

Episodic Growth and Relative Shoot:Root Balance in Loblolly Pine Seedlings

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ABSTRACT

Leaf, root and stem systems of loblolly pine seedlings are characterized by a seasonal periodicity in growth, during which they alternate in spurts of activity. Despite this periodicity, the allometric coefficient describing the ratio of the relative growth rates of leaf to root remains constant for at least the first two years of development. In part, constancy results from the inability of variation in the allocation of growth increment during brief periods to change a pre-existing structure accumulated over the life of the seedling. In addition, alternating periods of leaf, root and stem growth may represent the action of feedback mechanisms which operate to maintain an adaptive balance between organ systems.

Keywords: *Pinus taeda* L., loblolly pine, allometric coefficient, homeostatic control of growth.

INTRODUCTION

Allocation of photosynthate to dry matter sinks in the shoot and root systems of tree seedlings is governed by interrelated physiological needs and dependencies. Photosynthate appears to be partitioned between shoot and root organs in inverse proportion to relative activity (Davidson, 1969; Thornley, 1972); i.e. root weight $\times$ rate of water and nutrient absorption $\propto$ leaf weight $\times$ rate of photosynthesis. As need for water and minerals increases, a corresponding increase in root biomass takes place. Likewise, with increased photosynthetic needs, growth of the shoot results. A functional equilibrium is maintained.

Allometric analysis is an effective way of characterizing the dynamic balance between shoot and root biomass (Huxley, 1924). The allometric equation, $\log(\text{shoot d. wt}) = a + k \cdot \log(\text{root d. wt})$, expresses the balance between growth of these two organs during ontogeny. When the allometric coefficient, k , which is an expression of the proportionate constant in Davidson's (1969) equation, is less than 1.0, relative growth rate of the roots is greater than relative growth rate of the shoot. When k is greater than 1.0, the converse is true. The shoot:root ratio declines for at least the first few years in conifers; i.e. $k < 1.0$. Ledig *et al.* (1970) discuss some of the considerations involved in applying allometric growth analysis to studies on tree seedlings with special reference to loblolly pine (*Pinus taeda* L.).

It has been assumed that the allometric coefficient is constant, and therefore expresses the long-term balance or equilibrium between shoot and root development (Ledig *et al.*, 1970). Short-term determinations of the relative distribution of assimilate are often used to partition future dry matter increments by means of appropriate coefficients in

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iterative growth models (Ledig, 1969; Ledig and Botkin, 1974). However, Cannell and Willett (1976) have shown that allometric trends may in part reflect conditions at the time seedlings were sampled. Late fall and winter root growth can result in a rapid change in the pattern of growth distribution. Because relative distribution of dry matter depends on seasonal growth periodicities, the constancy of the allometric coefficient is in doubt. In conifers it is possible that allometric coefficients determined over several growing seasons may be lower than those calculated in short-term studies such as those of Ledig, Bormann and Wenger (1970) or Drew and Ferrell (1977). Cannell and Willett (1976) show that 'imbalances' in shoot and root development acquired during summer and fall growth of three tree species were 'corrected' each spring and early summer. 'Excessive' shoot growth was later balanced by compensatory root growth. Greater 'imbalances' were reversed by greater 'corrections'.

In the present study, progeny of controlled crosses in loblolly pine were analysed for d. wt change over two growing seasons to determine whether seasonal periodicities in relative growth of shoot and root are reflected by changes in the allometric coefficient.

MATERIALS AND METHODS

Seed representing six full-sib families of loblolly pine (*Pinus taeda* L.) was supplied by Weyerhaeuser Company. Three of the controlled crosses, 74×76 , 35×33 , and 76×31 were from the South Coastal Plain progeny test planting, Craven County, North Carolina and three others, 80×7 , 21×1 , and 8×141 were from the North Coastal Plain progeny test, Bertie County, North Carolina. Seed were stratified 60 days and sown between 23–24 April 1974, one per pot, in soil dug from respective progeny test planting sites. Families were confounded with soils to satisfy objectives of a broader study of which this is a part. The confounding has no importance for the results discussed below. Both soils were mixed thoroughly before potting. The Craven County soil was a black peat, rich in organic matter whereas the Bertie County soil was more of a brown loam with less organic matter.

Seedlings were germinated on 6 May 1974 in a greenhouse and placed in an outdoor nursery at New Haven, Connecticut between 9–13 May 1974 in clay pots sunken into soil to their rims. Mortality was replaced two to three weeks later (i.e. 30 May to 10 June) by transplanting extra seedlings from seed sown in small peat pots at the same time the main experiment was sown in clay pots. The small peat pots were sunk into soil in the larger clay pots and the roots allowed to grow through the decomposing peat wall. No differences in morphology or size of root system were observed between seedlings sown directly and those transplanted to the larger pots.

Clay pots were sunken into soil to their rims and the pots rotated periodically to restrict root growth to the pots and ensure recovery of the complete root system at harvest. While growth in containers might conceivably alter root growth, the use of pots was a necessary evil to permit recovery of the entire root system. Seedlings to be harvested during the first year were grown in 1.9 l clay pots. Those to be harvested the second year were grown in 3.8 l pots.

Because of the possibility of winter frost damage occurring in loblolly pine planted this far north, we protected the seedlings during the first winter by moving the pots to four-sided, plywood frames with corrugated fibreglass tops. The tops were removed during days of mild weather between 28 November 1974 and 17 March 1975, but remained in place almost continuously after 22 December. Lead-sheathed heating cable was strung through the frames and thermostated to turn on whenever temperatures fell below 0°C . The heating cable maintained temperature of air surrounding seedlings at -6.5°C during the coldest nights of -10°C .

Shoots of seedlings were damaged the second year by tip moth. This had been un-

anticipated in New Haven and virtually all seedlings showed some degree of damage. A spraying with malathion on 2 September 1974 had little effect as most damage had already occurred.

Seedlings were harvested for dry weight assessment at biweekly intervals between 6 June and 4 December 1974 for a total of 13 sampling periods. All six full-sib families were sampled near the beginning of each month, but at the mid-month harvest only crosses 74×76 and 80×7 were sampled due to a shortage of seed from the other crosses.

In 1975, harvests began on 6 February and ended on 13 December, totalling 12 in all. These were at biweekly intervals at the peak of growth during May and June, but at monthly and bimonthly intervals towards the beginning and end of this period, respectively. Again, crosses 74×76 and 80×7 were the only plants involved in some of the harvests. All seedlings were mycorrhizal irrespective of family or soil.

At each harvest period, seedlings were divided into green leaves, dead leaves, stem and branches, and roots. These portions were dried at 80°C for at least 2 days, transferred to dessicators containing drierite, and weighed after cooling.

The relative distribution of growth between leaves and roots, the primary physiological sinks, was examined allometrically. The regression of leaf or shoot d. wt on root d. wt was computed after transformation to natural logarithms.

RESULTS

For all six families the allometric relationships were remarkably similar (Table 1). There were no deviations from the general pattern in any instance nor were there any differences in slope. A common allometric constant of 0.90 characterized the logarithmic regression of leaf d. wt on root d. wt with little deviation over the 2 year period even for tip moth-damaged plants which might be expected to have suffered loss of leaf growth (Fig. 1).

TABLE 1. *Parameters of the allometric relationship of shoot to root, $\log(\text{shoot}) = a + k \log(\text{Root})$, for six full-sib families of loblolly pine seedlings*

Soil	Family	<i>a</i>	<i>k</i>
Craven Co.	74×76	-0.057	0.919
	35×33	-0.099	0.901
	76×31	0.018	0.896
Bertie Co.	80×7	-0.238	0.978
	21×1	-0.028	0.866
	8×141	0.007	0.891

Increment in leaf, stem, and root d. wt as a percentage of total d. wt increment varied substantially among harvest periods (Fig. 2). Data are not presented for the second year because tip moth damage resulted in erratic or dubious patterns and sampling was less intensive. An oscillation of leaf and root growth was obvious, but because of the manner in which growth increments were calculated, it was not possible to statistically test differences among sampling intervals. However, we were able to analyse differences in shoot:root ratio. A change in these ratios indicates that the increment in shoot or leaf was not in the same proportion as that in root. In fact, seasonal variation (i.e. variation among sampling dates) was highly significant. Fluctuations suggested a higher allocation to leaf than to root growth during some periods accompanied by reversals in subsequent periods.

Leaf and root incremental changes appeared inversely correlated over time (Fig. 2). When the proportion of total d. wt allocated to leaves increased, that allocated to roots decreased, and vice versa. A complementary pattern must be expected when only two

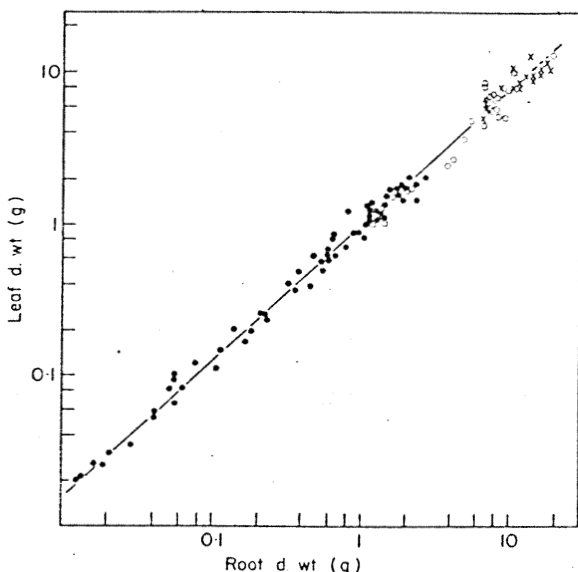


FIG. 1. The relationship of leaf d. wt to root d. wt for six full-sib families of loblolly pine over two growing seasons, a period from one to 20 months after germination ($n = 1$ to 6). ●, First year; ○, second year; X, tip moth damaged. $\text{Log}(L) = 0.902 \text{Log}(R) - 0.022$; $r = 0.99$.

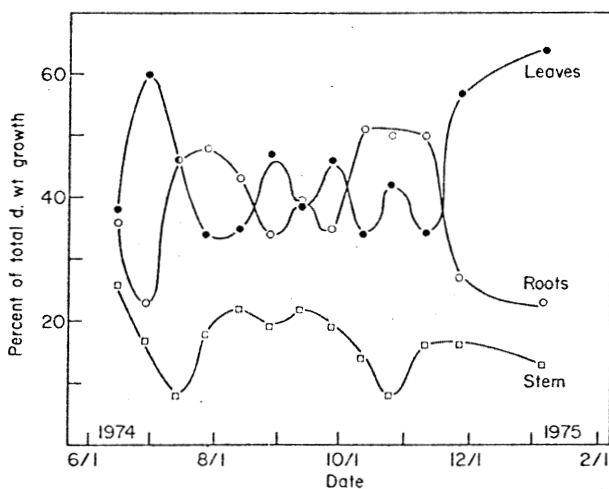


FIG. 2. The distribution of d. wt increment between leaves, roots, and stems, expressed as a percentage of total increment, for different periods during the first growing season in 74 × 76, a full-sib family of loblolly pine seedlings ($n = 6$). Ratios are plotted over mid-harvest date because they are derived from differences in dry weight between harvests and refer to increments during the interharvest period. ●, Leaves; ○, roots, □, stem.

components are expressed as a proportion of the total, but the present case is a three-component system. Large increments in stem growth generally occurred during times of reduced allocation of dry matter to leaf growth. For all six full-sib families, stem growth appeared better correlated with changes in leaf biomass than with root biomass. Depending upon harvest period, leaf growth in family 74 × 76 (illustrated in Fig. 2)

accounted for anywhere between 64 and 33 per cent of total growth, and there was a similar range for root growth. Though other crosses showed different patterns, nevertheless all maintained the same allometric relationship, partly because differences in allocation during any brief period is ineffective in changing the pre-existing structure, which has been accumulated over long periods.

DISCUSSION

The similarity among the six families in leaf:root relationships was striking. Ledig and Perry (1965) and Ledig *et al.* (1970) had previously noted genotypic variability in relative shoot:root growth in first-year loblolly pine, but they sampled a much larger number of families. The constancy of the allometric coefficient over time, i.e. from one season to the next during the two-year study, was obvious. Cannell and Willett (1976) showed that the ratio of shoot:root varied seasonally in Sitka spruce and lodgepole pine [*Picea sitchensis* (Bong.) Carr. and *Pinus contorta* Dougl.], a fact they attributed to periodicity of shoot development which is rigidly controlled by photoperiod and temperature. Growth of loblolly pine is under control of the same types of adaptive mechanisms, and seasonal changes in relative growth of leaf and root are evident. Nevertheless, the allometric coefficient appears relatively constant and retains a high degree of predictability ($r^2 = 0.98$).

For such uniformity in relative leaf:root growth to occur in loblolly pine, the allocation of dry matter to new plant tissue must be under the control of a sensitive feedback system, as suggested by Cannell and Willett (1976). Apparently, feedback mechanisms operate to correct seasonal 'imbalances' in pines, so that viewed from a broader perspective over a period of several years the relative growth of leaf and root mass retains its general pattern.

Because of the relatively rapid change in short-term pattern of allocation to leaf, stem, and root growth (Fig. 2) the control mechanism may be either substrate concentration acting directly as suggested by Thornley (1972) or by its influence on hormone production. The existence of such a system in the cyclic growth of leaves and root system in pitch pine (*Pinus rigida* Mill.) was apparent in Ledig, Drew and Clark (1976). Maximum rates of increase in size of either organ were separated in time, while the rate of change in total plant d. wt was constant. The physiological impulse behind shifts in allocation is probably hormonal but poorly understood.

Based on the model developed by Thornley (1972), an increase in root biomass would be accompanied by a decrease in specific activity of the root. Likewise, specific activity of the shoot would decrease with increased shoot biomass. Thornley's model, which has been verified experimentally (Davidson, 1969; Charles-Edwards, 1976; Cooper and Thornley, 1976), suggests that cyclic changes in specific activity of both shoot and root, such as changes in rates of carbon dioxide and nitrogen uptake, respectively, may be correlated with and perhaps responsible for oscillatory behaviour in partitioning of assimilate. Photosynthesis and root absorption are differentially rate-limited by environmental variability under temporally changing field conditions. For example, diurnal soil temperature lags behind air temperature; therefore, conditions favouring optimum photosynthesis occur prior to most favourable periods of root absorption and nutrient uptake. Such external regulation of internal plant processes may be basic to understanding homeostatic regulation of shoot:root development.

The major point is that pine seedlings during their early years do not deviate greatly from the generalized allometric relationship which describes leaf or shoot mass relative to root mass. This constancy is apparent despite comparison of different soils, different families, different sized containers in year one and two, damage from tip moth, and most importantly, short-term fluctuations in the fate of photosynthate. The short-term

pattern must reflect a homeostatic mechanism tending to maintain the seedling on an appropriate developmental path.

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