Pines

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Stand-level allometry in *Pinus taeda* as affected by irrigation and fertilization

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Summary Changing environmental conditions have the potential to alter allometric relationships between plant parts, possibly leading to ecosystem-level feedbacks. We quantified allometric shifts in field-grown loblolly pine (*Pinus taeda* L.) in response to altered resource availability based on data from multiple harvests to correct for size-related changes in biomass partitioning. A replicated factorial arrangement of irrigation and fertilization treatments was applied for 4 years to an g-year-old loblolly pine plantation on a well-drained, low fertility site in North Carolina. Destructive and nondestructive growth measurements were used to develop treatment-specific regressions to estimate stand-level biomass for ephemeral and perennial plant parts, both above- and belowground. Stand-level allometric analysis indicated that irrigation increased biomass partitioning to fine roots and decreased partitioning to foliage, relative to other plant parts. Fertilization increased partitioning to perennial tissues (coarse roots, taproots, and branches) and decreased partitioning to ephemeral tissues (foliage and fine roots). Changes in allometry were small (< 6 %) but statistically significant, indicating that biomass partitioning in loblolly pine changes with altered resource availability, but is probably under strong ontogenetic control.

foliage, loblolly pine, ontogenetic control, perennial tissues, resource availability.

Introduction

The response of terrestrial ecosystems to changing environmental conditions may provide a major feedback to global change (Mooney et al. 1991*a*, Woodward et al. 1991, Strain and Cure 1994, Melillo et al. 1996), reducing the extent to which the global cycles of carbon, water and nutrients are altered. Two aspects of global change critical to plant growth and function are increasing nitrogen deposition (Galloway et al. 1995, Vitousek et al. 1997) and the predicted increase in soil water (Houghton et al. 1996). These factors are likely to alter biomass partitioning within plants, affecting ecosystem-level processes such as decomposition and nutrient cycling. Belowground shifts in biomass partitioning are especially important. Increased partitioning to roots could increase carbon storage in soil, providing a negative feedback to further accumulation of CO_2 in the atmosphere (van Veen et al. 1991, Wisniewski and Lugo 1992, van de Geijn and van Veen 1993, Curtis et al. 1994).

Biomass partitioning between roots and shoots is generally considered as a functional balance between the acquisition of carbon and the acquisition of soil resources, as conceptualized by Brouwer (1962) and Davidson (1969), and modeled by Thomley (1972). In theory, when the uptake of a resource is limiting, biomass is preferentially allocated to the organ responsible for uptake of the limiting resource until all resources are equally limiting. For example, if growth is limited by nitrogen, more biomass is partitioned to roots relative to shoots to restore the balance of carbon to nitrogen. Although the functional balance theory does not consider simultaneous limitations by multiple resources (Mooney et al. 1991*b*), a large body of empirical evidence appears to support it (Robinson 1986, Wilson 1988, Ingestad and Agren 1991, Conroy 1992, Cannel1 and Dewar 1994, Proe and Millard 1994, Marschner et al. 1996). Furthermore, several studies with loblolly pine (*Pinus taeda* L.) seedlings also support the theory (Li et al. 1991, Green et al. 1994, Griffin et al. 1995, Gebauer et al. 1996). However, to test the generality of this theory for forests, it is necessary to determine if the results of seedling studies scale to the level of the stand for field-grown trees.

As plants increase in size, the relative partitioning of biomass between organs changes. A good example is provided by Ovington (1957). who obtained chronosequence data from plantations of *Pinus sylvestris* L. showing that root:shoot ratios reached a maximum of 0.82 at age seven and then declined to 0.29 by age 55. In addition. experimental treatments that accelerate growth, such as fertilization, may alter allometry simply because they increase plant size during the experimental period. Therefore, when examining shifts in biomass partitioning in response to experimental treatments, it is necessary to use statistical methods that allow the separation of direct treatment effects from ontogenetic effects. A convenient tool for this purpose is allometric analysis, a procedure that is widely used to evaluate how changing resource availability can alter biomass partitioning among plant parts (Pearsall 1927, Troughton 1955, Ledig et al. 1970).

Biomass partitioning responses seem to be partially dependent on the species of plant and the resources altered. Norby et al. (1992, 1993) demonstrated that, after 3-4 growing seasons in elevated CO_2, *Quercus alba* L. saplings partitioned more biomass to roots relative to shoots, whereas *Liriodendron tulipifera* L. showed no response. Similarly, Murray et al. (1996) found no shifts in biomass partitioning in *Picea sitchensis* (Bong.) Carr. after 3 years of exposure to elevated CO_2. Gebauer et al. (1996) showed that elevated CO_2 had no direct effect on biomass partitioning in *Pinus taeda* seedlings, whereas nitrogen deficiency caused biomass to be preferentially partitioned to lateral roots. King et al. (1996) demonstrated that *Pinus ponderosa* Dougl. ex Laws. seedlings partition less biomass to secondary roots relative to the primary and taproot fractions at elevated temperature, whereas *Pinus taeda* increased partitioning to the secondary (lateral) root fraction in response to both increased temperature and nitrogen; neither species altered biomass partitioning in response to elevated CO_2.

Despite several studies on biomass partitioning in field-grown trees in response to varying resource availablility (Keyes and Grier 1981, Linder and Axelsson 1982, Axelsson and Axelsson 1986, Snowdon and Benson 1992, Gower et al. 1993, Haynes and Gower 1995), it is not known whether mature trees growing in the field respond to varying resource availability with the same phenotypic adjustments as young trees grown under highly controlled conditions. Most studies on mature field-grown trees have not used the allometric approach to separate treatment effects from ontogenetic effects, or did not include belowground components, or did not examine responses at the stand level (but see Gower et al. 1992). In addition, the common practice of comparing root:shoot ratios combines perennial tissues (stems, branches, and coarse roots) with ephemeral tissues (foliage and line roots), which confounds our understanding of the functional response of biomass partitioning and does not account for the seasonal dynamics of ephemeral tissues. For example, because loblolly pine foliage biomass varies substantially over the course of the growing season in the southeastern USA (Kinerson et al. 1974, Allen et al. 1992), time of year has a large impact on allometric relationships between foliage and other plant parts.

To investigate the effects of water and nutrient availability on biomass partitioning in field-grown trees, we installed a factorial design of irrigation and fertilization treatments in an 8-year-old stand of loblolly pine (*Pinus taeda* L.). Data on the effects of the treatments on biomass production have been presented in Albaugh et al. (1998), and this study extends the analysis to determine if the changes in production resulted in quantifiable shifts in whole-tree biomass partitioning. Loblolly pine is the most economically important species of pine in the southeastern USA (Wahlenberg 1960, Baker and Balmer 1983, Allen et al. 1990, Gupta and Durzan 1991), and its extensive geographic distribution (Baker and Langdon 1990) makes it a major component of the biosphere's response to global change. We hypothesized that increased availability of water and nutrients would result in: (1) decreased biomass partitioning to roots relative to shoots for both the perennial tissues (tap and coarse roots versus stem and branches) and ephemeral tissues (fine roots versus foliage); (2) decreased biomass partitioning to fine roots (ephemeral) relative to coarse roots (perennial); (3) greater biomass partitioning to branches (perennial) relative to stems (perennial); and (4) increased biomass partitioning to foliage (ephemeral) relative to branches (perennial).

Methods

Study site

The Southeast Tree Research and Education Site (SETRES) is located in the Georgia-Carolina Sandhills in Scotland county, NC (35° N, 79° W) on an infertile, excessively well-drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakula series). Field capacity is approximately 6.5 cm (11% volumetric water content) in the upper 50 cm of the profile. Mean annual precipitation is 1210 mm, but extended droughts occur during the growing season.

In 1992, sixteen 50 x 50 m treatment plots with 30 x 30 m measurement plots were established in a plantation of eight-year-old loblolly pine. Plant material consisted of a mix of 10 one-half sib families of loblolly pine Piedmont selections that were hand planted at a spacing of 2.4 x 3 m in March 1985. Final tree stocking density was 1260 stems per hectare. Treatments were applied in a randomized complete block design with two nutrient regimes and two irrigation regimes, replicated four times. Nutrient treatments have been maintained since March 1992, and irrigation has been applied since April 1993. See Albaugh et al. (1998) for complete site and treatment descriptions.

Treatments

Nutrient treatments were (1) optimum nutrition or (2) control. Optimum nutrition was defined as maintaining dormant season foliar nitrogen concentration at 1.3% dry mass based on a branch terminal in the upper third of the crown in codominant or dominant trees (Allen and Duzan 1983, Adams and Allen 1985, Allen 1987). Other nutrients were applied in balance with nitrogen (N) to maintain nutrient:N ratios of 0.10 for phosphorus (P), 0.35 for potassium (K), 0.12 for calcium (Ca) and 0.06 for magnesium (Mg). Foliar boron (B) concentrations were maintained above 12 ppm. Foliar nutrient status was monitored monthly and fertilizer applied as necessary to maintain target values. A table of the quantity and timing of fertilization has been included as an appendix (Table 1A).

Irrigation treatments were (1) natural precipitation (control) and (2) precipitation plus supplemental irrigation. Irrigation events were targeted to maintain soil water content at 40% of field capacity in the surface 50 cm of profile as determined by volumetric water content measured by time domain reflectometry (TDR) (Topp and Davis 1985). Measurements were taken with a 50-cm TDR probe at ten random locations within each plot every 2 weeks from March to November. The irrigation system consisted of Rainbird irrigation nozzles (Rainbird Agricultural Irrigation Products, Glendora, CA) mounted on

35-cm high risers positioned on a 10 x 10 m grid throughout the treatment plots. Each irrigation event applied 2.5 cm of water to the plots. During the growing season, our soil water targets were achieved in 1994 and 1995; however two drought events in 1993 caused available soil water content to drop to 23 and 5% for a total of 8 weeks (see Albaugh et al. (1998) for details).

Stand-level biomass estimation

Whole-tree stem regressions were developed with D^2H and tree age as the predictor variables, where D is diameter at breast height (1.4 m) and H is total tree height (Albaugh et al. 1998). A total of 48 trees were used in the whole-tree stem regressions (Table I). Whole-tree foliage and branch wood regressions were developed with D^2L as the predictor variables, where L is length of the live crown. A total of 448 trees (Table 1) were used in the regressions for foliage and branch wood. Forty-eight of the trees were from the destructive harvests and the additional 400 trees were measured nondestructively. Branch-level regressions were developed for branches on the destructively harvested trees with branch diameter and distance from the top of the trees as predictor variables. The branch-level regressions *were* applied to each branch on the 400 nondestructively measured trees and then summed by tree for whole-tree foliage and branch wood biomass estimates.

Whole-tree coarse root and taproot regressions were developed with D as the predictor variable. Twenty-three trees (Table 1) were used in the whole-tree coarse and taproot regressions. Coarse root biomass was estimated for each of the destructively harvested trees by collecting, drying, and weighing all roots > 2 mm diameter in soil pits (1 m x 1 m x 50 cm deep) centered on the destructively harvested trees. Because we may have underestimated coarse root biomass by this sampling method, we have since begun sampling "between rows," which should provide more accurate estimates in the future. However, this possible underestimation would have little effect on our interpretation of shifts in allometry because the strong linear relationship between coarse roots and total tree size was consistent within and between treatments. Taproot biomass was estimated by complete excavation of taproots of 23 destructively harvested trees (Table 1). Fine root (< 2mm diameter) biomass was estimated from core samples collected monthly in each plot (Table 2) and scaled to an area basis. In 1992 and 1993, line roots were sampled with 20 6.6 cm diameter x 10 cm deep cores per plot per month (Mignano 1995). Visually estimated live and dead roots were sorted by hand (only live roots are presented here). Core samples were scaled to 50-cm depth based on root depth distribution data for this site (Mignano 1995). In 1994 and 1995, the same procedures were used to estimate fine root biomass; however, only five cores with dimensions of 15.2 cm diameter x 15 cm deep were collected per plot per month to limit the plot area disturbed by coring.

Statistical analysis

Treatment effects on biomass pools (ANOVA) Treatment main effects and interactions on stand-level biomass estimates for all tree components for all years of the study were tested by standard analysis of variance (Steel and Tonie 1980). Data were tested for normality and natural-log transformed where necessary to normalize variances among treatments. Statistical analyses were performed on data from February 1992 to insure that there were no pretreatment differences; however, estimates of belowground biomass were unavailable for this year. Treatment effects were considered significant if $P \leq 0.05$.

Shifts in biomass partitioning (ANCOVA) Changes in biomass partitioning among tree components were detected by allometric analysis (Pearsall 1927, Troughton 1955, Ledig et al. 1970, Niklas 1994). The analysis consisted of fitting linear models to stand-level estimates of tree-component biomass by treatment for data from January 1993 until December 1995. Natural log-transformed estimates of one component (response variable) were plotted against natural log-transformed estimates of another component (covariate), and shifts in biomass partitioning were identified by significantly different slopes between treatments (Niklas 1994). An analysis of covariance (ANCOVA) was used to determine if non-homogeneity of slopes was significant, as indicated by significant interactions

Table 1. Harvest schedule for tree components by treatment and year. Data were used to estimate stand-level biomass for allometric analysis.[1] Numbers indicate the number of *trees* harvested and letters signify treatments: C = control, I = irrigation, F = fertilization, and IF = irrigation + fertilization (adapted from Albaugh et al. 1998).

	Fine roots[2]	Coarse roots	Taproots	Stem	Branches[3]	Foliage[3]
1992	20 cores/plot	-		16C	16C	16C
1993	20 cores/plot	-				
1994	5 cores/plot	2C, 21, IF, 21F	2C, 21, 1F, 21F	4C, 4I, 4F, 41F	4C, 4I, 4F, 41F	4C. 4I, 4F, 41F
1995	5 cores/plot	-				
1996	5 cores/plot	4C, 4I, 4F, 41F	4C, 4I, 4F, 41F	4C, 4I, 4F, 41F	4C, 4I, 4F, 41F	4C, 4I, 4F, 41F

[1] Stem diameter at breast height and tree height were measured annually on all trees, and used to scale plant-part biomass estimates to the stand-level for each year of the study. Regressions were based on biomass data from the destructive harvests.

[2] Fine root core samples were collected monthly. In 1992 and 1993, core size was 6.6 cmdiameter x 10 cm deep. Starting in 1994. core dimensions were enlarged to 15.2 cm diameter x 15 cm deep.

[3] In all years. branch and foliage biomass were estimated nondestructively by means of treatment-specific regressions on 20 trees per treatment. Regressions were based on biomass data from the destructive harvests.

Table 2. Estimates (P-values) of tree biomass accumulation (Mg ha-‘) by component at the beginning and end of the treatment period (adapted from Albaugh et al. 1998).

Treatment	Stem	Branch	Foliage	Taproot	Coarse root	Fine root	Total
Beginning 1993							
Control	4.7	2.2	1.8	1.5	0.7	0.9	11.8
irrigation	4.4 (0.441)	2.0 (0.534)	1.7 (0.480)	1.4 (0.523)	0.6 (0.480)	0.9 (0.080)	11.0 (0.357)
Fertilization	6.6 (0.000)	3.1 (0.000)	3.6 (0.000)	2.7 (0.000)	0.8 (0.018)	1.3 (0.260)	18.1 (0.000)
Fert. + Irrig.	6.4 (0.857)	3.0 (0.867)	3.4 (0.000)	2.6 (0.934)	0.8 (0.921)	0.8 (0.085)	17.0 (0.886)
RMSE[1]	0.7	0.4	0.3	0.3	0.4	0.2	
End 1995							
Control	13.0	4.9	3.0	3.9	1.5	0.8	27.1
Irrigation	14.9 (0.113)	5.5 (0.152)	3.5 (0.016)	4.2 (0.218)	1.6 (0.222)	1.2 (0.018)	30.9 (0.092)
Fertilization	23.4 (0.000)	9.8 (0.000)	5.7 (0.000)	9.4 (0.001)	2.3 (0.000)	0.7 (0.104)	51.3 (0.000)
Fert. + Irrig.	26.4 (0.694)	11.1 (0.625)	6.9 (0.258)	10.2 (0.638)	2.5 (0.924)	0.9 (0.455)	58.0 (0.631)
RMSE	2.7	1.3	0.6	0.3	0.4	0.2	-

[1] RMSE = Root mean square error.

of experimental factors with the covariate. If significant interactions were found, the magnitude of the treatment-induced shift in biomass partitioning was determined following King et al. (1996). Statistical models were constrained to have parallel slopes between treatments by removing interaction terms with the covariate. Marginal means of the response were then calculated for the constrained and unconstrained models and compared as a percentage difference.

Results

Biomass accumulation

To demonstrate the effects of the irrigation and nutrition treatments on biomass accumulation, data obtained by Albaugh et al. (1998) for the period 1993-1995 are presented in Table 2. All plant components except fine roots (stems, branches, foliage, taproots and coarse roots) showed substantial increases in accumulated biomass in response to the treatments. In general, accumulated biomass of all components except fine roots was significantly increased by fertilization over the four-year study (Table 2; Albaugh et al. 1998), resulting in 86% greater total biomass in trees in fertilized plots compared with trees in non-fertilized plots. Irrigation did not significantly affect any biomass component in 1993 or 1994 (Table 2; Albaugh et al. 1998). However, in 1995, we observed a significant increase in foliage and fine root biomass in response to irrigation (Tables 2 and 3), resulting in 10% greater total biomass ($P = 0.092$) in trees in irrigated plots compared with trees in non-irrigated plots. The interaction between fertilization and irrigation was not statistically significant for accumulated biomass of any plant component during the study (Table 2). By the end of the study there had been no tree mortality and leaf area index was still increasing, suggesting that competition for light had not yet reached a critical level.

Allometric shifts in biomass accumulation

Throughout the treatment period, perennial roots (coarse roots plus taproots) accumulated more biomass relative to perennial shoots (branches plus stems) as a result of fertilization (Table 3), and though significant, the change in slope between fertilized and non-fertilized plots was small (Figure 1A). The linear models used in the ANCOVA fit the perennial root and shoot data well. A significant interaction between the irrigation factor and the covariate foliage (Table 3) indicates a shift in biomass partitioning between fine roots and foliage that appears to be associated with a relative increase in foliage biomass in the irrigation treatment (Figure 1B). Unfortunately, the poor fit of the linear models to the fine root data limits our

Table 3. Values of P for interactions between dependent variables and covariates used in the analyses of covariance. Tissue types are denoted by P = perennial and E = ephemeral.

Dependent variable	Covariate	Tissue-type contrast	Fertilization x covariate	Irrigation x covariate	Fertilization x irrigation x covaritate
Coarse + Taproot	Branch + Stem	P versus P	< 0.001	0.683	0.901
Fine root	Foliage	E versus E	0.095	0.002	0.387
Fine root	Coarse + Taproot	E versus P	0.096	0.007	0.602
Fine root	Coarse root	E versus P	0.098	0.006	0.580
Branch	Stem	P versus P	< 0.001	0.378	0.420
Foliage	Branch	E versus P	< 0.001	< 0.001	0.387

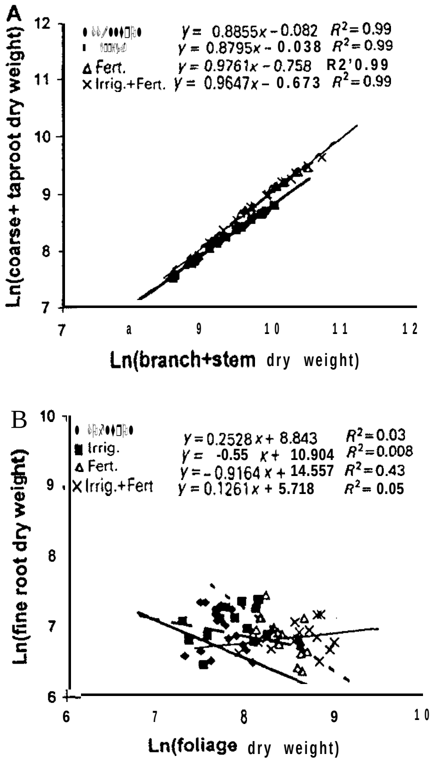

Figure 1. (A) Coarse root + taproot biomass versus branch + stem biomass (natural log transformed) and (B) fine root versus foliage biomass (natural log transformed) for the control, irrigated, fertilized, and irrigated + fertilized stands, for year-ends 1992, 1993, 1994 and 1995.

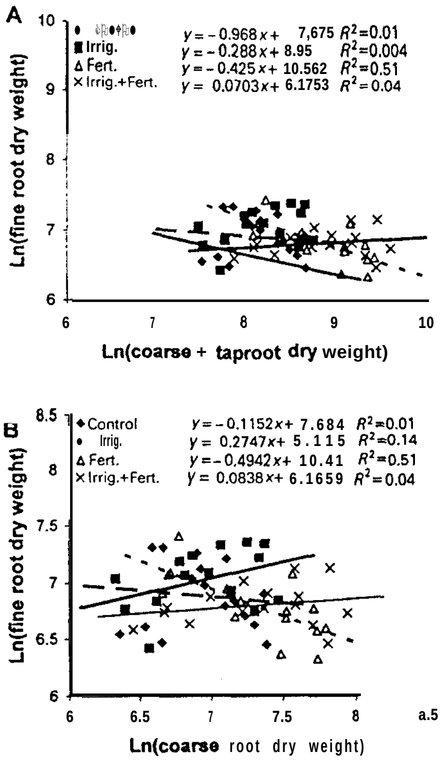

Figure 2. (A) Fine root biomass versus coarse mot + taproot biomass (natural log transformed) and (B) tine root versus coarse root biomass (natural log transformed) for the control, irrigated, fertilized, and irrigated + fertilized stands, for year-ends 1992, 1993, 1994 and 1995.

confidence in interpreting the allometric shifts between fine roots and foliage (Sokal and Rohlf 1995).

The irrigation treatment increased biomass partitioning to ephemeral roots (fine roots) relative to perennial roots (coarse roots plus taproots) (Table 3; Figure 2A) and increased biomass partitioning to fine roots relative to coarse roots (Figure 2B). Across treatments and years, the range in fine root biomass was less than the range for other plant components (Table 2; Figures 1B, 2A and 2B), contributing to the weakness of the linear relationships between fine roots and other plant parts. Again, the lack of fit of the linear models to the fine root data prevents an unequivocal interpretation of the shifts in biomass partitioning between fine roots and other plant parts (Figure 2).

Fertilization significantly increased biomass partitioning to branches relative to stems (Table 3); however, shifts in biomass partitioning between these plant parts were minor (Figure 3A). Improved soil resources affected the relationship between foliage biomass and branch wood, with less foliage accumulated per unit branch mass in the fertilization and irrigation treatments than in the controls (Table 3; Figure 3B). There was a good fit of the linear models used in the ANCOVA for branches, stems and foliage (Figure 3).

The comparison of constrained and unconstrained models provided estimates of the magnitude of the treatment-induced shifts in carbon accumulation between plant parts (Table 4). The differences between constrained and unconstrained models ranged from 0.61 to 5.87%, indicating that the treatments had small absolute effects on biomass partitioning.

Discussion

SETRES and plant allometric analysis

The sandy soil at SETRES permits imposition of well-controlled irrigation and nutrition treatments and monitoring of leaf nutrient concentrations insures adequate separation of treatment effects. In addition, the sandy soil facilitates recovery of root tissue, which is essential for the study of stand-level tree allometry. Few authors have examined allometry in large woody perennials by means of statistically robust methods that correct for ontogenetic shifts in biomass partitioning during growth (but see Gower et al. 1992). Stand-level allometric analyses are particularly useful because effects at the scale of the individual plant, such as increased leaf area display, are integrated with those at the stand level, such as canopy closure and competition for light. Although our stand-level estimates are based on regressions of relatively few trees, the results are similar to those obtained when examining specific trees, and are not a function of the scaling procedures.

Several global circulation model (GCM) simulations predict that soil water content over the southeastern USA will increase

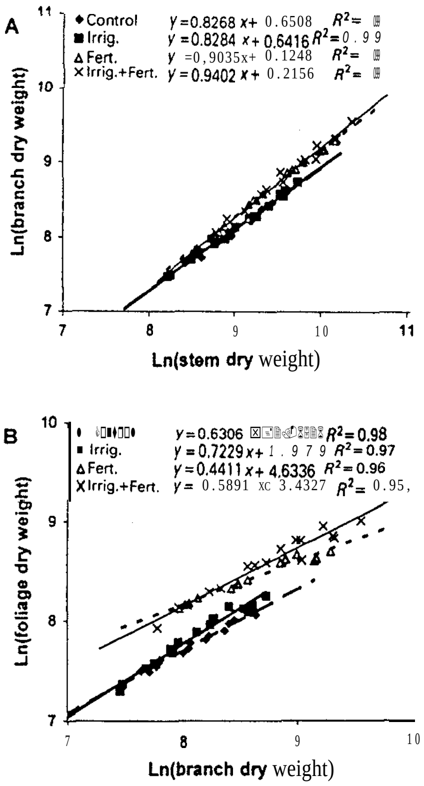

Figure 3. (A) Branch biomass versus stem biomass (natural log transformed) and (B) foliage biomass versus branch wood biomass (natural log transformed) for the control, irrigated, fertilized, and irrigated + fertilized stands, for year-ends 1992, 1993, 1994 and 1995.

by 1 to 4 cm (summer and winter) with a doubling in atmospheric CO_2 concentration (Houghton et al. 1996). On average, the irrigation treatment at SETRES added 4.6 cm per year to soil water content (1994-1996 data), which slightly exceeds the upper limit of the predicted increases. Although water was applied mainly during the growing season, responses to irrigation observed at SETRES may provide a good approximation of forest ecosystem responses occurring at similar sites. Similarly, current atmospheric N deposition in the southeastern USA (50 to 250 mmol N m^{-2} year-‘) is currently about 25 times pre-industrial rates (Galloway et al. 1995). The fertilization treatment at SETRES has added on average 105 mmol N m^{-2} $year^{-1}$ (1992-1996). Although actual N-deposition rates at SETRES have not been quantified, the amount of additional N applied approximates the projected rate of N deposition for the year 2020 (80 mmol N m^{-2} year-‘) in much of the world (Galloway et al. 1995).

Stand-level estimates of all biomass components, except fine roots, increased substantially in all treatments from 1992 to 1996 (Table 2; Albaugh et al. 1998). possibly indicating that fine roots have fully occupied the site (Ford and Deans 1977, Nambiar 1983, Bowen 1984). Among plant parts, irrigation had the greatest effect on ephemeral plant parts, i.e., fine roots and foliage (Table 2). However, over the four-year study, irrigation consistently increased foliage production, whereas it only affected fine root production in 1993 (Albaugh et al. 1998). The relatively small root response to irrigation may be attributable, at least in part, to the coarse texture of the soil. We have observed coarse lateral roots penetrating the soil to depths of 4 m (King and Albaugh, unpublished data). Although these “sinker” roots represent a small fraction of the total root biomass, they may be important for the uptake of water stored deep in the soil profile (Holmes and Colville 1970, Bowen 1984).

In all years of study, fertilization had a positive effect on all biomass pools except fine roots (Table 2; Albaugh et al. 1998). Fertilization generally decreased fine root biomass, but the effect was only significant in 1993. Several authors have reported that fertilization has no effect or reduces fine root biomass in forest ecosystems (Alexander and Fairly 1983, Axelsson and Axelsson 1986, Haynes and Gower 1995), presumably because of altered allometry between line roots and other plant parts. It has been suggested that the decreased allocation of biomass to line roots in fertile soils, with proportionate reductions in growth and respiration, result in greater biomass allocation to foliage and stems (Linder and Axelsson 1982, Axelsson and Axelsson 1986).

Allometric shifts

Root:shoot relationships Contrary to our first hypothesis, we found a slight increase in perennial root biomass (coarse and taproots) relative to perennial shoot biomass (branches and stems) in response to fertilization (Figure 1A). This response

Table 4. Percent difference in the dependent variable between unconstrained and constrained models for interactions that were significant in the analyses of covariance. Percentages were calculated on untransformed data.

Dependent variable	Covariate	Non-fertilized	Fertilized	Non-irrigated	Irrigated
Coarse + Taproot	Branch + Stem	***-4.80***	***-0.95***	***NS***[1]	***NS***
Fine root	Foliage	NS	NS	-3.09	***5.87***
Fine root	Coarse + Taproot	NS	NS	-0.81	4.79
Fine root	Coarse root	NS	NS	0.61	2.19
Branch	Stem	-3.79	***-0.808***	***NS***	***NS***
Foliage	Branch	***2.30***	***0.44***	1.67	0.79

[1] NS = Interaction was not significant in the analysis of covariance.

was driven by a preferential increase in allocation of biomass to taproots, which comprised 75% of total root biomass in fertilized plots at the end of 1995 (data not shown). The effect could be related to the functional importance of structural roots (Coutts 1983). The discrepancy between these data and the functional balance theory may be associated with the advanced stage of development of the study trees, because the theory was developed from studies on seedlings grown in pots. Chronosequence data from Ovington (1957) show that, in plantations of *Pinus sylvestris*, root:shoot ratios increase until about age7 and then decline over the life of the stands. Ontogenetically, the loblolly pine plantation at SETRES appears to be in the stage of decreasing root:shoot ratio (calculated from Table 2). Allometric analyses revealed that fertilization slightly reduced the rate at which this decline occurs.

Gedroc et al. (1 996) found increased root:shoot ratios in two species of annuals grown under low-nutrient conditions, consistent with functional balance theory. However, their allometric analyses indicated that relative growth of shoots exceeded that of roots under low-nutrient conditions, whereas the reverse occurred under high-nutrient conditions. This apparent contradiction to functional balance theory is in agreement with our findings. Gedroc et al. (1996) concluded that root:shoot partitioning is partially consistent with functional balance theory during the early stages of growth, but is also highly constrained by ontogeny. In loblolly pine, decreased relative root growth at high-nutrient availability in seedlings (Griffin et al. 199.5, Gebauer et al. 1996), followed by the converse in trees (Kinerson et al. 1977, this study) would tend to support this view.

Irrigation significantly decreased partitioning of biomass to ephemeral root tissues (fine roots) relative to ephemeral shoot tissues (foliage) (Table 3, Figure 1B). These. treatment effects are probably an expression of the functional linkage between fine roots, which supply water to the xylem, and foliage, which transpires water during photosynthesis (Givnish 1986, Cannel1 and Dewar 1994). Increased water availability appears to permit greater foliage display per unit fine root mass, thereby increasing potential carbon gain, and is consistent with other studies examining leaf:root partitioning in response to drought stress (Ibrahim et al. 1997).

Because fine root biomass at SETRES is relatively constant throughout the year (Mignano 1995), the allometric relationship between foliage and tine roots would be expected to change as foliage biomass increases over the growing season. Sufficient fine root biomass must be maintained to support maximum foliage display, which occurs in late August or early September. Our January sampling, therefore, quantified the relationship between foliage produced in the current year (because previous-year foliage has dropped by this time) with fine root biomass of the current year, and avoids confounding biomass produced in previous years with ephemeral tissues from the current year. We conclude that it is important to separate perennial tissues from ephemeral tissues when considering functional responses.

Fine root:coarse root relationships Because fine roots are the fraction mainly responsible for the uptake of water and nutrients, we hypothesized that partitioning to fine roots would decrease in response to irrigation in accordance with the functional balance model. The data did not support this hypothesis. Irrigation increased the amount of tine root biomass accumulated per unit of both coarse plus taproots and coarse roots only (Table 3; Figure 2). This finding appears to differ from that of Bongarten and Teskey (1987), who found greater partitioning to roots under drought stress. However, the generally held conception that dry matter partitioning to roots increases in response to drought, as it does for nutrient stress (Cannell 1985, Wilson 1988), is based largely on studies that did not differentiate between the perennial and ephemeral root fractions.

Improved nutrition resulted in a shift toward less fine root biomass per unit coarse root, consistent with our second hypothesis (Table 3; Figure 2B); however, this shift in partitioning was not statistically significant (P = 0.098). Several studies have reported decreased partitioning to fine roots in response to fertilization (Linder and Axelsson 1982, Axeisson and Axeisson 1986, Cower et al. 1994).

Absolute fine root biomass at the study site exhibited a narrow range of responses to a wide range of experimentally imposed environmental conditions. Similarly, Kurz et al. (1996) reported that fine root biomass is nearly constant for a wide range of aboveground biomass values for softwoods and hardwoods in Canadian forests. This finding highlights several important considerations when interpreting functional responses of forests to changing environmental conditions. Our data show that allometric analysis can be a powerful tool for examining biomass partitioning in trees and for detecting when inferences are weak because of the variance structure of the data (e.g., fine roots in this study). For example, the lack of a proportionate tine root response resulted in a "weak" relationship between fine roots and other plant parts. It may be an inherent property of fine root biomass, at least as estimated by coring, to scale poorly with aboveground biomass (*sensu* Kurz et al. 1996) or other plant parts (e.g., coarse roots), making interpretation of fine root responses difficult.

Foliage:branch:stem relationships The data in Table 3 and Figure 3A support our hypothesis that improved soil resources result in greater biomass partitioning to branches relative to stems. Increased foliage biomass is a major factor contributing to increased carbon gain by pines following fertilization (Gower et al. 1994. Dougherty 1996, Aibaugh et al. 1998). From a functional perspective, enough biomass must be allocated to branches to provide structural support and meet increased transpirational demands of peak foliage displayed during the growing season. In terms of forest productivity, the concern is that increased partitioning to branches does not occur at the expense of stem production or wood quality. Other studies have shown that branch:stem partitioning is mainly affected by light environment and stocking density (Cannel1 1985, Niisson and Hällgren 1993). We found that branch:stem allometry is also affected by the nutritional status of the stands, and that there is a small decrease (Table 4) in stem production relative to branch production in response to fertilization. Similarly, Gillespie et al. (1994) showed that fertilization resulted in increased partitioning to branches as a result of increased growth and retention of branches lower in the crown.

The final hypothesis tested was that improved soil resources would result in greater biomass partitioned to foliage relative to branches. We found a decrease in biomass partitioning to foliage relative to branches in response to improvement in both nutrition and water availability (Table 3; Figure 3B). Similar observations were reported by Gillespie et al. (1994), who attributed the response to fertilization-induced retention of branches in the lower crown. Lower-crown branches are retained longer in fertilized trees compared with non-fertilized trees, and accumulate biomass until canopy closure results in light limitation. Fertilization appears to extend the time to light limitation by enhancing light-use efficiency of lower-crown foliage (Gillespie et al. 1994).

Interpretation of allornetric shifts

The magnitude of the shifts in biomass partitioning in loblolly pine was on the order of a few percent of the response variables (Table 4). Such small shifts in biomass allocation have been reported previously for loblolly pine (King et al. 1996) and support the hypothesis that biomass partitioning is sensitive to environmental conditions, but is also probably highly constrained by ontogeny (Gedroc et al. 1996). In addition, decreases in partitioning to roots in response to fertilization during the early stages of development (Griffin et al. 1995, Gebauer et al. 1996) followed by the converse later in life (this study) lends support to the argument that biomass partitioning in loblolly pine is under strong ontogenetic control. Further, the robustness of the analyses depends, in part, on the degree to which linear models accurately describe the relationships between plant parts. In cases where the linear fit is good (foliage, branches, stems, coarse roots, taproots) we can be reasonably sure that the shifts in allometry are accurately described; however, in cases where the linear fit is less good (fine roots), the interpretation is equivocal.

Conclusions

We conclude that stand-level shifts in biomass partitioning among plant parts in large woody perennials growing in the field occur as a direct response to altered resource availability. However, the observed shifts were small and greatly affected by the ontogenetic development of the trees. Improved nutrition resulted in proportionately more biomass partitioned to perennial roots relative to perennial shoots, more partitioning to branches relative to stems, and more partitioning to branches relative to foliage. High water availability was important for biomass partitioning to both tine roots and foliage. Finally, when considering biomass partitioning among plant parts, it is important to consider the functional relationships between perennial and ephemeral tissue, and to account for the seasonal dynamics of foliage and fine roots.

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Appendix

Table I A. Annual nutrient application rates (kg ha^{-1}) and sources of fertilizer at SETRES, Scotland County, NC (adapted from Albaugh et al. 1998).

Year	N (Urea)	P (TSP[1])	K (KCl)	Ca Gypsum)	Mg (Sophomag)[2]	B (Borate)
1992	225	56	112	135	56	2
1993	82	50	113	0	56	0
1994	112	0	0	0	0	0
1995	56	28	56	24	34	1

[1] TSP = Triple super phosphate.

[2] Sophomag = Sulfate of potash magnesia.