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THE INFLUENCE OF THE GEOMETRY AND DISTRIBUTION OF ROOT SYSTEMS ON COPPICE REGENERATION AND GROWTH OF HYBRID POPLARS.

IOWA STATE UNIVERSITY, PH.D., 1978

The influence of the geometry and distribution of root systems on coppice regeneration and growth of hybrid poplars

by

Don Koo Lee

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Forestry
Major: Forestry (Biometry)

Approved:

Signature was redacted for privacy.

In Charge of ~~Major~~ Work

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

Iowa State University
Ames, Iowa

1978

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INTRODUCTION

The Problem

World-wide demand for wood products is expected to increase more dramatically than available wood supplies to the year 2000 (USDA Forest Service, 1973). Forest land, however, is continuously shrinking. The problem facing forestry is to efficiently increase production of wood fibre: that is, to produce more wood, in a short time, from a smaller land base.

Intensive culture of woody plants shows the possibility of increasing wood fibre productivity (McAlpine et al., 1966; Larson and Gordon, 1969; Schreiner, 1970; Steinbeck et al., 1972) and total tree utilization concepts increase potential raw materials (Young, 1964; Keays, 1971). Close spacing, short rotations and superior genotypes allow for high yields from small areas (Heilman et al., 1972; Smith and DeBell, 1973; DeBell, 1975; Dawson et al., 1976). In addition, woody plants at high densities and for coppice regeneration have several potential advantages in dry-matter productivity over annual crop plants (Gordon, 1975). Coppice regeneration systems are economically advantageous because replanting after each harvest, which is costly, is not necessary.

Among many factors influencing coppice regeneration, the most important are genotype, length of rotation, spacing of plantation, and proper management. Each of these must be evaluated on the basis of biological and economic criteria. To accomplish this most rapidly, both controlled environment and field studies are needed. Greenhouse studies can give information about early selection of the clones having not only good wood

properties and rapid growth but also high regeneration potential. With appropriate field studies, selected clones can be used as a basis for breeding programs. Furthermore, genotypes selected from greenhouse studies would have desirable coppice regeneration attributes such as the appropriate number of sprouts, fast sprouting and rapid sprout growth, and resistance to pests. However, control of genotype is very important for successful management programs. If certain clones show deep-rooting and late-sprouting characters but rapid growth potential, those may be suggested for mixed plantations with shallow-rooting and early-sprouting clones. Mixed stands may be more effective for utilization of site (Smith, 1962) and usually are more resistant to damage by biotic agencies (Graham, 1952) than pure stands.

If the relation between variables of roots and shoots is understood and the most desirable size of stump or root system for coppice regeneration is obtained, it may be possible to predict the effects of intensive yield on cultural treatments over several coppice rotations. Promnitz and Rose (1974) demonstrated that simulation models from laboratory experiments can predict the total production of young forest stands in the field.

To help identify superior genotypes and best plantation densities for intensive culture systems (Figure 1), I evaluated the growth performance following coppicing of six hybrid poplar clones in the greenhouse and four of them in two field locations. Effects of location, density and clone on growth variables and the relation between variables of shoots and roots were also examined to provide information about successful coppice regeneration.

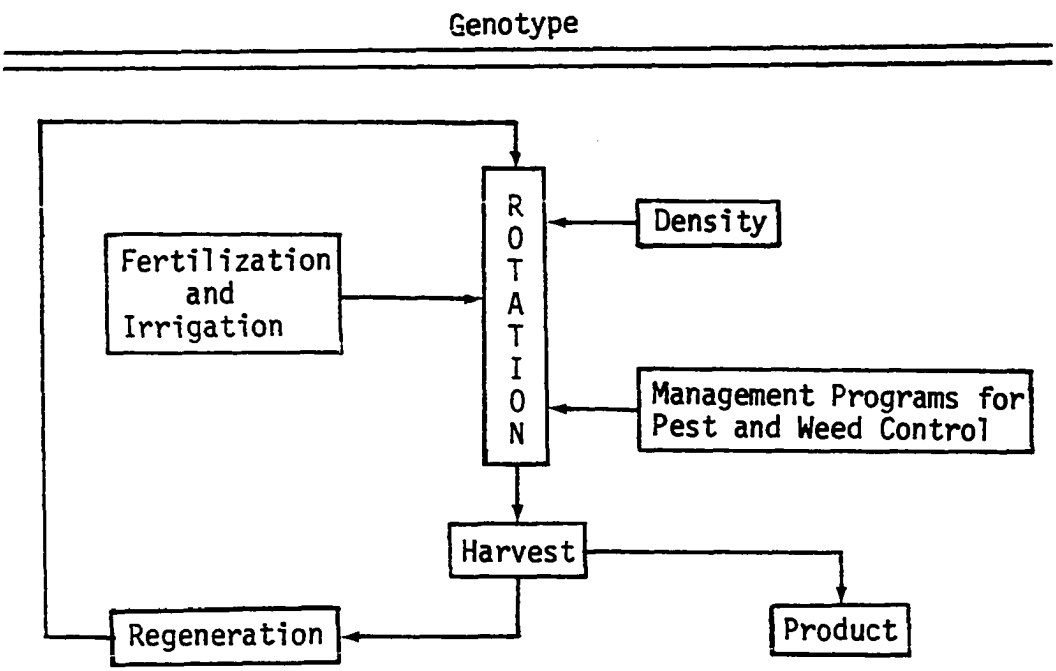


Figure 1. Intensive culture systems

Literature Review

The previous studies indicate that the major factors affecting coppice regeneration are tree species or genotypes, length of rotation, planting density, the height of stump cuts, season of cutting, characteristics of the residual stand (stumps and roots), fertilization and irrigation, pest and weed controls, and site fertility. These will be reviewed separately.

Species or genotypes

Dickmann (1975) pointed out that the ideal plant materials having such characters as rapid juvenile growth, erect branching and high leaf areas for maximum solar radiation interception, and acceptable wood properties are appropriate for intensive culture of wood fiber and must be easily regenerated.

Coppicing is one of the simplest regeneration methods and can be applied to most woody species having sprouting ability. Sprouting is a common character for hardwoods but is rare in conifers. Considerable variation also exists among species within each of these groups. White oak and post oak showed more but shorter sprouts per stump than black and scarlet oaks (Little, 1938). Sycamore and sweetgum sprouted better than yellow poplar (Kulchol, 1971). Hybrid poplar clones used in this study show vigorous sprouting in controlled environments and differ in sprouting characteristics; for example clone 5323 appears to sprout more per stump than clone 5377 but clone 5377 appears to sprout earlier after coppicing than clone 5323. In the field, moreover, clonal differences in sprouting characteristics would be large because the development of root systems among genotypes differs (Fasehun, 1975), which can affect the utilization of soil moisture and minerals. One of the major objectives of this study was to identify genotypes that sprout vigorously and produce appropriate numbers of sprouts per stump. This may be related to rapid mobilization of stored reserves in root systems. Vigorous sprouting will be important not only for the first rotation, but for the second and subsequent rotations.

Densities of sprouts per stump influence total dry matter production. If too many sprouts arise on a stump of one genotype, total growth might be less than those from the proper number of sprouts of another genotype because of severe competition for utilization of stored nutrients. Thus, regeneration with root suckers may not be appropriate for maximum production.

Length of rotation

Rotation length becomes a limiting factor to coppice regeneration because of its effects on root development, which in turn affects regeneration capabilities. The cutting cycles greater than two years had higher fresh or dry weight yields of sycamore than a one-year cycle (Kormanik et al., 1973; Kennedy, 1975). For the coppice growth of black cottonwood, a four-year cutting cycle showed higher dry weight yields than that with a two-year (DeBell, 1975). Thus, first coppice would be best when root systems are well-developed, at least three or four years after planting. Otherwise, sprouting abilities probably will be weak, especially when many short rotations are considered.

Density of plantation

Larson (1962) mentioned that yield as well as wood quality can be easily manipulated by the spacing of plantation. The effect of spacing on the total production of biomass becomes more important with shorter rotations (Zavitkovski, 1976). Although close spacings are better for the maximum utilization of the site, they will exhibit more severe competition for water or nutrients by roots and for light. The number of sprouts and number of surviving sprouts per stump increased with increasing spacing (Steinbeck et al., 1972). Relatively narrow spacings such as 30 x 60 cm to 60 x 120 cm in sycamore (Kulchoi, 1971; Steinbeck and May, 1971; Kormanik et al., 1973) and 30 x 30 cm in black cottonwood (Heilman et al., 1972) produced high yields and the highest initial sprouting, but closer spacings showed high stump mortality. This relationship between density and yield, however, changed with increasing age. For example, in 2- to 4-year-old

sycamore stands, established at four spacings (30 x 120 cm, 60 x 120 cm, 120 x 120 cm, and 180 x 120 cm), the most dense plantation showed the highest yield for the second and third years, but in the fourth year, the highest yield was shown by the 60 x 120 cm spacing followed by the 120 x 120 cm spacing (Saucier et al., 1972). Another study of Kennedy (1975) in intensively managed sycamore stands showed that the most dense spacing yielded the greatest fresh weight in the first, second, and third years while wider spacing produced greater biomass in the fourth year than close spacing. This implies that the establishment of very dense plantations may not be best in terms of yield production and plantation density should be considered with rotation age for the maximum biomass yields.

On the different density plantations, hybrid poplar clones showed clonal differences in root and top growth even before coppicing (Lee, 1975). Thus, large differences in coppice growth also could be expected to result from various combinations of spacings and clones.

Height of stump cuts and season of cutting

The height of the stump and time of cutting also have an important effect on the production of sprouts following cutting. High-cut stumps of swamp tupelo showed more sprouts and stumps sprouting than low-cut stumps in the nursery beds or in the 90-year-old stands (Hook et al., 1967; DeBell, 1971). If sprouts arise from the root collar at or below the ground, however, it is suggested to cut the stumps as low as possible (Hawley and Smith, 1954). Sprouting was poorest for stumps cut during the growing season, whereas best sprouting was exhibited by stumps cut during the dormant

season (Keller, 1942; DeBell and Alford, 1972; Belanger and Saucier, 1975). In these studies, however, the height of the stump was restricted to 10 cm above soil surface and cutting was done during the dormant season.

Characteristics of residual stand (stumps and roots)

Much attention had been given to the growth of above-ground plant parts until the idea of whole tree utilization was proposed. The close association of root development to the growth above ground has been examined (Foth, 1962; Eliasson, 1968; Kramer, 1969; Troughton, 1974). In particular, the above-ground biomass production from coppice regeneration could be even more related to the characteristics of stump and root systems. In red oak, stumps of large parent trees initially produced a greater number of sprouts, but differences disappeared with increasing age (Johnson, 1975). Similarly, Sander (1971) observed that oak sprouts from the largest stems were greatest in number and exhibited the fastest growth. Studies with stump diameters ranging from 3 through 33 cm have shown that coppice yields of sycamore increase as diameter of the stump increases (Belanger and Saucier, 1975).

Growth rate of sprouts can be accounted for by supplies of carbohydrates and the inheritance of the ability to form extensive root systems (Smith, 1962). Seasonal carbohydrate reserves fluctuated in a pattern similar to sprouting vigor (Smyth, 1934). In contrast with these facets, sprouting of sweetgum was not dependent on carbohydrate content; for instance, larger stumps contained a lower quantity of total carbohydrate than smaller ones but produced larger and more sprouts (Wenger, 1953). A hormone system related to that controlling apical dominance was thought to

be the chief factor governing the vigor of sprouting (Wenger, 1953). Similarly, Vogt and Cox (1970) observed that breaking of bud dormancy in oak stump was controlled by hormonal action, not by reserve carbohydrates. Moreover, the least vigorous sprouts were produced by cutting when the leaves were nearly full size (Stoeckeler, 1947), which is a time to produce the maximum growth substances of the leaves or needles. This indicates that sprouting may be more directly related to fluctuations in hormones.

Fertilization and irrigation

Greater attention to nutrient and water supplies is necessary because of the shortened time periods for harvest and increased intensity of biomass removal in this system and consequently of severe competition for available nutrient and moisture of soils.

Irrigation affects not only growth and yield but also wood properties. Diameter or height growth was increased by irrigation during the growing season (Broadfoot, 1964; Sagmuller and Sopper, 1967; Howe, 1968). The number of nonflattened tracheids and specific gravity of ponderosa pine showed an increase due to irrigation (Howe, 1967). The prolonged formation of earlywood tracheids was found in a growth study of red pine under irrigation (Zahner et al., 1964).

Growth was substantially increased by an application of fertilizer whereas wood properties such as cellulose yield, tracheid length, and specific gravity generally showed a decrease. Height and diameter of fertilized slash pines grew twice as well as those of controlled trees (Pritchett and Smith, 1969). Wood production on both a volume and a weight basis was remarkably increased by the application of fertilizer to a

Douglas fir plantation (Resler et al., 1974). Also, NPK applied to a plantation of southern pines, one year after planting, resulted at age 9 in a volume of nearly 112 m^3 per hectare compared to only 14 m^3 per hectare in the unfertilized stands (Schmidtling, 1973). Cellulose yield and tracheid length of loblolly pine were decreased with increasing dosage of N-P-K fertilizer (Zobel et al., 1961). Similarly, specific gravity was reduced as a result of the faster growth rate following the application of fertilizer (Williams and Hamilton, 1961; Posey, 1964). The increase in yields of quaking aspen as a result of fertilization was intensified by irrigation (Einspahr et al., 1972).

Pest and weed controls

Young leaves and stems developed from sprouting can frequently become subject to widespread attack by insect or disease because of such favorable conditions as physiological juvenility and abundant attractive materials contained for certain insects or diseases. Reduction of leaf area or even defoliation by pests affects tree growth primarily by reducing the amount of photosynthetic tissue and thereby the amount of carbohydrates available for growth. Leaf rust caused a great amount of leaf damage and defoliation and consequent damage to trees (Schipper and Dawson, 1974; Widin and Schipper, 1976). Stem cankers severely damaged hybrid poplars in experimental plots at Ames, particularly clone 5323 (Schipper et al., 1977). Phelps (1974) demonstrated that significant loss of dollar value could occur due to damage by fusiform rust.

Weeds can greatly influence tree growth. About 30 percent of plantation mortality in the southern region was attributed to stress by weed

competition (Fitzgerald et al., 1973). The control of weeds increased growth in some trees and decreased survival in others. A large increase in the growth of white ash and silver maple resulted from weed control (Von Althen, 1970). Twice as many sycamore cuttings with weed control survived than without control (McAlpine et al., 1972). In contrast to this result, application of herbicides to control weeds resulted in a lower survival for conifer species (Phipps and Noste, 1976). Furthermore, to attain the maximum fiber production in this system, weeds should be controlled because they compete severely with trees for sunlight, water, and mineral nutrients. As open spaces broaden from coppicing, weeds get favorable conditions although their growth beneath tree canopies has been suppressed. Therefore, mechanical and chemical control of weeds was suggested to establish successful short-rotation forest crops (Heiligmann, 1975).

Site fertility

Such environmental conditions as site characteristics and climatic factors, as well as cultural practices, also directly influence coppice regeneration. Sprouting is usually quicker and more vigorous on good sites than on poor sites. Auclair (1975) reported that black cherry showed the greatest growth rates and lowest incidence of sprouting on favorable sites. Quaking aspen and pin cherry had about 27 percent taller sprouts on good sites than on poor sites in northern Wisconsin (Stoeckeler, 1947). Sprout growth of red oak was also faster in height on good sites and the effect of site increased with age (Johnson, 1975). In hybrid poplars, coppice-shoot production was affected more by site quality than clonal parentage (Davidson and Davis, 1972). Better growth on favorable sites is probably

attributable to more available moisture and nutrients and better developed root systems. Thus, intensive cultural practices should be examined at a variety of locations.

Objectives

The primary objective of this study was to compare the coppice growth performance of hybrid poplars 1) by examining sprouting vigor in controlled environment, which gives useful information for early selection and on whether controlled-environment growth characters can predict coppice regeneration and performance in the field; 2) by evaluating responses to coppicing in the field as affected by two locations, four clones, and three densities; and 3) by determining important variables to predict effects of density changes on regeneration and growth responses, to maximize total coppice production.

GREENHOUSE EXPERIMENT

Materials and Methods

Plant materials

The sprouting vigor of six hybrid poplar clones (Zuuring, 1975), after coppicing, was examined (Table 1).

Table 1. Selected hybrid poplar clones

North Central Forest Experiment Station number	Name and parentage
5377	*Populus* x *euramericana* Guinier
5321	*Populus* x *euramericana* Guinier
5323	*Populus* x *euramericana* Guinier
5326	*Populus* x *euramericana* Guinier
5328	*Populus* x *euramericana* Guinier
5260	*Populus tristis* Fish. x *Populus balsamifera* L.

Eighteen rooted cuttings of each clone which were of uniform height, leaf area, and root length were selected and planted individually in 7400 cm^3 black plastic pots. The potting medium consisted of a 2:1 mixture of Jiffy Mix and Perlite. Plants were grown in a greenhouse bay for 24 weeks at 24°C during the day and 18°C during the night. An 18-hour photoperiod was maintained during the January 8 to June 25 growth-period by supplemental lighting with incandescent and fluorescent lights during dark periods between 6:00 AM and 12:00 midnight. All plants were watered

identically and fertilized once a week with a Peters 20-20-20 fertilizer solution containing 200 ppm N, 88 ppm P, and 166 ppm K.

Experimental design and statistical analysis

A split plot design was used with two treatments (control vs. coppiced) as whole plots. Each treatment had three replicates which served as blocks. Six clones were randomly assigned to each block and were grown under the controlled environmental conditions. At the end of the tenth week, three trees per clone were harvested for growth measurement and another three individuals of each clone were coppiced with a cutting height of 5 cm. Most of the new shoots died within 20 days of sprouting, so the experiment was revised as follows: all trees of three blocks selected at random were cut back to a 10 cm in height and sprouts were grown for ten weeks; only one tree of each clone was harvested for growth comparison. A randomized block design was adopted for the analysis of coppice growth performance. Most of the readily available food and nutrients necessary for shoot growth are stored in the stumps of the juvenile trees rather than in the root system (Balatinecz et al., 1966). Therefore stump volume was used as a covariate for the covariance analysis of the coppice yield.

Uni- and multi-variate analysis of variance was used to test whether or not there were any clonal differences in growth performance after coppicing. In addition, canonical correlation analysis was used to analyze the relationships between top and bottom variables after coppicing.

Tree measurements

The following variables were measured at the end of 10, 14, and 24 weeks after planting: height (HT), basal diameter (DIA), stem dry weight

(STDW), leaf dry weight (LFDW), basal diameter of stump (STMDIA), stump dry weight (STMDW), and root dry weight (RTDW). Maximum length (SPLN) and number of sprouts (SPNO) were additionally measured for the coppice treatment. In addition, top dry weight (TOPDW: STDW + LFDW), bottom dry weight (BOTDW; STMDW + RTDW), and top to bottom ratio (TBRO) were calculated from these values. Height and diameter were measured to the nearest 0.1 cm and dry weights to the nearest 0.01 g after drying for 72 hours in a 70°C oven. Sample leaves were selected systematically for leaf measurement, and then lengths and widths of them were measured with a plastic ruler to the nearest 0.1 cm. Leaf surface area (LFAREA) was calculated with regression methods (Zuuring, 1975). The measurements were done four times (the sixth, tenth, fourteenth, and twenty-fourth week) for the control plants and twice (nineteenth and twenty-fourth week) for the coppiced plants.

Results

Growth differences between treatments and between clones

Height and diameter No clonal differences in height growth were significant at the 5 percent level for the control plants and none of the clones showed consistent height growth throughout the growing period. However, diameter growth was significantly different between clones, and clone 5328 grew better than the other clones (Table 2).

For the coppiced plants, clonal differences in sprout length were highly significant. The largest mean sprout length was attained by clone 5321 although it showed the slowest height growth in the control (Table 3). This was probably because clone 5321 produced the least number of sprouts.

Table 2. Means of clones for the leaf surface area, height, and basal diameter of control plants at each harvest in the greenhouse

Clones	LFAREA (cm^2)				HT (cm)				DIA (cm)			
	Feb. 12	Mar. 19	Apr. 16	June 25	Feb. 12	Mar. 19	Apr. 16	June 25	Feb. 12	Mar. 19	Apr. 16	June 25
5377	1002.4	5812.9	9132.1	12581.6	33.7	120.8	208.8	292.9	0.6	1.1	1.3	1.8
5321	580.0	3874.8	7736.2	12126.6	33.8	110.2	199.4	253.0	0.5	0.9	1.3	1.6
5323	844.7	5593.1	10223.1	14738.5	36.3	122.6	196.9	312.7	0.5	0.9	1.2	1.8
5326	937.5	5360.7	10232.3	13112.2	33.4	118.0	186.8	276.4	0.5	1.0	1.3	1.9
5328	1170.5	6538.4	11283.1	15690.8	28.2	103.2	181.2	280.9	0.6	1.0	1.5	2.2
5260	822.3	3881.7	7784.5	9136.9	39.6	126.8	211.8	266.2	0.4	0.9	1.4	1.5
	0.064*	0.054	0.016	0.024	0.227	0.392	0.206	0.235	0.024	0.131	0.008	0.001

*Indicates significance level between clones.

Table 3. Means of clones for the leaf surface area, length, and number of sprouts after coppicing in the greenhouse

Clones	LFAREA (cm^2)		Maximum sprout length (cm)		Sprout no.	
	May 24	June 25	May 24	June 25	May 24	June 25
5377	1765.6	2388.8	25.3	33.2	6	6
5321	1628.6	2074.7	36.0	48.6	5	5
5323	2028.5	2791.3	26.8	42.2	7	6
5326	2439.6	2908.5	24.7	33.1	8	7
5328	2723.7	3939.2	25.3	33.9	7	7
5260	1790.0	1828.2	21.7	29.2	7	7
	0.162*	0.018	0.075	0.023	0.247	0.103

*Indicates significance level between clones.

Leaf surface area There were clear differences in LFAREA between clones in the control treatment, which increased in magnitude as the trees grew (Figure 2). Clone 5328 developed the largest LFAREA throughout the experiment, followed by clones 5323, 5326, and 5377 in descending order, and clones 5321 and 5260 had the smallest.

The coppiced plants were similar in their LFAREA development to the control plants except for clones 5323 and 5326. The largest mean LFAREA was shown by clone 5328 followed by clones 5326, 5323, and 5377 in descending order, and clones 5321 and 5260 had the smallest. Looking at the clonal means of the fifth week (May 24) after coppicing, the mean response of LFAREA of the coppiced plants was greater than that of the controlled grown for six weeks. This indicates that it may be possible to increase growth via coppicing.

Dry weight All variables showed highly significant differences between two treatments, and the control plants produced more dry weight

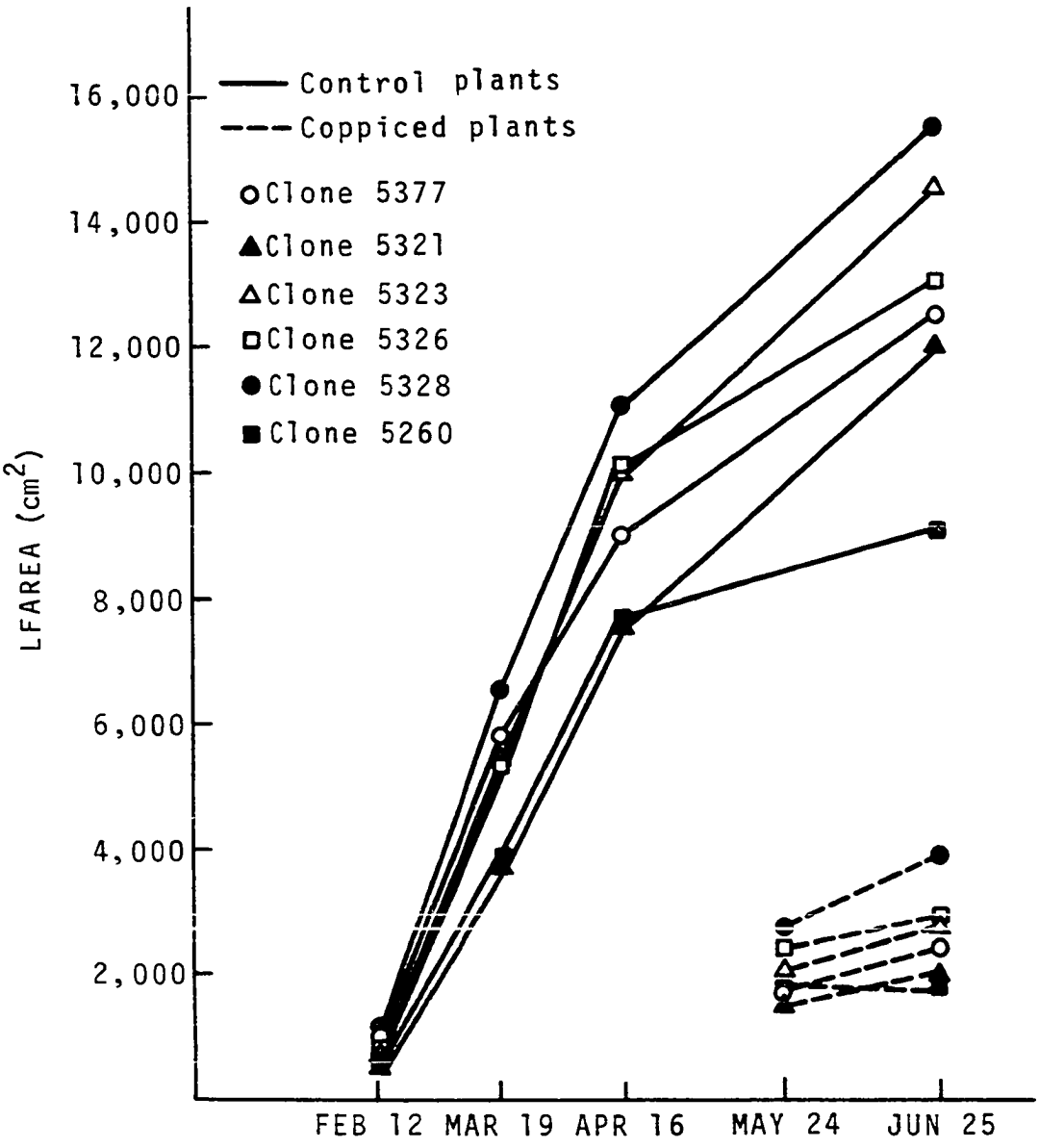


Figure 2. Comparison of leaf area development between six clones in the greenhouse (coppicing was done on April 16)

than coppiced plants (Tables 4 and 5): 3, 2, 2, and 4 times in STDW, LFDW, STMDW, and RTDW, respectively. The TOPDW produced by coppiced plants, however, surpassed that of the uncut plants when compared at the same age (Figure 3). This also implies that growth may be increased by coppicing if a longer growing period is provided.

Table 4. Mean squares from analysis of variance for the final yield in the greenhouse

Source of variation	d.f.	STDW	LFDW	STMDW	RTDW
Treatments (T)	1	$85244^{.01*}$	$22430^{.01}$	$226.2^{.02}$	$78596^{.00}$
E (a)	4	2302	837	16.4	276
Clones (C)	5	$2276^{.01}$	$3875^{.00}$	$27.0^{.00}$	$919^{.00}$
T x C	5	$1087^{.13}$	$429^{.21}$	$6.1^{.09}$	$225^{.20}$
E (b)	20	552	271	2.7	139

*Indicates significance level.

Clonal differences were also large. All dry weight variables of clone 5328 were greater than those of the other clones whether coppiced or controlled (Table 5). Particularly, at each harvest with control plants, the largest mean TOPDW was attained by clone 5328 followed by clones 5323, 5377, and 5326 in descending order. Two clones, 5321 and 5260, produced the lowest TOPDW (Figure 3).

Table 5. Means of clones by treatments for the final yield in the greenhouse

Treatments	Clones	STDW (g)	LFDW (g)	STMDW (g)	RTDW (g)
Control	5377	164.7	121.8	13.9	109.1
Control	5321	109.2	99.5	9.6	119.1
Control	5323	165.7	132.3	13.3	124.9
Control	5326	150.5	130.6	12.0	127.7
Control	5328	190.3	173.1	17.3	154.1
Control	5260	109.3	73.6	9.3	102.3
Coppiced	5377	66.4	69.3	6.9	27.0
Coppiced	5321	61.1	62.4	5.9	25.2
Coppiced	5323	73.7	74.7	6.0	26.2
Coppiced	5326	81.1	79.8	7.9	27.7
Coppiced	5328	99.9	103.4	9.7	44.5
Coppiced	5260	49.2	51.6	6.3	25.9

Similar trends were exhibited in the coppiced treatment: the largest mean TOPDW was shown by clone 5328 followed by clones 5326, 5323, and 5377 in descending order, and clones 5321 and 5260 had the smallest TOPDW.

Dry weights of stump and root of the control plants were larger than those of the coppiced plants, and again, clone 5328 had the largest mean dry weight.

Top to bottom ratio Shoot to root ratios as well as proportions of shoot or root to total dry weight were, in general, used for the expression of assimilate distribution. The TBRO, however, was calculated to examine how assimilates were distributed after coppicing. The TBRO decreased rapidly as growth period increased from 10 to 24 weeks for all clones (Table 6). Clones 5377, 5323, and 5328 had the largest TBRO, and clones 5321 and 5260 had the smallest in the control treatment, whereas in the

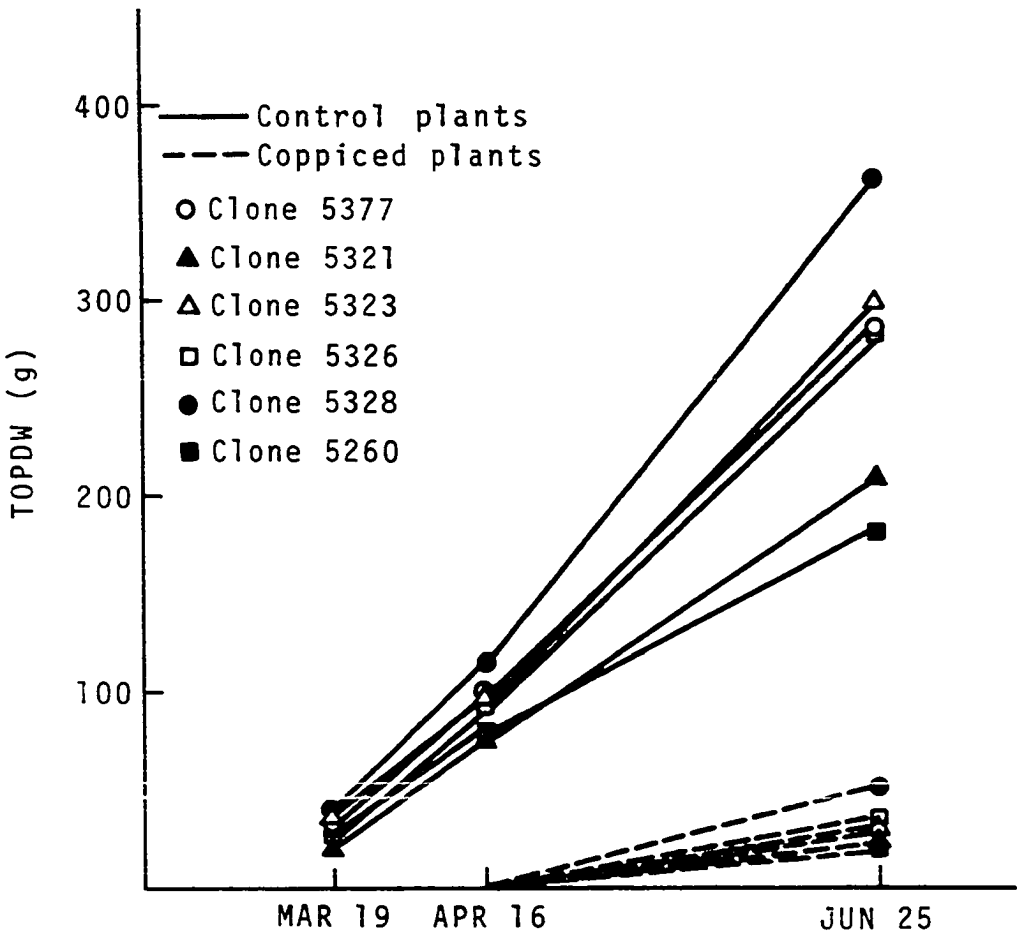


Figure 3. Comparison of top dry weight for six clones in the greenhouse (coppicing was done on April 16)

coppiced treatment clones 5326, 5323, and 5328 showed the largest ratio, and clones 5260 and 5321 showed the smallest (Table 6). Thus, clones 5260 and 5321 are not superior genotypes in terms of total dry weight accumulation because of less assimilate deposited in the top while clones 5323, 5328, 5326, and 5377 appeared to be good genotypes in terms of assimilate deposition in the top. The mean TBRO, at final harvest, showed that average values for plants coppiced at the end of 10 or 14 weeks were smaller than those of the control. Because of rapidly growing sprouts, the ratios of coppiced plants were expected to increase so that original growth balance could be recovered.

Table 6. Ratios of top to bottom for control and coppiced plants at 10th, 14th, and 24th week after planting in the greenhouse

Clones	Treatments	10-week	14-week	24-week
5377	Control	5.96	4.22	2.33
5377	Coppiced	--[a]	--	0.88
5321	Control	4.52	3.75	1.62
5321	Coppiced	--	--	0.86
5323	Control	6.07	4.22	2.16
5323	Coppiced	--	--	0.99
5326	Control	5.34	5.67	2.01
5326	Coppiced	--	--	1.04
5328	Control	4.76	3.21	2.12
5328	Coppiced	--	--	0.98
5260	Control	4.68	3.62	1.64
5260	Coppiced	--	--	0.66

[a]Indicates no measurement.

Comparison of top dry weight accumulation between coppiced clones after adjusting for initial stump volume

Except for clones 5328 and 5260, most sprouts had died after the first coppicing. This was probably due to a lack of stored materials in the root system necessary for sprout growth. Based on that assumption, the initial stump volume for all clones was adjusted to compare clonal differences in top dry weight. When the initial stump volume was not used as covariate, clonal differences in top dry weight variables were highly significant. However, the significant effect of clone on top dry weight yields was reduced by adjusting the initial stump volume (Table 7). After adjustment, the highest yielding clone 5328 was not significantly different in top dry weight from clones 5326, 5323, 5321, and 5377 but was much superior to clone 5260 (Table 8).

Table 7. Mean squares from analysis of variance for coppice growth variables adjusted and unadjusted by initial stump volume in the greenhouse

Source of variation	Unadjusted				Adjusted			
	d.f.	STDW	LFDW	TOPDW	d.f.	STDW	LFDW	TOPDW
Clones	5	$32.9^{.05*}$	$185.6^{.01}$	$372.3^{.01}$	5	$21.3^{.13}$	$96.4^{.05}$	$205.5^{.07}$
Error	10	9.7	26.6	67.7	9[a]	9.2	26.6	66.5

*Indicates significance level.

[a]One degree of freedom was lost due to covariate.

Table 8. Means of clones by treatments for the TOPDW adjusted and unadjusted by initial stump volume in the greenhouse

Clones	Control (g)	Coppiced	
		Unadjusted (g)	Adjusted (g)
5377	286.57	29.23	29.31
5321	208.70	26.70	30.54
5323	297.93	31.80	35.62
5326	281.10	37.07	37.84
5328	363.40	53.20	45.97*
5260	182.90	21.13	19.85

*Indicates significance at the 5 percent level.

Relationships between top and bottom growth variables after coppicing

The results obtained from univariate analysis for coppice growth performance show that most variables of clone 5328 had the largest increase after coppicing except for the sprout number (Table 9), and differences were generally significant (Table 10). The significant effect of clone on these variables was primarily due to the largest mean responses of clone 5328.

The mean responses of coppice growth variables indicated clonal ranks as follows: clone 5328 was the largest, clones 5326, 5323, and 5377 intermediate, and clones 5321 and 5260 the smallest.

In general, partial correlation coefficients holding block and clone constant indicated strong and positive relationships between coppice growth variables except for sprout number (Table 11): that is, all bottom growth

Table 9. Means of clones for coppice growth variables in the greenhouse

Clones	SPNO	TOPDW (g)	STMDIA (cm)	STMDW (g)	RTDW (g)
5377	6.00	29.83	1.53	6.93	26.97
5321	4.67	26.70	1.60	5.87	25.17
5323	6.33	31.80	1.57	6.03	26.17
5326	7.67	37.07	1.70	7.87	27.73
5328	7.00	53.20	1.93	9.73	44.50
5260	6.67	21.13	1.60	6.27	25.90

Table 10. Mean squares obtained from uni-variate analysis of variance for coppice growth variables in the greenhouse

Source of variation	d.f.	SPNO	TOPDW	STMDIA	STMDW	RTDW
Clones	5	$3.12^{.10*}$	$372.30^{.01}$	$0.06^{.01}$	$6.54^{.00}$	$166.40^{.00}$
Error	10	1.26	67.73	0.01	0.89	16.71

*Indicates significance level.

variables with the top dry weight and stump diameter with stump dry weight. However, relationships within top growth variables and within bottom growth variables were generally not significant. This strong association between growth variables of top and bottom was also evident when canonical correlation analysis was performed (Table 12).

Table 11. Partial correlation coefficients between coppice growth variables holding block and clone constant

	SPNO	TOPDW	STMDIA	STMDW	RTDW
SPNO	1.00	$0.42^{\cdot 20}$	$0.28^{\cdot 59}$	$0.07^{\cdot 83}$	$0.29^{\cdot 61}$
TOPDW	$0.42^{\cdot 20*}$	1.00	$0.81^{\cdot 00}$	$0.65^{\cdot 03}$	$0.84^{\cdot 00}$
STMDIA	$0.28^{\cdot 59}$	$0.81^{\cdot 00}$	1.00	$0.68^{\cdot 02}$	$0.49^{\cdot 12}$
STMDW	$0.07^{\cdot 83}$	$0.65^{\cdot 03}$	$0.68^{\cdot 02}$	1.00	$0.47^{\cdot 14}$
RTDW	$0.29^{\cdot 61}$	$0.84^{\cdot 00}$	$0.49^{\cdot 12}$	$0.47^{\cdot 14}$	1.00

*Indicates significance level.

Table 12. Canonical correlation coefficients relating coppice growth variables of top and bottom

Canonical variable number	Canonical correlation coefficient	χ^2-value
Var. #1	0.9616	$21.152^{\cdot 00*}$
Var. #2	0.2351	$0.455^{\cdot 80}$

*Indicates significance level.

Hotelling-Lawley's Trace used as a test criterion showed significance at the 0.3 percent level (Table 13), which illustrates that there were some clonal effects on those variables.

In addition, strong and linear relationship was exhibited between canonical variable #1 in group 1 (top growth variable) and canonical variable #1 in group 2 (bottom growth variable) (Figure 4). Figure 4 shows

Table 13. F-values from multi-variate analysis of variance for coppice growth variables

Test hypothesis	F-value
Ho: No clone effect	$3.39^{.003*}$

*Indicates significance level.

that the points for clone 5328 are located at the upper portion of the graph and quite far from those for the other clones. This indicates that clone 5328 is better in terms of those growth variables than the other clones and is also different from the other clones.

The first two canonical variables explained 86.7 percent of the variation due to clone (Table 14). In canonical variable #1, root dry weight, dry weight and basal diameter of stumps contributed the most to variations between clones (Table 15). The second canonical variable explained 13.6 percent of the variation due to clone. In this case, the dry weight of stump, top dry weight, and root dry weight contributed the most to variations between clones (Table 15).

In summary, such growth variables as root dry weight, stump dry weight, and top dry weight contribute the most to the clonal difference.

Discussion

Growth performance differences between two treatments

Leaf surface area as a measure of photosynthetic ability and dry weight as an expression of assimilate deposition were markedly different between clones in both control and coppiced experiments. Clone 5328 was

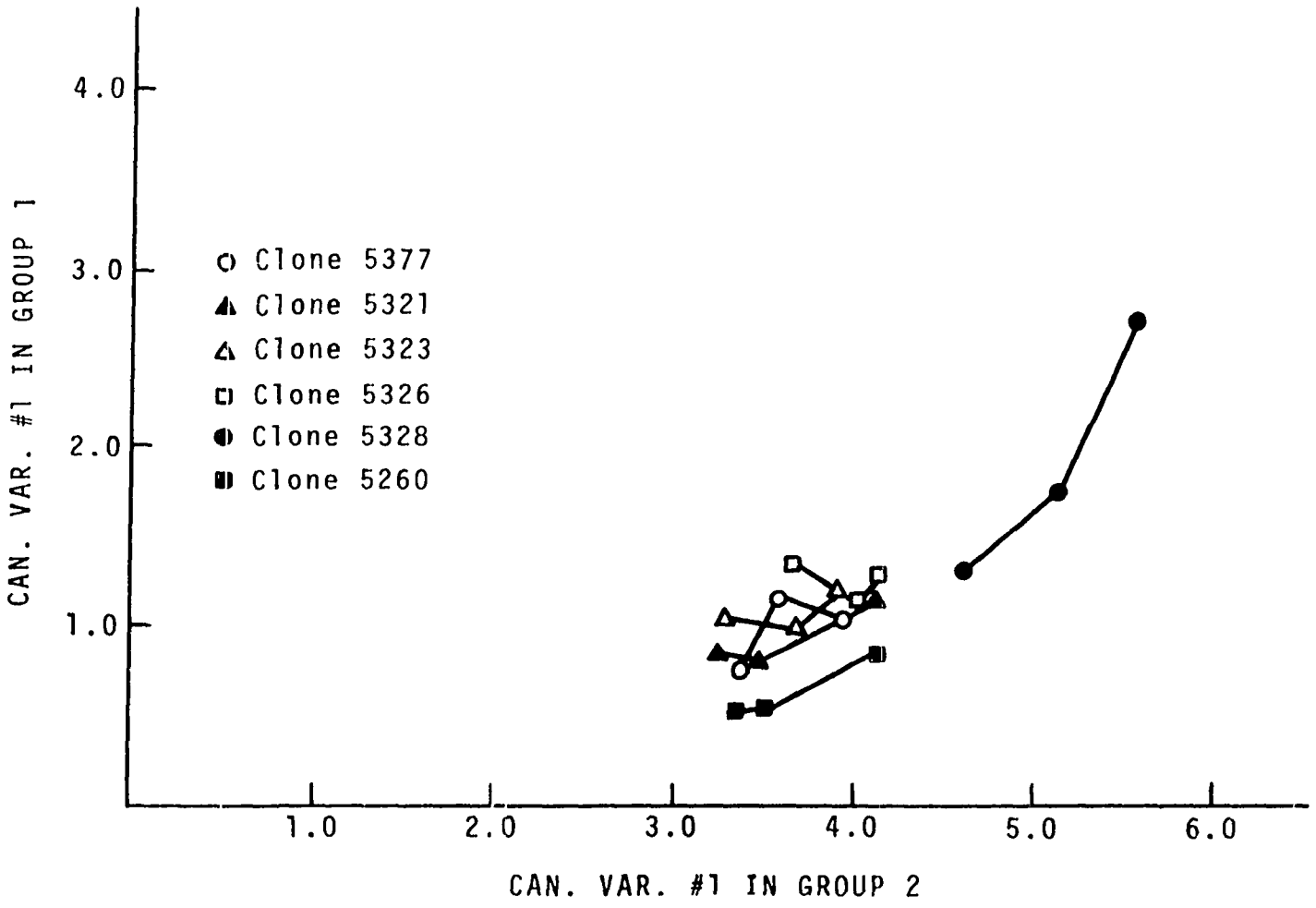


Figure 4. Canonical analysis of proportion of top and bottom growth elements for six clones

Table 14. Characteristic roots and vectors of canonical multi-variate analysis of the variation due to clone

Canonical variable number	Characteristic root	Percent of variation	Normalized characteristic vectors associated with characteristic roots				
			SPNO	TOPDW	STMDIA	STMDW	RTDW
Var. #1	14.079	73.14	0.107	-0.124	4.446	0.130	0.168
Var. #2	2.617	13.59	0.039	0.064	-3.531	0.263	-0.047
Var. #3	1.916	9.95	-0.280	0.041	0.041	-0.233	0.014
Var. #4	0.455	2.37	0.042	0.016	3.187	-0.188	-0.049
Var. #5	0.182	0.94	0.141	0.009	-0.750	-0.256	0.042

Table 15. Correlation coefficients between each canonical variable and dependent variables (variation due to clone)

Canonical variable number	Correlation coefficients between canonical variable and dependent variables				
	SPNO	TOPDW	STMDIA	STMDW	RTDW
Var. #1	0.1143	0.2655	0.3704	0.3870	0.5038
Var. #2	0.3724	0.7270	0.3981	0.7553	0.5968
Var. #3	-0.5353	0.3704	0.2214	0.0298	0.4811
Var. #4	0.4079	0.4758	0.7881	0.1800	0.0453
Var. #5	0.6287	0.1931	-0.1848	-0.4964	0.3955

always superior in these growth variables to the rest of the clones, whereas clones 5321 and 5260 were inferior whether control or coppiced. The results from control plants were not similar to those reported by Zuuring (1975) who found clone 5260 to have higher growth in leaf area and dry weight than other clones. In contrast to this experiment, Zuuring's experiment was done in controlled growth chambers, in which only relatively low irradiances were attainable. The results showing that clone 5321 had less RTDW than clones 5328, 5323, and 5326 are similar to those reported by Fasehun (1975) who showed that clone 5321 had the poorest root system developed at the full light intensity.

The coppiced plants yielded less growth in HT, DIA, LFAREA, STDW, LFDW, STMDW, and RTDW than controlled plants, which was probably due to a short growing period. The LFAREA and TOPDW after coppicing were higher than those of the controlled plants when compared at the same age. This implies that more yield can be produced via coppicing.

Growth responses due to coppicing

The results of the coppiced treatment can be used to select clones for sprouting ability in the field. The remarkable growth difference of clone 5328 in the coppiced treatment suggests that it may be a physiologically superior genotype, capable of producing a large fiber yield in coppice systems. Clone 5260 appeared to be one of the poorest clones in terms of dry weight accumulation. However, clone 5260 could be a good genotype for sprouting ability because it had the highest survival rate at the first coppicing.

The mean responses of the TOPDW and LFAREA at both treatments showed clonal ranks in the following order: clone 5328 was the largest, clones 5323, 5326, and 5377 intermediate, and clones 5321 and 5260 the smallest.

FIELD EXPERIMENT

Materials and Methods

The plantation

Hybrid poplar plantations in this study were located in Ames, Iowa (42°04'N, 93°37'W) and in Rhinelander, Wisconsin (45°38'N, 89°28'W). The Ames plot, on an area formerly used for agronomic crop production, was established in June of 1973 and the Rhinelander plot, on an area formerly used as a conifer nursery, was established in June of 1974 by planting rooted cuttings. Soil characteristics of the plantations are shown in Table 16.

The Ames plantation was weeded once a year and was fertilized only once in mid-July of 1976 with 370 kg/ha of urea nitrogen. The plantation was irrigated once during a dry period. The Rhinelander plot was treated in a closely similar manner but was regularly irrigated.

Four hybrid poplar clones were each planted at three densities: 5,000, 10,000, and 15,000 trees per hectare (Figure 5). The four clones are listed in Table 17.

Experimental design and statistical analysis

The experiment, done in Ames, Iowa, and Rhinelander, Wisconsin, was a split-plot design with two replicates at each location. The whole plot treatments were three densities; all densities were allocated at random to each of the two replicates. Four clones were randomly assigned to each density as sub-plot treatments. Trees were grown on the experimental plots for three years. All trees were coppiced during the dormant season at the end of the third year by cutting at 10 cm above the soil surface. Three

Table 16. Soil characters of the hybrid poplar plots in both locations

Location	Soil property	Soil by depth		
		Top 0-15 cm	Middle 15-30 cm	Bottom 30-45 cm
Ames	Physical			
	Texture	loam	silt loam	silt loam
	Sand %	35.3	19.5	15.1
	Silt %	46.1	59.9	59.4
	Clay %	18.6	20.6	25.5
	Chemical			
	O.M. %	3.3	3.4	3.4
	P ppm	21.1	25.8	14.3
	Ca ppm	71.8	71.6	76.1
	Mg ppm	27.5	27.8	23.3
	K ppm	52.5	41.3	25.0
	Mn ppm	8.0	8.0	9.0
	S ppm	1.3	1.2	1.0
	C/N	10.6	11.3	11.2
	$PH(H_2O)$	7.4-7.6	7.6-7.7	7.5-7.6
Rhinelander	Physical			
	Texture	loamy sand	loamy sand	loamy sand
	Sand %	78.4	78.9	81.6
	Silt %	16.4	16.1	13.8
	Clay %	5.2	5.0	4.6
	Chemical			
	O.M. %	2.2	1.3	0.7
	P ppm	136.5	102.0	109.5
	Ca ppm	45.1	42.6	63.7
	Mg ppm	7.4	3.5	5.2
	K ppm	65.5	64.5	71.5
	Mn ppm	8.6	7.7	3.7
	S ppm	1.2	1.2	1.3
	C/N	9.0	5.4	14.0
	$PH(H_2O)$	6.0-6.1	6.0-6.1	6.3-6.5

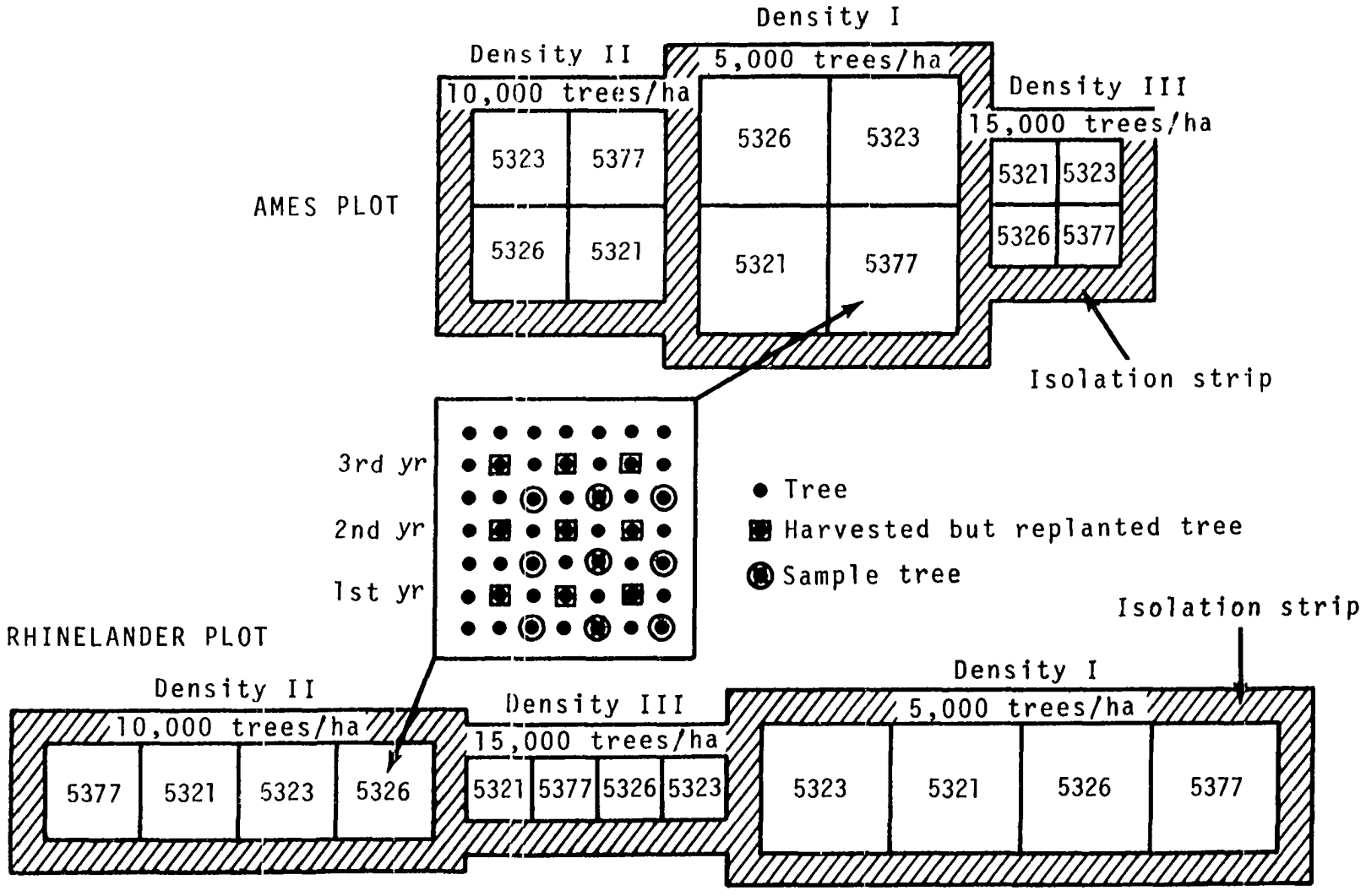


Figure 5. Split-plot experiment to test coppice yields of four Populus clones at three densities in two locations

Table 17. Selected poplar clones for field studies

North Central Forest Experiment Station number	Name and parentage
5377	Populus x euramericana Guinier
5321	Populus x euramericana Guinier
5323	Populus x euramericana Guinier
5326	Populus x euramericana Guinier

trees from each clone, density, replication, and location were chosen per year (Figure 5).

The following hypotheses were tested using uni- and multi-variate analysis of variance:

(1) Were there any locational differences in growth performance of plants before and after coppicing?

(2) Were there any planting density effects on growth performance before and after coppicing?

(3) Were there any clonal differences in growth performance before and after coppicing?

(4) Were there any interactions between the above two factors or between three factors?

In addition, canonical correlation analysis was used to analyze the relationships between top (total sprout number and top dry weight) and bottom (basal area of stump, stump dry weight, and root dry weight) variables after coppicing.

Since the size of roots is one of the important factors affecting the growth after coppicing, root size (root dry weight) was used as a covariate for the covariance analysis for the coppice yield.

Soil cores

Because of the evidence shown in previous study (Lee, 1975) that most root weight was concentrated near the tree stump in large roots including root stock, soil core sampling was not done in the immediate stump area (stratum 1 in Figure 6), which was instead excavated when harvested. Therefore, soil core samples were randomly located in strata 2 and 3 only and extracted from each stratum at three depths from the soil surface (Figure 6).

Core sampling was done on three sample trees at the end of the third year before coppicing. After coppicing two trees chosen randomly from the three selected sample trees were used. This sampling technique was applied only for the Ames plot and the methods for sampling, processing, and estimation of number and dry weight of roots were the same as those used in previous study (Lee, 1975).

Tree measurements before and following coppicing

Before coppicing, lengths and widths of sample leaves selected systematically were measured in mid-June each year for the estimation of the initial leaf surface area. Dry weights of stem and leaf were measured at the end of the growing season each year, and then final leaf surface area was calculated from the relationship with leaf dry weight.

To examine how leaf biomass changes during the growing season after coppicing, initial developed leaves, falling leaves, and remaining leaves

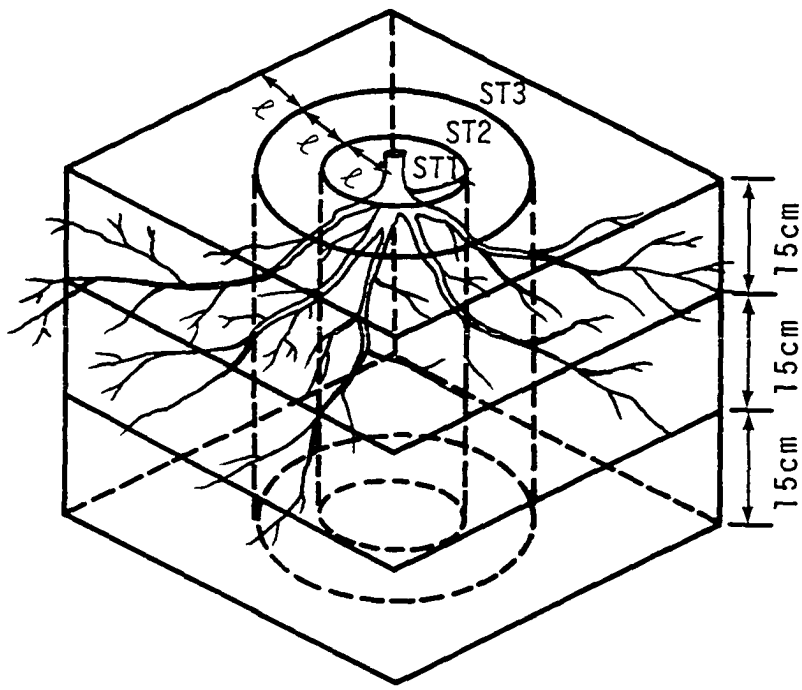


Figure 6. Diagram for soil core sampling. Three strata and three depths were defined by increasing distance from the sample tree and from the soil surface, respectively. The distance, ℓ, changes with the planting density, 23.6 cm for 5,000 trees/ha, 16.7 cm for 10,000 trees/ha, and 13.6 cm for 15,000 trees/ha

were separately observed. Lengths and widths of sample leaves selected systematically were measured in mid-June for the estimation of the initial leaf area, and falling leaves were collected five times from mid-July to early-September for the estimation of falling leaf area (LFFALL) by using a net under the sample tree. The remaining leaf area (final leaf area) was measured when harvested. Leaf surface area from either length and width of leaf or leaf dry weight was calculated by the method developed by Rose and Promnitz (1975).

Sprout length and number were measured only at the Ames plot and the measurement was repeated five times from late-May to mid-September.

The following variables were measured at the end of the first growing season after coppicing: number of sprout site (SPST), length and number of the most vigorous sprouts from each sprout site (SPLN and SPNO, respectively), stem dry weight (STDW), leaf dry weight (LFDW), stump diameter (STMDIA), stump dry weight (STMDW), and root dry weight (RTDW) at stratum 1 by excavation. From these variables, top dry weight (TOPDW; STDW + LFDW), total root dry weight (TRTDW; RTDW + root weight estimated from strata 2 and 3), basal area of stump (SBA), bottom dry weight (BOTDW; STMDW + TRTDW), and stem to bottom ratio (SBRO) were calculated later. The precision in measuring length and weight was similar to that of the greenhouse experiment.

Results

Productivity as related to crown geometry

Leaf area development With the exception of the initial leaf area in coppice stand, the three factor interaction, location by density by

clone, was not significant at the 5 percent level for the initial and final leaf areas (Table 18). This significance shown in coppice stand was ascribed to that of the two factor interaction, density by clone, at the Ames experiment. All clones developed greater leaf area at the Ames plot than the Rhinelander plot both before and after coppicing. There was no consistency in clonal superiority for the initial leaf area (Table 19). At the Ames plot, clones 5377 and 5326 produced more initial leaf area than clones 5323 and 5321 before coppicing. After coppicing, however, the largest mean area per tree was attained by clone 5377 followed by clones 5323 and 5326, and clone 5321 the smallest. For the Rhinelander plot, there were different trends: clones 5326 and 5323 had the largest mean leaf areas for the second year, and clones 5377 and 5326 had the largest mean areas for the third year. After coppicing, clones 5323 and 5326 had the largest leaf areas, clone 5377 intermediate, and clone 5321 the smallest leaf area.

The result of the final leaf area was different from that of the initial area: clone 5323 showed the largest mean area at both plots except for the second year in Ames and the third year in Rhinelander (Table 19). Clone 5377, in general, yielded smaller final leaf areas than the other clones.

Either before or after coppicing, the density by clone interaction was not significant at the 5 percent level (Table 18). None of clones showed unique trends with increasing planting density for the initial leaf area in the second year. Most clones exhibited a decreased leaf area with increasing planting density except for clone 5326 in the third year before coppicing and for clone 5377 after coppicing. None of clones showed its

Table 18. Mean squares from analysis of variance for the initial and final leaf areas

Source of variation	d.f.	Initial LFAREA		
		Before coppicing		After coppicing
		Year 2	Year 3	Year 1
Locations (L)	1	161035371$^{.05*}$	1089428662$^{.09}$	1212811011$^{.00}$
E (a)	2	8543116	112953003	4454469
Densities (D)	2	1066125$^{.79}$	643046928$^{.13}$	197082480$^{.00}$
L x D	2	2628504$^{.59}$	229557670$^{.37}$	68257637$^{.01}$
E (b)	4	4348567	179165242	3570244
Clones (C)	3	10785066$^{.00}$	607968932$^{.04}$	64914417$^{.01}$
L x D	3	2973599$^{.20}$	109368748$^{.62}$	45873060$^{.02}$
D x C	6	1120594$^{.70}$	146188262$^{.57}$	24345941$^{.09}$
L x D x C	6	1321240$^{.61}$	91709695$^{.79}$	34716566$^{.03}$
E (c)	18	1745428	177599956	10853334

*Indicates significance level.

Final LFAREA			
Before coppicing			After coppicing
Year 1	Year 2	Year 3	Year 1
5545655.60	425072367.33	14564070.57	4160342110.01
14835079	257709545	32669636	30760366
937333.20	276449585.02	1028747729.01	1483910913.01
481319.37	5249467.76	245447700.11	352083254.08
372758	17941387	62539327	70739118
1229170.28	34845577.10	151535400.14	138588153.05
885807.58	32484040.12	136815638.18	75620080.20
172979.97	28067067.13	38501591.79	75973814.17
586359.69	6688441.83	8209439.99	36694677.56
897547	14569444	74626597	43985163

Table 19. Means of clones by locations for the initial and final leaf areas

Locations	Clones	Initial LFAREA (cm^2)			Final LFAREA (cm^2)			
		Before coppicing		After coppicing	Before coppicing			After coppicing
		Year 2	Year 3	Year 1	Year 1	Year 2	Year 3	Year 1
Ames	5377	8074.5	39914.0	18700.9	1772.8	20026.0	22399.2	34667.2
Ames	5321	5328.4	27276.5	10159.8	2741.5	19715.2	25047.5	39785.9
Ames	5323	5998.5	35149.2	17772.3	2967.9	24701.5	32840.2	39990.1
Ames	5326	7704.3	49706.0	17538.8	2089.2	26111.0	23568.5	29065.1
Rhinelander	5377	3097.1	34356.7	5572.6	1619.8	16073.1	28943.1	15093.5
Rhinelander	5321	2124.8	21444.6	5356.2	1478.5	16950.6	17444.5	15427.6
Rhinelander	5323	3341.4	26814.8	8433.7	1951.3	17719.8	26957.0	21603.4
Rhinelander	5326	3889.3	31317.0	4596.4	1802.7	16003.5	26104.1	16904.9

superiority in the initial leaf development at all densities except that clone 5377 had the greatest mean area per tree at the intermediate density (10,000 trees/ha) before and after coppicing (Table 20).

The final leaf area per tree decreased as density increased from the lowest (5,000 trees/ha) to the intermediate density for all clones and then increased again at the highest density (15,000 trees/ha) during the first year before coppicing. On the other hand, during the second and third year before coppicing and the first year after coppicing, a decreasing trend with increasing density was shown by most clones with the exceptions of clone 5326 for the second and third year before coppicing and of clone 5323 after coppicing. With respect to clonal differences at each density, the greatest final leaf area was attained by clone 5323 at the medium density before coppicing, but it differed at the lowest and highest densities. After coppicing, clone 5323 was the greatest at the lowest and highest densities, and clone 5321 the greatest at the medium density (Table 20).

The density by location interaction was not significant before coppicing but was significant at the 5 percent level after coppicing (Table 18). The initial leaf area decreased with increasing planting density only for coppice growth at both locations (Table 21). Before coppicing there were not the same trends: in the second year, the intermediate and highest densities were the highest in the initial leaf area for the Ames and Rhinelander plots, respectively, but the lowest density was the highest for both locations in the third year. Final leaf area decreased with increasing planting density at the Ames plot in all years while at the Rhinelander plot there was the same trend only in the second year before coppicing and in the first year after coppicing. For the first and third years before

Table 20. Means of clones by densities for the initial and final leaf areas

Densities (trees/ha)	Clones	Initial LFAREA (cm^2)			Final LFAREA (cm^2)			
		Before coppicing		After coppicing	Before coppicing			After coppicing
		Year 2	Year 3	Year 1	Year 1	Year 2	Year 3	Year 1
5,000	5377	5199.6	43620.2	13506.7	1748.7	20455.1	32002.3	33227.1
5,000	5321	3732.4	27516.4	9790.7	2596.1	22456.0	31333.6	33572.1
5,000	5323	4664.7	45686.0	18289.2	2503.5	25350.9	42574.8	46269.7
5,000	5326	5883.3	44931.8	16509.5	2245.5	28723.0	32466.4	35691.4
10,000	5377	5332.8	36467.1	15333.5	1481.7	17015.2	23161.7	23603.2
10,000	5321	3986.2	26708.7	7722.5	1860.0	17584.5	16906.0	28818.2
10,000	5323	4705.5	26687.3	10531.4	2255.6	22919.8	27266.4	22647.8
10,000	5326	4904.7	33485.1	10493.9	1578.6	16896.2	20103.0	21345.6
15,000	5377	6224.9	31318.8	7570.0	1858.4	16678.4	21850.0	17810.9
15,000	5321	3461.2	18856.5	5760.9	1873.8	14958.3	15498.3	20429.8
15,000	5323	4639.7	20572.7	10488.4	2619.8	15361.1	19854.6	23472.7
15,000	5326	6602.4	43117.6	6199.5	2013.7	17552.6	21939.5	11918.0

Table 21. Means of densities by locations for the initial and final leaf areas before and after coppicing

Locations	Densities (trees/ha)	Initial LFAREA (cm^2)			Final LFAREA (cm^2)			
		Before coppicing		After coppicing	Before coppicing			After coppicing
		Year 2	Year 3	Year 1	Year 1	Year 2	Year 3	Year 1
Ames	5,000	6501.5	48216.9	20978.2	2707.2	27838.9	39371.9	51666.3
Ames	10,000	7030.4	36838.7	16987.7	2240.2	21478.1	21689.7	32239.8
Ames	15,000	6797.4	28978.7	10163.0	2231.2	18598.3	16829.8	23725.1
Rhinelander	5,000	3238.5	32660.3	8069.8	1839.7	20653.6	29816.6	22713.8
Rhinelander	10,000	2434.2	24835.5	5052.9	1347.8	15729.7	22028.8	15967.6
Rhinelander	15,000	3666.7	27954.1	4846.4	1951.7	13676.9	22741.2	13090.6

coppicing, the highest density produced rather larger leaf area than the intermediate density.

All main effects, location, density, and clone sources of variation were significant at the 5 percent level for the coppice growth performance, whereas before coppicing, both location and clone effects were significant for the initial leaf area in the first year, and density effect only for the final leaf area in the second and third year (Table 18).

The significant effect due to location in terms of leaf areas developed by the coppice stand indicated that the mean response of the Ames plot was significantly different from that of the Rhinelander plot (Figure 7), probably because of the soil differences between locations.

The remarkable density effect on the initial leaf area after coppicing was due to great mean differences among three densities, but that on the final leaf area of uncut and coppiced stands due to large mean differences between the lowest and intermediate densities (Figure 8).

The significant differences in the initial leaf area between clones either before or after coppicing were due to the smallest mean response of clone 5321 as compared to the rest of the clones (Figure 9) while those in the final leaf area were because of the greatest mean response of clone 5323 (Figure 10). Furthermore, clones 5377 and 5326, in general, produced larger initial leaf area than clones 5323 and 5321, whereas larger final leaf area was yielded by clones 5323 and 5321 (Figures 9 and 10). Looking at the leaf areas produced from leaf fall during the growing season revealed that the quantity of falling leaves from clones 5377 and 5326 were much greater than those from clones 5323 and 5321 (Table 22). Thus, clones 5323 and 5321 showed increased growth in the final leaf area.

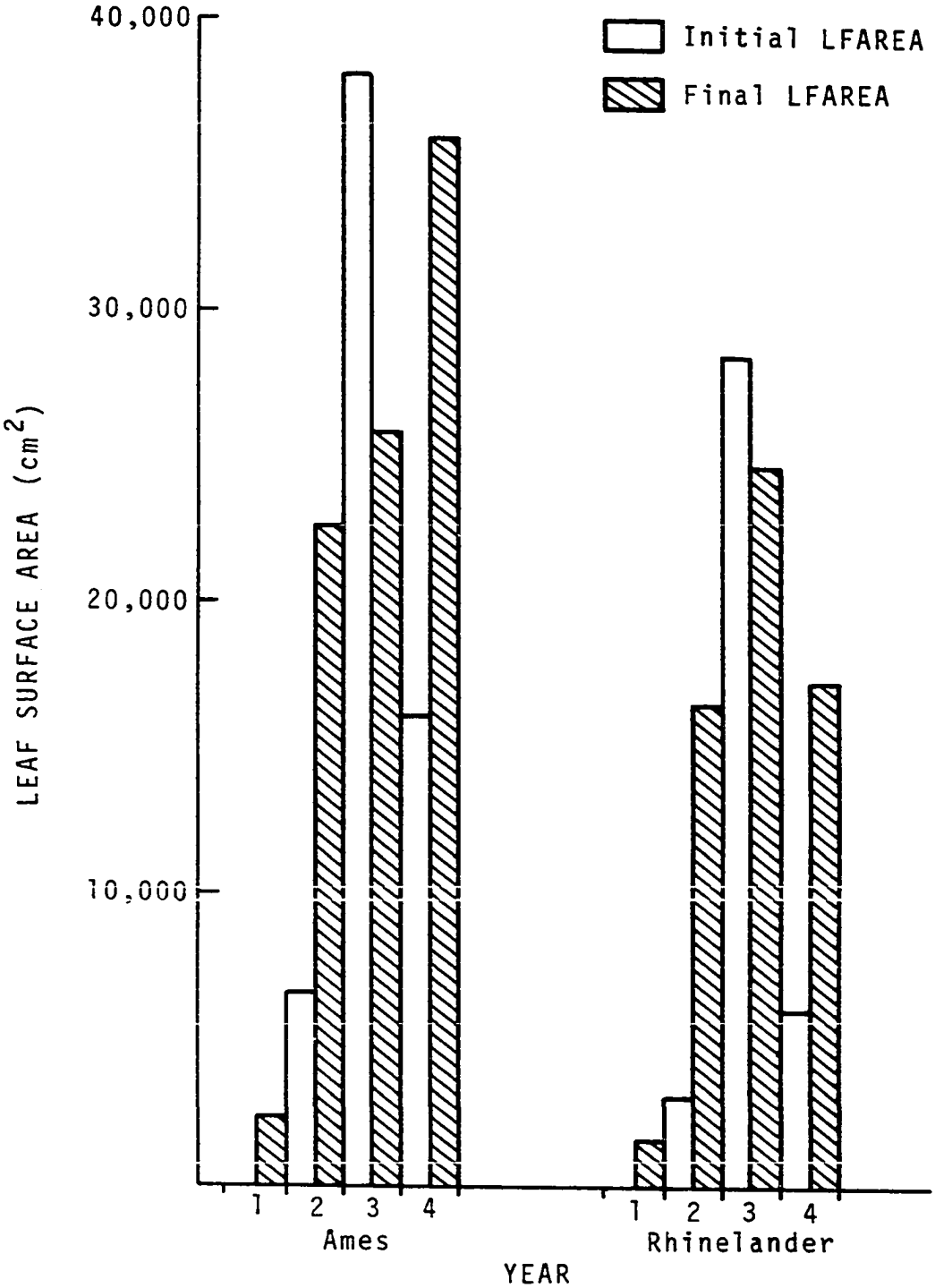


Figure 7. Comparison of initial and final leaf surface areas for the two locations (no initial leaf area was measured in year 1; coppicing was done in year 3)

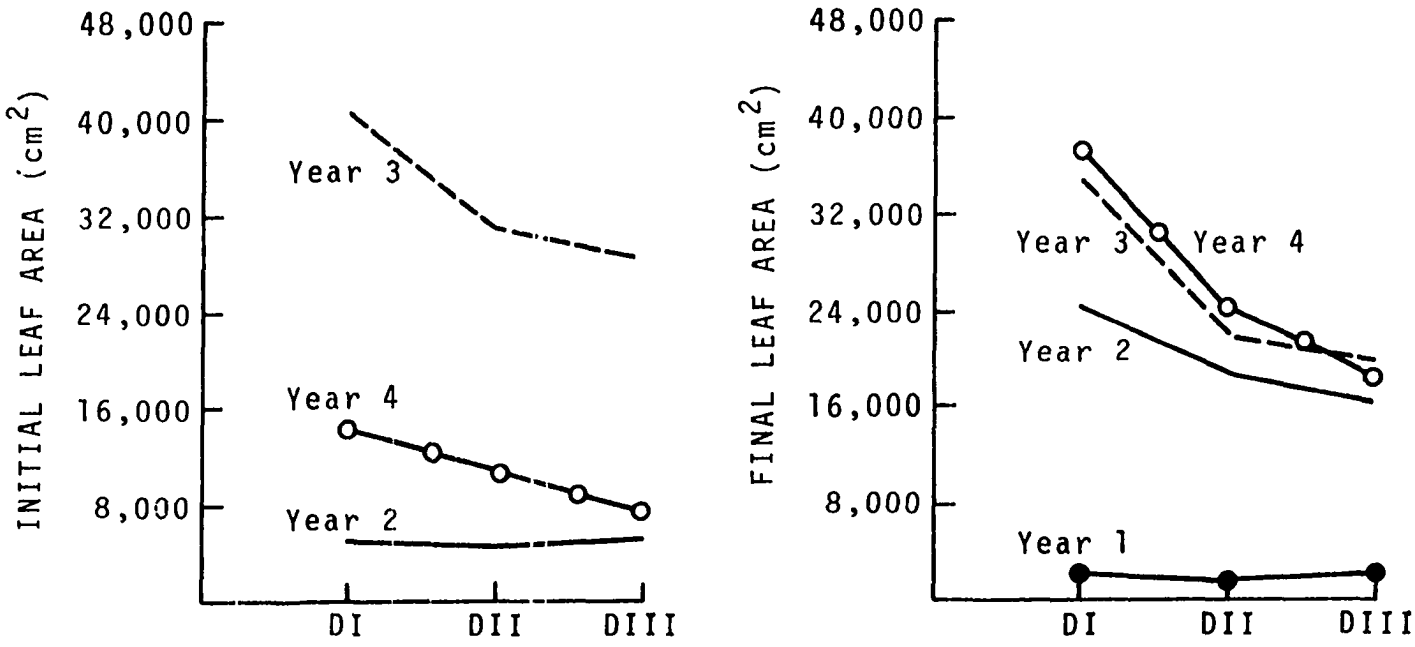
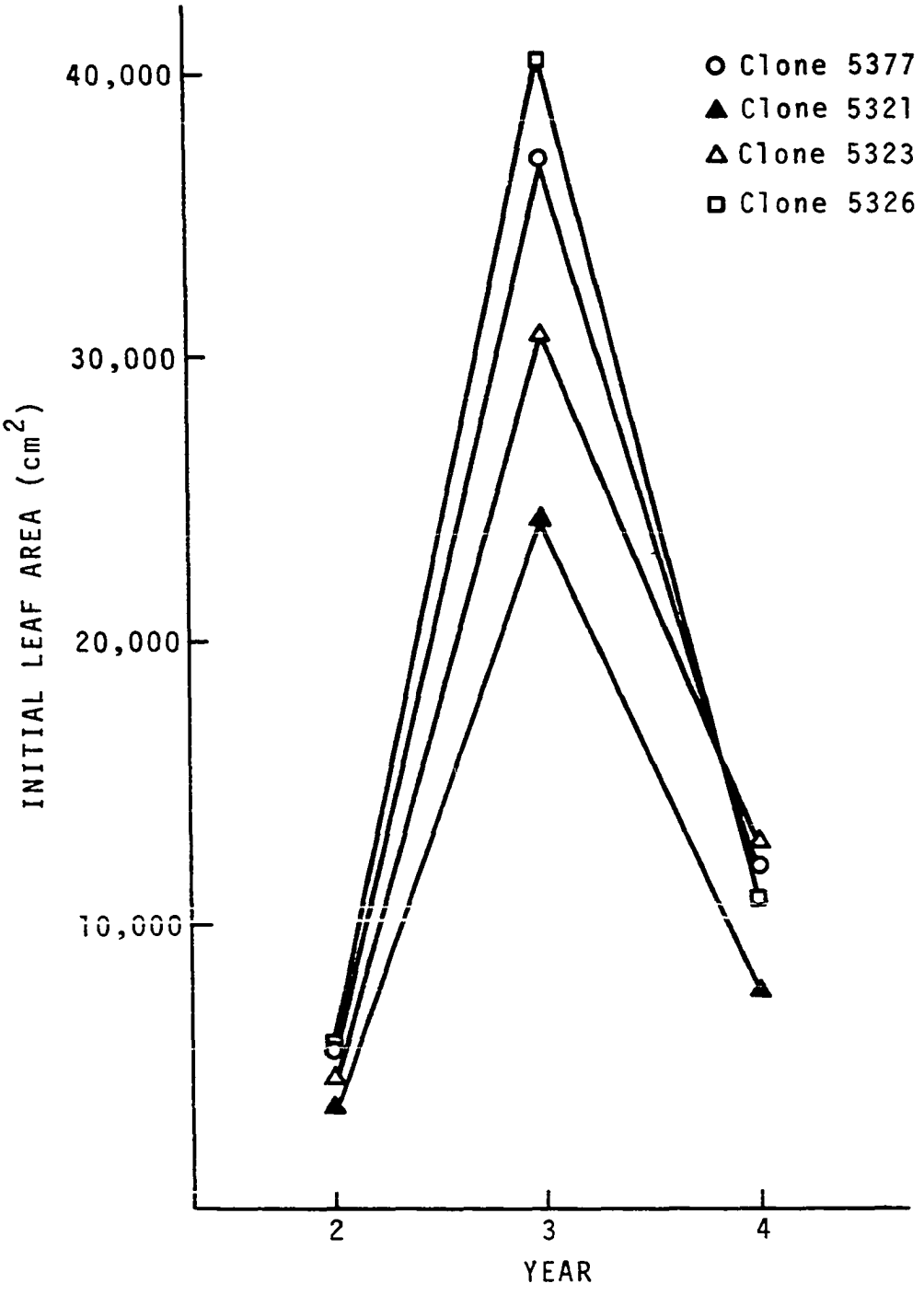


Figure 8. Comparison of initial and final leaf areas for each year at each density (DI, DII, and DIII indicate 5,000, 10,000, 15,000 trees per hectare, respectively)



Figur- 9. Comparison of initial leaf area for four clones before and after coppicing (coppicing was done in year 3)

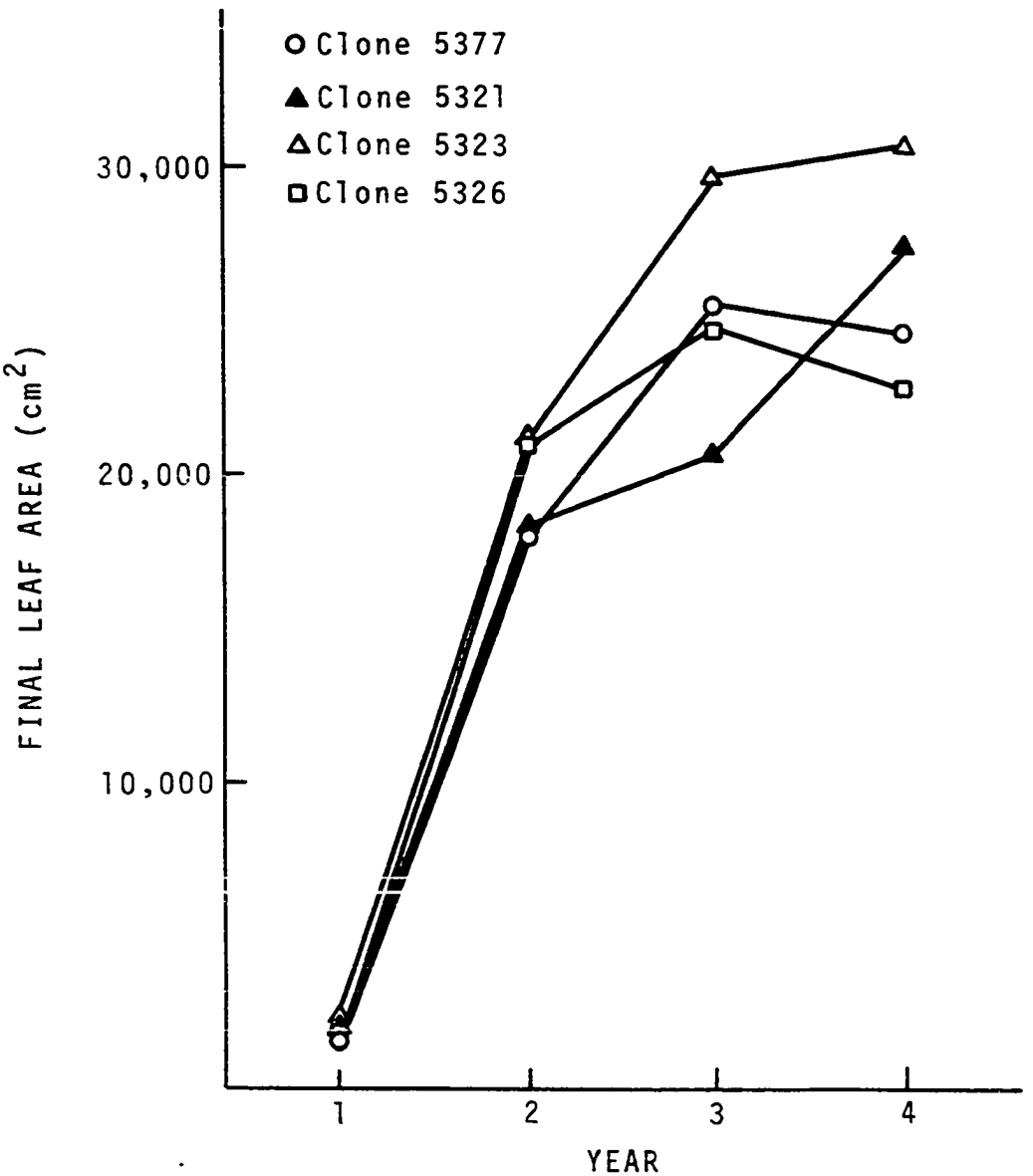


Figure 10. Comparison of final leaf area for four clones before and after coppicing (coppicing was done in year 3)

Table 22. Means of clones for leaf area development during the growing season in Ames coppice stand

Clones	Initial (cm^2)	LFFALL (cm^2)	Final (cm^2)
5377	18700.9	22316.0	34667.2
5321	10159.8	11049.1	39785.9
5323	17772.3	13378.3	39990.1
5326	17538.8	19384.9	29065.1

Sprout growth The two factor interaction, density by clone, was not significant at the 5 percent level for height growth and number of sprout site (Table 23).

For the sprout height at the lowest density, the largest growth was attained by clone 5377 followed by clones 5323 and 5326, and clone 5321 was the smallest. At the intermediate density, again clone 5377 was the largest and the rest of the clones were similar in growth. At the highest density, however, clone 5321 was the largest, and clones 5377 and 5323 intermediate, and clone 5326 the smallest (Table 24).

In contrast to height growth, the number of sprout site showed differently: clone 5321 had the smallest number at each density, and clones 5326, 5377, and 5323 the largest at the lowest, intermediate, and highest densities, respectively (Table 24).

The effect of density on sprout height was not significant at the 5 percent level during the growing season (Table 23). The lowest density showed the largest growth in height throughout season. The intermediate

Table 23. Mean squares from analysis of variance for the sprout growth variables

Source of variation	d.f.	SPLN	SPST
Densities (D)	2	$2247^{.07*}$	$56.2^{.05}$
E (a)	2	180	3.3
Clones (C)	3	$3074^{.08}$	$45.3^{.03}$
D x C	6	$1601^{.24}$	$19.5^{.15}$
E (b)	9	965	9.1
Times (T)	4	126068	20.8
D x T	8	$127^{.61}$	$0.2^{.98}$
C x T	12	$516^{.00}$	$0.7^{.58}$
D x C x T	24	$156^{.51}$	$0.2^{.99}$
E (c)	48	159	0.8

*Indicates significance level.

density was the next highest until the end of July, and after that the highest density showed better growth than intermediate density. The sprout site number, however, was not different between the lowest and intermediate densities throughout the season but decreased at the highest density (Table 25).

Looking at the clonal difference by time, the difference was significant at the 1 percent level for only the sprout height (Table 23). All clones showed an increase in height growth but showed a decrease in sprout site number from May through September (Figures 11 and 12). The greatest

Table 24. Means of clones by densities for the sprout growth variables

Densities (trees/ha)	Clones	SPLN (cm)	SPST
5,000	5377	153.0	7
5,000	5321	125.9	6
5,000	5323	150.3	7
5,000	5326	135.7	9
10,000	5377	140.5	11
10,000	5321	125.2	6
10,000	5323	124.2	7
10,000	5326	125.2	7
15,000	5377	137.5	6
15,000	5321	141.4	4
15,000	5323	134.1	7
15,000	5326	97.9	6

Table 25. Means of densities by time for the sprout growth variables

Densities (trees/ha)	Dates	SPLN (cm)	SPST
5,000	May 28	35.0	9
5,000	June 25	96.5	8
5,000	July 23	160.0	7
5,000	Aug. 20	203.9	7
5,000	Sept. 18	210.7	7
10,000	May 28	30.6	9
10,000	June 25	86.9	8
10,000	July 23	146.7	7
10,000	Aug. 20	183.3	7
10,000	Sept. 18	196.4	7
15,000	May 28	27.2	7
15,000	June 25	81.1	6
15,000	July 23	141.8	5
15,000	Aug. 20	185.4	5
15,000	Sept. 18	203.2	5

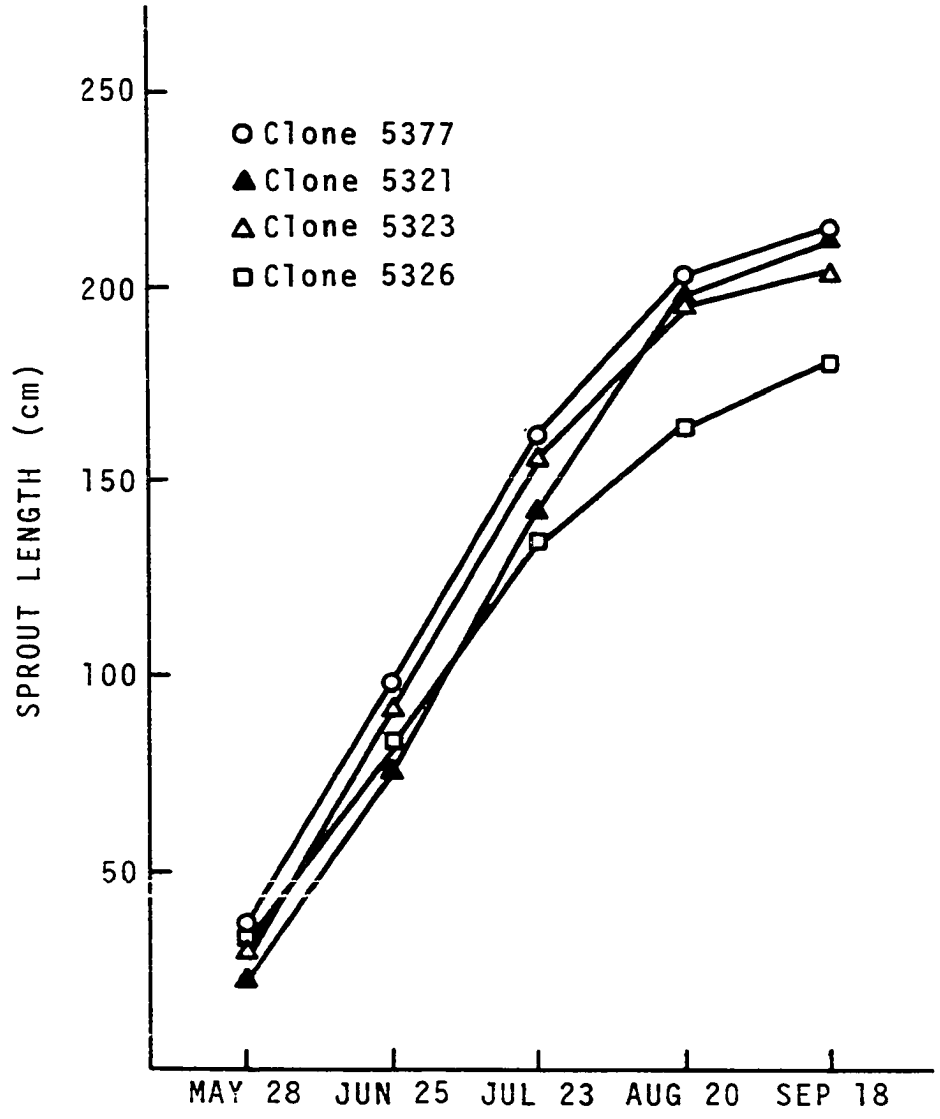


Figure 11. Comparison of height growth of sprouts per tree for four clones during the growing season

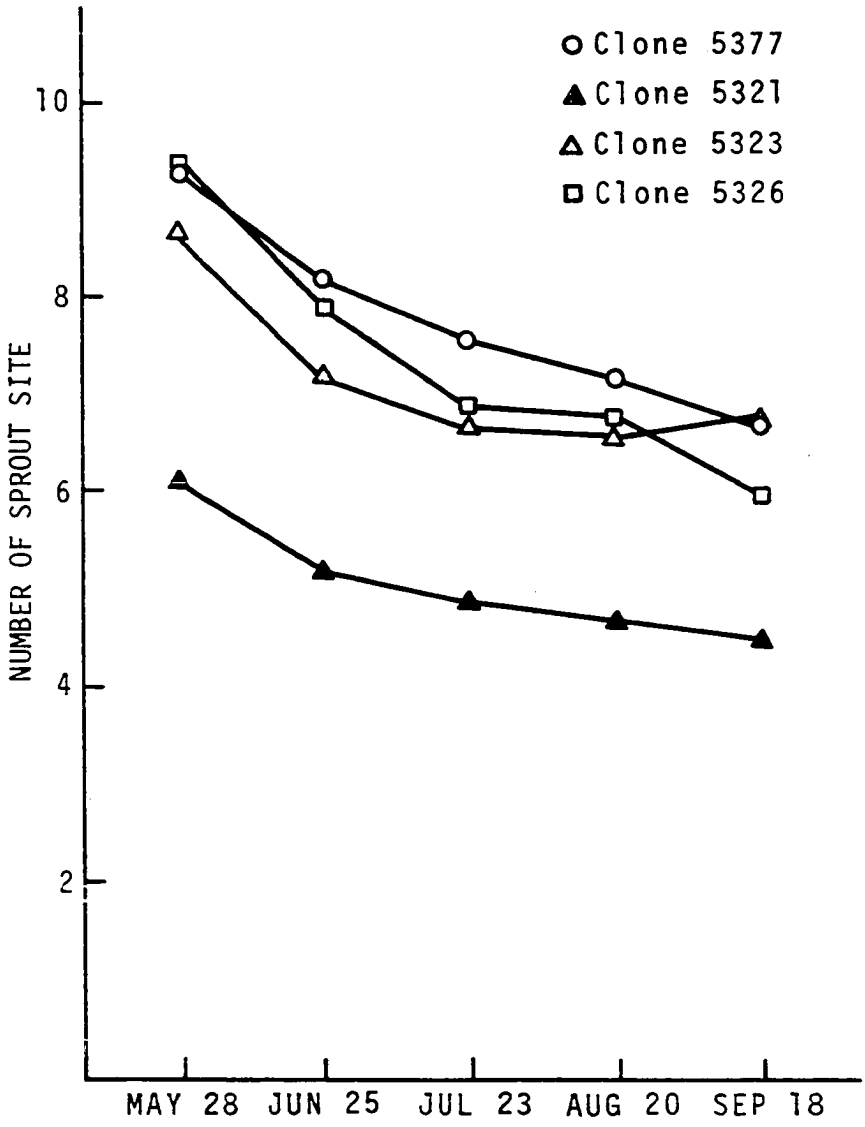


Figure 12. Comparison of sprout number per tree for four clones during the growing season

mean sprout growth in both height and number was shown by clone 5377 throughout the growing season and followed by clones 5323 and 5326 until the end of June, but after that the height of clone 5326 showed a slow growth and was the smallest when harvested.

Although neither of the main effects of density or clone on height growth was significant at the 5 percent level, the sprout of clone 5377 grew most vigorously, and the lowest density was the highest. On the sprout site number, however, both main effects were significant at the 5 percent level, and clone 5377 and intermediate density were the highest.

Dry weight production in woody tissue Since the three factor interaction, location by density by clone, was not significant at the 5 percent level for the dry weight of stem portion, it was appropriate to graph the mean response of each of the four clones over levels of location and density.

Greater stem dry weight was produced at the Ames plot than at the Rhinelander plot for all clones whether before or after coppicing (Table 26), but differences were not significant at the 5 percent level except for the stem weight after coppicing (Table 27). Looking at the mean dry weight of both plantations before coppicing, clones 5323, 5326, and 5377 yielded better than clone 5321 except for the first year, and differences were generally significant. Similar trends were exhibited after coppicing except that clone 5326 produced much less than clones 5377 and 5323 at the Ames plot. Before coppicing, the largest mean stem dry weight was attained by clone 5326 at the Ames plot when pooled over three years, whereas at the Rhinelander plot clone 5323 was the largest. After coppicing, however,

Table 26. Means of clones by locations for the stem dry weight per tree before and after coppicing

Locations	Clones	Before coppicing Year 1 (g)	Before coppicing Year 2 (g)	Before coppicing Year 3 (g)	After coppicing Year 1 (g)
Ames	5377	14.0	501.4	1711.6	920.6
Ames	5321	18.0	341.5	1168.4	643.9
Ames	5323	22.4	487.3	1759.6	908.8
Ames	5326	15.7	594.1	1764.8	711.2
Rhinelander	5377	4.5	221.5	907.2	371.0
Rhinelander	5321	6.1	128.2	441.2	245.8
Rhinelander	5323	11.0	268.7	941.8	397.8
Rhinelander	5326	7.3	212.7	771.2	387.1

clones 5377 and 5323 yielded the highest dry weight accumulation at the Ames and Rhinelander plots, respectively.

Either before or after coppicing, the density by clone interaction was not significant at the 5 percent level (Table 27). With the exception of the first and second year, stem dry weight decreased with increasing planting density for all clones (Table 28). At the lowest density, clone 5323 showed the greatest dry weight before and after coppicing except for the second year before coppicing. At the intermediate density, clone 5323 produced the greatest weight before coppicing, but clone 5377 produced the most after coppicing. At the highest density, clone 5323 was the highest in the first year, clone 5326 in the second year and clone 5377 in the third year, and clone 5323 again the highest after coppicing.

Again, density by location interaction was not significant at the 5 percent level before coppicing but was significant after coppicing (Table 27). Stem dry weight production from the Ames plot was higher than that

Table 27. Mean squares from analysis of variance for the stem dry weight per tree before and after coppicing

Source of variation	d.f.	Before coppicing			After coppicing
		Year 1	Year 2	Year 3	Year 1
Locations (L)	1	$1274^{.41*}$	$896643^{.18}$	$8381737^{.10}$	$2383901^{.00}$
E (a)	2	1179	223251	978372	9788
Densities (D)	2	$99^{.32}$	$88393^{.08}$	$1535627^{.11}$	$803361^{.01}$
L x D	2	$40^{.58}$	$55^{.99}$	$1012364^{.19}$	$178842^{.05}$
E (b)	4	63	18006	390557	25345
Clones (C)	3	$117^{.08}$	$67606^{.00}$	$777416^{.03}$	$115002^{.01}$
L x C	3	$8^{.90}$	$18308^{.15}$	$38008^{.90}$	$32077^{.25}$
D x C	6	$17^{.88}$	$5066^{.77}$	$27911^{.99}$	$54022^{.06}$
L x D x C	6	$41^{.51}$	$7706^{.56}$	$63129^{.92}$	$23830.^{40}$
E (c)	18	43	9228	201352	21525

*Indicates significance level.

from Rhinelander for all densities. Furthermore, the highest density, least productive at the Ames plot, produced even higher dry weight than the lowest density at the Rhinelander plot, which was most productive.

In general, stem dry weight showed a decrease with increasing planting density except for the first year growth (Table 29). When locations were compared, trends were different; at the Ames plot individual stem dry weight decreased with increasing density before and after coppicing (Table 30); at the Rhinelander plot, however, similar trends were exhibited only for the second year growth before coppicing and coppice yield.

Table 28. Means of clones by densities for the stem dry weight per tree before and after coppicing

Densities (trees/ha)	Clones	Before coppicing Year 1 (g)	Before coppicing Year 2 (g)	Before coppicing Year 3 (g)	After coppicing Year 1 (g)
5,000	5377	9.0	422.2	1679.0	876.4
5,000	5321	17.2	312.1	1083.7	541.1
5,000	5323	18.2	452.4	1819.9	1006.5
5,000	5326	15.0	533.6	1556.3	864.6
10,000	5377	7.8	325.6	1166.5	608.0
10,000	5321	8.3	193.8	702.9	456.8
10,000	5323	14.5	380.5	1223.8	456.7
10,000	5326	9.0	325.1	1167.6	519.2
15,000	5377	10.9	336.5	1082.8	453.1
15,000	5321	10.7	198.7	627.9	336.7
15,000	5323	17.4	301.1	1008.5	496.7
15,000	5326	10.4	351.5	1080.1	263.6

Table 29. Means by locations, by densities, and by clones for the stem dry weight per tree before and after coppicing

Factors	Before Year 1 (g)	Before Year 2 (g)	Before Year 3 (g)	After Year 1 (g)
Locations				
Ames	17.5	481.1	1601.1	796.1
Rhinelander	7.2	207.7	765.4	350.4
Densities				
5,000 trees/ha	14.9	430.1	1534.7	822.1
10,000 trees/ha	9.9	306.3	1065.2	510.2
15,000 trees/ha	12.3	296.9	949.8	387.6
Clones				
5377	9.3	361.4	1309.4	645.8
5321	12.1	234.8	804.8	444.8
5323	16.7	378.0	1350.7	653.3
5326	11.5	403.4	1268.0	549.1

Table 30. Means of densities by locations for the stem dry weight per tree before and after coppicing

Locations	Densities (trees/ha)	Before Year 1 (g)	Before Year 2 (g)	Before Year 3 (g)	After Year 1 (g)
Ames	5,000	21.1	565.8	2194.5	1163.6
Ames	10,000	15.8	441.7	1501.4	698.7
Ames	15,000	15.7	435.7	1107.5	526.1
Rhinelander	5,000	8.6	294.3	875.0	480.7
Rhinelander	10,000	4.0	170.8	629.0	321.7
Rhinelander	15,000	9.0	158.1	792.1	249.0

Again, all main effects, location, density, and clone sources of variation were significant at the 1 percent level for the coppice yield (Table 27). In contrast to the coppice yield, most main effects were not significant at the 5 percent level for the yield before coppicing except for clonal effect in the second and third year.

The significant effects of location on coppice yield were high, which implied that the mean response of the Ames plot was significantly higher than that of the Rhinelander plot. In addition, the significance of locational effects increased yearly. This was probably influenced by the differences in soil, length of the growing season, and temperature.

In particular, clonal effects were highly significant in this experiment with the exception of the first year growth, which suggests that certain clone would be superior genetically in terms of dry weight accumulation. Before coppicing, the highest mean stem dry weight per tree was produced by clone 5323 followed by clones 5326 and 5377 when pooled over three years and the smallest by clone 5321 (Table 29). After coppicing,

however, both clones 5323 and 5377 yielded the largest mean dry weight, clone 5326 the next, and clone 5321 the lowest again. Thus, clones 5323 and 5377 appeared to be good genotypes with respect to dry weight accumulation.

Root geometry and production before and after coppicing

Effects of stratification by distance and depth on estimates of root growth Most root growth variables in a given core showed a decrease with increasing distance from the tree stem both before and after coppicing (Table 31). These differences were highly significant before coppicing, but the dry weight of roots was only significant after coppicing (Table 32). This relationship was also evident when densities were compared, and again the only exception was the total root number after coppicing (Table 33). When four clones were examined, the relationship was different (Table 34): the total root number of clone 5326 showed an increase with increasing distance from the stem both before and after coppicing. The total root numbers of clones 5377 and 5323 increased after coppicing, and the number of roots greater than 1 cm of clone 5323 increased after coppicing. Root numbers showed a small decrease with increasing distance from the stem, but root dry weight reflected a large decrease. The largest decrease in root dry weight was shown at the intermediate density both before and after coppicing. The decrease of root dry weight with increasing distance was primarily due to this decrease at the intermediate density. With increasing distance, the root dry weight of clone 5323 greatly decreased before coppicing while the dry weight of clone 5377 decreased greatly after coppicing.

Table 31. Means by strata for the core measurements before and after coppicing

Strata[a]	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
	Before	After	Before	After	Before	After
2	47.3	35.0	8.3	6.4	69.1	47.6
3	41.9	36.6	6.9	6.2	17.4	18.4

[a]Strata 2 and 3 indicate a radial distance from the stem, and the distance changes with the planting density; distances for strata 2 and 3 are 23.6 to 47.2 cm and 47.2 to 70.7 cm for 5,000 trees/ha, 16.7 to 33.4 cm and 33.4 to 50.0 cm for 10,000 trees/ha, and 13.6 to 27.2 cm and 27.2 to 40.7 cm for 15,000 trees/ha, respectively.

All root growth variables tended to decrease with increasing depth from the soil surface (Table 35), and differences were highly significant (Table 32). A similar trend was shown in most densities and clones with the two exceptions of the root dry weight variable at the intermediate density (Table 36) and the root dry weight variable of clone 5323 (Table 37) after coppicing. The root dry weight at the intermediate density exhibited a great decrease with increasing depth before coppicing, but after coppicing there was a small increase followed by a small decrease.

Root dry weights of clones 5377 and 5323 showed a great decrease with increasing depth before coppicing while that of clone 5377 showed the largest decrease after coppicing. In contrast to the other clones, root dry weight of clone 5323 increased with increasing depth after coppicing.

Most root variables, in a short distance from the tree stem, showed greater growth than in a long distance at most soil depths. Exceptions were found in the total root number at both top and bottom of soil depths

Table 32. Mean squares from analysis of variance for root growth variables of four Populus clones before and after coppicing

Source of variation	d.f.	Total root no.		No. of roots (>1 cm)		Root dry wt. (mg)	
		Before	After	Before	After	Before	After
Densities (D)	2	$4887^{.46*}$	$5309^{.35}$	$23.2^{.75}$	$9.4^{.23}$	$30828^{.11}$	$519^{.88}$
E (a)	2	4077	2892	69.8	2.9	3599	3974
Clones (C)	3	$383^{.86}$	$1193^{.73}$	$108.3^{.08}$	$33.1^{.53}$	$19436^{.08}$	$13595^{.20}$
D x C	6	$1478^{.51}$	$1087^{.86}$	$41.6^{.38}$	$38.2^{.45}$	$5547^{.55}$	$5044^{.65}$
E (b)	9	1558	2721	34.1	36.1	6303	7065
Strata (S)	1	$3235^{.00}$	$185^{.51}$	$227.9^{.00}$	$3.4^{.58}$	$287687^{.00}$	$61299^{.00}$
D x S	2	$147^{.52}$	$2^{.99}$	$0.8^{.91}$	$0.7^{.94}$	$46666^{.00}$	$1055^{.82}$
C x S	3	$622^{.07}$	$252^{.56}$	$44.2^{.03}$	$3.7^{.78}$	$12509^{.06}$	$1500^{.83}$
D x C x S	6	$131^{.65}$	$127^{.88}$	$6.6^{.63}$	$5.8^{.74}$	$1964^{.75}$	$4069^{.61}$
E (C)	9	185	347	8.8	9.9	3480	5207
Depths (P)	2	$127532^{.00}$	$40508^{.00}$	$1456.0^{.00}$	$308.3^{.00}$	$152172^{.00}$	$23637^{.01}$
D x P	4	$6627^{.00}$	$2355^{.00}$	$42.6^{.02}$	$19.4^{.10}$	$14502^{.27}$	$5120^{.32}$
C x P	6	$49^{.99}$	$964^{.08}$	$9.5^{.65}$	$19.0^{.08}$	$6043^{.76}$	$8471^{.08}$
D x C x P	12	$353^{.91}$	$633^{.24}$	$10.6^{.66}$	$9.3^{.52}$	$5288^{.91}$	$3751^{.57}$
S x P	2	$215^{.74}$	$179^{.69}$	$11.7^{.57}$	$3.0^{.73}$	$91222^{.00}$	$6638^{.22}$
D x S x P	4	$377^{.72}$	$147^{.87}$	$7.0^{.73}$	$14.4^{.21}$	$14919^{.26}$	$3330^{.54}$
C x S x P	6	$341^{.82}$	$217^{.84}$	$10.0^{.62}$	$0.6^{.99}$	$5741^{.78}$	$3181^{.61}$
D x C x S x P	12	$89^{.99}$	$466^{.51}$	$5.1^{.96}$	$9.8^{.44}$	$5630^{.89}$	$4106^{.51}$
E (d)	48	709	478	13.5	9.5	10844	4236

*Indicates significance level.

Table 33. Means of strata (distance from the stem) by densities for the core measurements before and after coppicing

Densities (trees/ha)	Strata (cm)	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
		Before	After	Before	After	Before	After
5,000	23.6-47.2	43.1	42.4	7.8	6.6	40.0	45.4
5,000	47.2-70.7	36.6	44.3	6.5	6.4	20.0	22.9
10,000	16.7-33.4	44.4	27.7	8.5	5.9	104.4	52.5
10,000	33.4-50.0	41.3	29.2	7.0	5.9	13.5	16.7
15,000	13.6-27.2	54.5	34.9	8.7	6.6	62.8	45.0
15,000	27.2-40.7	47.7	36.3	7.1	6.2	18.9	15.7

Table 34. Means of clones by strata for the core measurements before and after coppicing

Clones	Strata	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
		Before	After	Before	After	Before	After
5377	2	45.4	39.0	7.9	6.1	84.7	72.6
5377	3	41.3	39.7	7.3	6.0	15.6	33.4
5321	2	50.1	36.7	8.1	6.9	40.5	35.1
5321	3	40.0	33.6	5.9	6.2	14.0	8.9
5323	2	51.2	35.5	10.4	6.8	92.7	36.1
5323	3	42.9	41.2	7.6	7.2	22.6	18.1
5326	2	42.6	28.8	6.9	5.6	58.4	46.6
5326	3	43.3	31.9	6.7	5.2	17.5	13.4

Table 35. Means by depths for the core measurements before and after coppicing

Depths (cm)	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
	Before	After	Before	After	Before	After
0-15	75.8	58.2	10.8	8.2	76.6	50.3
15-30	41.5	31.4	7.6	5.9	41.5	29.2
30-45	16.5	17.8	4.4	4.7	11.7	19.6

Table 36. Means of depths by densities for the core measurements before and after coppicing

Densities (trees/ha)	Depths (cm)	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
		Before	After	Before	After	Before	After
5,000	0-15	62.6	65.1	9.3	8.3	49.1	58.9
5,000	15-30	41.1	42.7	7.9	6.5	28.7	23.8
5,000	30-45	15.8	22.2	4.3	4.7	12.1	19.6
10,000	0-15	66.9	41.9	10.7	7.2	108.9	35.9
10,000	15-30	43.1	27.0	7.8	5.9	61.6	36.6
10,000	30-45	18.6	16.6	4.7	4.6	6.4	31.2
15,000	0-15	98.0	67.5	12.2	9.2	71.8	56.0
15,000	15-30	40.2	24.6	7.3	5.1	34.1	27.2
15,000	30-45	15.2	14.7	4.3	4.8	16.5	7.9

and the number of roots greater than 1 cm at the bottom of soil depths after coppicing (Table 38). These differences were generally not significant (Table 32). Root dry weight showed the greatest decrease with increasing depth in the short distance range from the stem. This is the

Table 37. Means of clones by depths for the core measurements before and after coppicing

Clones	Depths (cm)	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
		Before	After	Before	After	Before	After
5377	0-15	73.7	66.1	11.4	9.0	90.9	89.9
5377	15-30	41.1	33.2	7.4	5.1	50.2	53.4
5377	30-45	15.4	18.8	4.0	4.0	9.4	15.7
5321	0-15	76.9	50.1	9.7	7.3	39.3	37.9
5321	15-30	42.1	34.3	7.4	6.7	33.3	20.5
5321	30-45	16.2	21.1	3.9	5.6	9.1	7.4
5323	0-15	79.7	68.6	12.5	9.2	99.2	21.7
5323	15-30	42.7	29.5	8.9	6.0	51.9	21.9
5323	30-45	18.9	16.9	5.6	5.9	21.8	37.7
5326	0-15	73.1	47.9	9.5	7.4	77.0	51.6
5326	15-30	39.9	28.7	6.8	5.6	30.4	21.0
5326	30-45	15.8	14.4	4.0	3.4	6.4	17.5

Table 38. Means of depths by strata for the core measurements before and after coppicing

Strata	Depths (cm)	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
		Before	After	Before	After	Before	After
2	0-15	80.0	55.9	11.8	8.5	129.6	73.7
2	15-30	43.5	31.8	8.1	6.0	62.6	42.6
2	30-45	18.6	17.2	5.0	4.6	15.0	26.5
3	0-15	71.7	60.5	9.7	7.9	23.6	26.8
3	15-30	39.4	31.0	7.1	5.8	20.4	15.8
3	30-45	14.5	18.4	3.8	4.8	8.3	12.6

primary reason why there was a decrease of root dry weight with increasing depth before coppicing.

Effects of density on estimates of root growth Most root growth variables showed an increase with increasing planting density, before coppicing, except for root dry weight. This trend was quite different after coppicing. It was probably due to the immediate stump area (stratum 1 in Figure 6) excluded in the core sampling (Table 39).

Table 39. Means by densities for the core measurements before and after coppicing

Densities (trees/ha)	Total root no.		No. of roots (> 1 cm)		Root dry wt. (mg)	
	Before	After	Before	After	Before	After
5,000	39.9	43.3	7.1	6.5	30.0	34.1
10,000	42.9	28.5	7.7	5.9	58.9	34.6
15,000	51.1	35.6	7.9	6.4	40.8	30.4

Examining the estimates for accuracy Accuracy of root dry weight estimated by sampling was examined by comparison to the actual measured weight for four selected trees. Sample estimates were not significantly different from the actual measurements (Table 40).

Comparison of total root dry weight between locations, between densities, and between clones Greater total dry weight of roots was shown at the Ames plot than at the Rhinelander plot (Table 41). This fact was also evident when densities or clones were compared (Tables 42 and 43). The differences were not significant at the 5 percent level in the first and

Table 40. Root dry weight estimated by sampling technique compared with actual measured weight

Sample tree number	Estimated weight (g)	Actual weight (g)
1	548.3	320.6
2	483.5	499.6
3	209.1	226.7
4	177.4	159.6

Table 41. Means by locations, by densities, and by clones for total root dry weight per tree before and after coppicing

Source	TRTDW (g)			
	Before			After
	Year 1	Year 2	Year 3	Year 1
Locations				
Ames	9.3	225.8	625.6	406.0
Rhinelander	4.9	89.7	198.4	273.7
Densities				
5,000 trees/ha	8.4	216.1	567.2	519.8
10,000 trees/ha	5.8	141.9	403.2	289.9
15,000 trees/ha	7.2	115.3	265.7	209.8
Clones				
5377	5.7	175.6	451.8	410.8
5321	6.0	97.8	281.4	262.2
5323	9.4	157.5	489.4	333.4
5326	7.5	200.1	425.5	353.0

Table 42. Means of densities by locations for total root dry weight per tree before and after coppicing

Locations	Densities (trees/ha)	TRTDW (g) Before Year 1	Before Year 2	Before Year 3	After Year 1
Ames	5,000	11.1	303.6	875.0	617.4
Ames	10,000	8.9	207.2	633.3	369.3
Ames	15,000	8.0	166.7	368.5	231.3
Rhinelander	5,000	5.8	128.6	259.3	422.1
Rhinelander	10,000	2.7	76.5	173.1	210.5
Rhinelander	15,000	6.4	63.9	162.9	188.4

Table 43. Means of clone by locations for total root dry weight per tree before and after coppicing

Locations	Clones	TRTDW (g) Before Year 1	Before Year 2	Before Year 3	After Year 1
Ames	5377	8.8	247.5	671.5	512.8
Ames	5321	7.8	153.5	438.3	321.8
Ames	5323	10.5	217.9	732.8	380.4
Ames	5326	10.2	284.4	659.9	409.0
Rhinelander	5377	2.7	103.6	232.1	308.7
Rhinelander	5321	4.1	42.2	124.5	202.6
Rhinelander	5323	8.3	97.0	246.1	286.3
Rhinelander	5326	4.8	115.9	191.1	297.1

second years before coppicing but were significant in the third year before coppicing and in the first year after coppicing (Table 44).

Total dry weight of roots for an individual tree showed a decrease with increasing planting density both before and after coppicing (Table 41), and differences were generally significant (Table 44). When clones were

Table 44. Mean squares from analysis of variance for total root dry weight of four Populus clones before and after coppicing

Source of variation	d.f.	Before			After
		Year 1	Year 2	Year 3	Year 1
Locations (L)	1	$230^{.53*}$	$222483^{.06}$	$2189742^{.01}$	$210132^{.03}$
E (a)	2	286	14243	20906	8200
Densities (D)	2	$28^{.38}$	$43640^{.02}$	$364513^{.01}$	$414178^{.00}$
L x D	2	$24^{.42}$	$5290^{.29}$	$171459^{.04}$	$25344^{.00}$
E (b)	4	22	3099	19236	328
Clones (C)	3	$35^{.02}$	$22814^{.00}$	$99268^{.00}$	$45104^{.00}$
L x C	3	$9^{.36}$	$1950^{.07}$	$18289^{.25}$	$7202^{.34}$
D x C	6	$7^{.52}$	$2851^{.01}$	$11062^{.52}$	$13320^{.09}$
L x D x C	6	$11^{.30}$	$896^{.32}$	$14287^{.37}$	$2476^{.86}$
E (c)	18	8	701	12305	6037

*Indicates significance level.

compared, this relationship was also evident in the third year before coppicing and in the first year after coppicing (Table 45). Also, it was evident when locations were compared, except for the first year growth before coppicing at the Rhinelander plot (Table 42).

Although clonal differences in total root dry weight were highly significant (Table 44), none of clones showed a consistently high dry weight. Clone 5323 had the greatest dry weight in the first year, clone 5326 in the second year, clone 5323 in the third year before coppicing, and clone 5377

Table 45. Means of clones by densities for total root dry weight per tree before and after coppicing

Densities (trees/ha)	Clones	TRTDW (g) Before Year 1	Before Year 2	Before Year 3	After Year 1
5,000	5377	5.8	230.6	585.3	652.0
5,000	5321	8.4	135.3	432.8	363.3
5,000	5323	10.5	199.0	619.8	499.4
5,000	5326	9.1	299.4	632.8	564.4
10,000	5377	5.2	169.1	490.4	310.5
10,000	5321	4.7	92.6	213.1	256.8
10,000	5323	6.6	156.9	506.9	274.2
10,000	5326	6.8	148.8	402.4	318.2
15,000	5377	6.1	127.0	281.8	269.8
15,000	5321	4.8	65.6	198.2	166.5
15,000	5323	11.1	116.5	341.6	226.6
15,000	5326	6.6	152.2	241.1	176.5

in the first year after coppicing (Table 41). All clones performed similarly in both locations (Table 43).

Effects of root dry weight adjusted on coppice growth

The growth of sprouts depends upon the size of the residual stand such as roots or stumps. The root dry weight for all locations, densities, and clones was adjusted in this study to compare the differences in coppice growth performance between locations, between densities, and between clones. When the dry weight of roots was not used as a covariate, most coppice growth variables showed markedly significant differences between locations, between densities, and between clones. The significant effects of location, density, and clone on these variables, however, were remarkably reduced by adjusting the root dry weight (Table 46). The mean

Table 46. Mean squares from analysis of variance for coppice growth variables adjusted and unadjusted by root dry weight in the field

Source of variation	d.f.	Unadjusted			
		SPNO	SPST	STDW	LFDW
Locations (L)	1	$73.3^{.31*}$	$60.8^{.10}$	$2383901^{.00}$	$463681^{.01}$
E (a)	2	39.7	7.2	9788	3541
Densities (D)	2	$301.3^{.00}$	$27.5^{.01}$	$803361^{.01}$	$162744^{.01}$
L x D	2	$19.2^{.20}$	$9.3^{.04}$	$178842^{.05}$	$38421^{.09}$
E (b)	4	8.0	1.1	25345	8403
Clones (C)	3	$80.6^{.01}$	$11.5^{.12}$	$115002^{.01}$	$39443^{.00}$
L x C	3	$1.7^{.95}$	$5.2^{.41}$	$32077^{.25}$	$11077^{.13}$
D x C	6	$17.9^{.39}$	$5.9^{.38}$	$54022^{.06}$	$9506^{.15}$
L x D x C	6	$24.1^{.23}$	$7.7^{.24}$	$23830^{.40}$	$3858^{.63}$
E (c)	18	16.1	5.2	21525	5216

*Indicates significance level.

[a]One degree of freedom was lost due to covariate.

d.f.	Adjusted SPNO	SPST	STDW	LFDW
1	$135.1^{.23}$	$51.2^{.12}$	$346772^{.01}$	$53032^{.11}$
2	46.4	7.7	4606	6661
2	$10.5^{.29}$	$0.9^{.45}$	$2947^{.89}$	$230^{.97}$
2	$34.2^{.07}$	$10.9^{.02}$	$72702^{.17}$	$12888^{.32}$
4	6.1	0.9	24983	8502
3	$73.9^{.01}$	$10.3^{.14}$	$42823^{.06}$	$53476^{.00}$
3	$5.4^{.75}$	$2.4^{.70}$	$23047^{.22}$	$13187^{.02}$
6	$10.7^{.57}$	$4.3^{.54}$	$35735^{.06}$	$10130^{.02}$
6	$25.0^{.14}$	$8.5^{.18}$	$17074^{.35}$	$4016^{.30}$
17[a]	13.0	5.0	14070	3026

differences between locations were not significant for most growth variables except for the stem dry weight, while mean differences in stem dry weight between clones disappeared, and those in leaf dry weight rather increased (Table 47). This significant difference between locations for the stem dry weight was mainly attributed to large mean value at the Ames plot. So, Ames plot is significantly superior to Rhinelander plot in terms of stem wood production. Furthermore, significant differences between densities were removed for all variables after adjustment for size (Table 46). All relationships between the covariate and the variables were positive.

Table 47. Means by locations, by densities, and by clones for coppice growth variables adjusted and unadjusted by root dry weight in the field (values were based on an individual tree)

	Unadjusted				Adjusted			
Factors	SPNO	SPST	STDW (g)	LFDW (g)	SPNO	SPST	STDW (g)	LFDW (g)
Locations								
Ames	13.81	6.00	796.13	378.26	12.23	5.32	718.86	336.91
Rhinelander	16.28	8.25	350.40	181.69	17.98	8.85	427.70	223.05
Densities								
5,000 trees/ha	19.58	8.52	822.14	391.60	15.04	6.80	611.98	279.15
10,000 trees/ha	14.60	6.94	510.16	252.90	15.96	7.39	568.49	284.12
15,000 trees/ha	10.94	5.92	387.53	195.42	14.31	7.06	539.37	276.66
Clones								
5377	15.25	7.11	645.83	249.35	13.36	6.52	562.99	205.03
5321	12.36	6.17	444.83	299.08	14.31	6.79	535.53	347.61
5323	18.50	8.47	653.32	350.90	18.83	8.48	660.87	354.94
5326	14.06	6.75	549.14	220.58	13.91	6.55	533.73	212.33

Although differences in stem dry weight between clones were not significant, the mean value of clone 5323 was significantly different from clones 5321 and 5326. In addition, the significant effects of clone on the number of sprouts and leaf dry weight, even after adjustment for root size, were primarily due to larger values in sprout number and leaf dry weight from clone 5323. This may imply that clone 5323 is a good genotype with respect to coppice growth.

Relationships between top and bottom growth variables before and after coppicing

Since the leaf dry weight in the third year at the Rhinelander plot was obtained by regression estimation, it was appropriate to use the ratio of stem to root instead of top (stems + leaves) to root ratio for the examination of assimilate distribution. The ratio showed an increase as the tree grew before coppicing, whereas it showed a large decrease after coppicing (Figure 13). This decrease after coppicing was generally expected because of a lack of reserve materials available immediately for shoot growth. However, it appears to increase rapidly as trees grow because of top-root balance.

Ratio differences between clones were significant at the 5 percent level in the first and second years before coppicing but were not significant in the third year before coppicing and in the first year after coppicing. Clones 5323 and 5321 tended to show a large ratio at the early stage (in the first and second years) while clones 5326 and 5377 showed a large ratio at the relatively late stage (in the third year before coppicing). Great ratios attained by clone 5321 were not because of greater dry matter

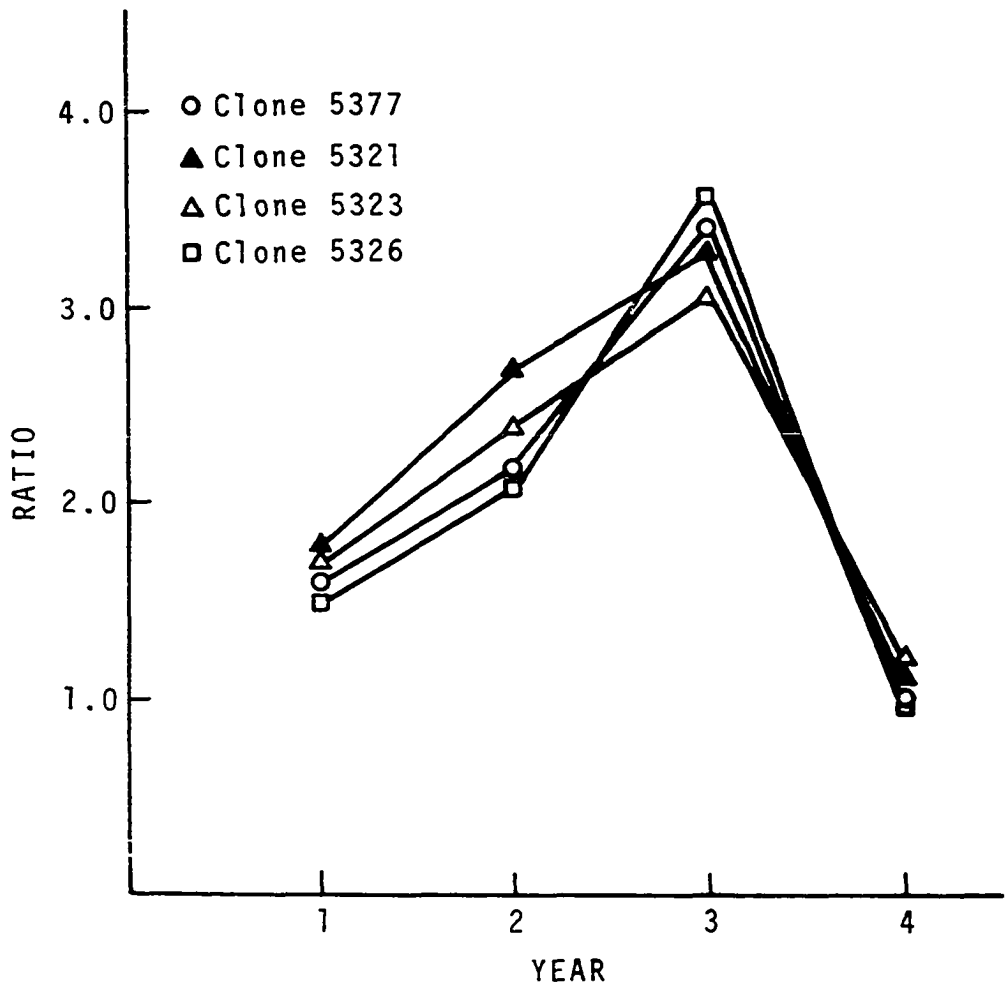


Figure 13. Comparison of ratios of stem to root dry weight for four clones in each year (coppicing was done in year 3)

deposition to the top but because of less root dry weight accumulation than the other clones. After coppicing, clone 5323 showed the largest ratio, clones 5321 and 5377 the intermediate, and clone 5326 the smallest. Thus, clone 5323 appears to mobilize reserve materials rapidly for early growth while clones 5326 and 5377 shows a possibility for late but large dry matter accumulation.

Most top and bottom growth variables after coppicing showed greater values at the Ames plot than at the Rhinelander plot except for total number of sprouts (Table 48). Location differences in top dry weight, basal area of stump, and root dry weight were significant (Table 49), and this significant effect was due primarily to the large mean response from the Ames plot. This relationship was also evident when densities or clones were compared (Tables 50 and 51).

Table 48. Means by locations, by densities, and by clones for coppice growth variables in the field (values were based on an individual tree)

Factors	SPNO	TOPDW (g)	SBA (cm^2)	STMDW (g)	TRTDW (g)
Locations					
Ames	13.8	1174.4	47.0	160.2	406.0
Rhinelander	16.3	532.1	24.8	140.1	273.4
Densities					
5,000 trees/ha	19.6	1213.7	49.6	230.0	519.8
10,000 trees/ha	14.6	763.1	32.3	121.0	289.9
15,000 trees/ha	10.9	583.0	25.8	99.6	209.8
Clones					
5377	15.3	895.2	42.2	166.6	410.8
5321	12.4	743.9	30.5	106.0	262.2
5323	18.5	1004.2	36.6	161.8	333.4
5326	14.1	769.7	34.4	166.2	353.0

Table 49. Mean squares from uni-variate analysis of variance for coppice growth variables in the field

Source of variation	d.f.	SPNO	TOPDW	SBA	STMDW	TRTDW
Locations (L)	1	$73.3^{.31*}$	$4950313^{.00}$	$5935^{.00}$	$4832^{.25}$	$210132^{.03}$
E (a)	2	39.7	20206	40	1889	8200
Densities (D)	2	$301.3^{.00}$	$1689219^{.01}$	$2420^{.03}$	$78146^{.00}$	$414178^{.00}$
L x D	2	$19.2^{.20}$	$382773^{.06}$	$437^{.30}$	$853^{.53}$	$25344^{.00}$
E (b)	4	8.0	61897	264	1125	328
Clones (C)	3	$80.6^{.01}$	$173923^{.03}$	$284^{.14}$	$10453^{.01}$	$45104^{.00}$
L x C	3	$1.7^{.95}$	$57766^{.32}$	$187^{.29}$	$1546^{.58}$	$7202^{.34}$
D x C	6	$17.9^{.39}$	$103902^{.08}$	$79^{.76}$	$2799^{.33}$	$13320^{.09}$
L x D x C	6	$24.1^{.23}$	$44792^{.53}$	$73^{.79}$	$1456^{.70}$	$2476^{.86}$
E (c)	18	16.1	45904	140	2257	6037

*Indicates significance level.

Table 50. Means by densities by locations for coppice growth variables in the field (values were based on an individual tree)

Locations	Densities (trees/ha)	SPNO	TOPDW (g)	SBA (cm^2)	STMDW (g)	TRTDW (g)
Ames	5,000	17.2	1707.6	65.4	235.2	617.4
Ames	10,000	14.4	1037.1	44.3	139.4	369.3
Ames	15,000	9.8	778.4	31.3	106.0	231.3
Rhinelander	5,000	22.0	719.9	33.8	224.6	422.1
Rhinelander	10,000	14.8	489.0	20.2	102.5	210.5
Rhinelander	15,000	12.1	387.5	20.4	93.3	188.4

Table 51. Means of clones by locations for coppice growth variables in the field (values were based on an individual tree)

Locations	Clones	SPNO	TOPDW (g)	SBA (cm^2)	STMDW (g)	TRTDW (g)
Ames	5377	14.2	1268.1	58.0	193.6	512.8
Ames	5321	10.6	1074.9	38.1	110.3	321.8
Ames	5323	17.4	1364.5	49.5	167.5	380.4
Ames	5326	13.1	990.2	42.5	169.5	409.0
Rhinelander	5377	16.3	522.3	26.3	139.6	308.7
Rhinelander	5321	14.2	412.9	22.9	101.8	202.6
Rhinelander	5323	19.6	644.0	23.6	156.2	286.3
Rhinelander	5326	15.1	549.3	26.3	163.0	297.1

All growth variables exhibited a decrease with increasing planting density (Table 48), and differences were highly significant (Table 49). This trend was also evident when locations were compared (Table 50). When clones were compared, the similar relationship was shown only for three clones, 5377, 5321, and 5326. Clone 5323, however, had increased growth of total sprout number, top dry weight, basal area and dry weight of stump with increasing density, from the intermediate to the highest (Figures 14, 15, 16, and 17). The high significance exhibited between densities was primarily due to the greater mean response at the lowest density over the rest of the densities.

Clone 5323 showed the largest growth of the top variables (total sprout number and top dry weight) whereas clone 5377 showed the largest growth of the bottom variables (basal area of stump, stump dry weight, and root dry weight) (Table 48). The smallest mean response of these growth variables was attained by clone 5321. This relationship between clones was

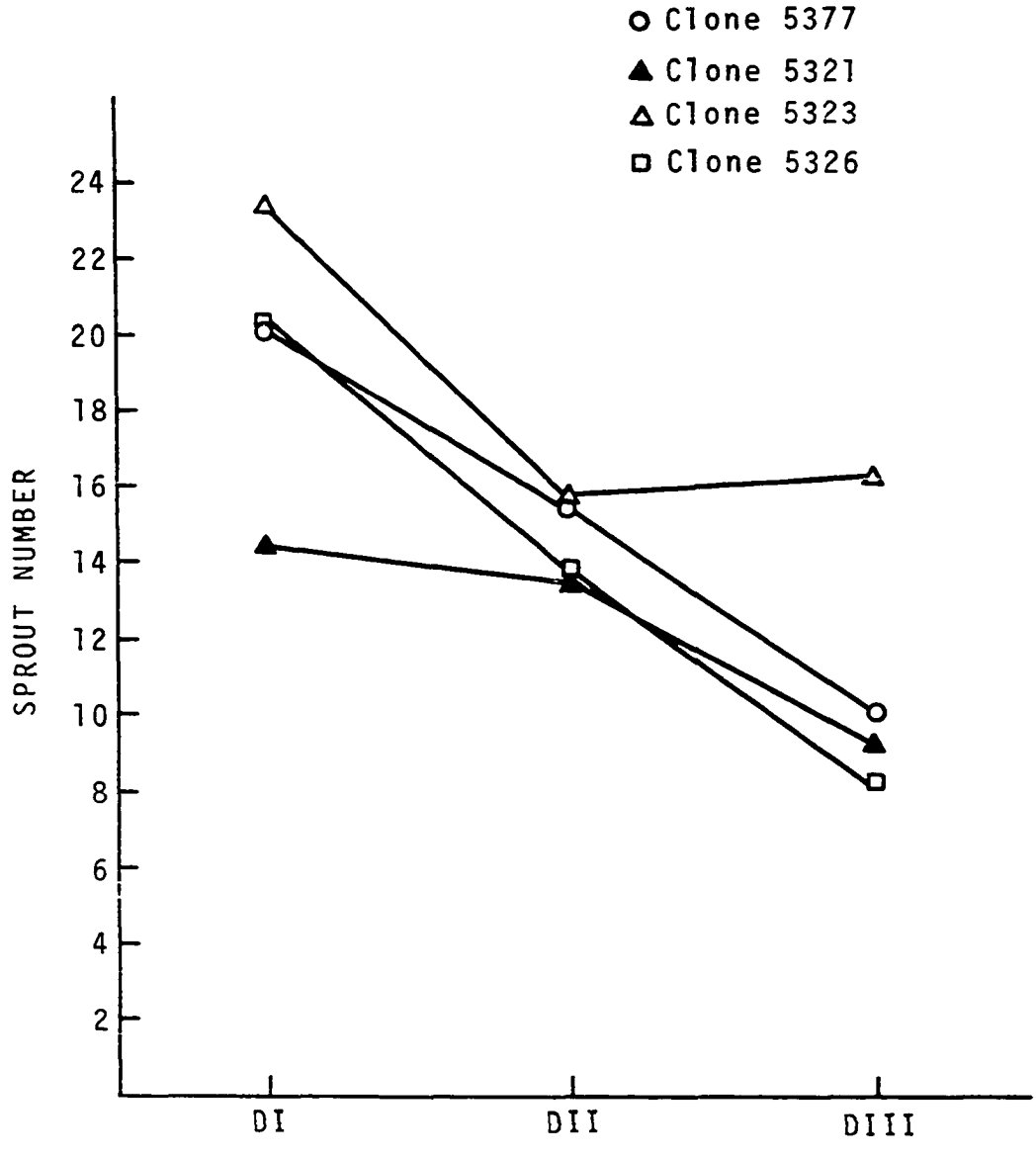


Figure 14. Comparison of sprout number for four clones at each density

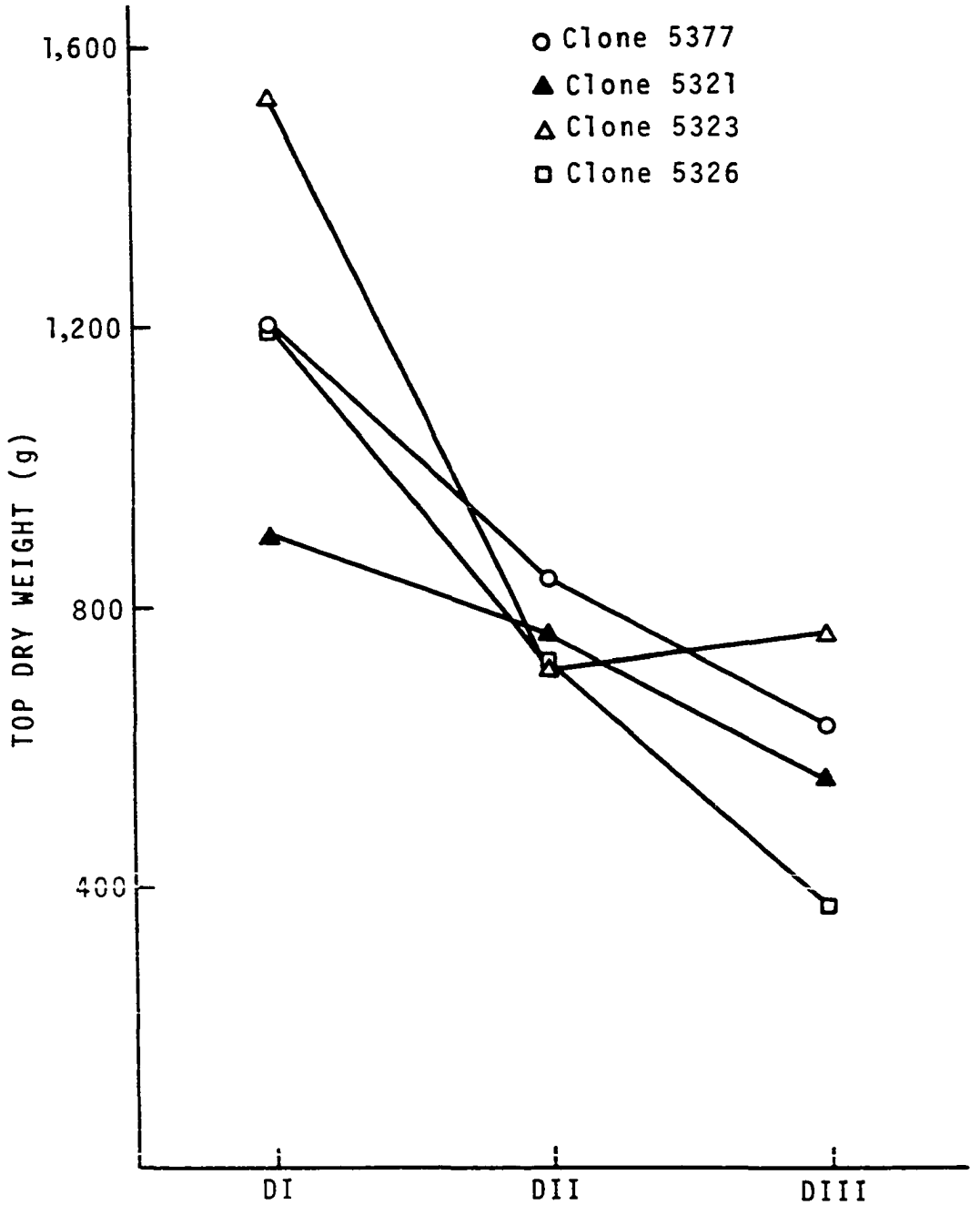


Figure 15. Comparison of top dry weight (stems + leaves) for four clones at each density

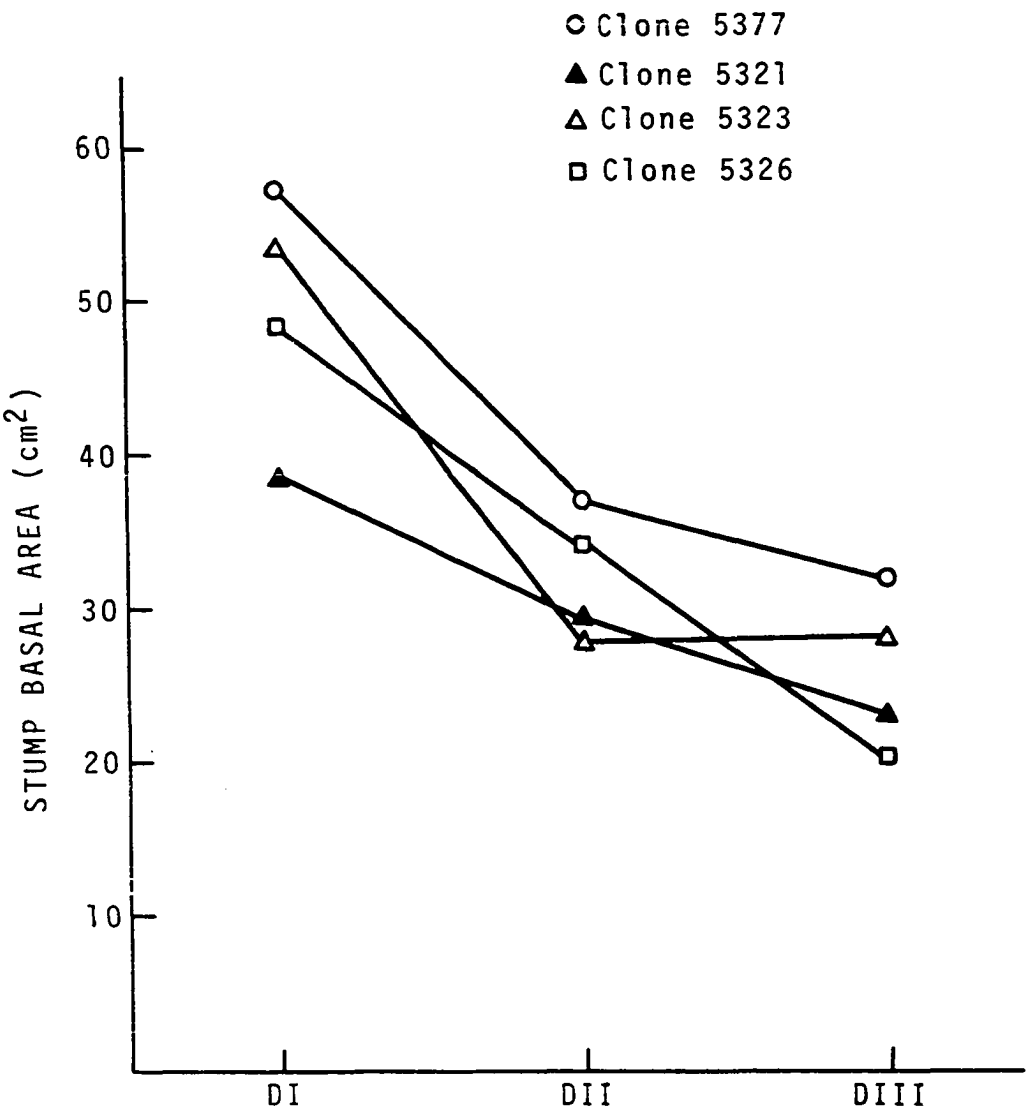


Figure 16. Comparison of stump basal area for four clones at each density

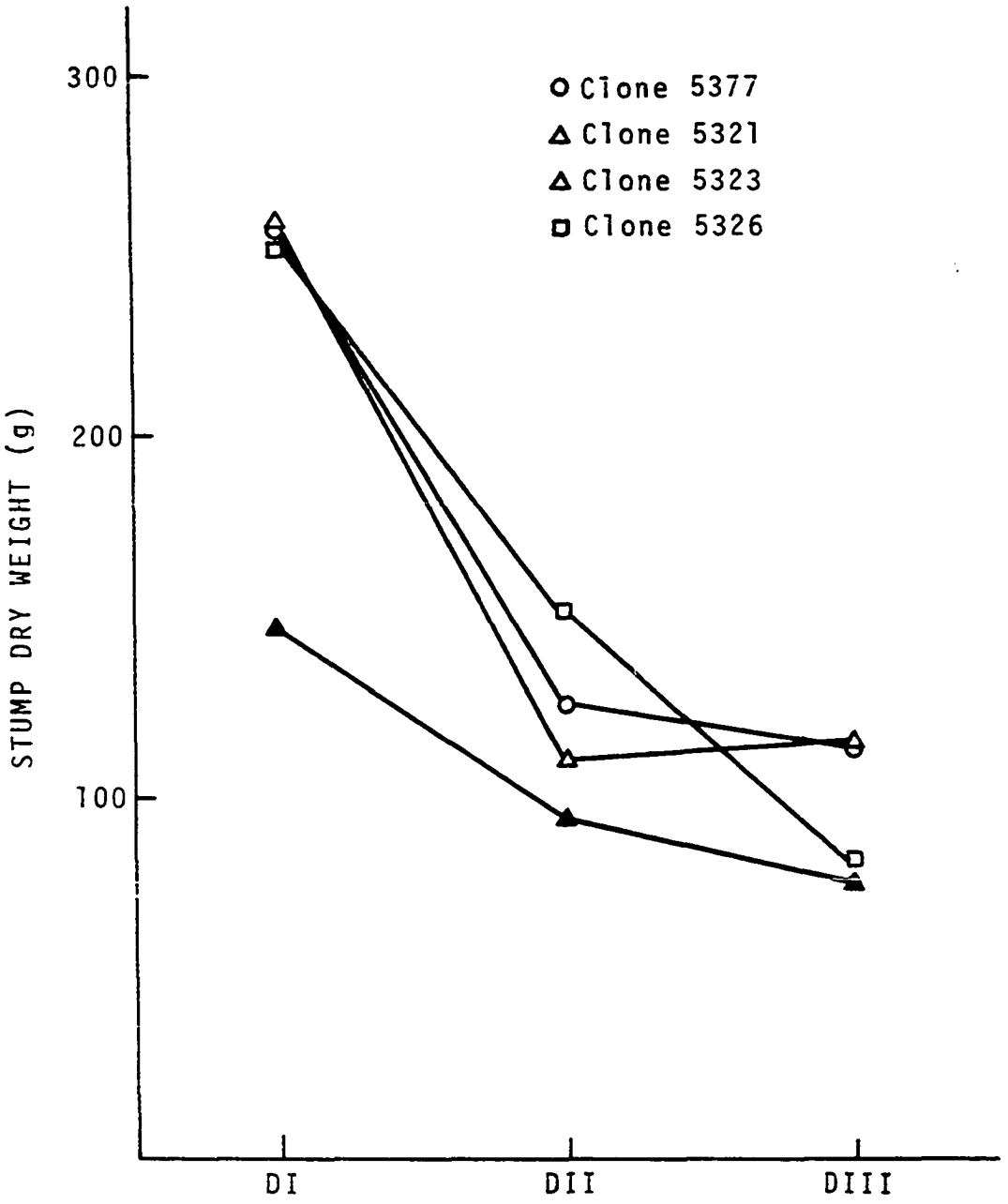


Figure 17. Comparison of stump dry weight for four clones at each density

generally evident at the Ames plot when locations were compared (Table 51). At the Rhinelander plot, however, clone 5323 had the largest top growth and stump dry weight while clone 5377 had the largest growth in the basal area of stump and root dry weight among bottom growth variables (Table 51). Again, the smallest growth responses for these variables were attained by clone 5321. At the lowest density, the largest top growth was shown by clone 5323 while the largest bottom growth was shown by clone 5377 (Figures 15 and 16; Table 45). At the intermediate density, none of clones were consistent for growth in these variables, but a similar trend to that at the lowest density was exhibited at the highest density.

The partial correlation coefficients holding location, density, and clone constant indicated strong and positive relationships between coppice growth of the following variables (Table 52): basal area and dry weight of the stump and root dry weight correlated with the top dry weight, basal area of the stump correlated with root dry weight, and total number of sprouts correlated with stump dry weight. This strong relationship between top and bottom growth variables was also evident when canonical correlation analysis was performed (Table 53).

Hotelling-Lawley's Trace, when used as a test criterion, indicated significance at the 1 percent level for all main effects and showed interaction effects between density and location (Table 54). This simply implies that there were some location, density and clone effects, and interaction effects between location and density.

The results obtained from canonical multi-variate analyses for coppice growth variables illustrated that the following dependent variables contributed most to the variation of each main effect. Top dry weight, basal

Table 52. Partial correlation coefficients between coppice growth variables holding location, density, and clone constant

	SPNO	TOPDW	SBA	STMDW	TRTDW
SPNO	1.00	$0.48^{.04}$	$0.53^{.02}$	$0.70^{.00}$	$0.49^{.03}$
TOPDW	$0.48^{.04*}$	1.00	$0.73^{.00}$	$0.71^{.00}$	$0.65^{.00}$
SBA	$0.53^{.02}$	$0.73^{.00}$	1.00	$0.72^{.00}$	$0.76^{.00}$
STMDW	$0.70^{.00}$	$0.71^{.00}$	$0.72^{.00}$	1.00	$0.61^{.00}$
TRTDW	$0.49^{.03}$	$0.65^{.00}$	$0.76^{.00}$	$0.61^{.00}$	1.00

*Indicates significance level.

Table 53. Canonical correlation coefficients relating top and bottom variables of coppice growth

Canonical variable number	Canonical correlation coefficient	χ^2-value
Var. #1	0.8598	$23.434^{.01*}$
Var. #2	0.3880	$2.601^{.63}$
Var. #3	0.0683	$0.072^{.78}$

*Indicates significance level.

area of stump, and root dry weight contributed the most to the variation between locations (Table 55). One hundred percent of the variation due to location could be expressed by the first canonical variable (Table 56). All growth variables used in this study, root dry weight, top dry weight, stump dry weight, basal area of stump, and sprout number, contributed most

Table 54. F-values obtained from multi-variate analysis of variance for growth variables after coppicing to test the following hypotheses

Test hypotheses	F-values
Ho: No location effect	$30.993^{.00*}$
Ho: No density effect	$13.676^{.00}$
Ho: No clone effect	$4.028^{.00}$
Ho: No location x density effect	$3.221^{.01}$
Ho: No location x clone effect	$0.856^{.61}$
Ho: No density x clone effect	$1.034^{.44}$
Ho: No location x density x clone effect	$0.869^{.66}$

*Indicates significance level.

Table 55. Correlation coefficients between each canonical variable and dependent variables (variation due to location)

Canonical variable number	Correlation coefficients between each canonical variable and dependent variables (variation due to location)				
	SPNO	TOPDW	SBA	STMDW	TRTDW
Var. #1	-0.1446	0.7357	0.4620	0.1037	0.4180

to the variation between densities (Table 57). One hundred percent of the variation due to density could be explained by the first two canonical variables (Table 58). Root dry weight, sprout number, stump dry weight, and top dry weight contributed the most to the variation between clones

Table 56. Characteristic roots and vectors of canonical multi-variate analysis of the variation due to location

Canonical variable number	Characteristic root	Percent of variation	Normalized characteristic vectors associated with characteristic roots				
			SPNO	TOPDW	SBA	STMDW	TRTDW
Var. #1	11.0689	100.00	-0.0234	0.0013	0.0045	-0.0033	0.0003

Table 57. Correlation coefficients between each canonical variable and dependent variables (variation due to density)

Canonical variable number	Correlation coefficients between each canonical variable and the dependent variables				
	SPNO	TOPDW	SBA	STMDW	TRTDW
Var. #1	0.4409	0.6364	0.4372	0.6167	0.8699
Var. #2	-0.4535	-0.1677	-0.0798	0.2080	-0.1086

Table 58. Characteristic roots and vectors of canonical multi-variate analysis of the variation due to density

Canonical variable number	Characteristic root	Percent of variation	Normalized characteristic vector associated with characteristic roots				
			SPNO	TOPDW	SBA	STMDW	TRTDW
Var. #1	10.0658	95.68	-0.0034	0.0003	-0.0175	0.0019	0.0034
Var. #2	0.4543	4.32	-0.0710	-0.0007	-0.0023	0.0079	0.0001

(Table 59). The first two canonical variables accounted for about 92 percent of the variation due to clone (Table 60).

Table 59. Correlation coefficients between each canonical variable and dependent variables (variation due to clone)

Canonical variable number	Correlation coefficients between each canonical variable and dependent variables				
	SPNO	TOPDW	SBA	STMDW	TRTDW
Var. #1	0.1785	0.1659	-0.1413	-0.2465	-0.4254
Var. #2	0.7925	0.6396	0.3656	0.6865	0.6640
Var. #3	-0.0337	0.3377	0.5296	-0.1286	0.5842

Table 60. Characteristic roots and vectors of canonical multi-variate analysis of the variation due to clone

Canonical variable number	Characteristic root	Percent of variation	Normalized characteristic vector associated with characteristic roots				
			SPNO	TOPDW	SBA	STMDW	TRTDW
Var. #1	3.1443	65.92	0.0498	0.0012	0.0033	-0.0056	-0.0030
Var. #2	1.2186	25.55	0.0357	0.0005	-0.0183	0.0009	0.0019
Var. #3	0.4067	8.53	0.0009	0.0003	0.0155	-0.0062	0.0017

A strong and linear relationship was present between canonical variable #1 in group 1 (top growth variable) and canonical variable #1 in group 2 (bottom growth variable) whether examined with planting densities or clones (Figures 18 and 19). Figure 18 shows that the points for the

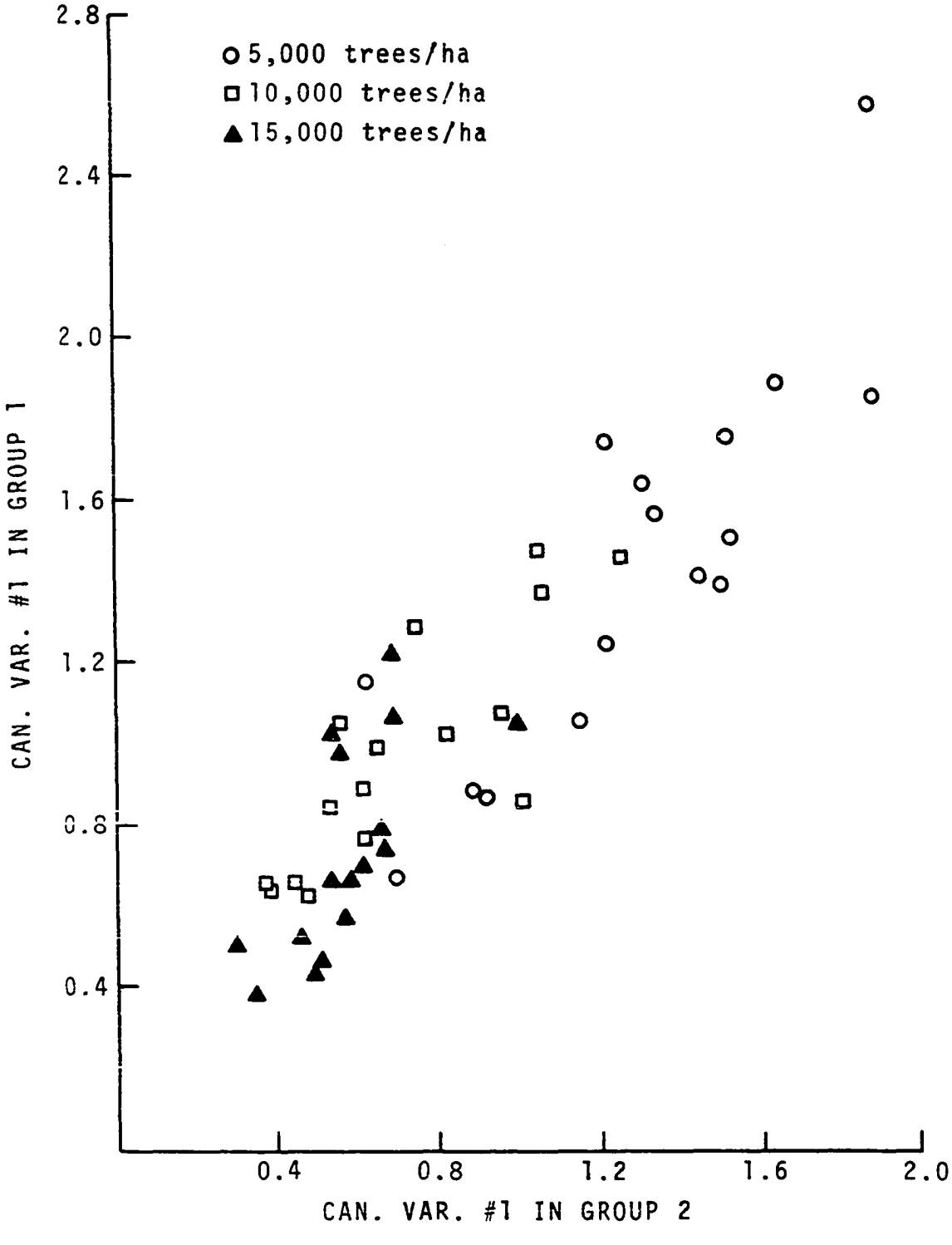


Figure 18. Canonical analysis of proportion of top (group 1) and bottom (group 2) growth elements for three planting densities

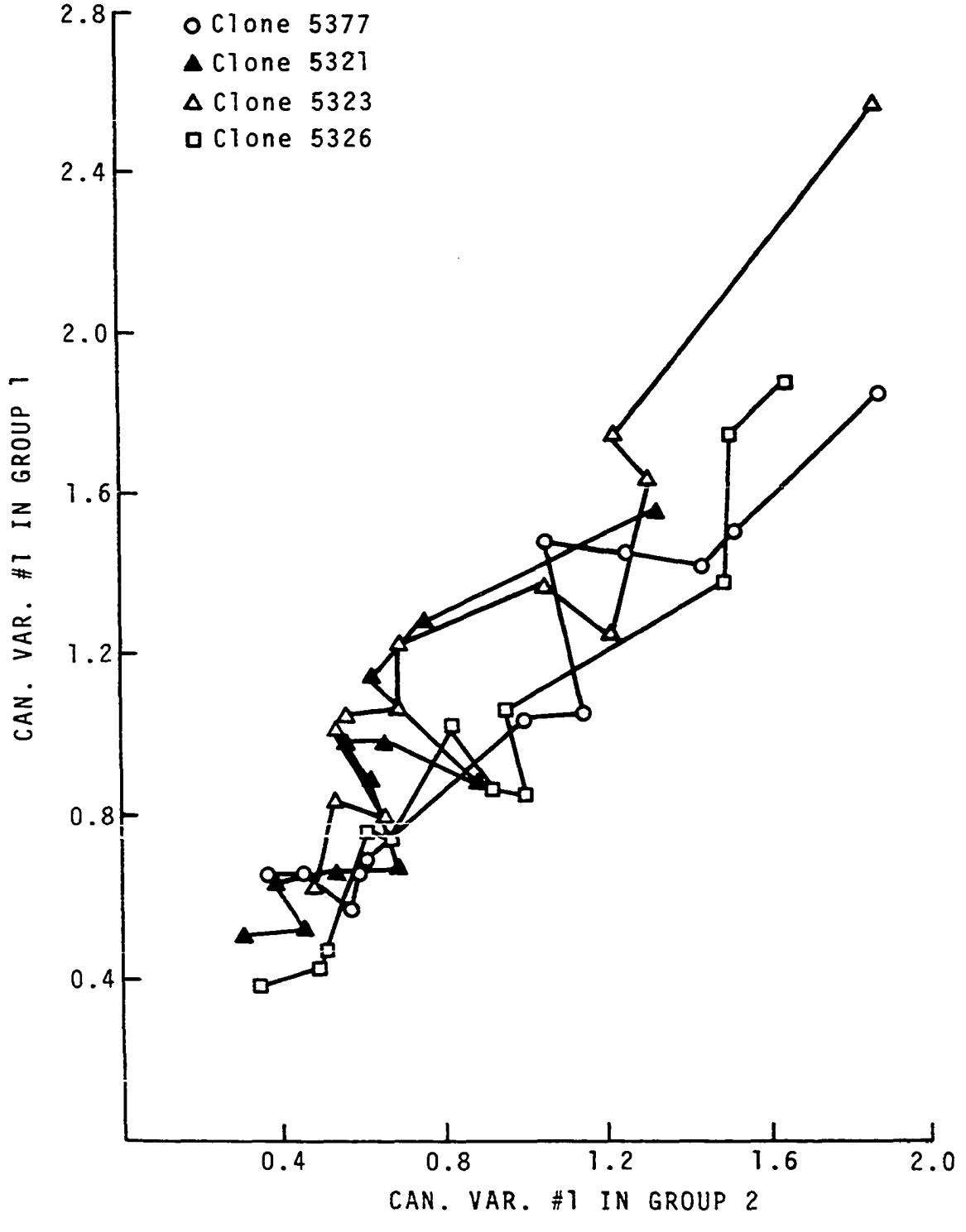


Figure 19. Canonical analysis of proportion of top (group 1) and bottom (group 2) growth elements for four clones

lowest density are clustered at the upper portion of the graph. This implies that the lowest planting density is more productive with respect to growth responses for groups 1 and 2 than the other densities. However, with respect to clustering, clonal observations are distributed differently (Figure 19); for instance, points for clone 5323 are located at the left-upper portion of the graph while those for clones 5377 and 5326 are located at the right-lower portion, in contrast, those for clone 5321 are clustered at the left-lower portion. This indicates that clones 5323, 5377, and 5326 are better in terms of the above growth variables because clone 5321 does not respond well to decreased planting densities.

The combined results of uni- and multi-variate analyses for coppice growth variables indicated a lack of interaction effects but strong main effects on most measured variables. Exceptions were for the strong effects of location by density on root dry weight. This significant effect of location by density on root weight was primarily ascribed to the highly significant effect of density.

Thus, the coppice growth differences between the two locations were mainly due to differences in environmental growth factors which were more favorable in Ames. Growth differences between the three planting densities were mainly due to greater growth at the lowest density, and those between the four Populus clones were due to better growth performances shown by clones 5323 and 5377 over clones 5326 and 5321.

Discussion

Growth performance differences between locations, between densities, and between clones, before coppicing

Greater initial and final leaf surface areas per tree were produced at the Ames plot than the Rhinelander plot, but differences were generally not significant except for the initial leaf area in the second year. This significant effect of location on the initial leaf area was primarily due to the large mean response of the Ames plot.

The dry weights of stems and roots yielded at the Ames plot were also greater than those at the Rhinelander plot. Location differences were not significant for the stem dry weight in all years but were significant for the root dry weight in the third year. These growth differences, leaf areas, stem and root dry weights, were probably due to the favorable environmental conditions for growth such as longer growing period and better soil characteristics.

Most measured variables, initial and final leaf areas, and dry weights of stems and roots, showed a decreasing trend with increasing planting density except for the first year's growth and second year's initial leaf area. Density differences were not significant for such top growth variables as initial leaf area and stem dry weight but were generally significant for root growth. This result that no significant differences in the top growth were found between planting densities was similar to that reported by Isebrands et al. (1977) who found that there was no significant difference in leaf areas per tree among spacings. This result probably occurred because of a competition between tops and roots for growth materials or foods (Loomis, 1953). Rapid top growth competing for light

reduces the allocation of available photosynthate to roots, and soil characteristics may also affect root growth.

In contrast to the above main effects, clonal effects on most growth variables were highly significant with the exception of the final leaf areas in all years and of the stem dry weight in the first year. Clones 5326 and 5377 produced initially more leaf surface areas but lost more leaves during the growing season than clones 5323 and 5321 whereas greater final leaf areas were yielded by clones 5323 and 5321 than those by clones 5377 and 5326. This illustrates that clones 5323 and 5321 retained leaves longer than clones 5377 and 5326.

The stem and root dry weight of clone 5323 showed generally the largest mean values except that the largest dry weights of both stems and roots were attained by clone 5326 in the second year. Also, dry weight production of stem wood was closely associated with leaf area production, particularly with the final leaf area production in clones 5323, 5377, and 5326. This relationship between stem dry weight and leaf area production was similar to that shown by Larson and Isebrands (1972) who observed the above ground wood dry weight to have a close relationship with the cumulative leaf area in young Populus clones.

Few interaction effects were significant and could be generally explained by random variation and small sample sizes. The location by density interaction of total root dry weight (Figure 20) may be due to the difference in tree sizes between Ames and Rhinelander.

The greater root growth, but larger decrease with increasing density, exhibited at the Ames plot is mainly attributed to the more favorable soil

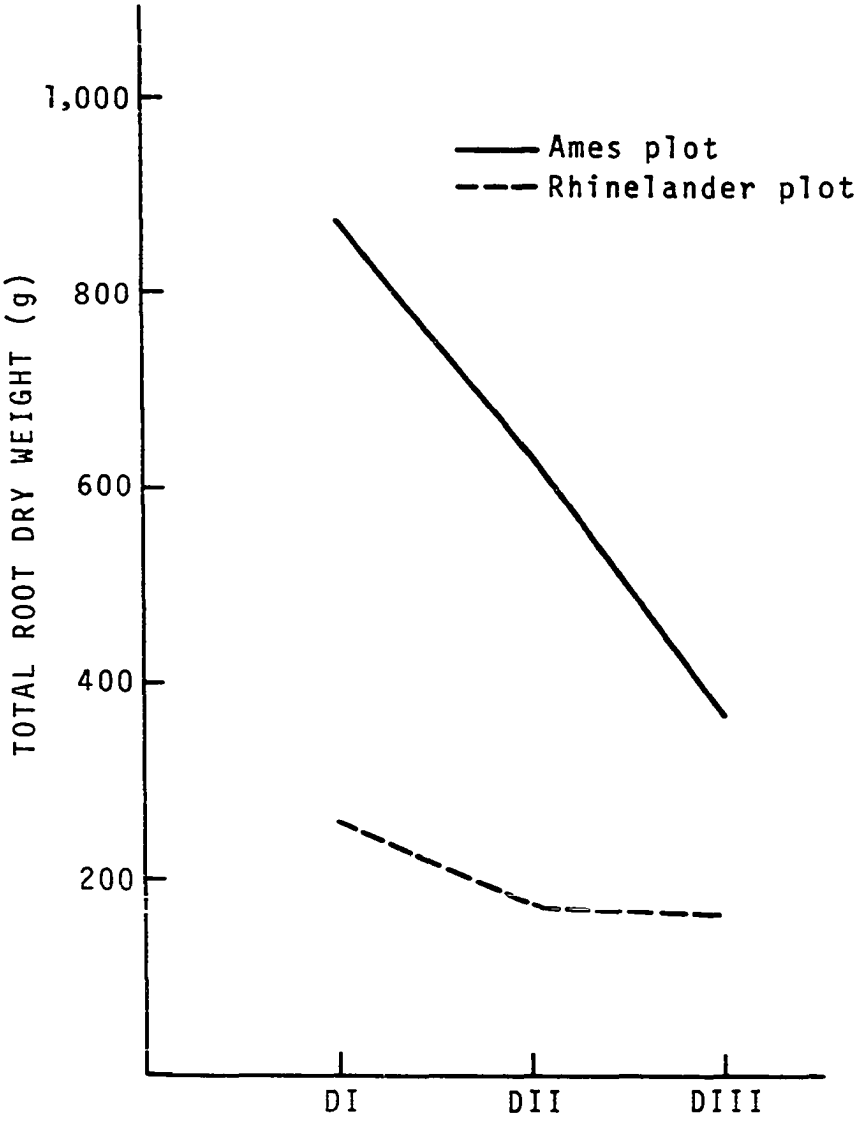


Figure 20. Comparison of total root dry weight for the two locations at each density in the third year before coppicing

environment, and thus considerable overlapping of root systems had already resulted in competition for moisture and nutrients. Marked density differences in root growth occurred, probably because of limitation of available soil moisture; roots growing at the low density thus can outgrow those at the high density. At the Rhinelander plot, however, water supply with frequent irrigations reduced root competition, and consequently root growth was not greatly affected by planting density. The results showing that the degree of root competition was in part dependent on planting density agrees with the work of Boswell et al. (1975) who stated that the root growth of orange trees was influenced by tree spacing.

With respect to the dry matter production per tree before coppicing, the following can be concluded: the Ames plantation, the lowest density, and clones 5323 and 5377 were the most productive among locations, among planting densities, and among clones, respectively.

Total biomass production per hectare, based on the tree average, exhibited an increasing trend with increasing spacing except for root dry weight in the third year (Table 61). The result for the stem dry weight, in particular, agreed with the work of Bowersox and Ward (1976) who reported that stemwood biomass of hybrid poplars increased with increasing growing space when pooled over the three years. The annual production of average stem dry weight, calculated over three years, ranged 2.6 tons/ha from the least dense plot (5,000 trees/ha) to 4.8 tons/ha from the most dense plot (15,000 trees/ha). The figure, 2.6 tons/ha/year, is larger than that reported by Einspahr and Benson (1968) who found 2.5 tons/ha/year of wood dry weight from a 12-year-old quaking aspen stand, of which spacing was similar to the lowest density of this study. Further, if spacing is

Table 61. Three-year growth of hybrid poplar at three planting densities (values for Ames, Iowa, and Rhinelander, Wisconsin, were pooled)

Densities (trees/ha)	Total dry weight (tons/ha)			Top dry weight (tons/ha)			Woody tissues: Stem dry weight (tons/ha)			Woody tissues: Root dry weight (tons/ha)			Leaf dry weight (tons/ha)		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
5,000	0.23	4.50	12.34	0.19	3.42	9.49	0.07	2.15	7.67	0.04	1.08	2.84	0.12	1.27	1.82
10,000	0.35	6.44	16.98	0.29	5.02	12.95	0.10	3.06	10.65	0.06	1.42	4.03	0.19	1.96	2.30
15,000	0.63	8.70	21.32	0.52	6.97	17.34	0.19	4.45	14.25	0.11	1.73	3.99	0.33	2.52	3.09

equal, stem dry weight productivity at the highest density could be equivalent to that reported by Dawson et al. (1976) who observed 6.0 tons/ha/year of stem weight from a Populus Tristis #1 stand planted in 0.6 m by 0.6 m spacing.

When clones were compared in terms of dry matter production, the largest biomass in either stem portion or total dry weight was yielded by clone 5323 followed by clones 5377 and 5326, and the smallest yield was shown by clone 5321, whether based on the average tree or the planting area (Tables 29 and 62).

In this study, Ames plot was more productive than Rhinelander plot, whether calculated on the individual tree or planting area basis. Particularly, an average stem dry weight per tree for clone 5377, grown for three years, was 1711 g at the Ames plot and 907 g at the Rhinelander plot. This result, however, was different from that reported by Hennessey (1976) who found better growth of clone 5377 at the Rhinelander plot than the Ames plot.

Growth responses due to coppicing

Most measured variables after coppicing showed decreased growth in most factors tested in this study as compared to the growth in the third year before coppicing. This result was generally expected because of no supply of carbohydrates from the shoots and because of carbohydrate reserves stored only in root systems to be used for both root and shoot growth. But exceptions were found: the final leaf areas when both locations were pooled and total root dry weight at the Rhinelander plot showed rather an increase for the first year after coppicing. This increase of

Table 62. Three-year growth of four Populus clones (values for Ames, Iowa, and Rhinelander, Wisconsin, were pooled)

Clones	Total dry weight (tons/ha)			Top dry weight (tons/ha)			Woody tissues						Leaf dry weight (tons/ha)		
							Stem dry weight (tons/ha)			Root dry weight (tons/ha)					
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
5377	0.33	6.80	18.52	0.27	5.22	14.50	0.10	3.47	12.10	0.06	1.58	4.02	0.17	1.75	2.40
5321	0.38	4.87	11.73	0.33	4.01	9.31	0.11	2.16	7.29	0.05	0.86	2.42	0.22	1.85	2.02
5323	0.55	7.20	19.57	0.45	5.76	15.14	0.17	3.53	12.16	0.10	1.44	4.43	0.28	2.23	2.98
5326	0.36	7.33	17.71	0.29	5.57	14.11	0.11	3.73	11.89	0.07	1.76	3.60	0.18	1.84	2.22

the final leaf areas was mainly due to the large increase at the Ames plot. Growth increase in root weight shown at the Rhinelander plot occurred probably because root growth continued due to frequent irrigations. This increasing trend was also evident when densities or clones were compared.

The differences in most growth variables between locations, between densities, and between clones were highly significant. Some of two or three factor interactions exhibited significant effects, but this was primarily caused by the high significance exhibited in the main effects.

After coppicing, such growth variables as initial leaf areas and stem dry weight showed much greater mean responses than those in the first year or second year before coppicing. This implies that more growth can be produced via coppicing.

In addition, total dry matter production per hectare, based on the tree averages, showed an increasing trend with increasing planting density (Table 63). The least dense plot (5,000 trees/ha) produced the equivalent of 4.11 tons/ha/year of stem dry weight, while the most dense plot (0.83 m x 0.83 m; 15,000 trees/ha) did 5.81 tons/ha/year. This figure is greater than that reported by Heilman et al. (1972) who found 2.76 and 5.51 tons/ha/year of wood dry weight from a black cottonwood stand established in spacings, 1.22 m by 1.22 m and 0.61 m by 0.61 m, respectively.

In terms of woody tissue production, clone 5377 ranked in first place, clone 5323 in second place, clone 5326 in third place, and clone 5321 in last place (Table 64). Mean stem dry weight among four clones varied from 4.11 to 5.75 tons/ha/year. This yield was not similar to that reported by Anderson and Zsuffa (1975) who found Populus hybrids to produce averagely 10.4 tons/ha/year from a coppice stand. Their experiment plots were

Table 63. One year coppice growth of hybrid poplar at three planting densities (values for Ames, Iowa, and Rhinelander, Wisconsin, were pooled)

Densities (trees/ha)	Total dry weight (tons/ha)	Top dry weight (tons/ha)	Woody tissues			Leaf dry weight (tons/ha)
			Stem dry weight (tons/ha)	Stump dry weight (tons/ha)	Root dry weight (tons/ha)	
5,000	9.82	6.07	4.11	1.15	2.60	1.96
10,000	11.75	7.63	5.10	1.21	2.90	2.53
15,000	13.39	8.74	5.81	1.50	3.15	2.93

Table 64. One year coppice growth of four Populus clones (values for Ames, Iowa, and Rhinelander, Wisconsin, were pooled)

Clones	Total dry weight (tons/ha)	Top dry weight (tons/ha)	Woody tissues			Leaf dry weight (tons/ha)
			Stem dry weight (tons/ha)	Stump dry weight (tons/ha)	Root dry weight (tons/ha)	
5377	12.90	7.99	5.75	1.43	3.47	2.24
5321	10.11	6.86	4.11	0.95	2.30	2.75
5323	13.02	8.76	5.68	1.38	2.88	3.08
5326	10.59	6.32	4.49	1.39	2.88	1.83

established with 4-year-old roots and 0.30 m by 0.91 m spacing in which age of roots and planting density were different from those of this study.

Root distribution before and after coppicing

All the root growth variables decreased with both the increasing distance from the tree stem and increasing depth from the soil surface before

coppicing. In general, this was also evident when densities or clones were compared. Total root number and the number of roots greater than 1 cm showed a small decrease with increasing distance or depth, but root dry weight showed a large decrease, which was particularly true of the medium planting density. This decreasing trend with increasing distance from the stem was similar to the results in earlier experiments (Lee, 1975). When the root growth change between two years was compared, the average values of root numbers in the third year were smaller than those in the second year whereas average root dry weight in the third year was larger than that in the second year. This may indicate that roots become thicker but degree of root branching decreases as the tree grows.

For the vertical distribution, root dry weight was mostly concentrated in the top 30 cm of soil. Similar results were reported by Bowen (1964) with monterey pine and Safford and Bell (1972) with white spruce. They observed most of the fine root weights distributed in the surface 30 to 45 cm. This is probably in part due to better nutrient level and aeration at the surface soil.

Although clonal differences in the horizontal and vertical distribution of root dry weight were not significant, clones 5323 and 5377 showed a large decrease with increasing depth from the soil surface. Clone 5323 had the largest mean values in all strata and depths, which implies that the roots of clone 5323 spread broadly and penetrate deeply.

Figure 21 shows clonal differences in root dry weight from the core sample at each planting density before coppicing. The largest root weight was found in the intermediate density followed next by the highest density, and the lowest density had the smallest. This was true of most clones

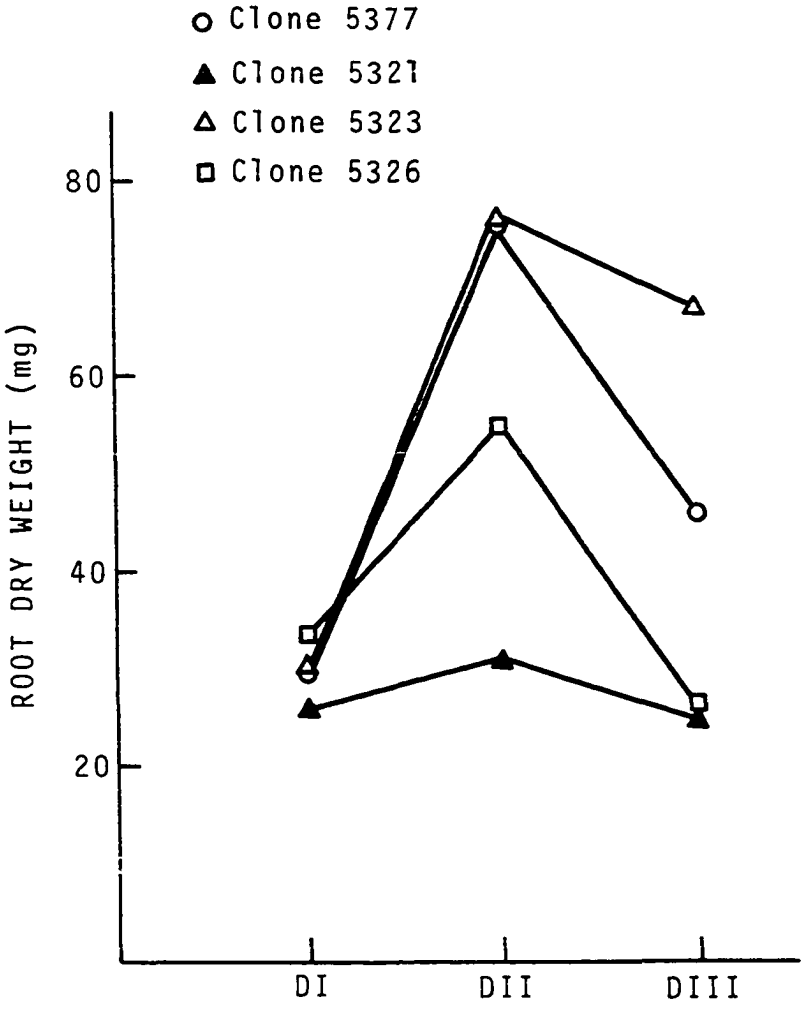


Figure 21. Comparison of root dry weight measured from the soil core for the four clones at each density in the third year before coppicing

except for clone 5326. Larger root weights found in the intermediate and highest densities were probably because of the root systems of adjacent trees overlapped and filled in all available spaces.

There were significant interaction effects of strata by depths on root dry weight. This interaction (Figure 22) is not because of decreasing mean response in one stratum and increasing mean response in another stratum as soil depth increased but rather because more roots were distributed near the tree stem (stratum 2 in Figure 6) where competition was more severe and thus differences in both strata became smaller as soil depth increased.

After coppicing, the decreasing trends for root variables were similar to those found before coppicing except for the horizontal distribution of total root number. Again, growth responses due to coppicing showed a large decrease in most root variables. This was generally expected because roots could not grow when shoots were removed (Eliasson, 1968), presumably due to a marked depletion of carbohydrate reserves stored in the root system. Therefore, many of growing roots probably died, which resulted in a large decrease in root growth. This result was similar to that reported by Visser (1969) who found that root weights were reduced by removal of shoots on tea plants. In contrast to this fact, root weight, after coppicing, in long distances (stratum 3) from the tree and all root variables at the bottom depth of soil exhibited greater values than those in the third year before coppicing. This implies that the growth of deeply penetrating roots may be less influenced by removal of shoots than roots distributed shallowly.

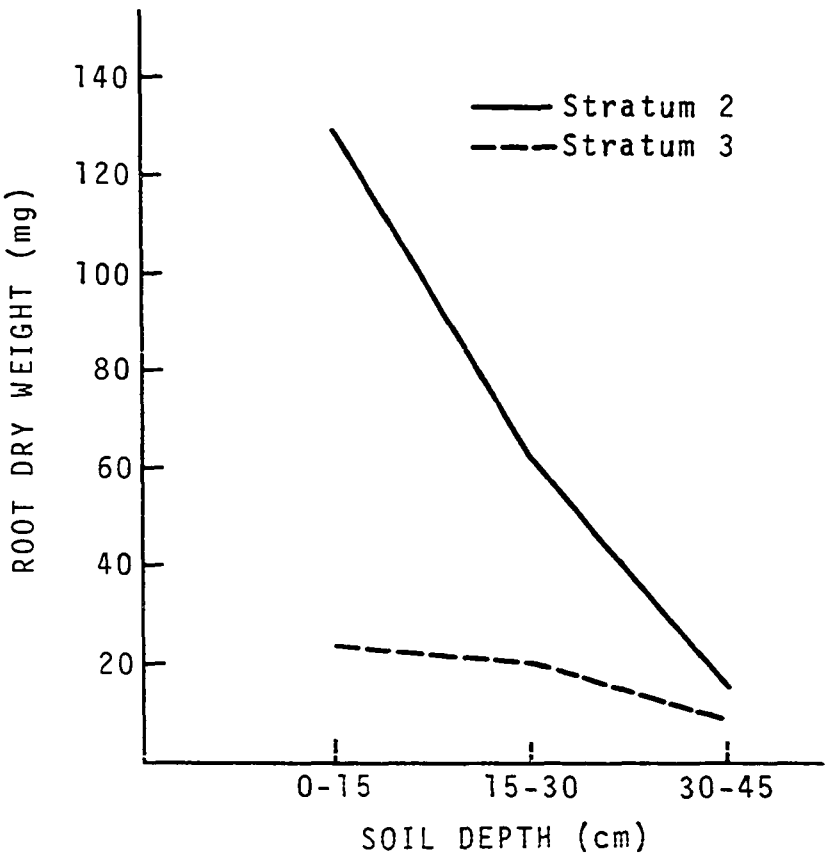


Figure 22. Comparison of root dry weight measured from the soil core for the two strata (distances from the stem) at each soil depth in the third year before coppicing

When densities were compared after coppicing, the values for root weight in response to coppicing showed an increase only at the highest density, but the differences were not significant. In contrast, this was not true of all clones; only the root weights of clones 5377 and 5326 exhibited a large increase at the highest density after coppicing. In addition, clone 5377 showed a large increase in the horizontal distribution of root weight (particularly at the further distance from the stem) while clones 5377, 5323, and 5326 showed increased root weights in the vertical distribution (particularly at the bottom depth).

In this study, the horizontal projection length of roots was not estimated by the previous method (Lee, 1975) because total root members counted from each core were usually 5.4 times larger than the number of roots greater than 1 cm. This was probably due to double counting of some unattached roots as separate units.

DISCUSSION

Coppice Growth Performance from Two Experiments

Coppice growth of hybrid poplars was examined in both controlled environmental condition and field condition. Yields from sprout growth generally declined after coppicing relative to yield before coppicing in both greenhouse and field experiments. Such above ground yields of coppiced trees as leaf surface areas and stem dry weight, however, were much higher than those of uncut trees; for example, leaf surface areas and stem weight were much greater 10 weeks after cutting than those of uncut plants 10 weeks after initial planting in the greenhouse while in the field, those of coppiced trees were higher one year after coppicing than those of uncut trees one year after initial planting. This result was similar to the work of Smith and DeBell (1973) who reported that greater dry weight yields of black cottonwood were obtained from coppice growth than from seedling growth. Furthermore, final leaf areas produced in the field after coppicing were even greater than those of uncut trees in the third year before coppicing. Thus, both greenhouse and field experiments show that growth can be increased via coppice regeneration method.

Growth Performances between Clones

In the greenhouse experiment, the highest top dry weight per tree before coppicing was shown by clone 5328 followed by clones 5323, 5377, 5326, 5321, and 5260 in descending order while the highest total dry weight per tree was shown by clone 5328 followed by clones 5323, 5326, 5377, 5321, and 5260 in descending order (Table 65). Clonal ranks for both top and total dry weight for three years before coppicing in the field were very

Table 65. Populus clonal rankings in field and greenhouse, based on top dry weight per tree before coppicing

Ranks	Field	Greenhouse
1	Clone 5323	Clone 5323
2	Clone 5326	Clone 5377
3	Clone 5377	Clone 5326
4	Clone 5321	Clone 5321

similar; clone 5323 was in first, clone 5326 in second, clone 5377 in third, and clone 5321 in last place (Table 65). Clonal rankings in dry matter production were quite consistent in both experiments. This agreed with the work of Gordon and Promnitz (1976) who reported that early growth differences between hybrid poplar clones in controlled environments resembled those observed after two year's growth in the field.

After coppicing, the highest top and total dry weight per tree were also attained by clone 5328 in the greenhouse and followed by clones 5326, 5323, 5377, 5321, and 5260 in descending order (Table 66). In the field, however, the greatest yield in either top or total dry weight per tree was attained by clone 5323 followed by clones 5377, 5326, and 5321 in descending order (Table 66). Clonal ranks were similar to those shown in the greenhouse except that clone 5326 ranked lower in both top and total dry weights than clones 5323 and 5377. In addition, the largest yield in either stem or whole woody tissue dry weight in the field was shown by clone 5377 and followed by clones 5323, 5326, and 5321 in descending order.

Table 66. Populus clonal rankings in field and greenhouse, based on top dry weight per tree after coppicing

Ranks	Field	Greenhouse
1	Clone 5323	Clone 5326
2	Clone 5377	Clone 5323
3	Clone 5326	Clone 5377
4	Clone 5321	Clone 5321

Thus, the results obtained from the greenhouse experiment can be useful to select clones and to expect growth performance in the field.

In contrast to dry weight yield, clones 5323 and 5321 showed more severe incidence of canker and higher mortality than clones 5377 and 5326 (Table 67). Therefore, clones 5377 and 5326 would be recommended for use of intensive culture system in the field. Also clone 5328 can be recommended, but further study on this clone is needed in the field.

Table 67. Means by densities and by clones for percentage of trees either infected or dead by cankers in Ames, Iowa (1977)

Densities (trees/ha)	Percentage of infected or dead trees	Clones	Percentage of infected or dead trees
5,000	36.7	5326	13.1
10,000	43.1	5377	16.0
15,000	48.4	5323	67.4
		5321	74.4

Effects of Planting Density on Coppice Growth Performance

Planting density influenced the coppice growth at both Ames and Rhinelander plantations. The lowest density (1.41 m x 1.41 m) produced the largest yield on the average tree basis whereas the highest density (0.83 m x 0.83 m) yielded the highest dry weight on the hectare basis. These results were similar to those of various tree species reported by many researchers. For example, Dawson et al. (1976) examined growth yields of the hybrid poplars with three different spacings (0.23 m x 0.23 m, 0.30 m x 0.30 m, and 0.61 m x 0.61 m), and the closest spacing produced the highest yield. Kennedy (1975) compared the coppice yield of sycamore with two planting densities (0.60 x 1.50 m and 1.20 m x 1.50 m), and the highest density also produced the largest yield. Heilman et al. (1972) reported the highest yield of black cottonwood from the closest spacing (0.30 m x 0.30 m) and the lowest yield from the widest spacing (1.22 m x 1.22 m).

Unfortunately, the highest planting density also showed the most severe canker attack and the highest mortality (Table 67). Similar results were reported by Bowersox and Merrill (1976) who found the most narrow spacing to have the greatest incidence of Septoria canker.

Therefore, considering costs for establishment and management, and disease problems, either the lowest (5,000 trees/ha) or the intermediate planting density (10,000 trees/ha) would be recommended as a planting space for intensive culture of hybrid poplars.

Effects of Residual Stand on Sprout Growth

Root dry weight in the field experiment and initial stump volume in the greenhouse experiment were adjusted to examine whether or not those

variables influence the growth following coppicing. After adjustment for size of residual stand, most coppice growth differences between clones were markedly reduced in both greenhouse and field experiments. Growth differences between locations were also remarkably reduced in the field studies, furthermore, significant differences between planting densities were removed for all coppice growth variables. Thus, characteristics of residual stand, roots or stumps, markedly affect coppice growth. These results were similar to those reported by Sander (1971) with oak and by Farrar (1975) with longleaf pine. Sander (1971) found the largest stems of advance reproduction to produce the fastest sprout growth and highest yield, and Farrar (1975) observed that sprouting was strongly related to initial plant size.

In addition, a more physiological study on the relationship between residual stand and sprout growth is necessary to find the major factors affecting sprout growth.

Effects of Coppicing on Root Growth and Distribution

Coppicing markedly affected the growth and distribution of roots; for example, dry weight and numbers of roots showed a decrease as compared to those shown before coppicing. When locations were compared, this trend was evident only at the Ames plot, however, root dry weight at the Rhinelander plot showed rather an increase. Also, roots were distributed deeply at the Ames plot while roots were shallowly distributed at the Rhinelander plot. This increase and shallow distribution of roots at the Rhinelander plot are probably due to frequent irrigation.

Decreasing trends were also true of the lowest and intermediate planting densities, but an increase in root weight was found at the highest density.

When clones were examined, clone 5321 showed a large decrease in all root variables after coppicing whereas clones 5377, 5323, and 5326 exhibited an increase in root weight. Particularly, clone 5377 showed an increase in both horizontal and vertical distribution of roots while clones 5323 and 5326 showed an increase in the vertical distribution of roots.

The decreased root growth shown after coppicing was mainly due to a lack of carbohydrates and growth hormones from the top. However, the increase in root weight shown after coppicing may be accounted for by genetic traits because root growth after removal of shoots is controlled by either materials stored in the root system or materials produced by the root tip itself.

Thus, a mixed planting of clone 5377 with clone 5326 would be recommended for better utilization of soil spaces for root growth.

SUMMARY AND CONCLUSIONS

Summary

The objectives of this study were to examine the coppice growth performance of hybrid poplars in the greenhouse situation, which gives useful information for early selection and prediction of coppice regeneration ability and growth performance in the field, to evaluate growth responses to coppicing in the field as affected by different locations, clones, and planting densities, and to determine important growth variables for maximum total coppice production.

In the greenhouse, six hybrid poplar clones, 5377, 5321, 5323, 5326, 5328, and 5260, were selected, planted individually in pots, coppiced at the end of 14 weeks and harvested at the end of 24 weeks. Comparisons were made for such growth variables as leaf surface areas, top and root dry weight, and height growth. In addition, effects of initial stump size on coppice growth performance were examined.

In the field, four clones, 5377, 5321, 5323, and 5326, were selected, planted at three different densities (5,000, 10,000, 15,000 trees/ha) at two locations (Ames, Iowa, and Rhinelander, Wisconsin), coppiced at the end of the third year, and harvested at the end of the fourth year.

Leaf surface areas, stem, top, stump, and root dry weight were compared for differences between locations, between densities, and between clones. In addition, effects of planting density and coppicing on root growth and distribution were examined. Finally, the effects of root size (dry weight) on coppice growth performance were studied.

Conclusions

1. Both greenhouse and field experiments show that yield increase can be made via the coppice regeneration method.

2. Coppice growth performance in the greenhouse can be used, to some extent, to predict growth performance in the field.

3. Growth both before and after coppicing was better at the Ames plantation than at the Rhinelander plantation, due to longer growing season, higher temperature, and more fertile soil characteristics at the Ames plantation.

4. In the greenhouse, clonal ranks with respect to leaf surface areas and dry matter production after coppicing as follows: the highest yield was attained by clone 5328 followed by clones 5326, 5323, 5377, 5321, and 5260 in descending order. In terms of sprouting ability, however, clones 5328 and 5260 were the best. In the field, the highest yield in either top or total dry weight, whether based on the average tree or on the hectare, was shown by clone 5323 and followed by clones 5377, 5326, and 5321 in descending order. With respect to stem, root, or whole woody tissue dry weight, clone 5377 was the best, clone 5323 second, clone 5326 third, and clone 5321 poorest.

5. Clones 5377, 5321, and 5326 showed a decrease in most coppice growth variables with increasing planting density, but clone 5323 showed a different trend. In such coppice growth variables as sprout number, top dry weight, and basal area and dry weight of stumps, it showed a decrease from the lowest to the intermediate density but showed an increase at the highest density.

6. With respect to dry matter production both before and after coppicing, the lowest planting density (5,000 trees/ha) was the best on the average tree basis whereas the highest density (15,000 trees/ha) was the best on the hectare basis.

7. Characteristics of residual stand (stumps and roots) markedly influenced the coppice growth performance; initial stump volume appears to be a more important factor affecting coppice growth in the greenhouse than the volume of the root systems while root dry weight appears to strongly affect coppice growth in the field. After adjustment for root system size, coppice growth differences between locations and between clones were markedly reduced, and those between planting densities were removed for all growth variables. However, a more complete study on the root and stump physiology relating to coppice growth is needed.

8. Clones 5377 and 5326 tended to produce more leaves initially but lose more leaves during the growing season whereas clones 5323 and 5321 tended to retain leaves longer and showed greater final leaf surface areas.

9. Most root growth variables showed a decreasing trend with both increasing distance from the tree and increasing soil depth before and after coppicing. This was particularly true of all planting densities before coppicing. Clone 5377 showed increased growth in both horizontal and vertical distribution of root weights after coppicing while clones 5323 and 5326 exhibited increased growth in the vertical distribution. Significant differences between clones in both horizontal and vertical distribution of root weights indicate that there is considerable genetic control over root development in Populus.

RECOMMENDATIONS

1. Considering disease problems, clones 5377 and 5326 are recommended for use in intensive culture system rather than clones 5321 and 5323. In addition, field growth test for clone 5328 is suggested to prove it to be a good genotype in terms of dry matter accumulation.

2. Considering costs for establishment, management, and disease problems, either the intermediate (10,000 trees/ha) or the lowest planting density (5,000 trees/ha) is recommended for use in intensive culture system.

3. A mixed planting of clone 5377, which appears to have horizontally oriented root systems, with clone 5326, which appears to have a predominantly vertical root system, would be recommended to reduce competition between the trees and also to allow a better utilization of soil water and nutrients.

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ACKNOWLEDGMENTS

I would like to express my sincere appreciation to Dr. John C. Gordon and Dr. Lawrence C. Promnitz for suggesting this research, providing their guidance, advice, and helpful suggestions, and reviewing this manuscript.

I also wish to thank Dr. George W. Thomson, all Forestry staffs and friends who provided a great amount of assistance in the preparation of this manuscript.

I am grateful to other members of the examining committee, Dr. Paul N. Hinz for his help in statistical analysis, Dr. Dwight W. Bensend, Dr. Harold S. McNabb, Jr., and Dr. Richard B. Hall for their valuable suggestions and contributions to my work.

I appreciate the help of Mr. David H. Dawson and Dr. J. Zavitkovski for providing assistance in measurement and harvest at Rhinelander, Wisconsin, and the help of Mr. Rich Faltonson in preparing plant materials and work in the greenhouse and field.

Finally, I would like to express my deepest appreciation to my wife, Young Sook, for helping me with much of the greenhose and field work and for her patience and understanding during my graduate student life, and to all my family and relatives for their encouragement and prayer.