Potential Effect of Stand Structure on Belowground Allocation

Thomas J. Dean

ABSTRACT. Stand structure affects two key variables that affect biomass allocation to the stem: leaf area and height to the center of the crown. By translating wind forces into a bending moment, these variables generate bending stress within a stem. The uniform-stress axiom of stem formation can be used to calculate current stem mass for a given bending moment and stem allocation for changes in bending moment over a time period. Stem allocation probably affects allocation to fine roots since the stem precedes the root system on the chain of carbohydrate sinks, and total net primary production is a linear function of leaf area. This study indirectly supports this link between stand structure and belowground allocation. A regression model based on the relationship between bending moment and stem allocation explained 98% of the variation in stand-level stem production of a 12-yr-old loblolly pine (*Pinus taeda* L.) plantation subjected to factorial combinations of irrigation and fertilization. Furthermore, relative fine-root allocation was inversely related to relative stem allocation and increases in apparent bending stress. Corresponding associations between bending stress and relative allocation between the stem and fine roots appear to exist for other species, providing additional support for the proposed link. FOR. SCI. 47(1):69–76.

Key Words. *Pinus taeda*, uniform-stress axiom, carbon allocation, fertilization.

TYPICAL FACTORS KNOWN TO INFLUENCE biomass allocation to fine roots in trees include light, soil water, and soil fertility (Cannell 1985, Gower et al. 1994). The simple response of fine-root allocation to these variables is typically calculated from the amount of carbon and nutrient elements used in new growth using the law of mass balance. For example, if it is assumed that new tissue has a fixed ratio of carbon and nitrogen, both shade and fertilization would increase shoot mass relative to root mass to compensate for either the reduction in carbon uptake caused by shade or the increase in nitrogen uptake due to fertilization. While an overall mass balance must exist, the basic mass-balance approach provides only a heuristic explanation for trees because only a portion of a tree's aboveground and belowground tissues acquire carbon or nutrients. The mass balance is also difficult to calculate for trees because of the varying distribution of biomass among the tree's components and their wide variation in nutrient concentrations. Consequently, when experimental results do not agree with the expected response of fine-root allocation to manipulation of environmental variables, it is difficult to judge whether the disagreement is due to the problems inherent in measuring fine-root production or the inaccurate modeling of the complicated mass balance equation for trees (e.g., Cropper and Gholz 1994).

How trees allocate biomass to fine roots has both positive and negative implications for forest management. Cultural treatments that reduce fine-root allocation and increase the harvest index (the fraction of total biomass that can be utilized commercially) are economically beneficial. In contrast, these same treatments can result in sharp decreases in stem growth and increased mortality during a severe drought

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(Linder et al. 1987). In addition, fine-root allocation is also a critical component of carbon-based process models that simulate forest growth. Such models have the potential of forecasting production in response to different sequences or timing of silvicultural treatments or to changes in soil or climate. However, this potential is yet to be realized because of the inability of these models to simulate the important factors that influence fine-root allocation.

Light, water, and nutrients not only affect the mass balance of resource acquisition of trees, but also affect the structure of the stand. Stand structure can be linked to fine-root allocation using several approaches, but the most general approach appears to be one that relates stem wood increment to mechanical needs of the crown. Annual stem increment may also be related to hydraulic needs of the foliage, but Kershaw and Maquire (2000) report that the cross-sectional area increment per unit foliage in western hemlock (*Tsuga heterophylla* Raf. [Sarg.]) and balsam fir (*Abies balsamea* [L.] Mill.) varies with tree size; consequently, this approach would require a coefficient to adjust for tree size. Simple, empirical relationships between crown size and stem size could be used to link stand structure and belowground allocation, but such relationships are weak when extrapolated beyond the range of tree sizes used to fit the equations. The mechanical relationship between the crown and the stem has been shown to uniformly apply to a wide range of tree sizes in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) (Dean and Long 1986); therefore, this relationship may apply to a broader range of stand structures without the need of adjustment factors or the limitations of empirical equations.

The amount of wood required to counter wind forces is a function of the leaf area the tree has accumulated and the vertical distribution of leaf area on the stem. Since the total amount of biomass produced in a stand is apparently a linear function of stand leaf area (Gower et al. 1992, Albaugh et al. 1998), root production is potentially limited by the physical requirements of the foliage. Fine-root production should be especially sensitive to the amount of new biomass needed for mechanical support of the crown because fine roots are at the distal end of the carbohydrate source-sink network (Kozlowski 1992). An inverse relationship between relative stem allocation and relative allocation to fine roots demonstrated by Santantonio (1989) for a number of northern coniferous species (Figure 1) supports the possibility that fine-root allocation is limited by the physical requirements of the stem as determined by stand structure.

The principal objective of this study is to evaluate the possible link between stand structure and fine-root allocation. The potential link between stand structure and fine-root allocation is evaluated with data from a controlled-field study of the effects of optimum soil water and nutrient availability on the growth of loblolly pine. Stand structure is expressed in terms of the amount and distribution of leaf area per tree and is translated into a cumulative measure of bending stress created by lateral wind movement through the stand. If stand structure affects fine-root allocation through its effects on stem allocation, the relative amount of biomass allocated to the fine-root system should be inversely related to the allocation to stem wood and the cumulative bending stress.

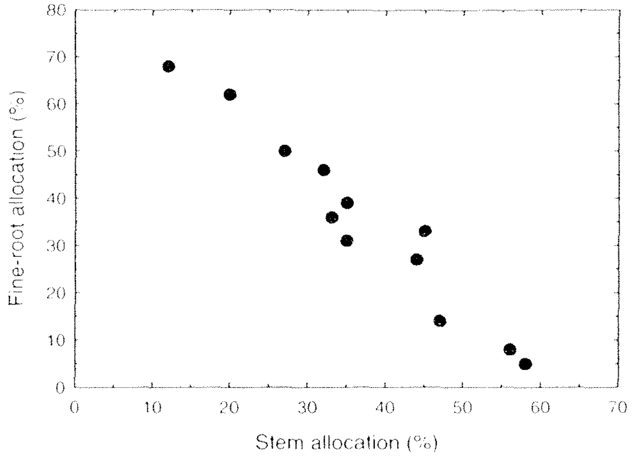

Figure 1. Fine-root allocation in relation to stem allocation for a number of northern coniferous species. Allocation to both biomass components expressed as a percent relative to total net primary production. Data from Santantonio (1989) for closed stands.

Theory

Stand structure is related to stem allocation through the uniform-stress axiom of stem formation, which describes stem size and shape from the principles of beam mechanics (Metzger 1893, Dean and Long 1986, Mattheck 1995). Assuming that bending stress is uniform across the surface of the stem, that wind drag is proportional to leaf area, and that wind velocity through the canopy is constant, Dean and Long (1986) found that the diameter of any cross section of the stem can be described in terms of the projected leaf area above the cross section at height *i* (A_i) and the length of the lever arm acting on the cross section (S_i) with the equation

$$D_i = p\,(A_i\,S_i)^{0.33} \tag{1}$$

where D_i = stem diameter at height *i*, and p = constant. Dean and Long (1986) found that the length of the lever arm could be calculated as the distance between *i* and the point in the crown that divides A_i into two equal parts. Several investigators have developed more precise descriptions of stem geometry from beam mechanics (West et al. 1989, Morgan and Cannell 1994), but according to Cannell and Dewar (1994), Equation (1) is a sufficient approximation. It is important to note, however, that Equation (1) does not describe stem strength (i.e., the lateral or vertical forces required for stem failure), it simply relates bending stress to stem geometry.

The combination of leaf area, leverage, and wind force is the bending moment exerted on the stem at height *i*. Obviously, bending moment is a dynamic value, but if wind force is a simple proportion of leaf area, the product of leaf area and leverage represents a static scalar of bending moment that is independent of wind speed. Replacing the product of A_i and S_i with the static scalar of bending moment at height *i* (M_i) changes the uniform-stress model [Equation (1)] to

$$D_i = p\,(M_i)^{0.33} \tag{2}$$

Stand structure affects stem size through its effect on the variables comprising the static scalar of bending moment. The number of trees per hectare and their average size has been shown to affect total stand leaf area (or total foliage mass) and average leaf area per tree (Turner and Long 1975, Mohler et al. 1978, Dean and Baldwin 1996). The length of the lever arm can be calculated with crown length and live-crown ratio (live-crown length divided by total tree height). Both of these variables vary with the number of trees per hectare and the average size of the trees (Beekuis 1965, Long 1985). Equation (2) implies that a specific quantity of stem volume is required to counteract bending stress coincident with a given stand structure. As stand structure changes, positive changes in bending moment should result in specific increases in stem volume. Since stem volume and mass are related linearly, Equation (2) further implies that carbon allocation to stem is specific for a given stand structure and the rate at which stand structure changes.

A simple expression for stem volume in relation to bending moment can be derived by setting i in Equation (2) to breast height (1.37 m) and substituting the allometric relationship between stem volume (V) and diameter at breast height (DBH), i.e., $V \alpha DBH^{2.4}$, (Tadaki 1977) for D_i. Converted to stem mass (W) by including wood density (s), Equation (2) becomes

$$W = s\,q\,(M)^{0.8}, \tag{3}$$

where q = constant, and M = the static scalar for bending moment acting at breast height. The change in stem mass per unit change in bending moment can be expressed in terms of annual, discrete changes in M:

$$P_t = a\,[(M_0 + \Delta M)^{0.8} - M_0^{0.8}], \tag{4}$$

where P_t = change in stem mass or stem production, a = a constant, M_0 = the bending moment scalar at the beginning of the year, and ΔM = the change in bending moment scalar during the year.

Since stand-level stem production is the summed stem production of all trees within a stand, the value of M_0 should correspond to the sum of the bending moments of individual trees at the beginning of the year, and the value of ΔM should correspond to sum of the changes in bending moment of individual trees during the year. Substituting the stand-level values of M_0 and ΔM into Equation (4) results in

$$P_s = b\left[\left(\sum_{j=1}^{k} (M_0)_j + \sum_{j=1}^{k} (\Delta M)_j\right)^{0.8} - \left(\sum_{j=1}^{k} (M_0)_j\right)^{0.8}\right] \tag{5}$$

where P_s = stand-level stem production, b = constant, j represents each tree within the stand, and k is the number of trees in the stand.

Equations (5) expresses stand-level stem production in terms of initial stand structure and the degree to which stand structure changes over an observation period. If the relative allocation to fine roots is inversely related to relative stem allocation, fine-root production should also be affected by stand dynamics. Sensitivity analysis of Equation (5) with ranges of realistic but arbitrary ranges of ΔM and M_0 and an assumed, linear relationship between leaf area and total net primary production indicates that both ΔM and M_0 must increase for relative allocation to stem wood to increase, and that the increase in ΔM must result from concomitant increases in both leaf area and lever arm. Consequently, if stand structure influences relative allocation through the uniform-stress axiom, systematic increases in relative allocation to the stem and systematic decreases in relative allocation to fine roots will be associated with systematic increases in both ΔM and M_0.

Methods

Data

Annual production and bending moments during 1996 were calculated with data collected in December 1995 and 1996 in a loblolly pine plantation growing in Scotland County, North Carolina, and being subjected to factorial combinations of irrigation and fertilization. The study site, study installation, experimental design, and sampling methods used in this study have been described by Albaugh et al. (1998). The topography at the study site is flat and underlain by an excessively drained, infertile soil of the Wakulla series, making treatment effects especially prominent. The cutover longleaf pine (*Pinus palustris* Mill.) site was hand-planted in 1985 with loblolly pine seedlings on a 2 × 3 m spacing. The plantation was 8 yr old when the four factorial treatments were randomly assigned to 16, 50 × 50 m plots. The fertilization treatments were initiated in March 1992, and the irrigation treatments began in April 1993. Fertilizers were applied as needed to maintain optimum nutrition or not applied, and plots were irrigated when the volumetric moisture content of the surface 500 mm of soil fell below 40% or received no supplemental water. The treatment protocols are described in detail by Albaugh et al. (1998).

Bending moment of individual trees at the beginning and end of the 1996 growing season were calculated from individual tree estimates of leaf area and length of the lever arm. Leaf area per tree was calculated from measurements of diameter at breast height and total height using a treatment specific biomass equation developed by Albaugh et al. (1998) and a specific leaf area of 3 m^2/kg. Specific leaf area was not significantly different across the four treatments (T.J. Albaugh, pers. comm.). Individual tree leaf areas and bending moments are, therefore, seasonal minimums. Lever arm length was assumed to be the distance between breast height and the middle of the live crown and was calculated from measurements of total height and the height to the base of the live crown according to Dean and Long (1986). Methods for determining production of the various biomass components are described in detail by Albaugh et al. (1998). Stem wood, coarse roots, and taproot production during 1996 were calculated with locally derived, treatment-specific, biomass equations using the diameter and height measurements made on individual trees before and after the 1996 growing season. The production of fine roots during 1996 was estimated with the procedures described by Fairly and Alexander (1985) using the root mass of live and dead roots < 2 mm in diameter washed from soil cores that were collected on a monthly basis. Albaugh et al. (1998) list the stand characteristics and production rates at the end of the 1995 growing season.

Analysis

The effect of stand structure on stem wood allocation was determined by analyzing how well variation in annual stem production was explained with cumulative bending moment at the beginning of the growing season and the cumulative change in bending moment during the growing season using Equation (5) as a model function. The following regression model was fit to the experimental data using a derivative-free, nonlinear-regression algorithm (Ralston and Jennrich 1978):

$$P_s = t_0\left[\left(\sum_{j=1}^{k}(M_0)_j + \sum_{j=1}^{k}(\Delta M)_j\right)^{t1} - \left(\sum_{j=1}^{k}(M_0)_j\right)^{t2}\right] \quad (6)$$
$$+\ t_3 I + t_4 F + t_5 (I \times F) + e$$

where t_0 to t_5 are regression coefficients and I and F are indicator variables for irrigation and fertilization, respectively, and e = error. The accuracy and precision of the fitted equation were evaluated with residual plots and the fit index [i.e., the fraction of variance in stem production explained by the model (Baldwin 1989)]. No tests were conducted on the fitted exponents in Equation (6) since their value reflects the aggregated allometric relationship between stem mass and *DBH* for all trees within the measurement plots regardless of crown position or vigor. Treatment effects on the fit of Equation [6] were determined with a general linear test approach (Neter et al. 1996). Briefly, this approach tests the null hypothesis $t_x = 0$ (where, in the case of Equation (6), x = 3, 4, and 5) by comparing the error sum of squares for the model with t_x and without t_x. The model without t_x represents the null hypothesis.

The hypothesized link between stand structure and the biomass allocation is evaluated by comparing the experimental results to the changes in relative allocation expected with increasing combinations of ΔM and M_0. As ΔM and M_0 increase across a series of stands, or in this case treatments, relative allocation should increase to the stem and decrease to the fine roots. Since this study did not trace the actual partitioning of carbon within the tree, this study must depend on correlation as evidence for a purported effect of stand structure on biomass allocation. A more direct evaluation of the hypothesis would involve artificial manipulation of the bending stress experienced in the stem and comparing the resulting translocation patterns with the patterns that would be expected to occur with changes in allocation.

Results and Discussion

Relation of Bending Moment to Annual Stem Increment

The fit of Equation (6) to the data indicates that stand-level stem production is related to stand structure and changes in stand structure during the growing season. The full model explains 98% of the variation in annual stem production, and the fit is unbiased across the observed ranges of cumulative bending moment and cumulative change in bending moment. The only treatment that significantly affected the fit of Equation (6) to the data was fertilization (Table 1). Nonlinear regression that includes only the significant indicator variable results in

$$P_s = 1405\,F + 62.6\,[(M_0 + \Delta M)^{0.53} - M_0^{0.52}]. \quad (7)$$

The significant coefficient for the indicator variable representing fertilization in Equation (7) indicates that for a given stand structure, fertilization increases stem production by 1.41 Mg ha^{-1} yr^{-1}. Stem volume in this study was calculated as a constant fraction of the stem filling a cylinder defined by diameter at breast height and total tree height (Albaugh et al. 1998). Jokela et al. (1989) found that stems of fertilized slash pine trees fill more of a cylinder than unfertilized slash pine trees. If fertilization affects stem taper in loblolly pine similarly, Equation (7) would require an additional term to account for differences in stem form. The presence of a significant indicator variable for fertilization in Equation (7) may actually be an artifact of using cylindrical form factors to calculate stem volume and mass, however. While Jokela et al. (1989) found differences in cylindrical form factor as a result of fertilization, when analyzed from the perspective of the uniform-stress axiom, taper for both fertilized and unfertilized slash pine trees could be described with a single equation.

According to Equation (7), the gains in stem production during 1996 in response to irrigation and fertilization are the result of two factors: (1) the widely different stand structures that existed at the beginning of the 1996 growing season after 4 yr of providing either optimal soil water or nutrition to these loblolly pine stands, and (2) the different rates in which stand

Table 1. Test results for the effects of irrigation, fertilization, and their interaction on the nonlinear curve fit of

$$P_s = t_0\left[\left(\sum_{j=1}^{k}(M_0)_j + \sum_{j=1}^{k}(\Delta M)_j\right)^{t1} - \left(\sum_{j=1}^{k}(M_0)_j\right)^{t2}\right] + t_3 F + t_4 I + t_5 (F \times I) + e$$

to stem production during 1996 for loblolly pine plantations growing in Scotland County, North Carolina. P_s = stem production (kg ha^{-1} yr^{-1}),

$\sum_{j=1}^{k}(M_0)_j$ = cumulative bending moment at the beginning of 1996 for tree j to k (m^3/ha),

$\sum_{j=1}^{k}(\Delta M)_j$ = cumulative change in bending moment during 1996 (m^3/ha), I and F = indicator variables for irrigation and fertilization, respectively (absent = 0, present = 1), t_0 to t_5 = regression coefficients, and e = error. Significance of t_3 to t_5 determined with the general linear test approach.

Treatment	F-statistic*	P-value
Irrigation (I)	0.01	0.93
Fertilization (F)	13.00	0.01
$I \times F$	0.15	0.15

* Degrees of freedom = 1 and 10

structure changed during 1996. The simple effects of irrigation and fertilization significantly increased M_0 by 32 and 166%, respectively (Table 2), and according to Equation (7), these differences alone (i.e., with $\Delta M = 0$) would result in respective increases of 20 and 40% in stem production. The respective 46 and 113% increases in cumulative bending moment that occur over the growing season produce substantial additions to stem production that would not occur if conditions were so poor that neither leaf area nor the length of the lever arm could increase.

The maximum value of ΔM is obviously constrained by the rates of leaf area accumulation, height growth, and self-pruning. Self-pruning affects the height to the base of the live crown and thus, the length of the lever arm. Under natural conditions, yearly and seasonal variation in weather conditions would cause these rates to vary, resulting in a cloud of points within a M_0 and ΔM plane. Occasional optimal weather conditions, however, should produce a distinct upper boundary in the data cloud that would represent the maximum possible rates in leaf area accumulation, height growth, and self-pruning. One of the goals in maintaining optimum soil water and nutrition in these 12-yr-old loblolly pine stands was to produce maximal biomass production. Consequently, the values of ΔM measured in the irrigation and fertilizer treated plots likely reflect yearly maximums for this particular soil type and location. Abundant rainfall occurred during 1996, which may explain why the values of ΔM also seemed to be maximal for the control plots. According to these results, the maximum value of ΔM is not a ceiling but a constant fraction of M_0 (Figure 2).

With stand age, annual stem production peaks at canopy closure and declines thereafter (Assmann 1970). This would seem to indicate that the existence of a linear relationship between maximum ΔM and M_0 throughout the lifetime of a stand is unlikely. The loblolly pine stands measured in this study are relatively young, 12 yr old, and only the fertilized stands have recently closed canopy. As the stands mature and approach their equilibrium leaf areas, the rate of change in ΔM will slow as the rates of leaf area accumulation and height growth slow. According to Equation (7), lower values of ΔM will be associated with lower values of stem production.

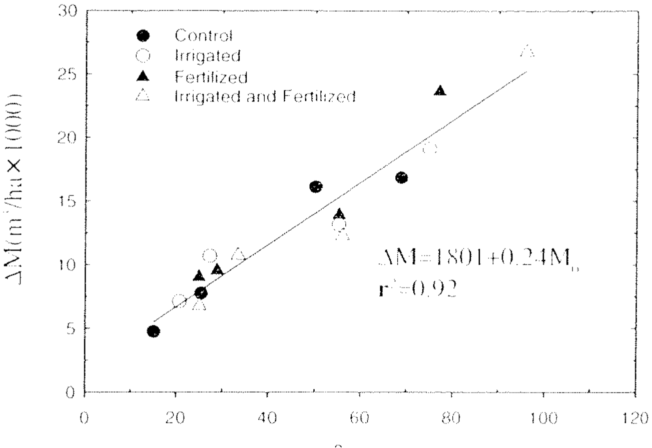

Figure 2. Change in cumulative bending moment during 1996 (ΔM) as a function of cumulative bending moment of the plot at the start of the 1996 growing season (M_0) for variously treated loblolly pine plantations growing in Scotland County, North Carolina. Line fitted with ordinary least squares.

Relation of Bending Moment to Fine-Root Partitioning

Unlike the previous years' results that were reported by Albaugh et al. (1998), neither irrigation nor fertilizer resulted in significant declines in the absolute value of fine-root production during 1996 ($P = 0.794$ and 0.541, respectively). Relative to total production, however, fine-root production was significantly reduced with fertilization (Table 2). The changes in relative allocation to the fine roots observed in these loblolly pine stands is consistent with the patterns that would be expected if reduced relative allocation to fine roots is caused by increased relative allocation to the stem. The largest values of relative root allocation occurred when the physical requirements of the crown were small as indicated by relatively small combinations of M_0 and ΔM, and the smallest values of relative root allocation occurred when the physical requirements of the crown were large as indicated by relatively large values of M_0 and ΔM (Figure 3a). The physical requirements of the crown implied by the various combinations of M_0 and ΔM are reflected in the values of relative stem allocation as expected; i.e., slowly increasing as the combination of M_0 and ΔM increases (Figure 3b).

Table 2. Treatment means and *P*-values for the effects of irrigation and fertilization during 1996 on the cumulative bending moment at the beginning of the growing season (M_0), the cumulative change in bending moment during the growing season (ΔM), relative stem allocation (r_s), and relative fine-root allocation (r_{fr}). Data collected from loblolly pine growing in Scotland County, North Carolina, and analyzed with the linear model for a randomized complete block design ($df_{error} = 9$).

	M_0	ΔM	r_s	r_{fr}
	(m³/ha)		(%)	
Treatment means				
I_0	39,492	10,592	32.1	14.6
I_1	52,154	15,419	33.4	11.6
F_0	25,048	8,296	31.2	17.6
F_1	66,600	17,715	34.3	8.6
Pooled SE*	9,507	3,069	2.3	4.1
P-value for effect				
Irrigation (*I*)	0.259	0.012	0.291	0.177
Fertilization (*F*)	<0.001	<0.001	0.024	0.002
I × *F*	0.269	0.375	0.262	0.357

* SE = standard error

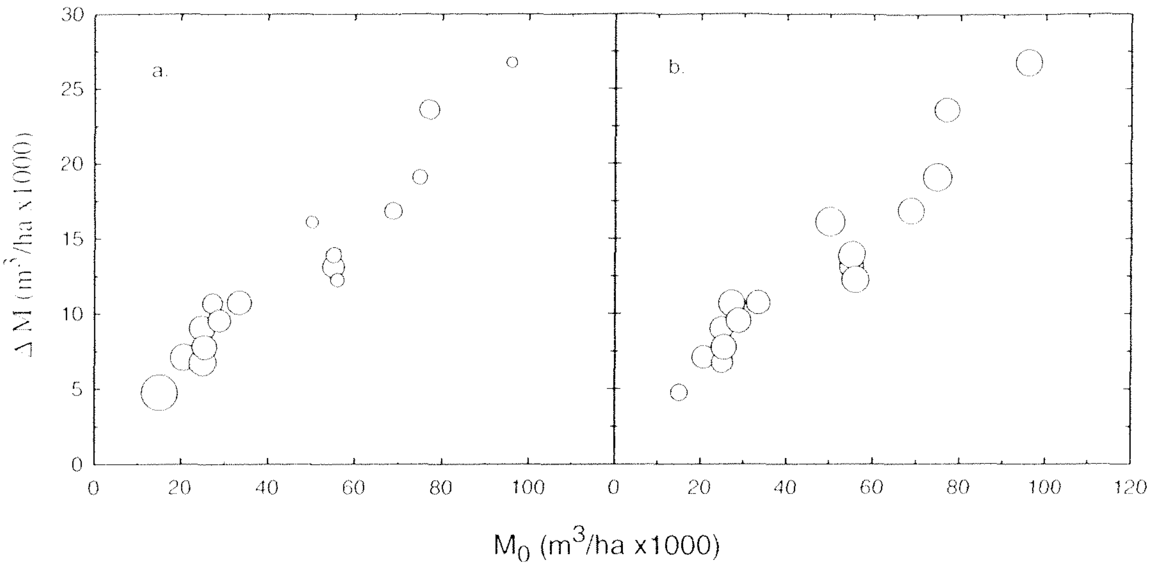

Figure 3. Change in cumulative bending moment during 1996 (*ΔM*) as a function of cumulative bending moment of the plot at the start of the 1996 growing season (*M_0*) for loblolly pine plantations growing in Scotland County, North Carolina. Size of symbols represents relative allocation of total net primary production to fine roots (a) and stem wood (b).

Consequently, across the range of M_0 and ΔM, increased partitioning to the stem is significantly correlated with decreased partitioning to the fine roots (Figure 4).

The inverse relation between relative stem allocation and relative *fine-root allocation (Figure 4) and its apparent* association with bending moment support the possibility of a link between stand structure and relative fine-root allocation. Similar influences of stand structure on relative fine-root allocation can be shown to exist for other species using the assumption that increasing stand density, in terms of either trees per hectare or basal area per hectare, increases the cumulative bending moment through an increase to the height to the middle of the crown and overall stand leaf area. Beets and Whitehead (1996) compared the effects of soil nutrition on the carbon allocation within radiata pine (*Pinus radiata* D. Don) stands across a range of stand densities. From the data they present in their Table 1, relative allocation to the fine roots decreases with relative allocation to the stem for all treatments, and within individual treatments, relative allocation to the fine-roots decreases and relative allocation to the stem increases systematically with increasing stand density with only one exception (Figure 5).

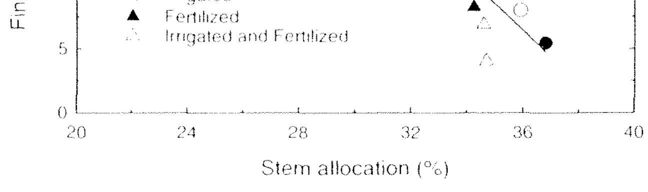

Figure 4. Fine-root allocation in relation to stem allocation for variously treated loblolly pine plantations growing in Scotland County, North Carolina. Allocation to both biomass components expressed as a percent relative to total net primary production. Line fitted with ordinary least squares.

An effect of stand structure on biomass allocation also seems evident in a study on biomass allocation in stands of 40-yr-old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) growing on good and poor sites (Keyes and Grier 1981). On the good site, Douglas-fir partitioned 46 and 7.9% of its growth to stems and fine roots, respectively, and on the poor site, it partitioned 27.3 and 36.4% of its growth to stems and fine roots. These allocation patterns corresponded with average tree heights on the good and poor sites of 33 and 23 m, respectively, suggesting that trees on the good site were subjected to greater wind forces than trees on the poor site.

Stand structure may add a new perspective to the somewhat anomalous results reported by Nadelhoffer et al. (1985), who reported a reduction in relative allocation to fine roots with decreasing site quality (the typical pattern is increased relative allocation to fine roots with decreasing site quality). While this anomaly is often attributed to the species changes that occurred across the sites (Cannell and Dewar 1994), the brief descriptions of the various stands used in the study suggest that the observed values of relative fine root allocation are due to stand structure, not the species dominating the stand, at least at the extremes. The largest value of relative partitioning to the fine roots was observed at the site with the greatest nitrogen availability. This stand was comprised of a few (i.e., 170 stems/ha) black oak (*Quercus velutina* Lam.), white oak (*Quercus alba* L.), black cherry (*Prunus serotina* Ehrh.), and shagbark hickory (*Carya ovata* [Mill.] K. Koch) in the overstory with a midstory of red maple (*Acer rubrum* L.). Ward (1964) has shown that both live-crown ratio and live-crown length decrease with increasing stand density in 10 to 40-yr-old stands of red oak (*Quercus rubra* L.). If these species react similarly, such low overstory densities would

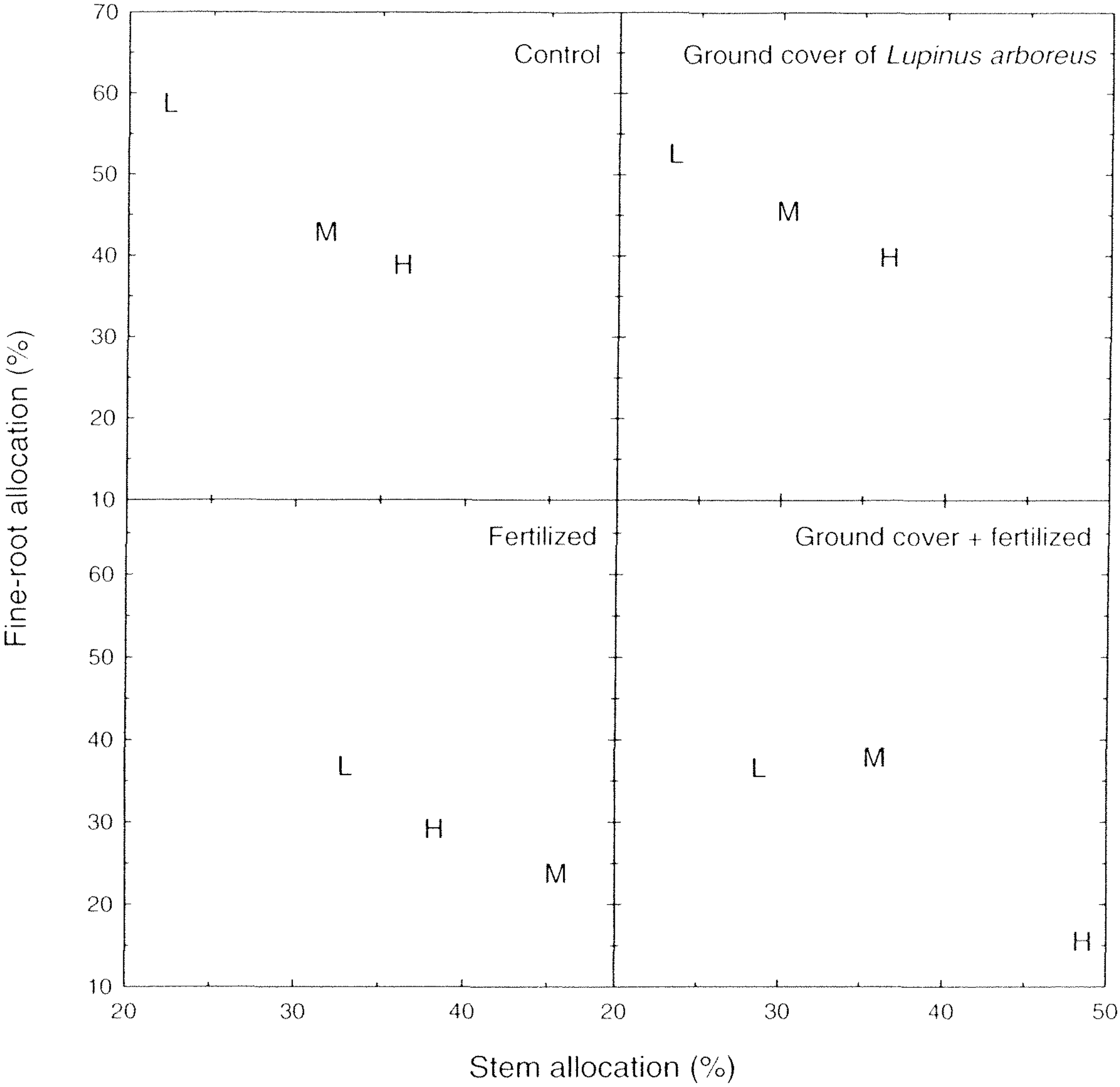

Figure 5. Fine-root allocation in relation to stem allocation for variously treated radiata pine plantations at the Woodhill Forest in New Zealand. Allocation to both biomass components expressed as a percent relative to total net primary production. Symbols refer to the number of trees per hectare of the stands in which allocation was determined: *H* = 2222; M = 1483; *L* = 741. Treatments used in this study were the control, ground cover of *Lupinus arboreus*, fertilized, and ground cover of *L. arboreus* combined with fertilization. Data from Beets and Whitehead (1996).

result in relatively small cumulative changes in bending moment. This would explain the relatively small allocation to perennial tissues in this stand compared to the other stands in this study. At the other extreme, the lowest value of relative allocation to the fine roots was observed at the site with the poorest nitrogen availability. The stand on this site consisted of uniformly sized white spruce (*Picea glauca* [Moench] Voss) growing at 2,024 trees/ha. The relatively high allocation to perennial tissues and low relative allocation to the fine roots corresponds with this stand's high density and uniformity.

These results support the possibility that stand structure affects the relative allocation of biomass belowground, especially to the fine roots. While more definitive experiments are required to confirm such a link, the patterns observed in this study and in published data suggest that stand structures that create greater physical stress on tree stems result in lower allocations of a fixed amount of production to the fine-root system. When the greater stress is created from treatments that increase resource availability, the capacity of the root system to acquire sufficient quantities of nutrients is probably unaffected. However, when the increased stress is simply the result of greater stand density with no change in resource availability, the sufficiency of the root system may decline, which may subsequently affect nutrient uptake and related physiological processes.

While stand structure appears to be a factor in the relative allocation of biomass to the fine-root system, these results indicate that stand structure alone cannot be used to calculate relative allocation to fine roots. One of the assumptions of this analysis is that the biomass allocated to the fine roots is that which remains after biomass is allocated to foliage, branch wood, stem wood, the tap root (if present), and the coarse root system. The link between stand structure and fine-root allocation apparently occurs through the effects of stand structure on the physical requirements of the stem. Until the principles governing biomass allocation to these other components are better understood or a different approach is discovered, the relationship between stand structure and fine-root allocation will necessary remain an empirical relationship and will need to be established experimentally if it is to be used in a growth simulation model.

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