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THE DISTRIBUTION OF DRY MATTER GROWTH BETWEEN SHOOT AND ROOTS IN LOBLOLLY PINE[1]

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ABSTRACT

The allometric relationship, $\log (y) = a + k \cdot \log (x)$—where x is one plant organ (e.g., dry weight of roots) and y is another (e.g., dry weight of shoot)—was used to study the relative distribution of growth within loblolly pine seedlings. The relative distribution of growth between shoot and roots or among needles, stem, and roots was unchanged by conditions ranging from full sunlight to one-third of full sunlight. There was an indication that the growth of the shoot was inhibited by soil moisture stress to a relatively greater degree than the growth of the roots, as shown by a decrease in slope of the allometric relationship. These results and data reanalyzed from the literature suggested that the relative growth of shoot to root in pine is surprisingly constant under the usual conditions of culture. The ontogenetic decrease in the ratio of shoot to root seems to be a common trend in woody seedlings, and this pattern can be interpreted as adaptive.

Introduction

The balance between the shoot and the root (or their relative growth rates) is important in understanding the mechanism by which plants adapt to their habitat, and perhaps in explaining variation in dry matter production. Ecologists and physiologists have suggested that relatively large tops and small root systems in shade-grown plants may be an environmentally induced adaptation which permits higher rates of photosynthesis per plant under low light intensity (BORMANN 1958). The utilization of available energy has resulted in the relative predominance of light-intercepting surface. Conversely, relatively large root systems and small tops would seemingly fit a sun-grown plant to conditions where energy is abundant, but where high rates of transpiration prevail. In dry matter production, an individual would be at an advantage if it distributed more of its photosynthate to the production of leaves, provided that the roots were of sufficient extent to supply water to the top.

Many investigators sought to determine the effect of environmental treatment on the growth of shoot and root by analysis of the shoot/root ratio (i.e., the weight of the plant top divided by the weight of the roots). The use of the shoot/root ratio frequently led to incorrect interpretations because of the failure to recognize that it changed with the growth of the plant. Comparison of the shoot/root ratio of plants of different sizes is, therefore, questionable, and reinterpretation of some previous studies was made by LEDIG and PERRY (1965).

Because many previous conclusions on the effect of light and moisture during ontogeny were based on shoot/root ratios, an allometric analysis of the effect of these variables on shoot and root growth in loblolly pine (*Pinus taeda* L.) is presented below. Allometry is the study of relative growth. The effect of light and moisture on seedling growth is reported. Data of other investigators were reinterpreted using the allometric formula to illustrate the dynamics of plant growth.

Review of the literature

SHOOT/ROOT RATIO.—The use of shoot/root or top/root ratios is common in the physiological and ecological literature. The ratio or its inverse, the root/shoot ratio, was cited as a growth correlation by MEYER, ANDERSON, and BÖHNING (1960), but the fact that the ratio changes as the plant grows was ignored. Among others, TURNER (1922) had observed that the shoot/root ratio was not a constant but changed as the plant grew. He felt that this was inexplicable, but PEARSALL (1927), TROUGHTON (1956), and LEDIG and PERRY (1965) have recognized that the change was the result of a difference between the rates of growth of the shoot and the root. Thus the shoot/root ratio of a single plant changes throughout its growth, making comparisons by analysis of the ratio difficult to interpret.

An effect of light intensity (i.e., shade or sun) on development of the shoot or root has been widely assumed by ecologists. Morphological development is obviously affected (e.g., BORMANN 1958). It was reported that the shoot/root ratio decreased with increasing light intensity for over-cup oak (*Quercus lyrata* Walt.) and loblolly pine by KOZLOWSKI (1949) and confirmed for loblolly by BORMANN (1958). Similar results, though not significant, were reported for ponderosa pine (*Pinus ponderosa* Laws.) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in the study of STEINBRENNER and REDISKE (1964). Alternate conclusions are possible based on the allometric formula.

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ALLOMETRIC GROWTH.—Shoot and root growth are logarithmic in seedling stages of many plants, and the ratio of the relative growth rates is a constant. The constant can be approximated by the regression coefficient of the logarithmic relationship between the dry weight of the shoot and the dry weight of the roots; that is, log (shoot dry weight) = $a + k \cdot \log$ (root dry weight). HUXLEY (1924) pioneered the use of similar relationships in animals and has termed the formula the allometric equation (HUXLEY 1932). It can be applied to investigation of the relative growth of shoot to root (*see* PEARSALL 1927; TROUGHTON 1955; LEDIG and PERRY 1965).

Comparison of the regression coefficients of the allometric formula is the most useful test of the effect of environmental factors on relative growth of shoot and root. The allometric relationship holds for plants grown under a single treatment (PEARSALL 1927; TROUGHTON 1955, 1956; LEDIG and PERRY 1965). Therefore, if two treatments differ in their effect on shoot-root balance, the slopes of their allometric regressions will differ.

Allometry has been treated mathematically by REEVE and HUXLEY (1945), PEARSALL (1927), TEISSIER (1948), and LEDIG and PERRY (1965), among others. The slope of the equation accounts for the dynamic aspect of shoot-root balance, and for this reason alone may be preferred to a static shoot/root ratio which applies to only one transient period in development. The formula has more biological meaning than any ratio, and its use is not restricted to the shoot-root relationship; for example, length-width changes in fruit development (SINNOT 1936), blade diameter-petiole length relationships in leaves (PEARSALL 1927), or almost any other conceivable pair of measurements can be studied by allometry.

Using various forage grasses, TROUGHTON (1955, 1956, 1960, 1961, 1963) has shown that the allometric constant for shoot on root increases as a result of nitrogen fertilization, soil moisture, and light intensity, and with photoperiods or temperatures above optimum. In other words, the shoot/root ratio increases at a faster rate under high nitrogen, moisture, and light treatments than at low levels. WAREING (1950) used the allometric equation to show that photoperiod had no effect on the relative growth of shoot to root in Scots pine (*Pinus sylvestris* L.), and he stressed that analysis of the shoot/root ratios would give the erroneous impression that long photoperiods decreased shoot-to-root balance.

Material and methods

FIELD.—Six plots were established in Atlanta, Georgia in a well-drained field in two rows of three plots each. Each plot was surrounded by a 1 ft × 8 ft × 8 ft wooden frame. By random choice, one plot in each row was left open (full sunlight), while screens were constructed over the remaining two plots. Using combinations of varnished screen and cheesecloth, the two plots in each row were screened to permit $\frac{1}{3}$ or $\frac{2}{3}$ of full sunlight at noon, as measured at ground level by a Weston Illuminometer Model II. The screens extended to within 1 ft of the ground on the east, south, and west sides of the plot, but were open on the north side. This permitted a relatively small amount of skylight (3%) to enter the screen plots from the north, but the arrangement promoted better ventilation on hot sunny days. Estimates of light reaching the plants are given in BORMANN (1956*b*).

Seeds were planted in flats on April 23. On May 2, 312 seedlings were transplanted to 8-inch clay pots, each containing a weighed amount of well-mixed composite soil. The mixture was local floodplain soil plus sand in a 2:1 ratio and contained 70% sand, 16% silt, and 14% clay with a field capacity of 11%, and a permanent wilting percentage of 4.7% providing 6.3% available water. The mixture was planned to facilitate the effectiveness of drought treatments and to increase the efficiency of root recovery by washing. Just prior to planting the seedlings, $\frac{1}{3}$ teaspoon of 4-8-4 fertilizer was stirred into the surface soil of each pot.

On May 18, the pots containing seedlings were randomly assigned, 52 to each plot. Each plot was randomly divided into two halves, each with 26 pots, to establish two watering regimes. On one half, pots were brought to field capacity each evening except when this was not necessary due to rain. Pots receiving the drought regime were treated the same way during the first 3 weeks in each of three 7-week growth periods. Thereafter, they were allowed to dry down as the weather permitted. Soil moisture was sampled gravimetrically; when soil moisture reached the permanent wilting percentage, the pots were rewatered for several days and then allowed to dry down again. Because all three growth periods contained extensive dry periods, it is certain that all drought plants received extensive amounts of drought, but it is unlikely that they received exactly equivalent amounts of drought.

At 7-week intervals, six seedlings were randomly selected, removed from each half plot (12 seedlings per treatment), and analyzed. Sampling dates were July 6, August 24, and October 12. Prior to the selection of seedlings, all plots were carefully examined and any seedlings showing signs of damage due to insects, fungi, or animals were removed. The experimental design yielded 12 seedlings from each of six light-moisture regimes at each of three ages—9 weeks, 16 weeks, and 23 weeks. The seedlings had been grown in the light moisture treatments for 7 weeks, 14 weeks, and 21 weeks, respectively. A total of 234 seedlings were analyzed in the experiment.

At harvest, roots were gently washed out of the soil. The length of roots from root crown to the tip of the longest root was measured, as was the hypocotyl and stem above the hypocotyl. A photograph of each treatment group was made and then each seedling was dissected into roots, hypocotyl, stem, and juvenile and secondary leaves. These were oven-dried and weighed. Numbers of primary and secondary leaves were counted.

Total dry weight, weight of individual organs, and number of needles were subjected to analysis of variance. For allometric growth, regressions were run for each treatment and differences among regressions were tested (STEEL and TORRIE 1960, p. 319).

Results

The data analyses showed that the effect of lifting time (i.e., age of seedlings) on all observed seedling characteristics was highly significant. This result was expected, since it means only that the average seedling grew appreciably in these characteristics. Data are summarized in table 1.

Stem and roots grew in length at a relatively uniform rate during the observation period, and

TABLE 1

EFFECT OF LIGHT AND MOISTURE ON DRY WEIGHT GROWTH OF SHOOT, ROOT, JUVENILE NEEDLES, SECONDARY NEEDLES, AND TOTAL SEEDLING, ON ELONGATION GROWTH OF SHOOT AND ROOT, AND ON NUMBER OF JUVENILE AND SECONDARY NEEDLES

	LIGHT[a]			MOISTURE[b]		MEAN
	Full	⅔ full	⅓ full	High	Low	
Total dry weight (mg):						
9 weeks	152	148	107	142	130	136
16 weeks	476	423	404	545	324	434
23 weeks	2,139	1,698	1,405	2,302	1,193	1,747
Shoot dry weight (mg):						
9 weeks	95	100	77	94	88	91
16 weeks	292	275	280	361	204	282
23 weeks	1,014	911	833	1,190	649	919
Root dry weight (mg):						
9 weeks	57	48	30	48	42	56
16 weeks	184	148	124	184	120	152
23 weeks	1,125	787	572	1,112	544	828
Juvenile needle dry weight (mg):						
9 weeks	77	78	60	74	69	75
16 weeks	173	164	148	188	136	162
23 weeks	291	237	192	261	218	240
Secondary needle dry weight (mg):						
9 weeks	0	0	0	0	0	0
16 weeks	55	49	63	89	23	56
23 weeks	481	471	425	316	286	459
Stem length (cm):						
9 weeks	1.7	2.4	2.9	2.5	2.1	2.3
16 weeks	4.6	5.7	7.3	8.0	3.7	5.8
23 weeks	8.1	8.3	9.8	11.0	6.5	8.8
Root length (cm):						
9 weeks	24.5	21.9	18.1	22.6	20.4	21.5
16 weeks	47.9	40.3	36.4	48.6	34.5	41.5
23 weeks	68.6	57.3	43.3	67.1	45.7	56.9
No. of juvenile needles:						
9 weeks	72	78	76	79	72	75
16 weeks	132	123	135	146	114	130
23 weeks	174	142	150	163	147	155
No. of secondary needles:						
9 weeks	0	0	0	0	0	0
16 weeks	23	24	30	40	12	26
23 weeks	68	61	62	81	46	63

[a] Each mean is based on 24 seedlings.

[b] Each mean is based on 36 seedlings.

watered plants grew more than unwatered plants. In contrast to growth in length, weight of both stems and roots increased rather slowly during the first 16 weeks, then increased sharply between the sixteenth and twenty-third week. The sharp increase paralleled the appearance and weight growth of secondary needles (table 1). The increase in total dry matter was greater in watered than in unwatered plants, and this effect was greatest at high light intensity.

Both juvenile and secondary needles were more numerous on watered than on unwatered seedlings, but light had no general effect on either characteristic. Among the unwatered seedlings, those under full light had more juvenile needles than those under less intense light, and the effect of age was negligible until the last 7 weeks. Among watered seedlings, more needles developed under full light during the first 9 weeks than under reduced light.

The dry weight of juvenile needles was increased both by watering and by light. The latter effect, although significant, was of small magnitude. The weight of secondary needles was not affected by light, but the effect of watering was much greater at 23 weeks than at 16 weeks.

There were no significant differences among the regressions for the six light-moisture treatment combinations in relative dry matter growth of shoot and root as shown by comparison of the slopes of the allometric formulae (fig. 1). This indicated that the ratio of shoot to root was on the average similar for two seedlings of the same dry weight, largely irrespective of either the light and moisture treatment combination under which they developed or their age.

The data were combined to test for differences in relative growth of shoot and root among the three light treatments and between the two moisture regimes. There were no differences among the slopes of the allometric equations for seedlings grown under conditions of full, two-thirds, or one-third light. There was a possibility that the moisture regime affected relative growth of shoot and root, with more root being produced under greatest moisture stress. The difference, however, was significant only at the .10 level of probability. If this was indeed biologically important, then the growth of the shoots was inhibited by the dry regime more than the growth of roots. This agrees with the popularly held belief on the adaptive nature of shoot-root development and the work of HARRIS (1914) in crop plants and TROUGHTON (1960) in forage grasses.

Analysis of variance of the shoot/root ratio indicated highly significant differences among treatments. However, this could not be interpreted as an effect of light or water on the growth of tops and roots. The difference existed because an increase either in light or water led to larger seedlings. Manipulation of the shoot/root balance was achieved by controlling seedling size. Large seedlings had a

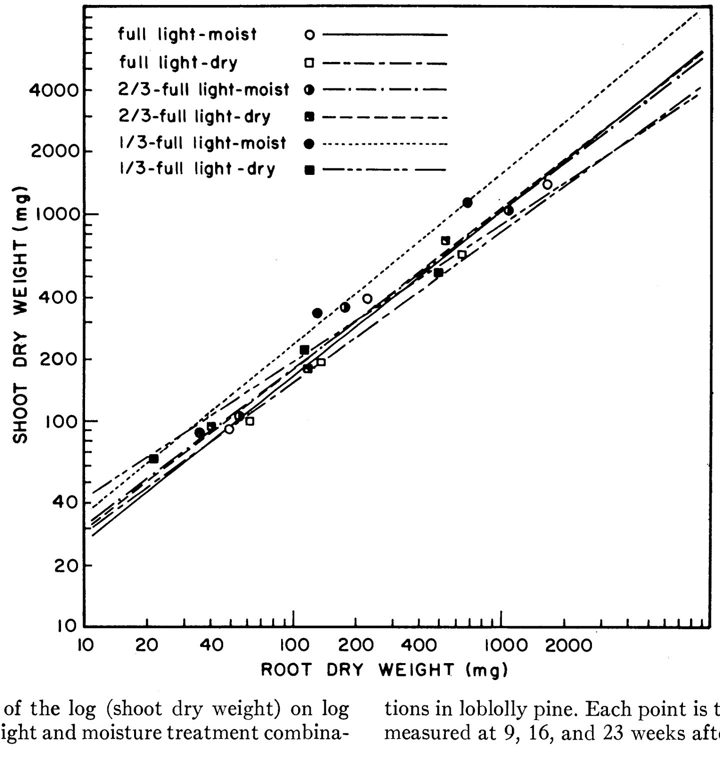

FIG. 1.—Regressions of the log (shoot dry weight) on log (root dry weight) for six light and moisture treatment combinations in loblolly pine. Each point is the average of 12 seedlings measured at 9, 16, and 23 weeks after germination.

relatively smaller shoot/root ratio than small seedlings.

Regression coefficients less than 1.0 signify a proportionately smaller increase in the shoot than in the root. As a result of a more rapid growth of roots than tops throughout seedling development, the shoot/root ratio decreased with growth (fig. 2), as has been reported previously in loblolly pine (LEDIG and PERRY 1965).

Regressions of the logarithms of the dry weights of needles and of stem on the logarithm of the dry weight of the roots paralleled those for shoot on roots (fig. 3).

Apparently, the obvious morphological change from juvenile to secondary needles was not accompanied by any shift in allocation of dry matter growth between shoot and root. The slope of the allometric relation between needles and roots was unchanged throughout the period of leaf development (fig. 4).

The strength of the allometric regressions suggested that they may have predictive value in sampling. From a harvest of seedling tops, the root weight can be predicted; the needle and stem weights can be estimated without stripping the foliage and weighing it separately (fig. 5, table 2).

While the allocation of dry matter increase among shoot and roots or needles, stem, and roots was relatively constant, showing little variation in response to the environments studied, there was no

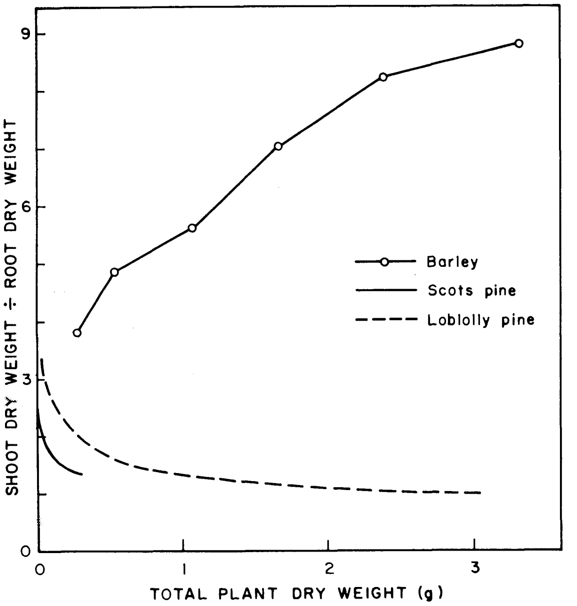

FIG. 2.—The change in shoot/root ratio with increase in total seedling dry weight (i.e., dry weights of tops plus roots) in loblolly pine (present study), Scots pine (after regressions in WAREING [1950]), and barley (after data of TURNER [1922]; $n = 4$).

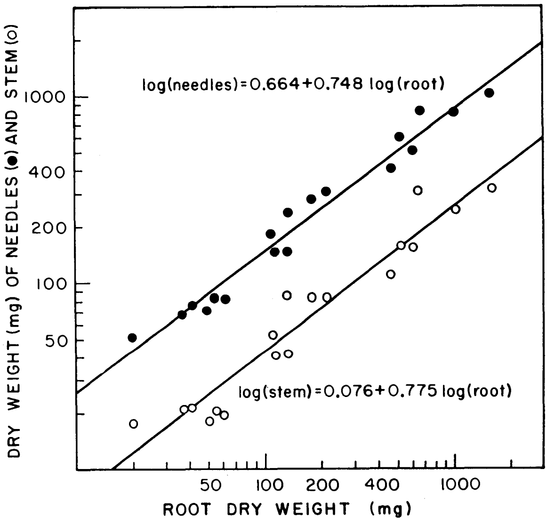

FIG. 3.—The logarithmic regressions of needle dry weight and stem dry weight on root dry weight in seedling loblolly pine. As in the relation of shoot to roots, there is no significant effect of light-moisture treatment combinations on the relative growth of needles or of stem to roots. Each point is the average of 12 seedlings for each of the six treatment combinations measured at 9, 16, and 23 weeks after germination.

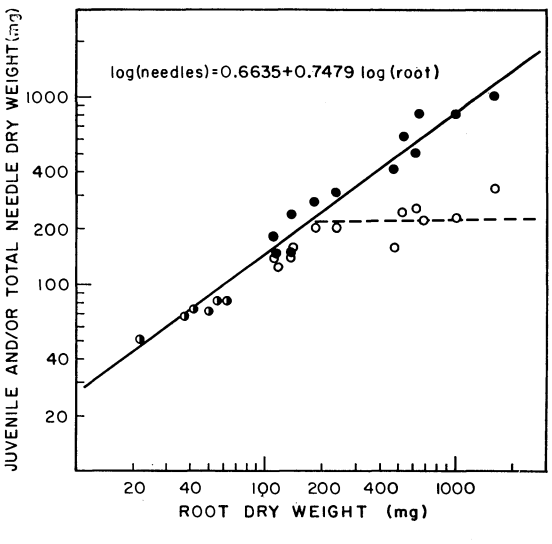

FIG. 4.—The logarithmic regression of total and juvenile needle dry weight on root dry weight in seedling loblolly pine sampled at periods of 9, 16, and 23 weeks after germination. Each point is the average of 12 observations. Averages for juvenile needles (○) represent the same seedlings as the averages for total needles (●) to which they correspond. Total needle dry weight for 9-week-old seedlings (◑) was entirely in juvenile needles. By 16 weeks there was some secondary needle growth, and by 23 weeks all needle growth represented secondary needles. The fact that the slope of the regression remains the same during and after the change from juvenile to secondary needle production indicates that the distribution of dry matter between needles and roots is not affected by the stage of ontogeny.

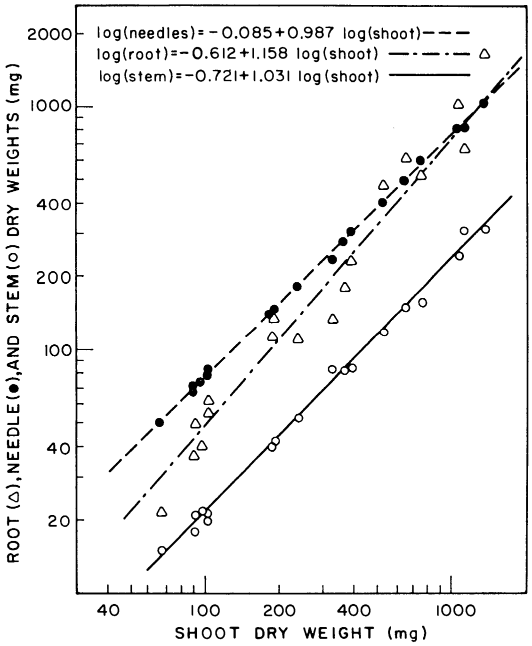

FIG. 5.—Regressions of the logarithms of needles, stem, and roots on the logarithm of top dry weight for loblolly pine seedlings. Each point is the average of 12 seedlings for each of the six treatment combinations measured at 9, 16, and 23 weeks after germination. Prediction of the dry weight of needles, stem, and roots from their regression on top dry weight is possible over the range of treatments tested in this study.

TABLE 2

PARAMETERS OF THE REGRESSION log (Y) = $a + k \cdot \log (X)$, CALCULATED OVER ALL TREATMENTS FOR VARIOUS COMBINATIONS OF ORGANS IN SEEDLING LOBLOLLY PINE

	a	*k*
Root(Y) on shoot(X)	−0.6120	1.1585
Needles(Y) on shoot(X)	−0.0851	0.9870
Stem(Y) on shoot(X)	−0.7206	1.0315
Shoot(Y) on root(X)	0.7638	0.7553
Needles(Y) on root(X)	0.6635	0.7479
Stem(Y) on root(X)	0.0764	0.7749

doubt of the effect of light and moisture on seedling morphology (fig. 6). The crown of shade-grown plants was more open than that of sun-grown plants. To quantify this, the ratio of number of needles/stem length for 23-week-old plants was subjected to an analysis of variance. The number of needles (primary plus secondary) per unit stem length was significantly greater at the .01 level of probability in sun-grown compared with shade-grown plants and in seedlings grown at the low moisture level compared with the high moisture level (table 3).

The reduction in number of needles per unit of stem was due both to a reduction in the total number of needles under less than full light conditions and to an increase in stem length (etiolation) under the maximum shade treatment (table 3). The low-moisture regime reduced both number of needles and stem length, but elongation of the stem was reduced proportionately more, resulting in a greater number of needles per unit stem than under the well-watered regime.

Discussion

The present investigation suggested that, within a range from one-third to full intensity, light had little effect on the relative distribution of dry matter growth amongst needles, stem, and roots in first-year loblolly pine seedlings. Very few experiments have been designed which could detect the effect of light and moisture on the relative growth of shoot and root. Previously, KOZLOWSKI (1949) reported an increase in the relative growth of shoot compared to root in loblolly pine as a result of shading, based on an analysis of the shoot/root ratio. More recently, it has been shown that the allometric relationship of shoot to root in the study by KOZLOWSKI had not actually been changed (LEDIG and PERRY 1965).

The treatments in our experiment affected seedling size and therefore, indirectly, the shoot/root ratio for a given time of lifting. Even though no effect of light or moisture on relative growth of shoot and root could be demonstrated, the possibility of such an effect cannot be ruled out; for example, the regression for one-third light-full moisture shows some departure from regressions for other treatments (fig. 1). However, the light intensities used in the experimental design may not have covered a wide enough range to indicate a potential response. Both TROUGHTON (1960) in grasses and PEARSALL (1927) in pea (*Pisum sativum*

TABLE 3

AVERAGE TOTAL NUMBER OF NEEDLES, STEM LENGTH, AND NUMBER OF NEEDLES PER CM OF STEM IN 23-WEEK-OLD LOBLOLLY PINE SEEDLINGS GROWN UNDER LIGHT AND MOISTURE TREATMENT COMBINATIONS

Treatment	Number of needles	Stem length (cm)	Needle number/ stem length
Full light, moist	263.33	10.43	26.43
Full light, dry	218.42	5.93	38.48
⅔ full light, moist	224.92	10.35	22.09
⅔ full light, dry	180.58	6.23	31.19
⅓ full light, moist	242.08	12.30	20.17
⅓ full light, dry	181.83	7.36	26.94

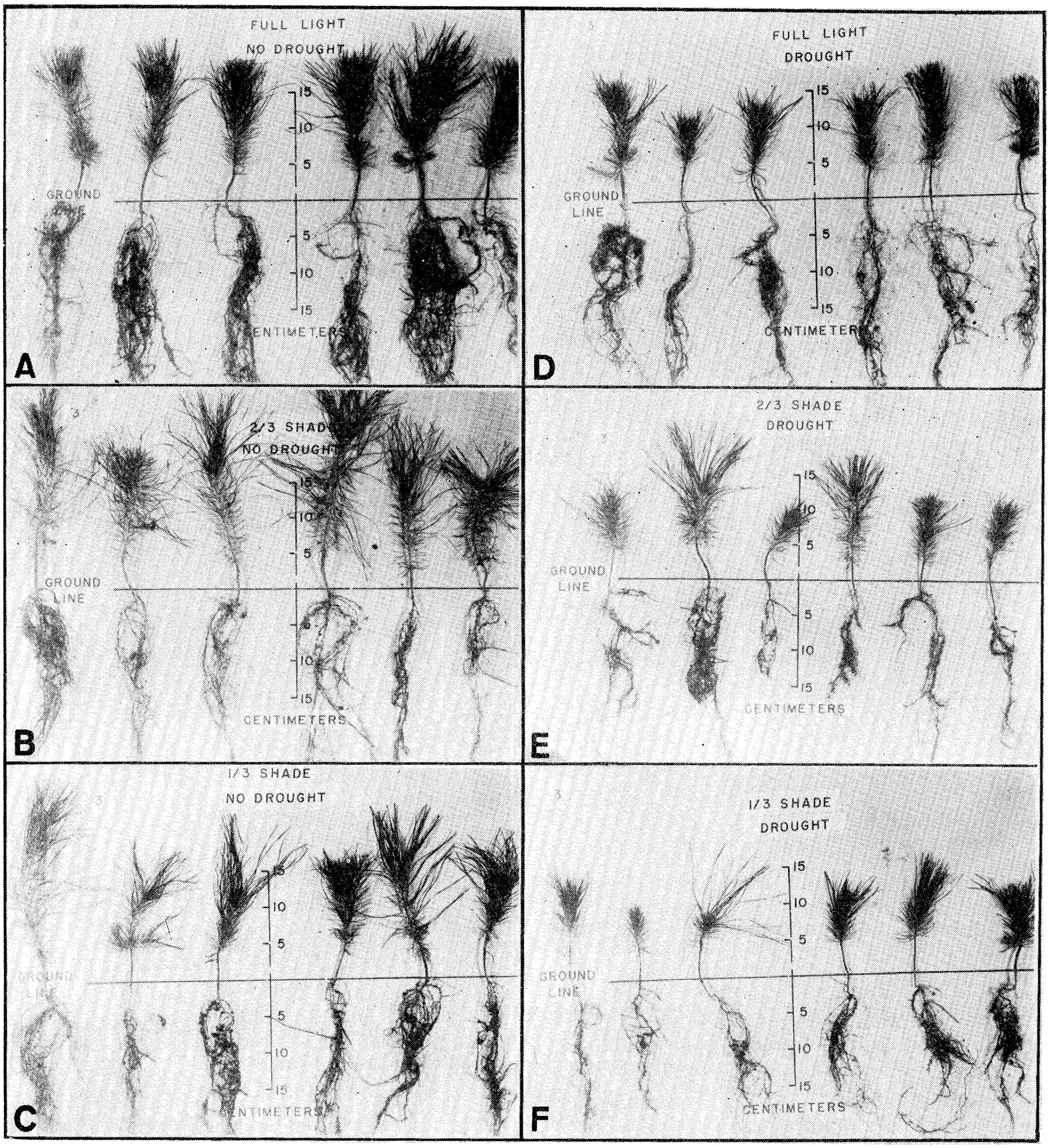

FIG. 6.—Loblolly pine seedlings at 23 weeks of age from the 6 light-moisture treatment combinations: *A*, *B*, *C*—ample soil moisture; *D*, *E*, *F*—soil moisture stress; *A*, *D*—full light; *B*, *E*—$\frac{2}{3}$ full light; *C*, *F*—$\frac{1}{3}$ full light. Seedlings grown in full sunlight have brushlike crowns with short internodes, while those grown under shades which reduced solar intensity have relatively open crowns with long internodes.

L.) have shown that the growth of the roots is inhibited more than the growth of the shoot by shading; TROUGHTON also found an effect due to soil moisture treatments. Perhaps the response of herbaceous plants does not require as drastic a modification of the environment as is necessary for pine.

Data from a growth-chamber experiment with ponderosa pine and Douglas-fir reported by STEINBRENNER and REDISKE (1964) were also analyzed. Their data failed to show any difference between the logarithmic regressions of shoot on root for two levels of light: 1,600 ft-c and 400 ft-c (fig. 7), but a significant interaction occurred between high

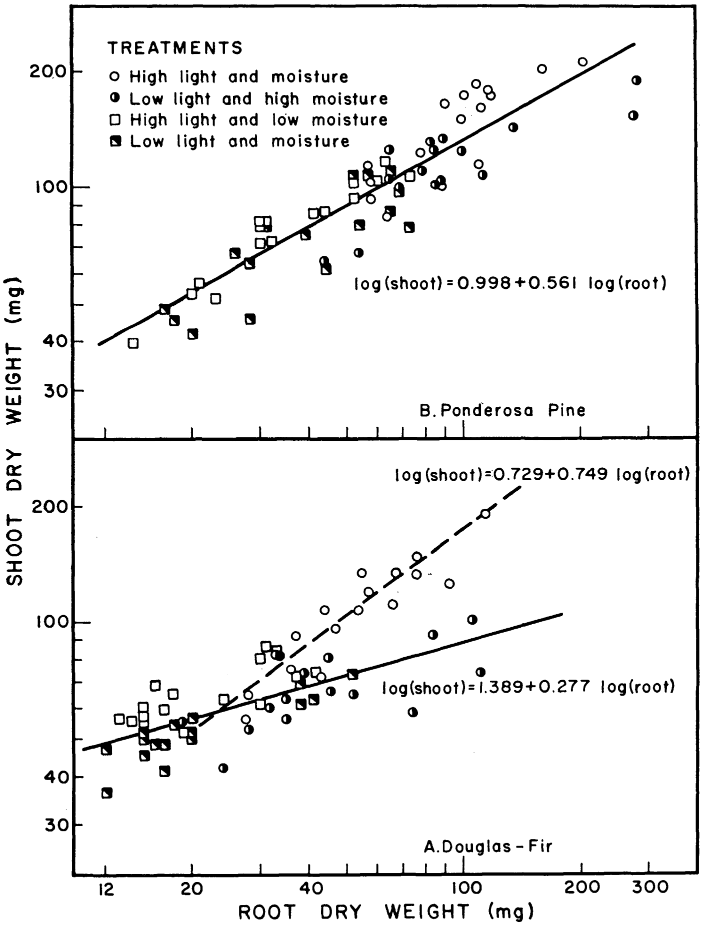

FIG. 7.—Logarithmic plots of shoot dry weight on root dry weight for Douglas-fir (*A*) and ponderosa pine (*B*) grown under four light-soil moisture treatment combinations. Only the logarithmic regression of the high light-high soil moisture treatment combination in Douglas-fir is significantly different from the common regression (after data of STEINBRENNER and REDISKE [1964]).

light and high soil moisture treatments for Douglas-fir, resulting in a greater slope for the logarithmic regression of shoot on root than that observed for the other treatments. No similar response was apparent for ponderosa pine.

The regression coefficients of log (shoot) on log (root) calculated from the data of STEINBRENNER and REDISKE (1964) for ponderosa pine and Douglas-fir (fig. 7) are lower than those reported here for loblolly pine, but all are less than 1.0. It is interesting to note that the regression coefficients reported by LEDIG and PERRY (1965) for the allometric relationship of shoot and root in loblolly pine range from 0.42 to 0.92, in good agreement with those found in this study, 0.67 to 0.83. Unpublished data from a study by LEDIG, based on over 4,500 seedlings, indicated a range from 0.62 to 0.77 among progeny of control-pollinated crosses among loblolly pine native to Georgia. WAREING (1950) calculated regression coefficients of 0.75 to 0.82 in Scots pine. In contrast, MONK (1966) reported data which indicated regression coefficients greater than 1.0 for loblolly pine (as computed by taking the reciprocal of MONK's regressions of root on shoot). This may reflect the greater difficulty in recovering the entire root system in the field sampling technique employed by MONK. The similarity of shoot-root relationships for loblolly pine in all of the other studies cited, suggests that the relative growth of shoot to root is unchanged by a broad spectrum of environmental conditions in which the species is ecologically successful.

Although the change in shoot-root ratio with growth or increasing age has become generally recognized, there is still confusion over the direction of the change. MONK (1966) stated: "The root/shoot ratios decrease with increase in plant size."

However, four out of six of the tree species studied by MONK showed larger ratios with increase in seedling size. In loblolly pine, the results of this study (fig. 2) and those of LEDIG and PERRY (1965) suggested that the shoot/root ratio decreased for the first year. The data of KOZLOWSKI (1949), as redrawn by LEDIG and PERRY (1965), indicated that the allometric coefficient was constant for the first 3 years in loblolly pine and that the shoot/root ratio was decreasing. The shoot/root ratio of Scots pine (WAREING 1950) also decreased with increasing seedling size throughout the first year (fig. 2). In white spruce (*Picea glauca* [Moench] Voss) there was a decrease in the shoot/root ratio from the first through the second year, although the ratio increased during the third growing season in the nursery (MULLIN 1963). In general, the shoot/root ratio seems to decline at least for the first few years in conifers.

In a study of 3- to 55-year-old plantations of Scots pine, OVINGTON (1957) wrote of the shoot/root ratio that "the ratio tends to increase with greater age." A logarithmic regression of his data (fig. 8) has a slope of 1.1, indicating that the shoot did increase at a more rapid rate than the root. A slope greater than 1.0 may mean that a change in the allometric pattern occurred after the first few years of seedling growth, and may result because the accumulated investment in stem and branch biomass was proportionally greater than root accumulation. Or perhaps, the relationship between shoot and root growth over the life of a tree is expressed by a more complicated equation. The onset of sexual reproduction, for example, might alter the relationship between top and roots. However, the slope of the regression based on OVINGTON's data was not much greater than 1.0, and the steeper slope could be the result of experimental procedure; in field sampling, relatively large portions of the root system might be lost because of the obvious difficulties of extraction, thus artificially increasing the shoot/root ratio. Also, OVINGTON did not measure loss of roots through abscission or decay in older trees, while needle shed was estimated with some precision. Thus, the significance of the allometric relationship for mature trees is not clear and the situation will be difficult to study because of the natural loss and decay of below-ground plant parts.

In general, published data have indicated that the shoot/root ratio in herbaceous plants does increase with growth of the plant (fig. 2)—that is, the allometric constant is greater than 1.0 (TURNER 1922; TROUGHTON 1955, 1956; MONK 1966). In fact, a trend is apparent from coefficients greater than 1.0 in the annuals (i.e., greater shoot-to-root growth) to coefficients less than 1.0 in perennials (i.e., greater root-to-shoot growth). This may reflect a difference in the function of the root; that is, perhaps it is predominantly an organ of water and nutrient absorption in annuals, but an organ of increasing importance as a storage and anchoring structure in woody perennials. Root crops are an exception to this trend. Crop plants with large subterranean storage organs, generally biennials, exhibit a decrease in shoot/root ratio with increasing age (PENKA 1965).

If shade and sun plants are adapted to their habitats by the balance between their tops and their roots, then this adaptation could be achieved through the control of the growth of the entire plant. Because the shoot/root ratio changes rapidly with increasing plant dry weight in small seedlings, a retardation or stimulation of total growth, affected by the level of light intensity or other factors, would either maintain or develop what has been considered an adaptive balance between aerial and subterranean parts by many authors (e.g., KRAMER and KOZLOWSKI 1960; KOZLOWSKI 1949; BORMANN 1958).

The highest mortality within seedling populations usually occurs among the youngest (i.e., smallest) seedlings, which are most vulnerable to environmental stress and competition. An adaptive advantage would seem to be gained by a developmental pattern that allowed a seedling to pass most rapidly through this vulnerable period. Such a strategy seems apparent in loblolly pine, where the new seedling invests a high proportion of its stored energy in photosynthetic shoot tissue. Given favorable light

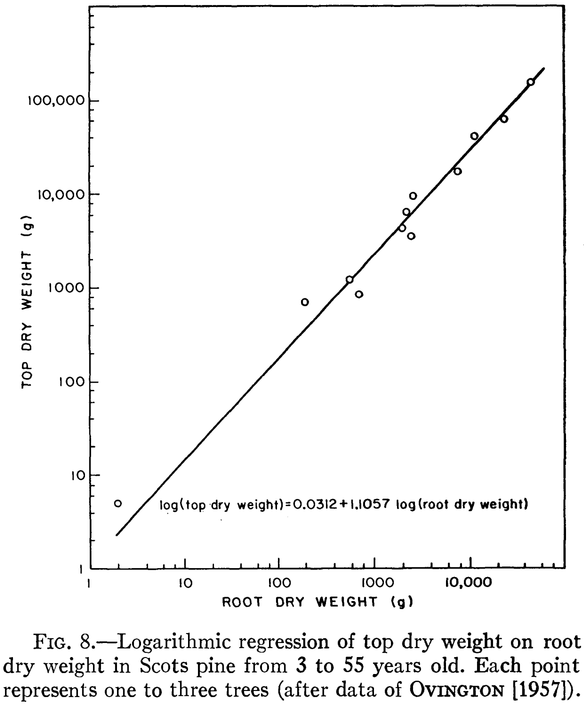

FIG. 8.—Logarithmic regression of top dry weight on root dry weight in Scots pine from 3 to 55 years old. Each point represents one to three trees (after data of OVINGTON [1957]).

conditions and even temporarily favorable moisture conditions, the seedling has a high capacity for rapid growth and accumulation of energy. As the seedling gains in biomass, there is a shift toward relatively more rapid root growth, and a more balanced relationship between absorbing and transpiring surfaces is achieved. There is a consequent increase in drought resistance. Such a response is the normal pattern of growth.

If the young seedling develops in shade, the initial high proportion of photosynthetic tissue might convey a temporary advantage, as long as favorable moisture conditions exist. However, this advantage would soon be lost with an increase in biomass and a decrease in the proportion of growth energy invested in shoot tissue.

Conclusions based on the allometric approach to dry weight growth of shoot and roots do not shatter the concept that a plant makes phenotypic adjustments to its environment. Instead, they indicate a developmental pattern which—within a wide range of environments—operates to maintain a generally balanced growth of shoot to root. The developmental sequence is in itself adaptive in a sense, and serves to regulate plant proportions through control of total growth or the rapidity of change from one stage to the next along a continuum. Further basic adaptive changes in the allometric growth pattern may occur under environmental extremes.

Within the range of environments which are ineffective in altering allometric growth patterns, other types of adaptations occur. For example, the effect of light and moisture per se on seedling morphology was very pronounced, as measured by the openness of the secondary leaf fascicles (BORMANN 1958) and the number of needles per unit stem. The adaptive nature of these changes is apparent. The foliage of shade-grown seedlings was spaced along a greater length of stem, reducing mutual shading by the needles. Mutual shading greatly reduced photosynthesis in pine seedlings (KRAMER and CLARK 1947), and the effect was especially pronounced at low light intensities (BORMANN 1956*a*, 1958). Short internodes would be particularly detrimental to growth in shady habitats. On the other hand, short internodes might result in less water loss from transpiration and better water absorption-transpiration balance than long internodes. Thus, more needles per unit stem in seedlings grown under dry conditions is adaptive. If one assumes a positive correlation in natural environments between dry sites and high light intensity, the dense clustering of needles is not an insurmountable obstacle to high rates of CO_2 assimilation.

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A CONOSTOMA WITH A TENTACULAR SARCOTESTA FROM THE UPPER PENNSYLVANIAN OF ILLINOIS

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ABSTRACT

A new species of the lagenostomalean seed genus *Conostoma* (*C. villosum*) is described from Illinois coal ball petrifactions of upper Pennsylvanian age. In longitudinal sections, the body of the seed measures approximately 4.5 mm long and 2.8 mm in maximum diameter and is ovoid with a rounded chalaza and a tapering apex that is bluntly flattened at the summit. Specimens are circular in transverse sections of the chalazal and midregions, becoming four-angled at the apex, and are characterized by tentacle-like, sarcotestal appendages that radiate outward from the seed body for approximately 0.7 mm. These appendages are abundantly distributed over the seed body and vary considerably in form; some are essentially uniseriate except at their bases, while others are multiseriate for varying distances outward from the seed body. The presence of the appendages increases the overall dimensions of the seed to approximately 6.0 mm long and 4.2 mm maximum diameter. Features of the nucellus and pollen-receiving structures correspond to those present in other species of the genus. Scalariform wall thickenings are present in cells of the lagenostome and central column. A single vascular bundle enters the chalaza and undergoes two closely spaced dichotomies producing four terete vascular bundles. These bundles extend distally toward the seed apex where they occur opposite the four angles of the integument. The traditional zonation of the integument into endo-, sclero-, and sarcotesta is more clearly evident in *C. villosum* than in any other lagenostomalean ovule.

Introduction

The genus *Conostoma* was instituted by Williamson in 1877. Of the three species originally described by Williamson (1877), only *Conostoma oblongum* is retained in the genus and may be considered as the type species. *Conostoma ovale* and *C. intermedium* have been redescribed by Benson under the name *Sphaerostoma ovale* (Benson 1914). Subsequent work on *C. oblongum* includes descriptions by Oliver and Salisbury (1911), Krick (1932), Reed (1939), Kern and Andrews (1946), and Rothwell (in press). Additional species include: *C. anglo-germanicum* (Oliver and Salisbury 1911), *C. platyspermum* (Graham 1934), *C. quadratum* (Graham 1934), *C. kestospermum* (Taylor and Leisman 1963), and *C. leptospermum* (Taylor 1967). The names *Conostoma laculatum* and *C. laculatum* var. *quinquangulum* are *nomina nuda* used by Leisman and Sudweeks (1963). The name *Conostoma quadrivasatum* var. *hirsutum*, also used in the above paper, is apparently an error since no species of *Conostoma* bears this specific name.

General features of *Conostoma* include a single three-layered integument to which the nucellus is fused except at its summit, where a large dome-shaped pollen chamber is present and at the apex of which a small, ovoid to spherical, lagenostome occurs. The floor of the pollen chamber has a centrally placed mound of tissue (central column) that extends upward toward the base of the lagenostome. A single vascular system is present in the inner layer of the integument (endotesta) except at the apex of the ovule, where the vascular strands enter the middle integumentary layer (sclerotesta). Species of the genus are characteristically radially symmetrical and have four vascular bundles. Exceptions to this are *C. oblongum*, in which six vascular bundles occur, and *C. platyspermum*, which has been described as having two vascular bundles. This latter species has also been described as bilaterally sym-