EFFECTS OF SHADING ON GROWTH AND DEVELOPMENT OF NORTHERN RED OAK, BLACK OAK, BLACK CHERRY, AND RED MAPLE SEEDLINGS. II. BIOMASS PARTITIONING AND PREDICTION[1]

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Abstract.--Northern red oak, black oak, black cherry, and red maple seedlings were grown under light treatments ranging from 8 to 94% of full sunlight for 2 years. Growth was least at the lowest light level and total dry weight increased with increasing light. Total dry-weight rankings (largest to smallest) at all light levels were black cherry, northern red oak, black oak, and red maple. As light increased, allocation of biomass into leaves and stems decreased while branch biomass held constant except for black cherry, which increased. Allocation of biomass into roots increased significantly with increased light. Seedling biomass could be predicted with a reasonable degree of accuracy across light levels from D^2H measurements taken late in the growing season. Data on biomass accumulation and root development suggest that increasing light to 20% or more will help advanced regeneration seedlings become well established, giving them the potential to grow rapidly after release.

Keywords: light, root development, natural regeneration

INTRODUCTION

Successful regeneration of the mixed oak forest type requires an adequate number of large stems of advance regeneration in the understory before the overstory is harvested (Sander 1972, 1977; Sander et al. 1976, 1984). Of the numerous environmental and biotic factors that affect the development of advanced regeneration, light is one of the most important. Initial germination and growth of oak seedlings are often not limited by the low light levels under hardwood canopies, but many seedlings fail to survive at these low levels once cotyledonary reserves are exhausted (Tryon and Carvell 1958; Carvell and Tryon 1961). Increased light levels have resulted in increased height growth and usually in increased root development and root/shoot ratios (McGee 1968; Musselman and Gatherum 1969; Phares 1971; Jarvis 1964; Loach 1970). Oak seedlings and saplings growing in shade break bud and develop leaves earlier than seedlings and saplings growing in full sunlight (McGee 1985). Earlier work showed that height and diameter growth for seedlings of black cherry, red maple, northern red oak, and black oak reached a plateau at 20 to 94% light, while root/shoot ratios increased linearly for all species except black cherry, which showed a hyberbolic response to increased light (Gottschalk 1985).

Total dry weight (TDW) of seedlings increases as light level increases: in some cases to a plateau at around 50% of full sunlight for Norway and red maple (Yakshina 1978; Loach 1970); for baldcypress and pondcypress (Neufeld 1983); for sessile oak (Jarvis 1964); and for northern red oak (Musselman and Gatherum 1969). In other cases, TDW continues to increase up to full sunlight for several eucalypts and associates (Withers 1979); for Douglas-fir (Reed et al. 1983); for birch (Atkinson 1984); and for northern red oak (Loach 1970; Phares 1971; Farmer 1975; Ashby 1976). In studies where TDW was followed over only a small range of low light levels, a similar increase was found for several oak species (Racine 1971; Shirley 1929a, b).

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Changes in biomass distribution were found as light levels increased. Allocation to roots generally increased, while the relative amounts in leaves and stems decreased, though stems remained constant in many cases (Yakshina 1978; Musselman and Gatherum 1969; Phares 1971; Loach 1970; Jarvis 1964; Neufeld 1983; Atkinson 1984). A number of studies have shown a change in allocation patterns as tree size increases (Farmer 1980; Gottschalk 1984; Switzer et al. 1976), so these differences in allocation patterns may be due to differences in overall tree size under the shading treatments rather than a direct effect of the treatments themselves.

On many good sites in the Allegheny Plateau region, harvested, mixed-oak stands are being regenerated to red maple or cherry-maple. In this area of transition, little large oak advance regeneration is present in the stands. To be successful on these sites, oak must be able to compete with these other species. Therefore, the two major competitors of oaks on these transition sites (red maple and black cherry) were included in the study. Shelterwood cutting may allow oak advance regeneration to grow large enough to compete with these species after harvest, while maintaining the competitors in a less favorable position. Ideally, it would be desirable to identify a light level(s) for establishment and growth of oak regeneration that would not be as favorable for black cherry and red maple, or at least would not give an advantage to them. Then the stand could be cut to that light level using a basal area to light penetration guide (Marquis 1973; Chambers and Jenkins 1983).

METHODS

Field and Laboratory

Twenty-four 8-foot-square plots were each covered with one of eight Saran[3] shade-cloth screen treatments, providing three replications of each treatment. The screen tents were 6 feet tall, were covered on all four sides and the top, and transmitted 94, 70, 57, 45, 37, 27, 20, and 8% of full sunlight. The study area is an abandoned agricultural site on the flood plain of the Allegheny River near Warren, PA. The plots were not watered nor fertilized. Although there were minor differences in soil moisture under the different shading treatments, there were no significant differences in water-stress levels because of the frequent and abundant rainfall during the two growing seasons. Each plot was rototilled before planting and an aluminum flashing border, buried to a 6-inch depth, was installed to prevent rodent damage. Open-pollinated seeds from one tree each of northern red oak, black oak, and black cherry were sown in November 1980. Open-pollinated seeds from one red maple tree were collected and sown in June 1981. Each species was planted in row plots of five points with 1-foot spacing between and within rows (4x5 feet). Northern red oak, black oak, and black cherry seed germinated in May and grew unshaded until June 15-17, 1981, when the shade-cloth tents were erected. Initial measurements of height, diameter at 2 cm above ground, and number of leaves were taken as soon as the shade-cloth tents were erected. Red maple seed did not germinate until after the tents were installed, so no initial measurements could be taken on them. Three seeds were sown at each point. Seedlings were thinned to one per point when the tents were installed. Red maple seeds germinated in mid- to late June and seedlings were thinned to one per point in early July. No mortality occurred in black cherry and northern red oak the first year, but black oak seedling and 10 red maple seedlings died (no more than seedlings from any one treatment plot). During the second year, one additional black oak seedling and three additional red maple seedlings died.

In mid-October 1981, the height and diameter of all seedlings were measured. In addition, one seedling from each species-light-replication combination was randomly selected for harvest. These seedlings were excavated by hand to recover as many roots as possible. The harvested seedlings were partitioned into stem, leaves, and roots, dried at 75°C, and weighed to the nearest 0.001 g. The leaves were photocopied before they were dried, and leaf areas were measured with an integrating planimeter. The shade-cloth tents were taken down in November after leaf fall was complete.

The shade-cloth tents were erected again in April 1982 before budbreak. In late September-early October 1982, the height and diameter of all seedlings were measured. Since some black cherry seedlings had reached the top of the tents, the study was terminated. All of the seedlings were harvested in the same way as in the first year, except that branches were partitioned into a separate category and leaf area was measured with a LiCor Leaf Area Meter.

Data Analysis

The study design was a split plot with randomized blocks. However, since the differences in the means between species were large, and the variances were heterogeneous, the data were analyzed by species. Individual component and total dry weights were averaged for each plot and the plot averages were used in analysis of variance. Dry-weight ratios (DWR) were calculated by dividing each component dry

[3] The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitite an official endorsement or approval by the U.S. Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

weight by total dry weight and transformed using arcsine. Ratios used were LWR (leaf-weight ratio), BWR (branch-weight ratio), SWR (stem-weight ratio), and RWR (root-weight ratio). If the analysis of variance showed statistically significant differences attributable to levels of light, treatment means were separated using Tukey's HSD procedure. The 0.05 level of probability was accepted as significant.

Ten models were fitted to the data using least squares regression to quantitatively describe the relationships between the various seedling-biomass variables (Y in grams) and light level (X in percent of full sunlight) (see Dell et al. 1984 for examples of these models). The models that were fitted are:

(1) $Y=b_0+b_1X$, Linear function

(2) $Y=b_0+b_1(1/X)$, Hyperbolic function

(3) $Y=b_0+b_1X+b_2X^2$, Quadratic function (second degree polynomial)

(4) $Y=b_0+b_1X^2$, Power function

(5) $\ln Y=b_0+b_1X$, Exponential function (exponential growth curve)

(6) $\ln Y=b_0+b_1(\ln X)$, Power function (log-transformed allometric equation)

(7) $\ln Y=b_0+b_1(\ln X)+b_2X$, Hoerl's special function

(8) $1/Y=b_0+b_1(1/X)$, Hyperbolic function

(9) $Y=b_0+b_1(\ln X)$, Logarithmic function

(10) $\ln Y=b_0+b_1(1/X)$, Special function

In addition, equation 6, the log-transformed allometric equation, was used to develop prediction equations for component and total dry weights using diameter squared times height (D^2H, cm^3) values. Because of few differences in partitioning across light levels and the small numbers of samples within light levels (3), the data for all light levels were pooled to develop the prediction equations. A correction factor for the bias due to transformation was calculated and used in the prediction equations (Baskerville 1972; Sprugel 1983).

RESULTS

Biomass

Leaves

First-year leaf biomass was not affected significantly by shading (Table 1). Since most of the northern red oak and black oak leaves were formed prior to application of the shading treatment and leaf biomass was fairly constant across treatments (fig. 1), this result is not surprising. Red maple seedlings grew under the shading treatment, but because of their late germination, small growth, and large variation, they did not show significant differences. However, the leaf biomass in the 8% treatment was considerably smaller than in the other treatments (fig. 1). Black cherry had considerable variability across light levels that masked any differences that may have been present. Small sample size contributed to the lack of significance. Seedlings in the 8% treatment had only one-third or less of the dry weight of any of the other light levels.

In the second year, red maple and black oak leaf biomass did have significant responses to shading (Table 1). All four species had considerably less leaf biomass in the 8% treatment (fig. 2). In red maple, the 8% value was significantly less than the 57% value, while in black oak it was significantly less than all of the other treatments.

Branches

Branches were produced in the second year and on a few of the unharvested first-year black cherry. There were no significant differences in branch biomass due to shading (Table 1), though the 8% treatment tended to have lower absolute values (fig. 2).

Stems

Stem biomass was not affected significantly by shading in the first year (Table 1). Northern red and black oak had fairly uniform stem values across all light levels, while the red maple and black cherry 8% treatments had stem values that were one-third or less of the other treatments (fig. 1). Second-year values were significantly affected only for northern red oak (Table 1), but all four species had considerably smaller values in the 8% treatment (fig. 2).

Roots

The roots were the part of the seedlings most affected by the shading treatments (Table 1); only black cherry in both years and red oak in the first year showed no significant differences due to variation in shade. Northern red oak is the only species that did not have less root dry weight in the 8% light treatment as compared to the other treatments in the first year (fig. 1). In the second year, root production was significantly less in the 8% treatment than in the other treatments for all of the species except black cherry (fig. 2). In both years there was a general trend toward an increase in root weight with increased light levels for all of the species.

Table 1.--Analysis of variance for component and total dry weights of seedlings of four tree species grown under different light level treatments.

Species	Source of variation	First year				Second year				
		Leaves	Stem	Roots	Total	Leaves	Branches	Stem	Roots	Total
Red maple	Light level	ns[1]	ns	**	*	*	ns	ns	**	*
Red oak	Light level	ns	ns	ns	ns	ns	ns	*	*	*
Black oak	Light level	ns	ns	*	*	*	ns	ns	*	*
Black cherry	Light level	ns	ns	ns	ns	ns	ns	ns	ns	ns

[1] ns = Not significant at 0.05 level.
* = Significant at 0.05 level.
** = Significant at 0.01 level.

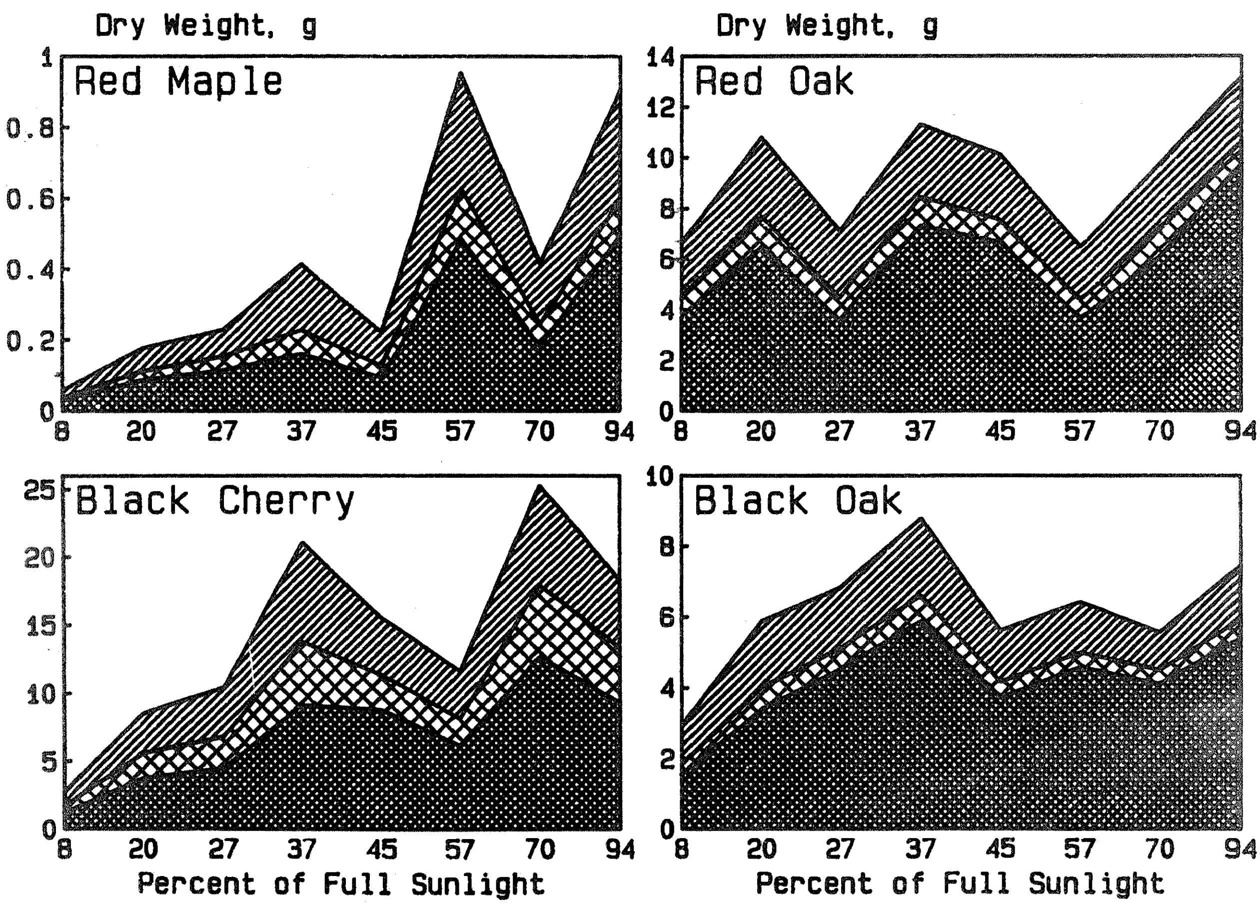

Figure 1.--Total and component dry weights of seedlings of four tree species grown under different light levels for the first growing season (leaves ▨, stem ⊠, roots ▩). Significant differences due to light level occurred only in red maple root and total dry weights and black oak root and total dry weights according to Tukey's HSD procedure at the 0.05 level.

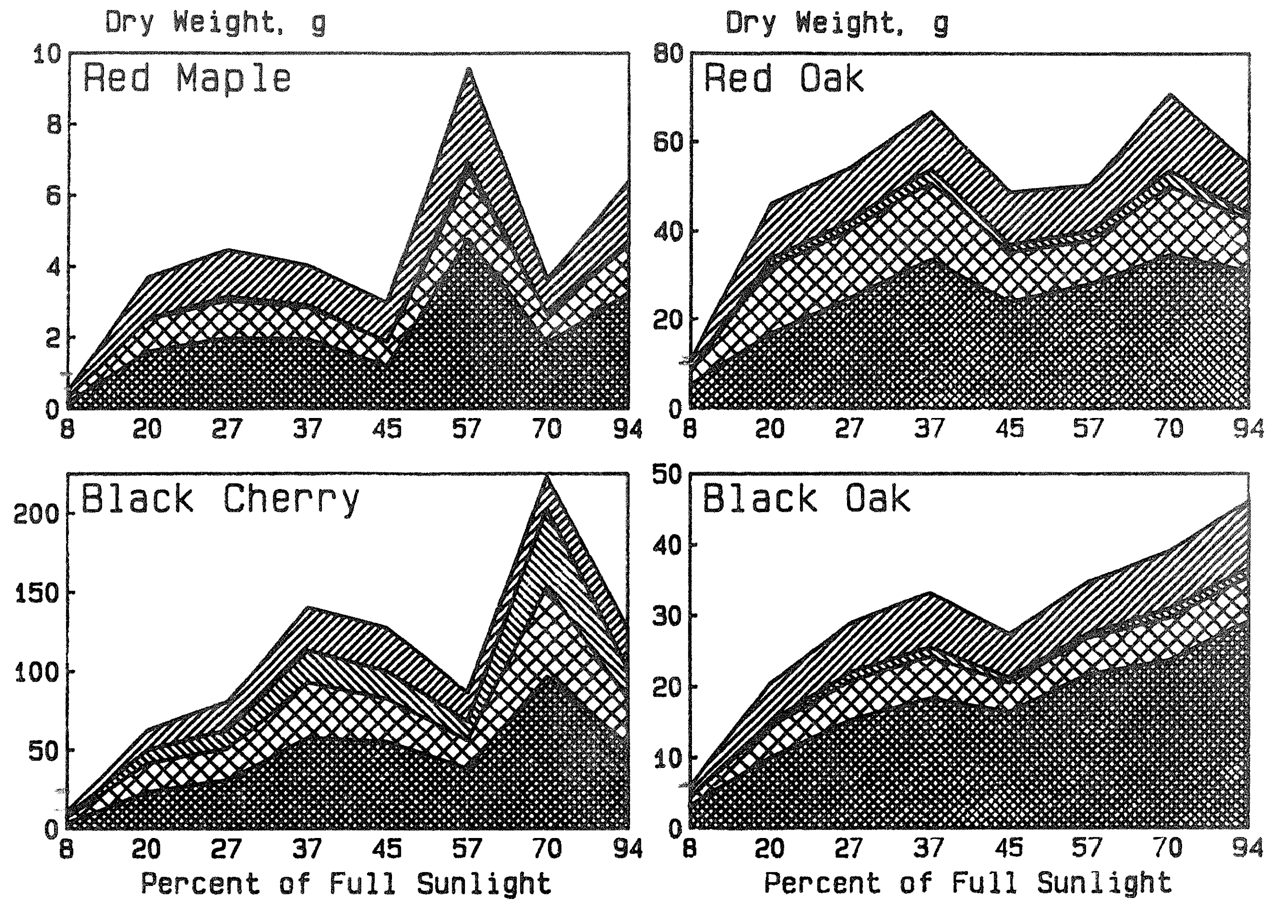

Figure 2.--Total and component dry weights of seedlings of four tree species grown under different light levels for the first two growing seasons (leaves ▨, branches ▧, stem ⊠, roots ▩). Significant differences due to light level occurred in red maple leaf, root, and total dry weights according to Tukey's HSD procedure at the 0.05 level.

Total

The shading effects on total seedling biomass are identical to those of the roots, indicating that the root biomass is the major influence on total biomass (Table 1, figs. 1-2). There was considerable fluctuation in total biomass within a species due to light level. In the first year, this variation was from 2 to 13 times and from 7 to 15 times in the second year. Black cherry produced the most biomass followed by northern red oak, black oak, and red maple, as shown by the following overall means for the first and second years, respectively: 14.17, 9.43, 6.18 and 0.421 g and 111.32, 50.24, 29.42, and 4.4 g. Second year biomass increased 5- to 10-fold over first-year values. Total biomass also showed a generally increasing trend with increased light level in both years.

Quantitative Models

At best, seedling development is difficult to model. Northern red oak biomass in the first year was not described well by any of the models tested (Table 2). Second-year biomass was described better than first-year values in all cases. Most of the best-fitting models were hyperbolic, showing large increases in biomass at lower light levels and correspondingly smaller increases at higher light levels. Red maple in the first year was the major exception as it was best described by a series of exponential functions.

The best models for first-year biomass were for black cherry roots (R^2=61%) and black oak roots (R^2=54%) followed closely by red maple total (R^2=51%), black cherry total (R^2=50%), and red maple stem (R^2=49%) biomass (Table 2). Northern red oak's poor fit in the first year was reversed in the second year where it provided several of the best fits: leaves (R^2=78%), total (R^2=76%), and roots (R^2=74%), along with black oak branches (R^2=76%). Red maple was close behind northern red oak while black oak and black cherry had somewhat poorer fits. There is a tendency for one model or closely related models to provide the best fit for all of the seedling components within a year and species combination. This shows that the components have a tendency to change in proportion to each other in response to changes in light level.

Table 2.--Relationship of light level treatments to seedling dry weights of four tree species grown under different light level treatments.

Species	Model parameters[1]	First Year				Second Year				
		Leaves	Stem	Roots	Total	Leaves	Branches	Stem	Roots	Total
Red maple	Model	6	6	6	6	10	8	10	10	10
	R^2	.40	.49	.42	.51	.61	.71	.55	.71	.66
	b_0'	-6.30**[2]	-6.91**	-5.87**	-5.18**	0.735**	-51.8ns	0.407*	1.31**	2.01**
	b_1	1.09**	1.02**	1.05**	1.07**	-21.05**	389.5**	-19.1**	-24.4**	-22.2**
Red oak	Model	-	-	4	-	8	8	8	8	8
	R^2	-	-	.18	-	.78	.65	.60	.74	.76
	b_0'	-	-	4.60**	-	0.007ns	-0.037ns	0.035ns	0.009ns	0.004ns
	b_1'	-	-	0.0005*	-	3.489**	31.1**	2.41**	1.44**	0.703**
Black oak	Model	-	8	8	8	10	8	10	9	10
	R^2	-	.17	.54	.44	.57	.76	.48	.55	.54
	b_0'	-	1.91**	0.146**	0.121**	2.30**	2.32*	1.93**	-18.97*	3.81**
	b_1'	-	15.1*	4.56**	1.94**	-16.0**	168.0**	14.4**	-10.1**	-17.5**
Black cherry	Model	8	10	10	10	8	10	10	8	8
	R^2	.43	.38	.61	.50	.52	.44	.38	.69	.58
	b_0'	0.052ns	1.34**	2.39**	3.02**	-0.005ns	3.20**	3.52**	-0.026ns	-0.003ns
	b_1'	10.9*	-18.8**	-19.96**	-18.16**	3.16**	-29.0**	16.9**	2.49**	0.753**

[1] Model = Number of best-fitting model (number defined in text under Data Analysis).

R^2 = Adjusted R^2 value of the regression.
b_0' = Estimate of intercept parameter of model.
b_1' = Estimate of slope parameter of model.

[2] ns = Not significant at 0.05 level.
* = Significant at 0.05 level.
** = Significant at 0.01 level.

Biomass Partitioning

Because of a tendency for seedling components to change together, dry-weight ratios were calculated for each component to determine if differences in biomass partitioning were occurring due to shading.

First Year

First-year dry-weight ratios were largely unaffected by the light treatments (Table 3, fig. 3). LWR's of black oak and black cherry both show significantly higher percentages of biomass partitioned into leaves in the 8% treatment than in several of the highest light treatments. Black oak RWR shows statistically less biomass partitioned into roots in the 8% treatment than in the three highest light levels. The oaks allocated relatively more biomass to roots and less to stem and leaves than red maple and black cherry, as shown by their means across all light levels:

	LWR	SWR	RWR
Red maple	.368	.151	.481
Red oak	.292	.106	.602
Black oak	.265	.081	.654
Black cherry	.313	.186	.501

With the exception of red maple, which was constant for all components, RWR tended to increase, LWR tended to decrease, and stem weight ratio (SWR) remained constant as light level increased (fig. 3).

Second Year

Second-year dry-weight ratios were still largely unaffected by shading (Table 3, fig. 4). Northern red oak's RWR at 20% was significantly less than the 57% and 94% values. Its 20% SWR

Table 3.--Analysis of variance for component dry weight ratios ($g\ g^{-1}$) of seedlings of four tree species grown under different light level treatments.

Species	Source of variation	First year LWR[1]	First year SWR	First year RWR	Second year LWR	Second year BWR	Second year SWR	Second year RWR
Red maple	Light level	ns[2]	ns	ns	ns	ns	ns	ns
Red oak	Light level	ns	ns	ns	ns	ns	**	*
Black oak	Light level	*	ns	*	ns	ns	ns	ns
Black cherry	Light level	*	ns	ns	ns	ns	**	**

[1] LWR = Leaf weight ratio.
SWR = Stem weight ratio.
RWR = Root weight ratio.
BWR = Branch weight ratio.

[2] ns = Not significant at 0.05 level.
* = Significant at 0.05 level.
** = Significant at 0.01 level.

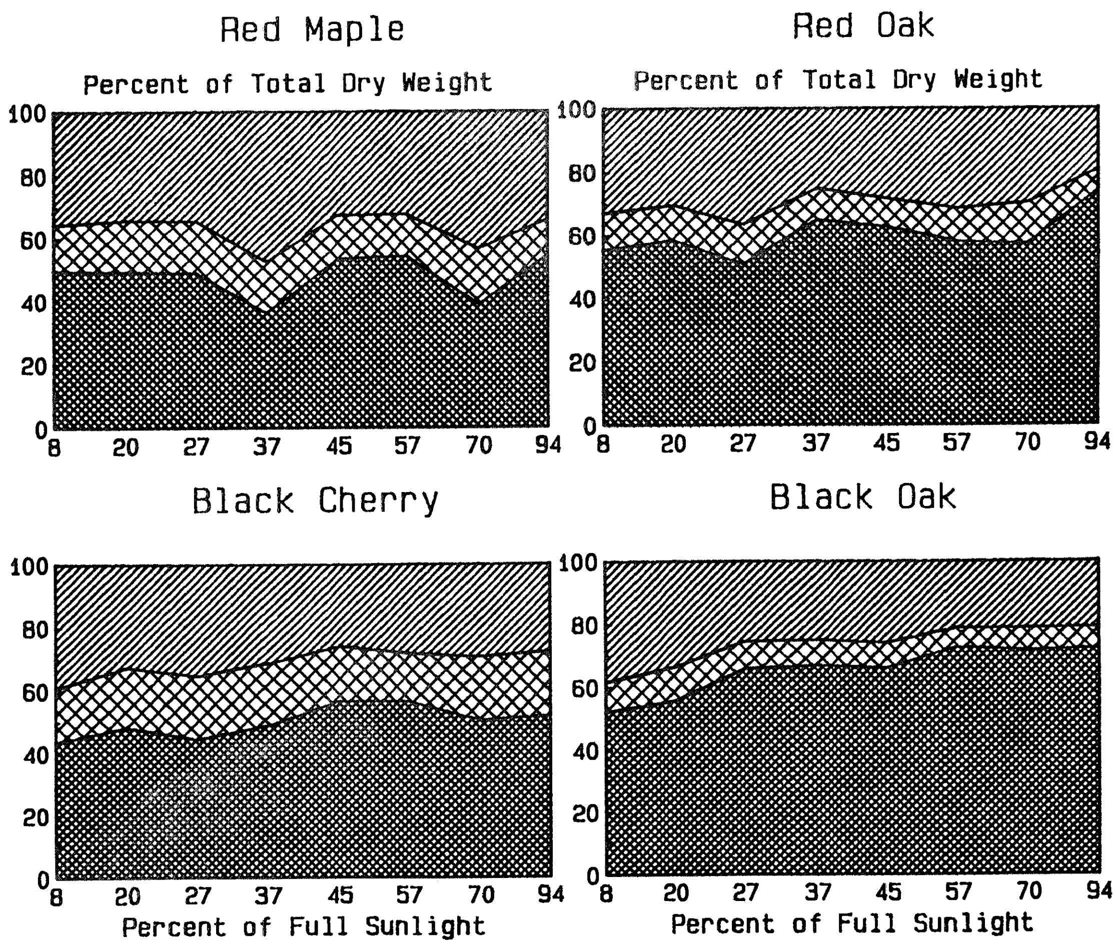

Figure 3.--Allocation of total biomass into components (dry weight ratios x 100%) for seedlings of tree species grown under different light levels for the first growing season (leaves ▨, stem ⊠, roots ▩). Significant differences due to light level occurred only in black oak leaves and black cherry leaves according to Tukey's HSD proceure at the 0.05 level.

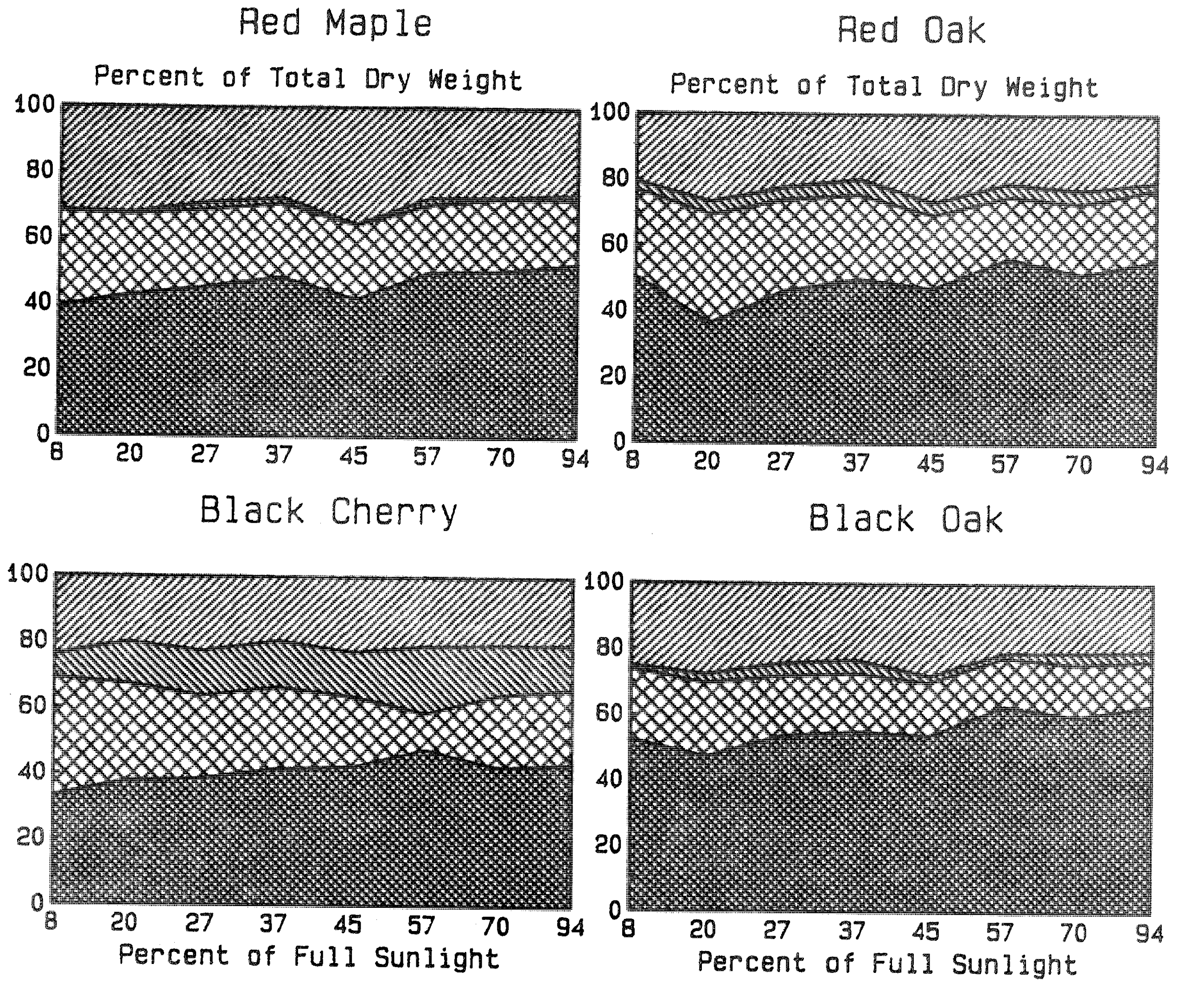

Figure 4.--Allocation of total biomass into components (dry weight ratios x 100%) for seedlings of four tree species grown under different light levels for the first two growing seasons (leaves, branches, stem, roots). Significant differences due to light level occurred only in red oak stem and roots and black cherry stem and roots according to Tukey's HSD procedure at the 0.05 level.

was significantly greater than all light levels above 27%, while the 57% value was significantly less than all light levels below 45%. Black cherry's 8% RWR was significantly less than the 57% value and its 8% SWR was significantly greater than all light levels larger than 37%. The oaks still partitioned relatively more biomass into their roots than black cherry and red maple but the difference was less than in the first year. Black cherry partitioned the highest biomass percentage into branches,as shown by the means across all light levels:

	LWR	BWR	SWR	RWR
Red maple	.296	.011	.230	.463
Red oak	.226	.036	.246	.492
Black oak	.238	.027	.176	.559
Black cherry	.214	.125	.252	.408

During the second year, LWR and branch-weight ratio (BWR) remained relatively constant for all species, while SWR decreased slightly and RWR increased slightly as light level increased (fig. 4).

Quantitative Models

Dry-weight ratios in general were not fit as well by the models as the absolute dry weights (Table 4). This result is due to less change in the relative values as compared to the absolute ones. There was a variety of model types that provided the best fits; linear for several RWR's, hyperbolic for some ratios, and exponential and power functions for others. The lack of a clear trend in dry-weight ratio with increasing light resulted in one-third of the ratios not being described by any of the models. With the exception of RWR, the trends shown by the dry-weight ratios reflect the influence of tree

Table 4.--Relationship of light level treatments to seedling component dry weight ratios of four tree species grown under different light level treatments.

Species	Model Parameters[1]	First year LWR[2]	First year SWR	First year RWR	Second year LWR	Second year BWR	Second year SWR	Second year RWR
Red maple	Model	-	-	-	-	-	9	1
	R^2	-	-	-	-	-	.41	.34
	b_0'	-	-	-	-	-	0.358**[3]	0.396**
	b_1'	-	-	-	-	-	-0.036**	0.01**
Red oak	Model	5	5	4	-	7	1	1
	R^2	.18	.17	.16	-	.30	.39	.22
	b_0'	-1.04**	-2.06**	0.556**	-	-5.51**	0.298**	0.427**
	b_1'	-0.005*	-0.005*	0.0004*	-	0.942**	-0.001**	0.001*
	b_2'	-	-	-	-	-0.029**	-	-
Black oak	Model	9	6	6	5	-	5	1
	R^2	.54	.23	.55	.17	-	.44	.31
	b_0'	0.539**	-1.86**	-0.957**	-1.31**	-	-1.52**	0.483**
	b_1'	-0.077**	-0.192*	0.146**	-0.003*	-	-0.005**	0.002**
Black cherry	Model	9	-	6	-	8	2	8
	R^2	.42	-	.17	-	.30	.57	.49
	b_0'	0.490**	-	-1.027**	-	5.58**	.202**	2.22**
	b_1'	-0.049**	-	0.091*	-	125.2**	1.33**	7.07**

[1] Model = Number of best-fitting model (number defined in text under Data Analysis).

R^2 = Adjusted R^2 value of the regression.
b_0' = Estimate of intercept parameter of model.
b_1' = Estimate of slope parameter of model.

[2] LWR = Leaf weight ratio.
SWR = Stem weight ratio.
RWR = Root weight ratio.
BWR = Branch weight ratio.

[3] ns = Not significant at 0.05 level.
* = Significant at 0.05 level.
** = Significant at 0.01 level.

size more than light level. RWR shows an increase to increasing light level.

Biomass Prediction

Seedling diameter and height (Equation 6, the log-transformed form) were used to develop prediction equations for component and total dry weights for each species (Table 5). With the exception of the first-year northern red and black oak roots and total biomass, tł regressions all do a good job of predict biomass from D^2H. The best second ȝ predictions are for stem biomass and the wc ones are for branches and roots, though both relatively good. Black cherry had the ŀ prediction equations in both years, followed red maple, black oak, and northern red oak.

Table 5.--Biomass regression and prediction equation parameters for D^2H versus component and total dry weights of seedlings of four tree species grown under different light level treatments with seedlings from all treatments pooled.

Species	Model parameters[1]	First Year				Second year				
		Leaves	Stem	Roots	Total	Leaves	Branches	Stem	Roots	Total
Red maple	R^2	0.80	0.87	0.77	0.87	0.90	0.47	0.90	0.89	0.91
	b_0'	-0.626**[2]	-1.689**	-0.485*	0.290ns	-0.675**	-3.923**	-0.901**	-0.266**	0.542**
	b_1'	0.878**	0.779**	0.811**	0.809**	0.823**	0.933**	0.784**	0.879**	0.840**
	CF	0.153	0.076	0.156	0.082	0.044	0.586	0.038	0.060	0.040
Red oak	R^2	0.64	0.91	0.20	0.42	0.86	0.72	0.98	0.68	0.86
	b_0'	0.378**	-0.900**	1.127**	1.633**	-0.313ns	-2.895**	-0.430**	0.672ns	1.214**
	b_1'	0.523**	0.787**	0.523*	0.542**	0.769**	0.969**	0.831**	0.708**	0.763**
	CF	0.020	0.008	0.124	0.052	0.032	0.120	0.005	0.078	0.031
Black oak	R^2	0.68	0.96	0.41	0.58	0.90	0.73	0.96	0.84	0.90
	b_0'	0.236**	-1.000**	1.154**	1.595**	0.066ns	-3.360**	-0.242**	0.559**	1.315**
	b_1'	0.539**	0.791**	0.610**	0.588**	0.794**	1.317**	0.794**	0.974**	0.894**
	CF	0.022	0.005	0.086	0.040	0.027	0.202	0.010	0.070	0.034
Black cherry	R^2	0.90	0.97	0.87	0.93	0.92	0.93	0.97	0.91	0.94
	b_0'	-0.253*	-1.194**	0.146ns	0.818**	-1.133**	-3.699**	-0.812**	-0.731*	0.229ns
	b_1'	0.708**	0.913**	0.746**	0.761**	0.864**	1.296**	0.8244**	0.917**	0.905**
	CF	0.038	0.018	0.052	0.028	0.038	0.080	0.015	0.054	0.031

[1] Prediction equation: $DW=e^{[b_0+b_1(\ln D^2H)+CF]}$ or $DW=a(D^2H)^{b_1}$.

Regression equation: $\ln DW=b_0+b_1(\ln D^2H)$ which is the transformed form of $DW=a(D^2H)^{b_1}$.

Where: DW= Component or total seedling dry weight in g.
D= Diameter at 2 cm above ground level in cm.
H= Height in cm.
D^2H= Mensurational variable, diameter squared times height in cm^3.
ln= Natural logarithm (base e).
e= Exponential function.
CF= Correction factor due to bias of transformation = $^2/2$.

a= Constant which equals $e^{(b_0+CF)}$.

[2] ns = Not significant at 0.05 level.
* = Significant at 0.05 level.
** = Significant at 0.01 level.

DISCUSSION

The increases in both total dry weight and root dry weight that occur with increased light levels generally agree with the patterns shown in the literature. Roots have been the most sensitive component to changes in light level (Neufeld 1983; Atkinson 1984) and especially so for the oaks (Musselman and Gatherum 1969; Phares 1971; Loach 1970; Jarvis 1964). As light level increases, root dry weight increases. These absolute increases have generally been associated with changes in the relative proportions of roots, leaves, and stem. This result is in part a redistribution of dry weight from roots to leaves under increasing amounts of shade, which is probably an adaptation to maximize light interception under low light conditions. The linear relationship between RWR and light level confirms this trend. The changes in most of the other ratios as well as the absolute dry weights show relationships that have large changes at low light levels and progressively smaller changes at higher light levels. This result may be an effect of tree size rather than light level.

The development of biomass prediction equations will allow adequate estimates of seedling dry weights from easily obtained field measurements of diameter and height. Farmer (1980) and Williams and McClenahen (1984) also published equations for estimating dry weights, though they did not include root dry weights in their equations and the latter did not include leaves. The equations in this paper will work for seedlings grown under a wide range of light conditions; however, they will probably underestimate TDW and RDW if used on seedling-sprouts or stump sprouts. The leaf and stem equations should give reasonable estimates for these two types of regeneration.

The interpretation of these results requires some caution. The uniform shade provided under these shade-cloth tents is a poor representation of the actual light conditions in forests due to the sunflecks and other irregularities in the quantity and quality of light reaching the understory. However, it seems clear that seedlings of all four species grow poorly and produce low amounts of biomass under 8% light (similar to uncut stands); increasing light to levels above 20% will increase seedling growth and especially increase root dry weights as light increases to full sunlight. Marquis (1973) found that similar cautions were needed in a study using black cherry grown in pots under shade cloth-tents.

This conclusion supports increasing light to obtain better establishment and growth of red oak, black oak, red maple, and black cherry seedlings. Shelterwood cutting to increase light levels from the 5 to 10% available in uncut stands (Chambers and Jenkins 1983) to 20% or higher should result in increased growth of the seedlings present in the stand. The general trend toward an increase in root growth at higher light levels supports maintaining as high a light level as possible. While this would support clearcutting to obtain maximum light, previous work has shown that unless oak seedlings are already large and well established, they cannot compete with the woody and herbaceous competitors (Sander 1972). Shelterwood cutting may hold the key to success as the more root growth an oak seedling produces, the better its chances of competing sucessfully once it is released from the shelterwood.

The use of shelterwood cutting to favor oaks over black cherry and red maple does not look promising because of the favorable responses of these two competitors across all light levels. However, the oaks will partition more biomass to their root systems than red maple and black cherry that could result in more rapid regrowth of the seedling sprouts following the removal cut or application of some form of competition control to favor the oaks.

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