EFFECT OF APICAL MERISTEM CLIPPING ON CARBON ALLOCATION AND MORPHOLOGICAL DEVELOPMENT OF WHITE OAK SEEDLINGS[1]

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Abstract—Seedlings from three open-pollinated half-sib white oak seedlots were clipped in mid-July and their development was compared to nonclipped controls after one growing season. In general when date were analyzed by family clipped seedlings were significantly less desirable in three to six of the eight variables tested. Numerically, In all families seedlots, the clipped seedlings were Inferior to the controls. Regardless of clipping treatment, the growth variable that affected seedling development the most was the Innate ability to develop lammas shoots. Seedlings that produced late season lammas shoots also produced the largest numbers for each of the eight variables tested.

INTRODUCTION

The range of white oak (*Quercus alba*) includes the entire eastern half of the United States because it can adapt to many climatic, edaphic and topographic conditions. It is one of the most commercially valuable oak timber species. White oak is also an important mast producer for wildlife such as squirrels, bluejays, crows, red-headed woodpeckers, deer, turkey, quail, mice, chipmunks, ducks, and raccoons (Rodgers 1990). Currently, whiie oak plays a major role in multiple use management and is usually included in other biodiversity and restoration ecology efforts.

Unfortunately, artificial regeneration of this valuable and adaptive species has been generally unsuccessful. Even though State nurseries have been providing white oak seedlings for over 50 years, successful plantings or plantations are diicult to find (Boyette 1980; Hill 1986; Kormanik and others 1989). In many instances, planting white oak is not recommended because attempts to artificially regenerate the species consistently fail (Russell 1971; Boyette 1980; Clausen 1983; Hill 1986). Most plantings fail because seedlings show poor growth and survival rates when they compete with herbaceous weeds and other woody, perennial plants. To assess the competitive ability of these seedlings, grading standards are needed. However, developing grading standards for the small white oak seedlings, which range from 25-30 cm in size, has been difficult.

At the Institute of Tree Root Biology (ITRB), we are developing a nursery fertility/management protocol for growing various species of oak and other hardwoods similar to the protocol for loblolly pine (Kormanik and others 1992). In one of the hardwood nursery trials at the Whitehall Experimental Nursery, deer browsed some of the white oak seedlings in mid-July. By mid-August we noted that browsing had affected the morphological development of the seedlings. We found a large variation in growth among the browsed seedlings: however, some of the browsed seedlings were 20 to 30 cm taller than adjacent nonbrowsed seedlings.

Normally, few axillary buds of white oak elongate in the nursery during the year of initiation except perhaps those at the terminal end of the initial flush. This strong apical control on axillary buds (Brown and others 1967) is evident even when cultural treatments result in five flushes instead of the three flushes typical in white oak seedlings. Browsing, however, resulted in rapid axillary bud elongation and lammas-like shoot development in some seedlings in late July. This shoot development is not usually observed on white oak seedlings until mid-August. We were unable to obtain reliable estimates of root and stem development of the browsed seedlings because (1) the number of seedlings affected was limited and (2) the seedlings were from a mixed seedlot

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and obvious seed source differences *were* apparent within the nursery beds.

The objectives of thii study were to determine the effect of dipping on (1) seedling height, root collar diameters (RCD) and number of elongated **axillary** buds, (2) **total** weight and weight of component parts of seedlings; and (3) root/stem morphology of seedlings.

METHODS

White oak acorns were collected daily from three different mother trees from **seedlots 2, 3,** and 4 in Clarke County, Georgia, during October-November 1992. The acorns were immediately placed in water and those that floated were discarded. Acorns that sank and showed no evidence of weevil or other damage were placed in plastic bags and stored at 2 to 4 °C until sown.

b Us December 1992, acorns were sown in a single raised nursery bed described in detail earlier (Kormanik 1986; Kormanik and others 1990). Based on soil sample analyses from **A&L** Laboratories, Memphis, TN, the soils were amended with the **appropriate** fertilizers to obtain the following levels of P, K, Ca, Mg, Cu, **Zn,** and B, respectively **80, 80, 500, 50, 2.5, 5,** and 0.8 ppm, and a pH of 5.8. In other nursery studies these levels had been shown to be appropriate for many species of hardwood including white oak (Kormanik and others 1993; 1994).

Nitrogen, applied as NH_4NO_3 at rates equivalent to 1345 **kg/ha** (1200 lb/acre) began in mid-May and continued at 10 day intervals until mid-September. Four different rates were used in the 11 applications. The first two applications were at a rate equivalent to 28 kg/ha (25 lb/acre), the third at 56 kg/ha (50 lb/acre), the next six applications were at 168 **kg/ha** (150 lb/acre) and the final two at 112 **kg/ha** (100 lb/acre). If needed, seedlings were watered daily until the first growth flush was essentially complete for all **seedlots** and some seedlings were beginning their second flush. At this point, seedlings received water when moisture tensiometers registered 30-50 centibars at a depth of 15 to 20 cm. During excessively hot periods, watering occurred at 30 centibars, while during cooler periods, watering was delayed until 50 centibars.

Sixteen continuous rows were assigned to each half-sib mother tree **seedlot** with 13 acorns placed in each row. This resulted in effective seedling density of 54 to $57/m^2$. Within each half-sib **seedlot** one row of each of the *seven* pairs of *rows* was randomly chosen to be clipped. The remaining row in each pair became the nonclipped control row. Clipping was completed on July 13, 1993, and consisted of cutting approximately 3 to 5 cm off the current flush. The clipping was internodal and just above either a developed or immature **axillary** bud. In mid-December 1993, the seedlings were lifted and heights, RCD, first-order lateral root (FOLR) numbers, stem, and root green weights, lammas shoot development and seedling survival rates were obtained.

In this study, each **seedlot** was treated as a separate experiment. The'experiments were analyzed as randombed block designs where the treatments were nonclipped and clipped. Since there were only two treatments, this analysis was equivalent to **a'paired t-**test Blocks were defined as adjacent pairs of rows in the nursery bed to which the two treatments were assigned at random, one to each row. The experimental unit was a row and the response variables were defined as row means based on thirteen seedlings. Similarly, survival percent and lammas shoot percent were computed on a row basis. Multiple embryos in about 10 to 15 percent of the acorns complicated survival data. Usually the largest seedling was maintained and measured when multiple embryo clusters occurred. Treatment differences were tested at the 0.05 probability level using PROC GLM (SAS Institute 1988).

RESULTS AND DISCUSSION

In this study, the clipping treatment and the innate ability of individual seedlings to develop lammas shoots affected seedling development and survival. Lammas shoot development was the most significant biological response and *may* be the most important factor in the artificial regeneration of white oak.

Effects of Clipping on Seedling Development

Clipping significantly affected seedling development in some half-sib mother tree **seedlots** for specific measured variables. However, because the overall responses were sometimes marginal and variable, they may not be of practical significance. Table 1 shows the sample means for clipped and nonclipped white oak seedlings for the eight variables and the associated P values from the analysis of variance. Half-sib **seedlot** differences in how clipping affected the variables were significant. However, the number of variables significantly different varied by family; the progeny from mother tree 4 were the most consistent. Numbers and

Table I-Effects of clipping on growth, survival, and P- values for white oak seedlings from three open-pollinated half-sib seedlots

	RCD mm	Hgt cm	FOLR[a] No.	Top wgt g	Root wgt g	Total wgt g	Survival pct	Lammas shoot pct
				Family 2[b]				
Nonclipped	5.46	30.8	3.02	18.7	43.0	61.8	81.3	37.7
Clipped	5.17	27.7	2.00	14.4	33.1	47.5	73.6	15.8
P-value[c]	0.257	0.185	0.123	0.084	0.042	0.051	0.086	0.009
				Family 3[b]				
Nonclipped	5.68	29.2	4.21	16.4	37.2	53.6	71.4	37.5
Clipped	4.61	27.0	1.94	12.1	26.4	38.5	63.7	8.9
P-value[c]	0.090	0.465	0.043	0.150	0.086	0.101	0.449	0.001
				Family 4[d]				
Nonclipped	7.34	53.6	5.51	29.9	49.1	79.0	96.2	69.1
Clipped	6.15	47.4	2.95	19.5	32.6	52.1	91.0	54.1
P-value[c]	0.005	0.059	0.013	0.006	0.002	0.002	0.235	0.179

[a] FOLR = first-order lateral root

[b] Based on 7 blocks.

[c] The pvalue obtained from testing the hypothesis that nonclipped and clipped means are equal.

[d] Based on 6 blocks.

proximal diameters of FOLR ≥1 mm were used to assess potential competitiveness of white oak seedlings (Kormanik and others 1989). Clipping reduced numbers of FOLR exceeding this minimum diameter which in turn, reduced root weights by approximately 30 percent

Like deer browsing, clipping resulted in the release of exillary buds, usually immediately below the severed internode. The degree of elongation of these stimulated shoots varied considerably, both within and among half-sib mother tree seedlots. Several weeks passed before the axillary buds were released from their quiescent condition. During this period, the nonclipped seedlings continued to undergo sequential flushes so commonly observed in oak seedlings In nurseries. Even with continued flushing, the overall mean sizes of seedlings (table 1), except those from half-sib seedlot 4 were no larger than normally reported (Boyette 1980; Hill 1966). Past and ongoing research at this location indicates that the time period when FOLR development of nonclipped seedlings accelerates is between flushes 3 and 4 and 4 and 5. Although the study design did not allow for periodic seedling excavation to follow seasonal FOLR development, the lag period between clipping and axillary bud elongation suggests a wound response in terms of carbon sink relationships. We believe that root growth was restricted while carbon was shunted to repair dipping damage to the stem.

When the study was terminated, the clipped seedlings with no significant elongation had few, if any, FOLR that were ≥1 mm in diameter and had poorly developed root system. However, clipping wss not the cause of poor root development We found that nonclipped seedlings exhibiting poor growth were similar to the smaller clipped seedlings in both stem size and red system morphological development Seedlings with undersirable growth and development had a significant impact on the mean growth variable shown in table 1. Unsatisfactory nursery development of open-pollinated half-sib progeny of white oak below a variables mean value has been shown to be accompanied by poor development of FOLR. Unfortunately, a high percentage of white oak seedlings from specific mother trees may be so affected (Kormanik and others 1989) Many of these inconsistencies were observed in the past and can now be explained, in part, by iammas shoot development recorded in thii study.

Effect of Lammas Shoots on Seedling Development

The response of white oak seedlings to the clipping treatment was of minor significance compared to normal iammas shoot development it is well known that white oak seediings tend to develop iammas shoots in late summer and early faii (Busgen end Münch 1929; Zimmermann and Brown 1971; Kramer and Kozlowksi 1979). In our nurseries studies, with white oak when either or both fourth and fifth flushes occur, these flushes can readiiy be classified as "lammas" rather then "proleptic" shoots (Kramer end Kozlowski 1979). Characteristically, these lammas shoots produce leaves that may be 3- to 7-fold larger in surface rrea than leaves produced earlier in the growing season. in the past, we have paid little attention to lammas shoots of white oak except to note their presence (Komanik and others 1989; 1993).

Lammas shoot development is believed to be under genetic control (Cenneii end Last 1976; Kramer end Kozlowski 1979). Our study supports this theory because 38 to 69 percent of the nonclipped seedlings produced iammas shoots. Moreover, in seediots 2 and 3 clipping significantly reduced lemmas shoot development We found lemmas shoots always developed from the terminal bud end the shoots from axiiiery buds released by clipping rarely exhibited typical lemmas growth characteristics.

Mean values of the growth variables for clipped end nonciipped seedlings by iammas shoot development show the impact of lemmas shoots on stem and root development (tabie 2). Because lemmas shoot growth was a dichotomous response variable (yes or no) end was not en independent experimental variable, we feit that formal statistical tests for differences were inappropriate end might be misleading.

Ail individuals with lemmas shoots were superior in ail *seedling* development characteristics (table 2). Most pronounced differences occurred in FOLR numbers and weight of component seedling parts. These growth responses related to lammas shoot development help to explain early FOLR development patterns in white oak (Kormenik end others 1989; 1993). Normeiiy, diameter growth of FOLR accelerates in late summer or early feii. This acceleration coincides closely with lemmas shoot development with white oak seedlings in this study.

Table 2-Effect of iammas shoot development on growth of clipped end nonciipped white oak seedlings

Family	Treat-ment[a]	Shoot[b] growth	RCD mm	Hgt cm	FOLR[c] No.	Top wgt g	Root wgt g	Total wgt g
2	1	0	4.7	24.7	1.4	11.7	28.1	39.8
	1	1	7.7	43.9	5.2	28.0	58.2	86.2
2	0	0	3.9	19.6	0.7	6.5	21.5	28.0
	0	1	8.0	48.1	6.5	37.4	76.2	113.5
3	1	0	4.4	24.9	1.5	10.2	23.6	33.8
	1	1	7.4	48.4	6.8	32.4	56.5	88.9
3	0	0	4.6	20.2	1.9	8.7	24.2	32.8
	0	1	7.3	43.2	7.6	29.0	57.1	86.0
4	1	0	4.5	33.6	0.7	8.9	18.8	27.7
	1	1	7.5	58.8	4.9	28.2	44.3	72.5
4	0	0	5.6	34.0	1.8	9.8	30.0	39.9
	0	1	8.0	62.1	7.1	38.7	57.1	95.9

[a] 1 = clipped; 0 = control.
[b] 1 = iammas shoot; 0 = NO lemmas shoot.
[c] FOLR = first-order lateral root.

Table **3--Characteristics** for **leave6** grown on normal shoot and **lammas** shoot of White oak Seedlings.

Leaf type	Leaf area cm'	**Photosynthesis** rate **umol/m^2.sec**	Total leaf **photosynthesis nmol/leaf.sec**	**mg/cm^2 Leaf specific weight**
Mature normal	23	14.1	32.4	0.6
Mature normal	51	14.5	74.0	0.2
Mature **lammas**	132	14.6	102.7	11.0
Mature **lammas**	140	13.5	180.0	**9.3**

Seedling6 exhibiting lammas shoot development were taller and had higher number6 of FOLR regardless of clipping treatment This observation parallel6 earlier observations where seedlings with **six** or more FOLR were two time6 taller and had **RCDs** twice as large a6 those with **less** than **six** FOLR. Earlier research had **shown** even greater variation among root and stem weight6 where **4-** to **7-fold differences** in root and stem weight were associated with greater number6 *of* FOLR (Kormanik and other6 1080; 1000). The largest seedlings in all studies frequently had two consecutive lammas shoot **episodes.**

Based on **these** data (table6 1 and **2),** a direct genetic correlation between FOLR development and lammaa shoot6 with **this species** appear6 to exist Our research support6 the hypothesis that the most dominant and codominant oak tree6 in the forest were those that were able to make rapid juvenile growth **(Korstain** 1927). **This** permitted them to get ahead of the **herbaceous** competition **that is** encountered after **overstory** harvesting. Therefore, the innate abilii to produce **lammas** shoot6 may be significant in whiie oak seedling establishment **How** long seedling6 have the potential to produce lammas **shoots is** unknown. Even a lammas **shoot** development period of only 3 to 4 **years,** may contribute'to seedling **success.**

We **also measured photosynthesis** and found that photosynthetic rate6 per unit leaf **area are the** same for the large lammas **shoots/leaves** and the smaller leave6 produced earlier in the summer. The advantage of lammas leave6 **lies** in their greater total leaf **area** that contribute6 significantly more carbon for seedling development (table 3).

We **have a&o observed** in several ongoing **research** studies at the **ITRB** that seedlings that develop **lammas shoots** the **first** year may **also** develop **lammas shoots** in the second growing season. When grown **under** proper nursery cultural conditions, transplanted **white oak** that developed lammas **shoots** the first **and second years,** attained height6 from 1.7 to 1.8 m **after the second** growing season.

CONCLUSION

Clipping whiie oak seedlings do66 not improve **seedling** qualii and **is** not recommended for improving seedling **size** or qualii. Although lammas shoot development in nursery stock production **has not been** studies extensively, **this** innate trait may **be important in** early selection of competitive individual **seedlings for** outplanting. Clipping can **significantly reduce the** development of lammaa **shoots.** When **clipped** seedlings develop lammas shoots, total **height and** RCD are comparable, but weight of other **component** part6 of seedlings may be significantly **reduced.**

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