

Above- and Belowground Net Primary Production in a Temperate Mixed Deciduous Forest

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ABSTRACT

Our current ability to detect and predict changes in forest ecosystem productivity is constrained by several limitations. These include a poor understanding of belowground productivity, the short duration of most analyses, and a need for greater examination of species- or community-specific variability in productivity studies. We quantified aboveground net primary productivity (ANPP) over 3 years (1999–2001), and both belowground NPP (BNPP) and total NPP over 2 years (2000–2001) in both mesic and xeric site community types of the mixed mesophytic forest of southeastern Kentucky to examine landscape variability in productivity and its relation with soil resource [water and nitrogen (N)] availability. Across sites, ANPP was significantly correlated with N availability ($R^2 = 0.58$, $P = 0.028$) while BNPP was best predicted by soil moisture content ($R^2 = 0.72$, $P = 0.008$). Because of these offsetting patterns,

total NPP was unrelated to either soil resource. Interannual variability in growing season precipitation during the study resulted in a 50% decline in mesic site litter production, possibly due to a lag effect following a moderate drought year in 1999. As a result, ANPP in mesic sites declined 27% in 2000 compared to 1999, while xeric sites had no aboveground production differences related to precipitation variability. If global climate change produces more frequent occurrences of drought, then the response of mesic sites to prolonged moisture deficiency and the consequences of shifting carbon (C) allocation on C storage will become important questions.

Key words: carbon allocation; interannual variability; mesic; mixed mesophytic forest; nitrogen mineralization; *Quercus*, soil moisture; total belowground carbon allocation; xeric.

INTRODUCTION

Forest ecosystems play a principal role in the terrestrial carbon cycle, accounting for 76% of biomass C and 42% of annual net primary

productivity of terrestrial vegetation, while covering only 29% of the terrestrial surface (Schlesinger 1991). Increased effort has been placed on understanding and modeling the terrestrial carbon (C) cycle, as global climate change, elevated nitrogen (N) deposition, and land-use changes threaten to alter the patterns of C and energy flow. To detect and predict future changes in forest ecosystem function, the patterns, controls, and variability of forest productivity within and among stands must be better understood. However, our understanding of these relationships is constrained by several limitations.

A major constraint to our consideration of forest productivity patterns is that the majority of work

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to date has been restricted to measurements of aboveground net primary productivity (ANPP). Although belowground net primary productivity (BNPP) has been estimated to account for up to 70% of total NPP (Vogt and others 1996), the allocation of C belowground has received relatively minor investigation and results are often contradictory. Precipitation and temperature are generally thought to limit temperate forest production at a continental scale (Leith and Whitaker 1975), but at smaller geographic scales, climatic patterns are typically too broad to account for the observed variations in productivity. Regionally, relationships have been described between ANPP (and its components) and local resource availability, for example, soil water and N (Van Cleve and others 1983; Pastor and others 1984; Zak and others 1989; Fassnacht and Gower 1997; Reich and others 1997). Fine root responses to soil resource availability are often assumed to be similar to aboveground foliar dynamics, although few studies have addressed this prediction (for example, Hendricks and others 1993; Ostertag 2001). Fine roots may respond differently than foliage to soil resource availability, resulting in a spatially dynamic allocation of C above- and belowground based on relative soil resource availability. This concurs with our current understanding of allocation priorities, wherein C is allocated to tissues where resources are most limiting (Chapin and others 1990). These responses can also be related to the particular soil resource that is most limiting (Ostertag 2001). Therefore, if soil resource availability is positively related to patterns of ANPP and negatively related to patterns of BNPP, soil resources can potentially have a smaller influence on total NPP at regional and local scales than has been previously observed in studies of ANPP. This would suggest that total NPP is largely controlled by climate. To understand the controls on forest total NPP, we must examine how these relationships, developed for ANPP, relate to BNPP and, consequently, to total NPP.

A second limitation to our knowledge of forest productivity patterns is that relatively few studies are longer than a single year. If climate and precipitation exert strong control on forest total NPP and C allocation patterns, then variation in annual and seasonal precipitation potentially drives inter-annual variability in NPP and C allocation. The long-term implications for this variability relate to the ability of forest stands to respond to changing resource conditions and the turnover time of C allocated to different tissues. An understanding of

the natural variability of NPP in forest stands will be crucial in detecting directional changes associated with subtle disturbances such as global climate change.

A further complication to our understanding of NPP in forest stands is that different species assemblages function differently (Pastor and others 1984) such that the response to resource limitations may be different among community types. This may be particularly pronounced in adaptations to soil water availability through leaf morphology and physiology, where species growing on xeric sites have higher guard-cell length, leaf mass per area, and leaf thickness compared to those on mesic sites (Abrams and others 1994). These morphological properties have direct implications for photosynthetic capacity and stand productivity as well as tolerance of drought conditions.

The northern Cumberland Plateau region in southeastern Kentucky, USA (Keys and others 1995) supports a significant gradient of microclimates due to the dissected landscape and is the geographic center of the mixed mesophytic hardwood forest (Braun 1950). The distribution of community types is correlated with variables associated with topographic aspect and hillslope position (for example, soil moisture and nutrients; Muller 1982). This region is opportune for examining forest productivity patterns and the effects of interannual variability in precipitation on productivity in contrasting community types due to their close proximity to one another. Precipitation during the growing season (April–November) in this area was highly variable during this study (1999–2001), ranging from –32 to +34% of the 30-year mean (M. Hamilton, unpublished data).

We quantified ANPP, BNPP, and total NPP on mesic and xeric forest stands within the Cumberland Plateau. We hypothesized that mesic sites would have greater ANPP and total NPP than xeric sites due to greater soil water and N availability, while xeric sites would have greater proportional allocation belowground in response to lower resource availability. We were able to follow shifts in ANPP across widely variable precipitation years.

METHODS

Site Description

The University of Kentucky's Robinson Forest is located in southeastern Kentucky, on the Cumberland Plateau and within the Mixed Mesophytic Forest Region described by Braun (1950) (Figure 1). The 90-year-old second growth forest

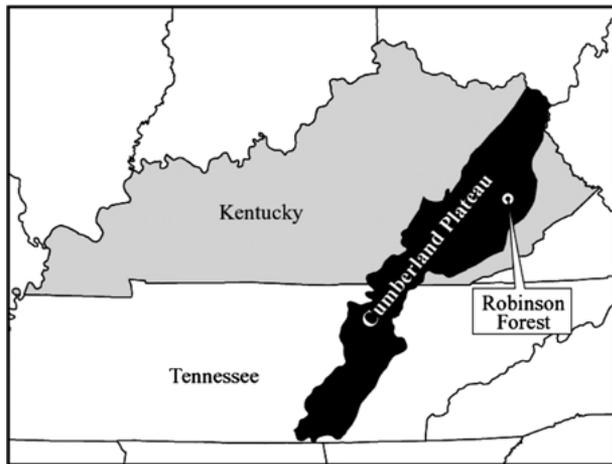


Figure 1. Location of the northern Cumberland plateau and the study site, University of Kentucky's Robinson Experimental Forest.

regenerated following clear-cut through vigorous stump sprouting, largely retaining the original forest composition (Arthur and others 1997). The mean annual precipitation is 963 mm, with approximately 70% falling during the 7-month growing season (M. Hamilton, unpublished data). Soils formed in residuum and colluvium from horizontally interbedded sandstone, siltstone, and shale are well-drained, stony silt loams (McDowell and others 1981) and are classified as mesic Typic Hapludults. Soils are acidic (pH 4.4–6.0), have low total C and N (0.9–5.1% and 0.1–0.4%, respectively), and low soil nutrient levels (G. Newman, unpublished data).

The mixed mesophytic forest on the Cumberland Plateau is noted for its high overstory species diversity (high α diversity: Muller 1982). The dissected landscape of this region creates a range of topographical microenvironments that support very different overstory and understory plant communities. Species composition across this topographic gradient is associated with strong gradients of surface soil moisture and soil fertility (Muller 1982) with upper slope topographic positions exhibiting relatively xeric temperature and moisture regimes and lower slope positions exhibiting more mesic microclimates. There has been a long history of microclimatic analysis from this region and the effects of slope aspect on soil moisture, temperature, and, consequently, species composition are well known (Wolfe 1951; Hutchins and others 1976; Stephenson 1982). Four ridges were selected for this study, with four 0.05 ha plots established on the upper slopes of opposing NE (mesic) and SW (xeric) aspects (a total of eight

plots; Figure 2) to represent contrasting forest communities and soil water availability regimes, while occurring on the same soil substrate and at the same elevation.

Soil Nitrogen Availability and Gravimetric Water Content

Net N mineralization was measured during 28-day incubations in August 2000 and April 2001 using an in situ closed core method (Adams and Attiwill 1986). Two paired 1.5 inch diameter PVC cores per plot were inserted to a depth of 10 cm within 15 cm of each other in ten locations per plot selected at random. One core was immediately removed for time zero extractions of NH_4^+ and NO_3^- while the other core was left in situ, loosely capped to prevent leaching by rain for the duration of the incubation. Initial and incubated cores were sieved to pass a 2 mm screen within 24 h of collection, extracted with 1 M KCl (Maynard and Kalva 1993), and analyzed for nitrate and ammonium on a Bran+Luebbe Auto Analyzer III (Hamburg, Germany). All samples were subsampled and analyzed for gravimetric water content during these incubations as well as in June 2000. The three measures of soil water content were averaged and used as an index of soil water availability.

To determine forest floor masses, the organic horizon down to mineral soil was removed from within six 729 cm² frames per plot, dried to constant mass at 50°C, and weighed. Forest floor C and N values were determined on each sample on a LECO CN 2000 (LECO Corp., St. Joseph, Minnesota, USA).

Net Primary Productivity

Aboveground NPP was determined for each of the 3 years from 1999–2001. All trees greater than 10 cm DBH were identified to species. For each tree, DBH was measured and one increment core was taken at breast height (1.37 m) parallel to the slope using an increment borer in November 2001. Mean tree height was determined on five co-dominant canopy trees per plot using a Vertex III hypsometer (Haglof, Inc., Madison, Mississippi, USA). Cores were mounted, sanded, and incremental growth was measured for each of the previous 10 years. Species-specific allometric equations from southeastern West Virginia (Brenemann and others 1978) were applied to changes in individual tree diameters to calculate annual aboveground woody growth per plot. Litter fall was collected every 2 weeks during September–November and once in

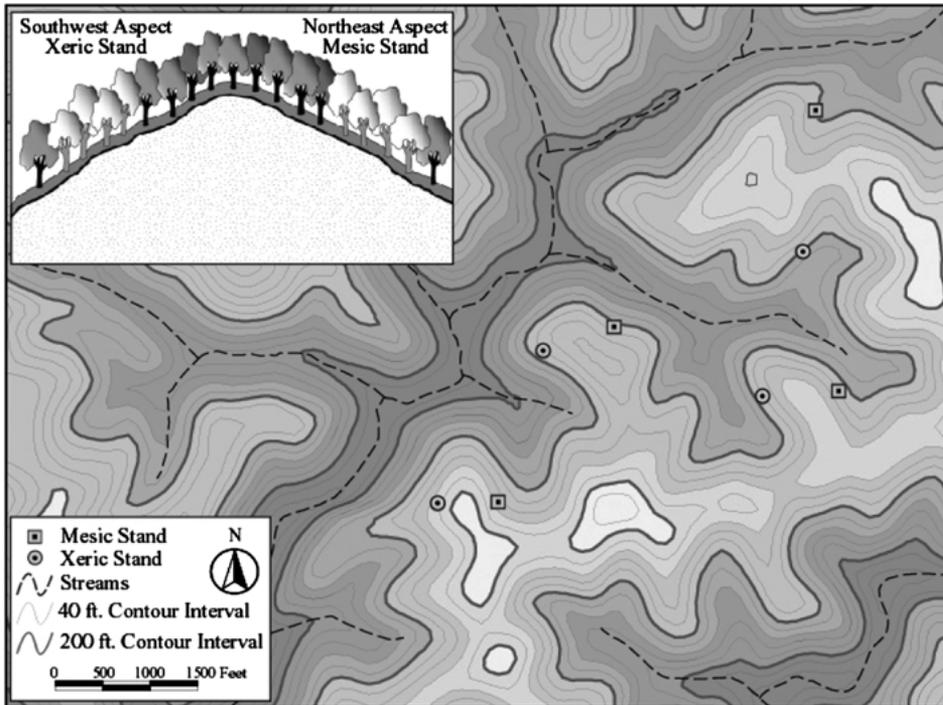


Figure 2. Topographic map section of University of Kentucky's Robinson Forest with the location of four permanent mesic and xeric sites. The *inset* is a graphic depiction of the opposing slope aspects of mesic and xeric stands.

late winter from 1999–2001 within six randomly located 0.22 m² traps per plot. Litter was sorted by species, dried to constant mass at 50°C, and weighed. Litter samples for C and N content were collected on mesh tarps placed adjacent to each plot and retrieved during peak leaf fall. Tarps were cleared following precipitation events to prevent collection of leaves exposed to leaching by rain. Litter samples were ground in a Wiley mill to pass a size 20 screen and total C and N was analyzed on a LECO CN 2000 (LECO Corp., St. Joseph, Minnesota, USA). ANPP was calculated as the sum of incremental woody growth and litter mass. Leaf area index (LAI) was determined using annual plot litter mass values (kg) multiplied by weighted-average specific leaf area (SLA, m² kg⁻¹) measurements. SLA measurements were made during July 1999 and 2000 by removing 10 mid-canopy leaves from two to three dominant trees of representative species using a 12-gauge shotgun and determining individual leaf area on an area meter (LI-3100, Li-Cor, Inc., Lincoln, Nebraska, USA) and then individual dried leaf masses.

Soil respiration measurements were conducted on eight 10 cm diameter permanent PVC collars per plot during 2000 and 2001 with a Li-Cor 6400 portable photosynthesis system attached to a Li-Cor 6400-09 soil CO₂ flux chamber (Li-Cor, Inc., Lincoln, Nebraska, USA). Measurements were conducted during mid-day at monthly intervals

during the growing seasons and every 2 months during the dormant season from December to March. During one day in April 2000 and again in July 2000, four measurements from 5 a.m. to 8 p.m. were taken on all collars in four of the plots which showed no statistically significant diurnal fluxes at this site (G. Newman, unpublished data). Therefore, the mid-day measurements were scaled to a 24-h period. To calculate annual CO₂ flux, daily fluxes from each measurement date were used for the periods during which measurements were not made.

Using a C budgeting approach, total below-ground C allocation (TBCA) was estimated as the difference between annual soil CO₂ efflux and average annual litter C (Raich and Nadelhoffer 1989). Coarse woody root production was estimated as 20% of annual aboveground woody growth (Giardina and Ryan 2002; Jackson and Chittenden 1981; Misra and others 1998). Davidson and others (2002) addressed the limitations and constraints of the TBCA method and concluded that estimates of TBCA may be most appropriate when interannual variability is averaged over several years and where steady-state assumptions are least problematic. Because the interannual variability of the largest components of the TBCA calculation (litterfall C and soil C efflux) may not operate at the same temporal scale, 2 year mean values for litterfall C and soil C efflux were

used to compute a single mean value for TBCA rather than interannual values similar to ANPP estimates. We assumed no change in soil organic C during this period (Giardina and Ryan 2002) and other deviations from steady-state C pool sizes would not be expected to cause detectable differences in the TBCA calculations at this site.

TBCA numbers were converted to production estimates (BNPP) by assuming that 50% of the C efflux was root and mycorrhizal respiration (the other 50% incorporated in new tissue) and that roots and mycorrhizae are 50% C (after Ryan 1991; Vogt 1991). The assumption that tissues are 50% C to convert TBCA to BNPP is robust (Vogt 1991). The assumption of 50% production efficiency (50% tissue incorporation and 50% respiration of TBCA) contains uncertainties, although small manipulations of these values did not significantly alter the results. These estimates of TBCA serve to constrain estimates of belowground production and allow limited interpretation of total NPP values in this region. Total NPP was estimated as the sum of ANPP and BNPP.

Interannual Variability in Precipitation

Precipitation at this site was measured using a tipping bucket rain collector within a permanent weather station operated by the Robinson Experimental Forest staff (M. Hamilton, unpublished data). The steep slopes, well-drained soils, and absence of winter snowpack at these sites make growing season (April–November) precipitation a more significant index of interannual variation in water availability than annual precipitation. The first year of study (1999) was characterized by 32% lower than average (growing season) precipitation following a high precipitation year (+34%) in 1998 (Figure 3A). Precipitation in 2000 (–1%) and 2001 (–17%) was average and moderately below average, respectively. Although precipitation patterns do not necessarily translate into soil water availability, the regional Palmer Drought Severity Index (PDSI) can be used to indicate periods of prolonged and abnormal moisture deficiency or excess (University of Kentucky, Agricultural Weather Center 2002). The regional PDSI for the period of this study exhibited a similar trend to growing season precipitation, with 1998 being an unusually high moisture year, 1999 a moderate drought year, and 2000 and 2001 increasing to positive levels during the growing season (Figure 3B). Therefore, the growing season precipitation recorded at Robinson Forest can be regarded as a reasonably accurate representation of water stress at these sites.

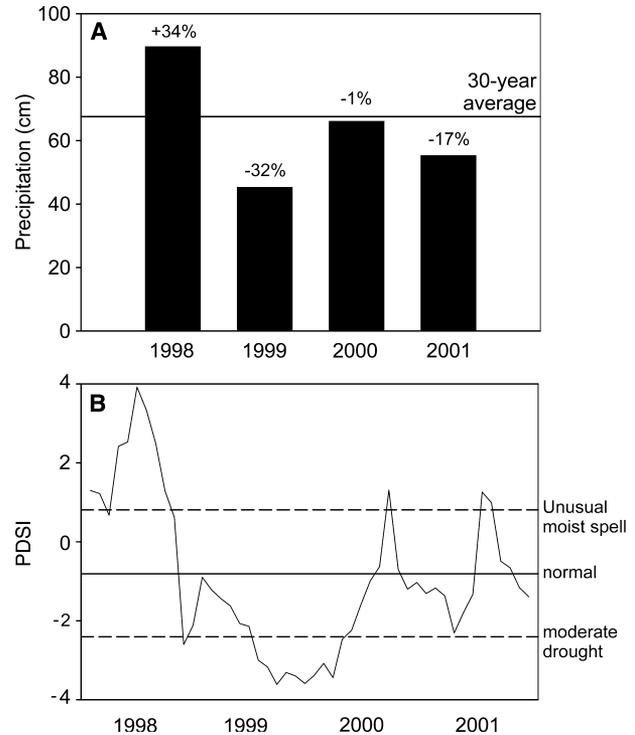


Figure 3. **A** Interannual variability in growing season precipitation from 1998–2001 and the 30-year mean precipitation record at Robinson Forest. **B** Palmer Drought Severity Index for eastern Kentucky during the growing season 1998–2001. The PDSI is a regional index of moisture excess or drought compiled by the Agricultural Weather Center, University of Kentucky, Lexington, Kentucky.

Statistical Analyses

There were four plots representing experimental units per aspect and all sampling within an experimental unit was averaged to provide a mean value per unit. Two-sample *t*-tests were used to compare variables between mesic and xeric sites. Variable means were considered significant at $\alpha = 0.05$. Linear regressions were developed to analyze productivity relationships and two-way ANOVAs were used to analyze interannual aboveground productivity while paired *t*-tests were used to analyze interannual relationships for only mesic sites (since only mesic sites showed significant interannual variability) using JMP 4.0 (SAS Institute, Inc., Cary, NC).

RESULTS

Species composition of sites on mesic aspects is characteristic of cove hardwoods (Muller 1982) whereas xeric aspects support predominantly

Table 1. Relative Basal Area (≥ 2.5 cm DBH) of Tree Species on Mesic (NE) and Xeric (SW) Upper Slope Aspects in Southeastern Kentucky

Mesic		Xeric	
<i>Magnolia acuminata</i>	23.9%	<i>Quercus prinus</i>	26.3%
<i>Liriodendron tulipifera</i>	11.8%	<i>Quercus coccinea</i>	25.3%
<i>Acer saccharum</i>	10.5%	<i>Quercus velutina</i>	16.7%
<i>Tilia americana</i>	8.5%	<i>Acer rubrum</i>	12.0%
<i>Quercus rubra</i>	8.1%	<i>Quercus rubra</i>	5.4%
<i>Acer rubrum</i>	7.3%	<i>Quercus alba</i>	3.9%
<i>Fraxinus americana</i>	6.0%	Other ²	10.4%
<i>Juglans nigra</i>	5.2%		
Other ¹	18.7%		

¹Other mesic species: *Fagus grandifolia*, *Carya ovata*, *Nyssa sylvatica*, *Ulmus rubra*, *Asimina triloba*, *Cornus florida*, *Cercis canadensis*, and *Vitis* spp.

²Other xeric species: *Amelanchier arborea*, *Liriodendron tulipifera*, *Oxydendrum arboreum*, *Carya glabra*, *Fraxinus americana*, *Carya ovata*, *Nyssa sylvatica*, *Carya tomentosa*, *Cornus florida*, *Acer saccharum*, *Carpinus caroliniana*, *Fagus grandifolia*, *Magnolia acuminata*, *Tsuga canadensis*, *Betula lenta*, and *Pyrolaria pubera*.

Quercus spp. (Table 1). Mesic and xeric stands had generally similar structure (Table 2), although mean annual aboveground litter production and LAI were 48% and 126% greater, respectively, on mesic sites. In spite of this difference in litter production, forest floor masses were similar, possibly due to greater decomposition rates resulting from higher litter quality (that is, lower C:N) and higher soil moisture content on mesic aspects (Table 2).

Net Primary Productivity

We measured a range of NPP across the sites and related NPP to resource availability, regardless of site type (mesic or xeric). Mean annual ANPP (513–1,156 g m⁻² y⁻¹) during three years of measurement, and BNPP (741–1,382 g m⁻² y⁻¹) and total NPP (1485–2153 g m⁻² y⁻¹) during 2 years of measurement, showed wide ranges across the eight sites. The range in ANPP was similar to that of BNPP and on average, 54% of total NPP was allocated belowground. The components of ANPP, annual litter production (211–553 g m⁻² y⁻¹) and aboveground woody production (265–945 g m⁻² y⁻¹), also showed wide ranges across the sites.

Aboveground net primary productivity was significantly correlated with net N mineralization, an index of soil N availability (Figure 4A), but was not significantly correlated with soil moisture (Figure 4B). Gravimetric soil moisture measurements were used as an index of soil water availability among sites. However, when ANPP was broken into its two components, mean annual litter production was positively correlated with soil moisture ($R^2 = 0.54$; $P = 0.038$), suggesting that soil

moisture constrains stand canopy size. In contrast, aboveground wood production was correlated with net N mineralization ($R^2 = 0.60$; $P = 0.025$).

Unlike ANPP, BNPP was unrelated to net N mineralization (Figure 4C). Rather, a significant negative relationship was observed between BNPP and soil moisture content (Figure 4D), although the simple approach used here may have introduced biases or missed temporal variations. BNPP also showed a moderately significant negative relationship with litter production ($R^2 = 0.38$; $P = 0.102$). This suggests a possible spatial trade-off in C allocation between above- and belowground resource acquisition sinks in response to soil moisture availability, although our calculations of BNPP are not independent of litterfall measurements which are a component of the TBCA equation. When wood production, a structural C sink, was included, there was no relationship between BNPP and ANPP ($R^2 = 0.01$, $P = 0.785$). Total NPP (ANPP+BNPP) was not correlated with either net N mineralization or soil water content (Figure 4E, F).

Interannual Variability in Aboveground Productivity

Interannual precipitation patterns can impose strong variability in annual soil moisture availability in this region (Figure 3). ANPP was affected more strongly by interannual variation in precipitation in mesic than in xeric sites (Figure 5A). Annual litter production showed the greatest response (Figure 5B) and there was a significant aspect by year interaction ($P < 0.001$). Mesic site litter production was substantially greater than litter production in xeric sites in 1999, a moderate drought year. Production levels then declined on mesic sites by 50% in 2000, a year of average precipitation. This was most likely a lag effect from drought conditions the prior year as mesic site litter production was statistically similar in 1999 and 2001. Conversely, litter production on xeric sites showed no significant variability during this 3-year period.

Although litter production varied considerably among years, wood production was not statistically different across years or aspects (Figure 5C). In a separate analysis, we determined that there was no correlation at these sites between growing season precipitation and the mean annual tree ring increment during the past 10 years for all stems larger than 10 cm (G. Newman, unpublished data). Although not significant, xeric sites consistently had greater wood production compared to mesic sites, which partially compensated for their lower

Table 2. Stand Characteristics and Soil Resource Availability on Mesic and Xeric Deciduous Forest Stands in Southeastern Kentucky

	Mesic	Xeric	<i>P</i>
Basal area (m ² ha ⁻¹)	27.4 (5.9)	30.4 (3.2)	0.665
Density (stems >10 cm dbh ha ⁻¹)	950 (230)	1,565 (332)	0.189
Aboveground woody biomass (Mg ha ⁻¹)	108.3 (21.4)	111.0 (19.4)	0.949
Canopy height (m) (<i>n</i> = 5)	31.9 (1.6)	26.6 (2.4)	0.127
Litter production (g m ⁻² y ⁻¹)	419 (13)	283 (27)	0.011
Leaf Area Index (m ² m ⁻²)	7.9 (0.4)	3.5 (0.3)	<0.001
Litter C:N	55.6 (5.6)	78.9 (5.6)	0.026
Forest floor mass (g m ⁻²)	130.8 (16.6)	135.2 (22.7)	0.884
Forest floor C:N	27.5 (0.4)	39.0 (3.8)	0.058
Gravimetric soil moisture content (%)	35.2 (2.0)	24.8 (1.9)	0.010
Net N mineralization (mg N kg ⁻¹ d ⁻¹)	0.43 (0.08)	0.50 (0.14)	0.690

Values are the means of four plots per aspect. Gravimetric water content was measured on three dates and net N mineralization during two 28-day incubations. Values are means (1 SE).

litter mass and made ANPP statistically similar between aspects for all three years (Figure 5A).

We were not able to assess interannual variability in BNPP or total NPP and therefore calculated 2-year mean values. Unlike ANPP, there was no statistical difference in these production values between mesic and xeric sites (Figure 6). Similarly, the 2-year mean C allocation values between mesic and xeric sites showed only significant differences in litter allocation (Figure 7).

DISCUSSION

Net Primary Productivity and C Allocation

Rates of ANPP at this site were within the ranges previously reported for eastern deciduous forests (Liu and Muller 1993; Reich and others 1997; Bolstad and others 2001; Curtis and others 2002). Mesic sites had litter production and LAI values roughly twice as high as xeric sites and at the upper range of previously reported values for this region (Jose and Gillespie 1996; Bolstad and others 2001). Our study corroborates previous reports of strong correlations between ANPP and net N mineralization (see Reich and others 1997).

Our range of belowground productivity estimates is consistent with previously reported values (see Nadelhoffer and Raich 1992) and similar to values from other eastern deciduous forests (Curtis and others 2002; Davidson and others 2002) using similar techniques. Our estimates of BNPP using the C budget approach are potentially higher than

direct estimates (for example, sequential coring, minirhizotrons), which tend to underestimate root and belowground productivity (Publicover and Vogt 1993). Soil respiration and annual litter production estimates measured in this study are similar to estimates used in a global review of the TBCA method by Davidson and others (2002) and are most closely related to other eastern temperate forest values.

We observed a strong negative correlation of BNPP with soil water content. It is not apparent whether this is a direct effect of soil moisture availability or a species effect within this study design, because xeric sites tended to have higher belowground production than mesic sites. This is consistent with the work of Dress and Boerner (2001), who found greater root productivity in xeric sites in southern Ohio than in mesic sites despite similar standing biomass. In a throughfall manipulation experiment in southeastern Tennessee, net root production was significantly greater in deciduous forest stands subjected to several years of lower soil precipitation input while fine root mortality was not different between treatments (Joslin and Wolfe 1998). Although BNPP was not statistically different between mesic and xeric sites in this study, regression analysis suggested that elevated root production in this region may be required in sites with lower soil moisture availability.

Based on a tight correlation between soil moisture content and litter production, we speculate that soil water availability constrained canopy size and annual leaf production in these forest stands. The negative relationship between BNPP and leaf

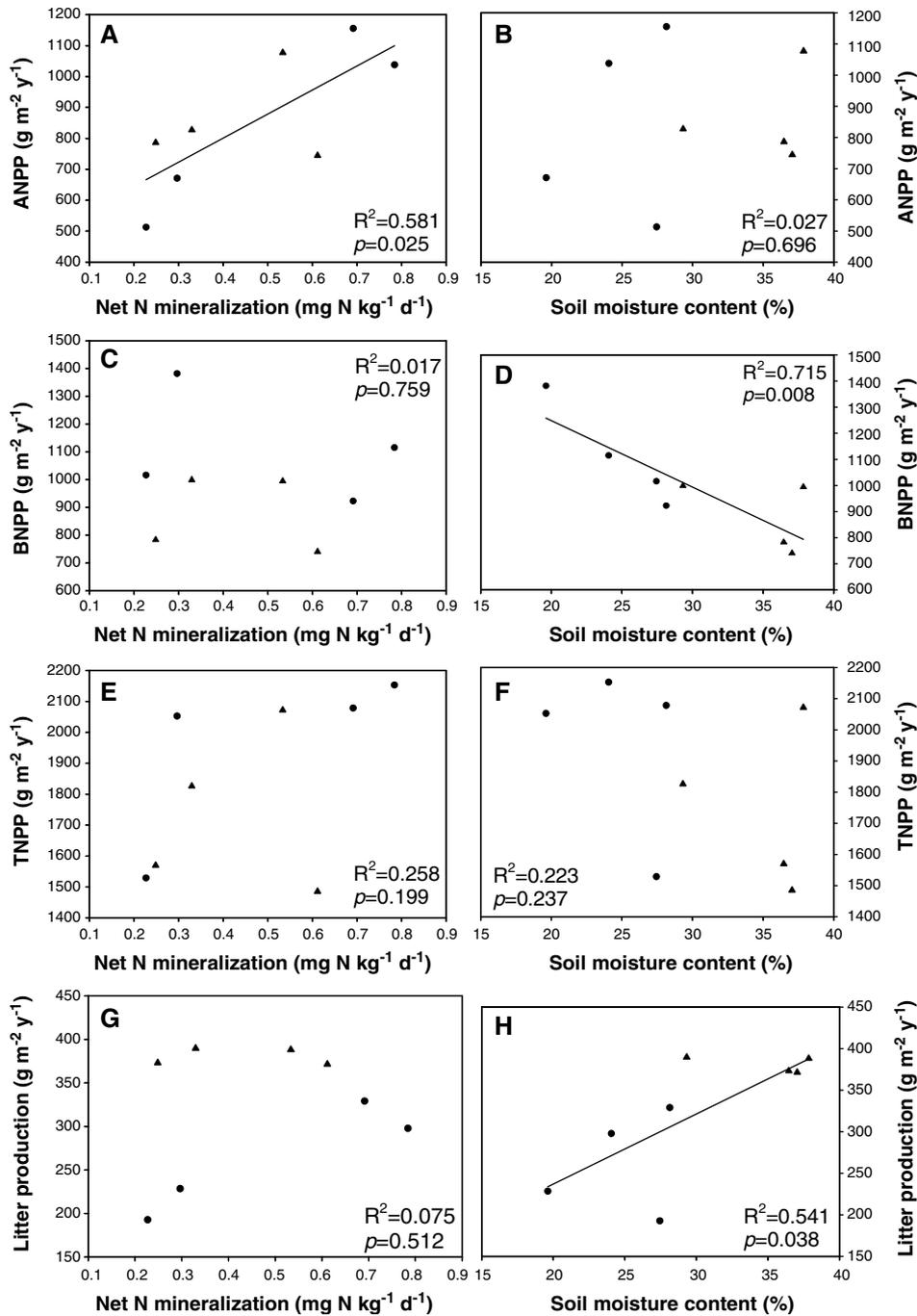


Figure 4. Productivity relationships with indices of soil resource availability for mesic and xeric sites in southeastern Kentucky. Productivity values are two-year means of annual measurements on $n = 8$ plots. Net N mineralization is the mean of 28-day in situ incubations in August 2000 and April 2001. Gravimetric soil moisture content is used as an index of soil moisture availability and is the mean of measurements in June 2000, August 2000, and April 2001. Mesic sites are represented by triangles and xeric sites are represented by circles.

production likely is a reflection of spatial shifts in C allocation as a result of soil water availability, where sites with greater soil water content can support higher foliage production and allocate less C belowground. General ecological theory would predict that belowground C allocation would increase with decreasing soil resource availability (Santantonio and Hermann 1985; Gower and others 1992; Haynes and Gower 1995) as greater C is

allocated to structural tissues where resources are most limiting (Chapin and others 1990). Although ANPP at our sites was positively correlated with net N mineralization and BNPP was negatively correlated with soil water content, neither soil resource predicted total NPP. The offsetting responses of ANPP and BNPP to spatial patterns of soil N and water availability seem to have negated any influence of either soil resource on total NPP. This may

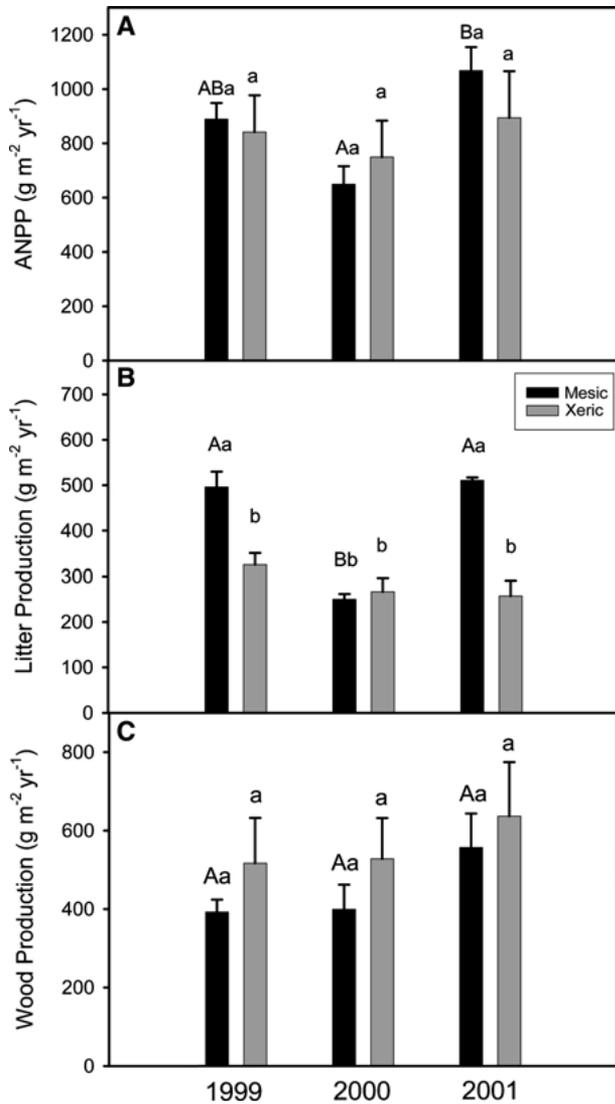


Figure 5. Interannual variability in **A** ANPP **B** litter mass, and **C** wood production, on mesic and xeric deciduous forest sites in southeastern Kentucky. Values are means ($n = 4$) and 1 SE. Different letters refer to significantly different values ($\alpha = 0.05$); lower case letters correspond to all sites while capital letters correspond to paired t test analyses of mesic sites only.

be particularly true for soil water, which was positively correlated with litter production and negatively correlated with BNPP. Therefore, our data do not support the generally accepted paradigm that temperate forests are N-limited (Vitousek and Howarth 1991), only that ANPP is N-limited. It would seem that N availability at these sites controls rates of ANPP whereas water availability constrains C allocation between above- and belowground resource acquiring tissues. Understanding interannual variation in productivity and

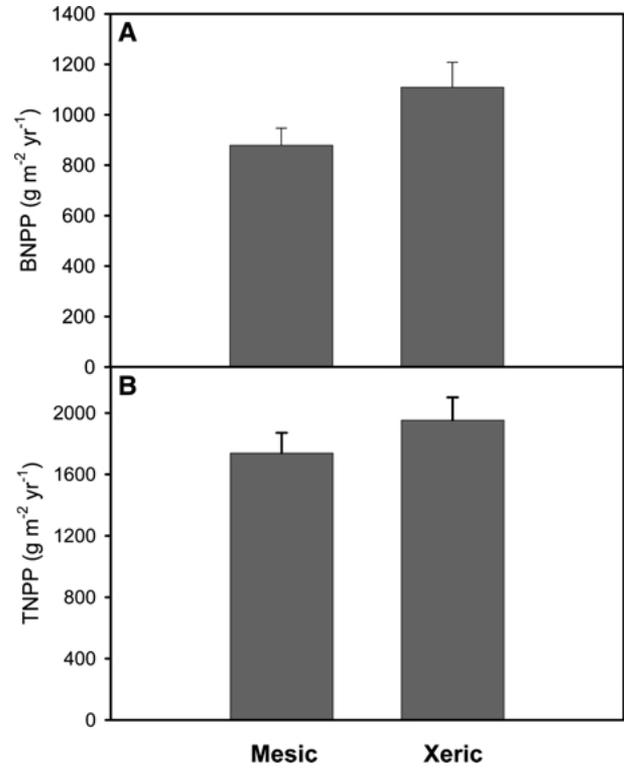


Figure 6. Mean 2-year values for **A** BNPP and **B** total NPP on mesic and xeric deciduous forest sites in southeastern Kentucky. Values are means ($n = 4$) and 1 SE. Values were not significantly different ($\alpha = 0.05$) between mesic and xeric sites.

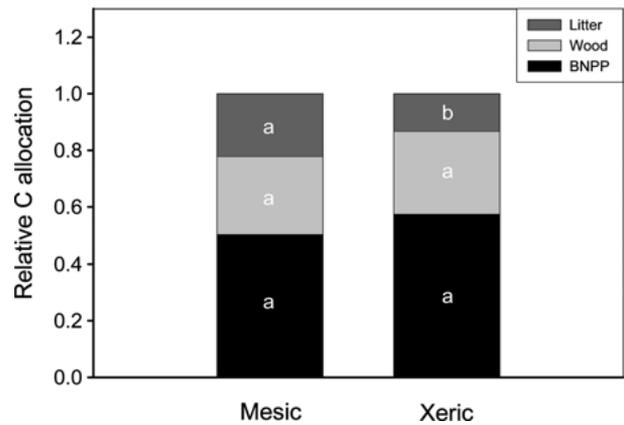


Figure 7. Two-year mean allocation of total NPP to litter, aboveground wood, and belowground tissue production on mesic and xeric deciduous forest sites in southeastern Kentucky. Different letters refer to values that are significantly different ($\alpha = 0.05$) within each component of NPP.

C allocation will require more detailed analysis of the influences of soil resources on the components of NPP.

Interannual Variation in Aboveground Productivity

On mesic sites, interannual variation in productivity and C allocation was related to annual growing season precipitation; however, this effect was delayed until the following growing season. Notably, a significant decline in leaf production was observed in 2000 following a moderate drought in 1999. Annual litter production represents the largest aboveground input of C into the soil and is a principal means of nutrient flux within forest ecosystems (Attiwill and Adams 1993). The 50% decline in mesic litter production in 2000 is substantial and resulted in a 27% decline in ANPP. Differences in interannual litter production were not attributable to variable leaf morphology because there were no statistical differences in mesic species leaf size or leaf mass per area (g m^{-2}) between 2000 and 2001 (G. Newman, unpublished data). Annual variability in litter production of this magnitude has not previously been documented for temperate deciduous forests.

Our C flux estimates of BNPP did not allow examination of interannual variability in belowground production, but annual and multiple-year variation in precipitation and soil water availability may lead to variability in belowground production and possibly C allocation between above- and belowground sinks, particularly on more mesic sites which were more susceptible to annual precipitation than xeric sites. More direct estimates of BNPP will be required to address this subject.

LAI and litter production are strongly influenced by site water balance (Gholz 1982; Burton and others 1991; Jose and Gillespie 1997) and originate from the number of leaf initials that are produced during the previous year (Kozlowski and Pallardy 1997). Drought acts to reduce the assimilation of CO_2 through stomatal closure and the subsequent storage of C reserves for bud initiation at the end of the drought year and lamina expansion the following year. This can result in the observed 'lag effect' of drought on the following year's litter mass. Previous studies have related variations in litter mass and LAI with AET (Berg and Meentemeyer 2001), temperature (Kouki and Hokkanen 1992), and water stress (Le Dantec and others 2000). Le Dantec and others (2000) also documented a 'lag effect' of lower LAI following years of water stress, but only in high ($> 5.5 \text{ m}^2 \text{ m}^{-2}$) LAI stands. This is in accord with the dramatic mesic ANPP responses to annual precipitation variability and no statistical production response in xeric sites within this study.

Although average ANPP is positively correlated with precipitation at a continental scale, Knapp and Smith (2001) found maximum interannual variability in aboveground production occurred in biomes with the highest potential growth rates (that is, grasslands and herbaceous ecosystems) and was not related to the magnitude of precipitation variability. Because of small coefficients of variation in northeastern mixed deciduous and Alaskan balsam poplar forests, they concluded that productivity of forests was distinctly less variable than other biomes. However, these forest soils probably do not experience soil drought events to the same extent as in other forest regions (for example, southeastern forests) due to lower potential evapotranspiration. Also, potentially slower decomposition rates leading to greater forest floor mass and soil organic matter may act to buffer variation in precipitation by retaining soil water. The deciduous mesic forests in the southeastern USA are likely more susceptible to drought and will potentially show larger variation in leaf production and ANPP in response to changes in precipitation patterns than previously reported for temperate forests.

The only precipitation manipulation experiment to date in southeastern deciduous forests, summarized by Hanson and others (2003), found minor or inconsistent interannual variability in forest productivity. Their study was conducted on a southeast facing slope with similar species composition as our xeric sites, which also showed no production response to changes in precipitation. Hanson and others (2003) also concluded that stand composition in these forests could be maintained due to reduced growth of certain seedlings and saplings due to lower soil water availability. For example, *Liriodendron tulipifera* is a mesic canopy species (Table 1) that often occurs in the understory of xeric sites in Kentucky but rarely reaches the canopy. Interannual variability of precipitation in this region may exert a strong positive feedback on microsite species composition via interspecific competition for soil water that results in the observed composition across microclimatic gradients associated with slope position and aspect (Muller 1982).

The stronger response of mesic canopies to water stress compared to xeric canopies can be supported by differences in leaf morphology and physiology. Xeric sites in our study are dominated by *Quercus* spp. and have consistently higher leaf mass per area (LMA) than mesic species (G. Newman and others, unpublished manuscript). In a study of leaf physiology during wet and dry years, Abrams and others (1994) found increasing guard cell length, LMA,

and leaf thickness with increasing site dryness in central Pennsylvania. During the wet year, xeric (including *Quercus velutina*) and mesic (including *Fraxinus americana* and *Juglans nigra*) species had more similar net leaf photosynthesis (A) and leaf conductance (g_{wv}) than wet-mesic species (including *Acer saccharum*, *Carya cordiformis*, *Prunus serotina*, and *Tilia americana*). However, during the dry year, A and g_{wv} decreased in mesic and wet-mesic species but not xeric species. Kubiske and Abrams (1994) also found greater drought effects on predawn leaf water potential (ψ), g_{wv} , and A in mesic species of central Pennsylvania compared to xeric species. It seems that xeric species are physiologically more adapted to periodic water stress and are able to buffer drought effects on physiological performance. These leaf-level physiological measurements corroborate our ecosystem-level patterns of ANPP and litter production, where mesic and xeric sites had similar ANPP during the 1999 drought year, but physiological limitations of mesic foliage resulted in a lower leaf production and ANPP the following year.

Stem production should be a lower C allocation priority than resource acquiring tissues (Waring and Schlesinger 1985). C allocation was fairly evenly distributed between foliage, stem production and roots, with the exception of lower foliar allocation in xeric sites (Figure 7). By this reasoning, mesic sites might be expected to show declines in wood production similar to leaf production during or following drought. However, we did not find any statistical difference in annual woody increment across years or aspect. Jenkins and Pallardy (1995) found a significant correlation between annual basal area increment and measures of drought severity for *Quercus coccinea* and *Quercus velutina* in the Missouri Ozarks. These Ozark sites receive considerably less precipitation than southeastern Kentucky and may develop stronger soil water deficits. Further, our study may not have been large enough in spatial or temporal scope to detect changes in incremental woody growth associated with precipitation variation. Nonetheless, the dramatic canopy reduction on mesic sites deserves consideration as a mechanism of drought attenuation in these forests via reduced transpiration losses.

Although only interannual variability in ANPP was measured in this study, the interannual response of BNPP and above- and belowground C allocation to climate variability are potentially important and may have strong genetic controls between forests of different species composition. The inclusion of belowground production is there-

fore an integral, albeit difficult to measure, component of forest NPP and must be incorporated into analyses of the patterns and controls on forest productivity. Further, if global climate change produces more frequent occurrences of drought, then the response of mesic sites to prolonged moisture deficiency and the potential consequences of shifting C allocation on C storage will become important questions.

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