r^2=0.62, Figure 6). The observed linear ANPP vs. LAI relationship was not significantly different (P > 0.1) from that reported by Fassnacht and Gower (1997) for deciduous broadleaf stands across a range of site qualities in Wisconsin, suggesting some generality in the ANPP-LAI relationships across diverse deciduous forest types. Variation in site quality reported by Fassnacht and Gower (1997) was due primarily to differences in water holding capacity in glacially derived soils, and related differences in soil properties. Site quality in our study was related to elevation and terrain position. Despite the differences in environmental conditions between these two studies, we observed strong evidence for a common ANPP-LAI relationship among eastern deciduous forests.

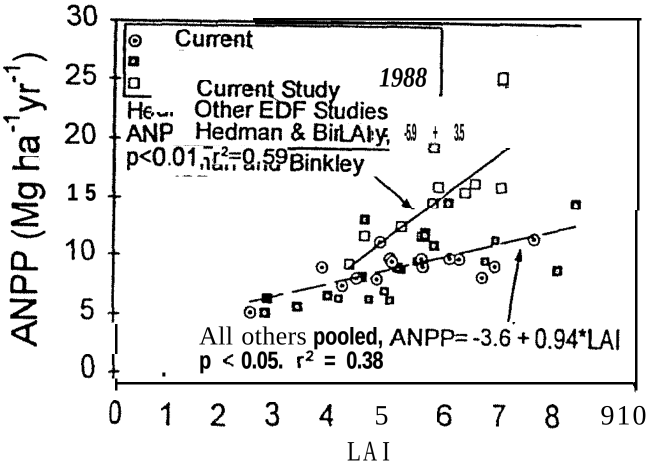

Figure 6. ANPP vs. LAI for this study and for other reported eastern deciduous forest stands. The pooled eastern deciduous study regression was significant ($P < 0.01$), and significantly different from Hedman and Binkley (1966).

The ANPP-LAI linear regression based on data from this study was not significantly different from a regression using a pooled set of ANPP-LAI measurement from a number of studies in North America (Figure 6). These "other" studies each reported ANPP and LAI for one to a few mature, relatively undisturbed eastern deciduous forest stands (Whittaker 1966, Johnson and Risser 1974, Whittaker et al. 1974, Crow 1978, Whittaker et al. 1979, Monk and Day 1988). Although the relationship between ANPP and LAI was more variable for the pooled data for North America, it shows a similar trend of increasing ANPP with increasing LAI. The linear relationship for these other studies was not significantly different from that based on Fassnacht and Gower (1997) or this study. Data from this study and those studies listed above were pooled to fit a single ANPP-LAI relationship:

$$ANPP = 3.6 + 0.94 * LAI, \quad (P < 0.01, r^2 = 0.37)$$

We note two data points in the pooled data set that contribute significantly to the variation observed in this general eastern deciduous forest ANPP-LAI relationship. Both points were well above the regression line for the pooled data (Figure 6). These points are based on measurements reported by Whittaker (1966) and Johnson and Risser (1974). Neither point was an outlier according to Cook's-D and other outlier tests (Draper and Smith 1981, p. 170–171), but removal of these two points reduced the mean-squared error by more than 23% and increased the adjusted r^2 from 0.38 to 0.49. However, neither the slope nor intercept of the regression line were significantly changed ($P > 0.05$) when these two points were omitted, and results are reported with these points included.

The linear regression for the data reported in Hedman and Binkley (1988) was significantly different ($P < 0.05$) from regressions based on all other North American eastern deciduous forest data sources (Figure 6). These differences were maintained with all combinations of the three other data sets, e.g., combining Fassnacht and Gower (1997) with the current study only, with the pooled studies only, or combining all three. Regressions were significantly different from the Hedman and Binkley (1988) line ($P < 0.05$) in all cases. The Hedman and Binkley (1988) data resulted in a higher, steeper regression line across the range of LAI values observed. Their observed LAI ranged from 4.5 to 7.4, within the range observed in other studies. However, their ANPP values range from 9.3 to 25 Mg^{-1} ha^{-1} yr, higher than those reported for most other mature eastern deciduous forest stands.

The ANPP-LAI relationship found for pooled eastern deciduous forest data was also significantly different ($P <$ 0.05) from a linearrelationship based on a global compilation of temperate deciduous forest ANPP-LAI measurements (Figure 7). The global dataset combined measurements of ANPP and LAI reported for deciduous forests outside of

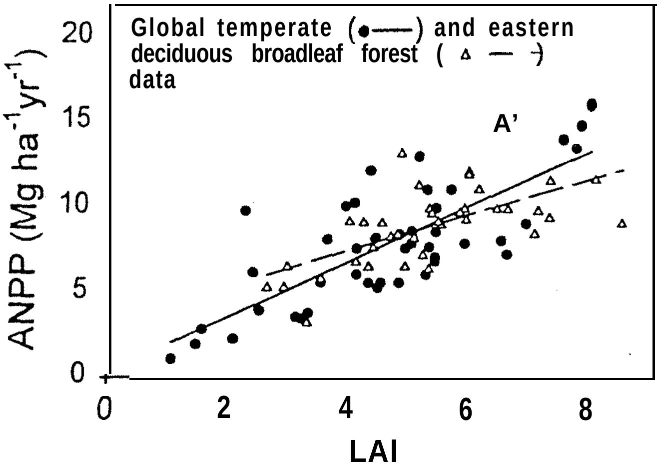

Figure 7. ANPP vs. LAI for the pooled eastern deciduous forest studies and for a global set of studies. The regression line for the eastern deciduous forest data **(ANPP** = 3.2 + 1.1 * LAI, r^2 = 0.39) **differed** significantly **(P < 0.05)** from the regression line for the global data set (ANPP = 0.17 + 1.6 * LAI, r^2 = 0.59).

eastern North America (Möller et al. 1954, Ovington and Madgewick 1959, Tadaki et al. 1969, Hughes 1971, Sato 1974, Hytteborn 1975, Persson 1975, Kakubari 1977, Kawahara 1979, Lossaint and Rapp 1978, Reichle 1981, p. 103–155, Decei 1991). A majority of these data were from Europe and Japan. LAI values ranged from 1.1 to 8.0, corresponding to a range of ANPP between 1.0 and 15.2. The linear regression based on the global dataset had a higher slope and lower intercept than the line for eastern deciduous forests, although the lines intersected near the middle of the range of measured values. The difference in these lines, although statistically significant, was small over the range where most data were observed. However, the difference may be large near the outer ranges of observed LAI values.

Our extreme observed LAI values were 2.7 and 8.2. The difference between predicted ANPPs using the global and eastern deciduous regressions at the midpoint of this LAI range was 0.13 Mt ha^{-1}yr^{-1}. The differences in predicted ANPP were 1.7 Mt ha^{-1}yr^{-1} at an LAI of 2.7, and 1.0 Mt ha^{-1}yr^{-1} at an LAI of 8.2. These differences correspond to a 27% underprediction when the global relationship was used near the lower end of observed LAIs in the eastern deciduous forest biome, and an 8% overprediction when the global relationship was used at the upper end of observed eastern deciduous forest LAI values.

We noted a significant (P < 0.05) non-zero intercept for the eastern deciduous forest ANPP-LAI model, and non-significant intercept (P < 0.05) for the global linear model. We expected a zero intercept for the ANPP-LA1 relationship in deciduous broadleaf forests. Zero leaf biomass indicates zero leaf area and zero production, and thus one might argue the model should be constrained to pass through the origin.

Taken together, the global data set provides strong evidence for a significant ANPP-LA1 relationship that passes through the origin, and no evidence that this relationship is nonlinear. However, there are slight differences between local and global models, indicating the global relationship may be different from local or regional relationships between LAI and ANPP. Differences in the relationships may be due to “sampling errors” in the literature-derived dataset, or in our eastern deciduous forest data set with few low LAI samples. Tests with an expanded dataset that includes low ANPP-LA1 values sampled in eastern North America are warranted.

Conclusions

LAI averaged 5.8 and ANPP averaged 9.2 Mg ha-' yr^{-1} in our southern Applachian forest sites, similar to values reported for other eastern deciduous forest sites. LAI decreased from cove to ridge sites. ANPP varied with LAI and both decreased with elevation. ANPP was not strongly related to precipitation differences along the elevation gradient at our study sites. While our observed productivity and LAI values were similar to those reported elsewhere for eastern deciduous forest stands, we did not observe LAI to be strongly related to previously reported local variation in soil nitrogen availability or trends in leaf nitrogen content.

ANPP-LA1 relationships were significant for the data in this study and when pooled with most other studies in eastern deciduous forests. The quantitative linear relationship between LAI and ANPP appeared the same in this study as one developed from deciduous forest stands across eastern North America. These results suggest a general quantitative relationship between LAI and ANPP across the eastern deciduous forest biome. Finally, we noted small but significant differences between the ANPP-LAI relationship observed in deciduous forests of North America and the ANPP-LA1 relationship based on a global combination of ANPP-LA1 data. We note that more ANPP-LAI measurements should be made in the eastern deciduous forest biome, particularly at sites with low LAI and ANPP, if a more exact characterization of the ANPP-LA1 relationship is to be established.

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