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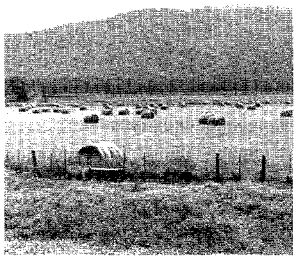

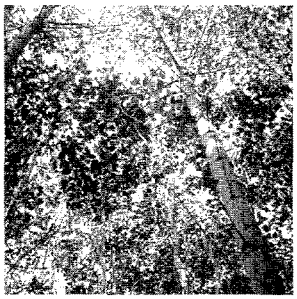

INCREASING THE PRODUCTIVITY OF SHORT-ROTATION *POPULUS* PLANTATIONS

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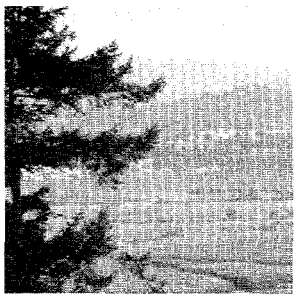

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USDA Forest Service
Pacific Northwest Research Station
Olympia, Washington

Prepared 1997

Research supported by
Biofuels System Division
Office of Transportation Technologies
Activity No. EB 52 03 00 0

for
Bioenergy Feedstock Development Program
OAK RIDGE NATIONAL LABORATORY
Oak Ridge, Tennessee 37831-6422
managed by
LOCKHEED MARTIN ENERGY RESEARCH CORP.
for the
U. S. DEPARTMENT OF ENERGY
under contract DE-AC05-96OR22464

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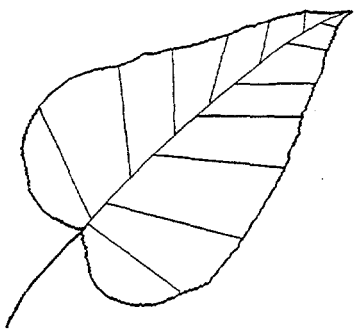
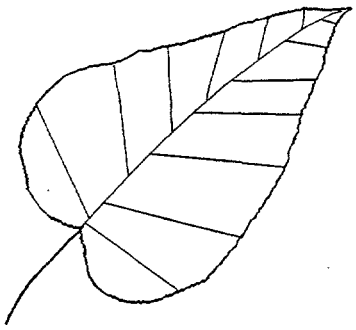


Chapter 1
Introduction

This final report represents the culmination of eight years of biological research devoted to increasing the productivity of short rotation plantations of *Populus trichocarpa* and *Populus* hybrids in the Pacific Northwest. Studies described herein provide an understanding of tree growth, stand development and biomass yield at various spacings, and how patterns thereof differ by *Populus* clone in monoclonal and polyclonal plantings. Also included is some information about factors related to wind damage in *Populus* plantings, use of leaf size as a predictor of growth potential, and approaches for estimating tree and stand biomass and biomass growth.

The work was accomplished in three research plantations, all established cooperatively with the Washington State Department of Natural Resources (DNR) and located at the DNR Tree Improvement Center near Olympia. The first plantation was established in Spring 1986 to evaluate the highly touted "woodgrass" concept and compare it with more conventional short-rotation management regimes, using two *Populus* hybrid clones planted at five spacings. Besides providing scientific data to resolve the politicized "wood-grass" dispute, this plantation has furnished excellent data on stand dynamics and woody biomass yield. A second plantation was established at the same time; groups of trees therein received two levels of irrigation and different amounts of four fertilizer amendments, resulting in microsites with diverse moisture and nutrient conditions. Individual tree and leaf characteristics were assessed over the wide range of growth performance to identify traits useful as predictors of growth potential over very different growing environments. The third plantation was established in Spring 1990 with four clones planted in pure and mixed blocks at three spacings; this plantation provided information on yields from alternate strategies of clonal deployment and on stand development patterns by clone and clonal mix. A storm with gale-force winds hit the study area on January 20, 1993; the latter plantation sustained considerable damage and thus provided an opportunity to assess tree and stand characteristics associated with susceptibility to wind toppling of young *Populus*.

The next six chapters (Chapters 2 through 7) of this report provide detailed methods, results, and interpretations of these topics. Chapter 8 describes techniques used to develop biomass equations and their application to assess the dynamics of stand biomass growth and yield over time and in response to various clonal and spacing treatments. These seven chapters were developed as "stand-alone" manuscripts that have been published or accepted for publication in refereed journals. A final chapter (Chapter 9) summarizes and discusses major findings about operational implementation and the need for or potential usefulness of additional research and development.



Chapter 2

Growing *Populus* Biomass: Comparison of Woodgrass Versus Wider-Spaced Short-Rotation Systems[1]

Dean S. DeBell, Gary W. Clendenen, and John C. Zasada

Abstract: Growth and yield of *Populus* were examined in a 5-year test of five spacing-harvest regimes in western Washington. Two hybrid clones (D-01 and H-11) were planted at two woodgrass spacings (0.18- and 0.3-m) and three wider spacings (0.5-, 1.0-, and 2.0-m). All treatments were replicated three times in a randomized block design; all plots were fertilized, irrigated, and weeded uniformly. Mean annual harvest yields in the woodgrass treatments did not differ significantly between the two clones (D-01 and H-11) or two spacings (0.18- and 0.3-m), averaging 6.4 to 7.0 Mg ha^{-1} (tonnes ha^{-1}) over the 5-year period. The highest yield in woodgrass treatments was produced in the second year (first year of coppice), and it declined thereafter. Cumulative growth in the wider spacings was significantly greater than in the two woodgrass spacings. Per hectare yields of clone H-11 in the wider spacings at age 5 were two to three times greater than cumulative yields obtained with annually cut woodgrass, averaging 15.7 to 18.8 Mg ha^{-1} yr^{-1}. Fifth-year increments in all wider spacings (0.5-, 1.0-, and 2.0-m) of clone H-11 exceeded 30 Mg ha^{-1}. Yields of clone D-01 in the wider spacings ranged from 8.1 to 10.9 Mg ha^{-1} yr^{-1} and thus were also substantially greater than cumulative yields of woodgrass. We conclude that annually harvested woodgrass shows little promise as a viable system for growing *Populus* for biomass. On the other hand, yields in the wider spacings with a longer harvest cycle were substantially higher than previously expected, especially for clone H-11. Thus, possibilities for application of the wide-spaced regimes and longer cutting cycles appear promising.

Keywords: Poplar, cottonwood, coppice, spacing, yields, bioenergy, stand density, intensive culture

Farm production of woody biomass was proposed more than two decades ago in the southeastern United States (McAlpine and others 1966; Herrick and Brown 1967). The concept, called "silage sycamore" by the proponents, included establishing rapid-growing trees at dense spacings, applying intensive cultural practices, harvesting in cycles of 10 years or less, regenerating subsequent crops via sprouts or coppice arising from stumps, and using a high degree of mechanization. Trials were soon initiated elsewhere in the country (Heilman and others 1972; Dawson 1976; Geyer and others 1985), with emphasis on *Populus* species and hybrids. During the first energy crisis, this short-rotation approach was suggested as a means to produce wood for energy (Szego and Kemp 1987). Subsequently, considerable research was conducted on biomass plantations for fiber and energy, much of it funded by the Short Rotation Woody Crops Program (now the Biofuels Feedstock Development Program) of the U.S. Department of Energy. Other public agencies and utilities have also funded or established projects, particularly in the northeastern and north central states. In general, such work indicated that spacings should be wider and harvest cycles longer than those evaluated in many of the early trials. Stand densities of 2500 to 4000 trees per hectare (i.e., square spacings of 2.0 to 1.6 m) and rotations of 5 to 8 years are now perceived as optimum for bioenergy crops (Ranney and others 1987). Other ongoing research suggests that even wider spacings and longer rotations may be preferable in some situations and for some objectives.

[1] Published in *Biomass and Bioenergy* 4 (5): 305-313 (1993).

In the late 1970's and early 1980's, however, a nurseryman in Oregon proposed a radical departure from the above trends in woody biomass farming (Dula 1984). The proposed system entailed establishing a *Populus* hybrid (clone D-01) at densities of 100 thousand to 600 thousand rootstocks per hectare with annual harvests of coppice. Biomass yields were purported to exceed 100 Mg ha^{-1} (tonnes ha^{-1}) annually. Economic analyses performed by coupling such yield data with estimated costs suggested that the system — dubbed "wood-grass" — compared favorably with other short-rotation density regimes (Vyas and Shen 1982). Considerable interest developed in the energy conversion community; some political representatives and agency administrators also became intrigued with the concept. Some forest biologists, however, remained skeptical. Clearly, a scientific evaluation of the woodgrass concept was needed. Our study compares two *Populus* hybrids (D-01 and H-11) at five square spacings — ranging from two woodgrass spacings (0.18 and 0.30 m) to one approaching a conventional pulpwood spacing (2.0 m). This report describes growth and yield of the plantings over a 5-year period.

METHODS

Our experiment was established in cooperation with the Washington State Department of Natural Resources at the Tree Improvement Center, located 12 km east of Olympia, Washington. Climate is mild with an average growing season of 190 frost-free days and a mean July temperature of 16° C. Precipitation averages more than 1000 mm per year, falling mostly as rain from October through May; summers are periodically dry. The land was previously farmed for strawberry and hay crops, and topography is relatively level. The soil is Nisqually loamy fine sand (a sandy, mixed, mesic Pachic Xerumbrept); it is a deep, somewhat excessively drained, medium acid (pH 5.6) soil formed in glacial outwash. The land was prepared for planting by plowing and disking in winter 1985-86.

The study was established as a factorial design with two *Populus* clones and five spacing treatments, replicated in three blocks. One clone, D-01, was a *Populus* hybrid (taxonomic identity unknown, but suspected to be either *P. trichocarpa* x *P. nigra* or *P. trichocarpa* x *P. angustifolia)* developed originall at University of Idaho and subsequently selected from a Canadian planting by Dula's Nursery of Canby, Oregon (Dula 1984). The other clone, H-11, was a *P. trichocarpa* x *P. deltoides* (11-11) hybrid developed and tested by University of Washington and Washington State University (Heilman and Stettler 1985). Square spacings (m by m) were 0.18, 0.3, 0.5, 1.0, and 2.0 m. Equivalent trees per hectare were ca. 310,000; 110,000; 40,000; 10,000; and 2,500. The first two spacings (0.18 and 0.3 m) were woodgrass treatments recommended by Dula [i.e., three and one plant(s) per square foot, respectively]. Size of treatment plots varied with spacing; all plots were sufficiently large to provide at least 100 interior measurement trees (400 trees for woodgrass harvests) and a border approximately one-half as wide as the projected height of trees at harvest. Thus, trees spaced at 2.0 m were grown in the largest plots (32 m by 32 m) and plants in the 0.18-m woodgrass treatments were grown in the smallest plots (~ 10 m by 10 m). Clone-spacing treatments were assigned randomly within each replicate block, with one minor stipulation. The annually harvested woodgrass plots were always assigned to outside positions in the block, so as to minimize future shading as well as root competition from trees in wider spacings.

Both clones were planted by hand as unrooted, hardwood cuttings in late April 1986. All cuttings were 30 cm long and had a minimum upper diameter of 1 cm; they were planted 20 cm deep with at least two healthy axillary buds remaining above ground.

Supplemental nutrients and water were provided uniformly in plots of all treatments. A pre-planting application of fertilizer (16-16-16) provided the equivalent of 100 kg per hectare each of nitrogen, phosphorus, and potassium. Additional nitrogen fertilizer (ammonium nitrate) was applied at 100 Kg N per hectare in May 1988. Plots were irrigated throughout each

summer by a drip system; amounts applied were equivalent to 400-500 mm per growing season. All plots were kept free of weeds during the first year by tilling and hoeing; in the second and third year, developing weed patches were controlled by spot applications of herbicides (oxyfluorfen, pronamide, and glyphosate) and hoeing. Little such work, however, was needed after the second year. At the end of the first year, all positions occupied by dead trees were replanted with unrooted cuttings; also, any secondary shoots on plants in the wider spacings (0.5, 1.0, and 2.0 m) were removed, resulting in stands composed solely of single-stemmed trees.

Survival, height, and basal diameter were recorded at the end of each of 5 growing seasons on the central 100 trees in each plot. Number of living and dead sprouts per rootstock were also tallied after the second and subsequent growing seasons in woodgrass plots. Yield data for the woodgrass treatments were based on annual harvests after leaffall of 400 trees in the center of each plot. Moisture contents were determined on subsamples to convert fresh weight to oven-dry (105° C) weight. Yields for the wider-spaced plots were estimated from oven-dry biomass component equations applied to diameter and height measurements of the trees. The equations were developed via destructive sampling of trees representative of the spectrum of sizes in each spacing of each clone. Equations of the form Ln(Y) = f (diameter, spacing, height, and age) were fit independently for each clone. R^2 ranged from 0.972 for branch weight of D-01 to 0.997 for stem weight of H-11. Stem weights and branch weights were estimated by separate equations and summed to provide above-ground, woody dry biomass. Above-ground woody biomass estimates for all trees on each plot were summed, and the resulting plot sums were expanded by appropriate multipliers to provide yield per hectare.

Plot means were calculated for each variable and displayed in tables or figures to illustrate trends in development of the plantings. All data have been analyzed by standard ANOVA techniques, and treatment means were compared by Bonferroni's test using $P \leq 0.05$ as the level of significance.

RESULTS AND DISCUSSION

Establishment year (general)

Survival at the end of the first growing season averaged 96% for D-01 and 98% for H-11. Average heights for D-01 and H-11 were 1.4 and 1.8 m, respectively. In the two woodgrass spacings, mean heights of the two clones were very similar, averaging 1.3 m. As spacing widened from 0.18 to 1.0 m, mean height of both clones increased to 2.3 m for H-11 and 1.7 for D-01. Trees of both clones, however, were shorter at 2.0-m than at 1.0-m spacing. Mean heights for the clones at spacings of 0.5, 1.0, and 2.0 m differed by 50 cm or more. Effects of spacing on basal diameter were of greater magnitude than effects on height. Both clones had similar diameters at the 0.18- and 0.3-m spacings (6 mm and 8 mm, respectively); mean diameter of both clones was greater at wider spacings and response to increased spacing was greater for H-11. Diameters of the latter clone were nearly four times greater at the 2.0-m spacing (i.e., 22 mm) than at 0.18-m spacing. Patterns of leaf, bud, and branch production also differed markedly between clones and among spacings during the first growing season. Average distances between leaves (hence, axillary buds) were greater in H-11 (about 4 cm) than in D-01 (about 3 cm). Moreover, H-11 exhibited sylleptic growth; that is, branches developed from axillary buds during the same growing season in which the buds formed. The proportion of buds producing sylleptic branches ranged from none in the densest woodgrass spacing to 31% in the widest (2.0-m) spacing. Growth in D-01 was predominantly proleptic with axillary buds remaining dormant until the next growing season; no buds produced sylleptic branches in the two woodgrass spacings and only 3.3% and 2.0% produced sylleptic branches in the 1.0-m and 2.0-m spacings.

The substantially reduced first-year growth in the woodgrass spacings as compared with growth at wider spacings indicated that competition among plants was sufficient to depress individual tree growth. Contrasted with trees in the 1.0-m spacing, trees in the densest

woodgrass spacing averaged 41% shorter in height and 71% smaller in basal diameter. Moreover, leaf area per tree in the densest spacing was less than one-fifth of that in the 1.0-m spacing. Because of the intense competition in the woodgrass plots, and, in accord with Dula's (1984) procedures, we harvested trees in all woodgrass treatments at the end of the growing season to establish coppice.

The growth patterns, morphological traits, and competitive stresses observed in the establishment year were harbingers of major differences in performance among clones and spacings in subsequent years.

Woodgrass

Yields from the first (non-coppice) harvest of the woodgrass spacings and those of four subsequent (true coppice) harvests are shown in Table 1. First-year yields of the two clones were nearly identical, averaging 3.5 Mg ha^{-1}. Dry-matter production averaged 4.0 Mg ha^{-1} in the 0.18-m spacing, and 3.0 Mg ha^{-1} in the 0.3-m spacing, but differences were not statistically significant ($p = 0.09$).

In April following winter harvest, vigorous coppice developed on the stumps, and growth was excellent throughout the season. Yields from the second cutting were more than double those of the first cutting, and ranged from 7.7 to 9.6 Mg ha^{-1} (Table 1). Although yields did not vary significantly at $p < 0.05$, production tended to be greater for clone D-01 than for H-11 ($p = 0.16$, 9.1 vs. 8.0 Mg ha^{-1}) and in the 0.18-m than in the 0.3-m spacing ($p = 0.31$, 9.0 vs. 8.2 Mg ha^{-1}).

Table 1. Effects of clone and spacing on dry yield of woodgrass during 5 years after planting.*

	Clone D-01 Spacing		Clone H-11 Spacing	
Year	0.18-m	0.30-m	0.18-m	0.30-m
	Mg ha-1			
1	3.9	3.1	4.1	3.0
2	9.6	8.7	8.3	7.7
3	8.6	7.9	8.3	7.5
4	7.0	5.0	7.8	7.3
5	5.9	7.3	5.9	6.6
Total	35.0	32.0	34.4	32.1
Mean	7.0	6.4	6.9	6.4

*Above-ground, leafless biomass dried to constant weight at 105° C.

Coppice development on stumps after the second harvest (or first coppice harvest) was also vigorous, but it became increasingly less so with each successive harvest. Third- and fourth-year yields continued to be somewhat greater ($p = 0.35$ and $p = 0.17$, respectively) in the 0.18-m than in the 0.3-m woodgrass spacing (Table 1). Fourth-year yields of H-11 were significantly greater ($p = 0.02$) than those of D-01 (7.6 vs. 5.7 Mg ha^{-1}). Production was declining, however, and by the fifth harvest, average yield was about 25% lower than that obtained in the second harvest. The reductions in yield (5th- versus 2nd-year) were greater for clone D-01 (-28%) and in the densest (0.18-m) spacing (-34%). By the fifth year, annual production in the 0.3-m spacing was somewhat, but not significantly, greater ($p = 0.08$) than that at the 0.18-m spacing.

Increased biomass production in the second harvest and patterns of production in subsequent harvests were associated with sprouting characteristics—number of sprouts per rootstock, size of dominant sprouts on the rootstocks, and number of rootstocks surviving (Table 2, Fig. 1). The tendency for clone D-01 to produce higher yield per hectare in the second harvest was related mostly to dramatic differences between the clones in the total number of sprouts initiated ($p < 0.01$) and the number surviving at harvest ($p < 0.01$) (Table 2). Averaged across spacings, D-01 produced 7.4 sprouts per rootstock whereas H-11 had only 4.6.

Clonal differences in total sprout production may be related in part to differences in patterns of bud and branch production during the establishment and subsequent years. Numbers of axillary buds per centimeter were about one-third greater in D-01 than in H-11; also, a larger percentage of the H-11 buds formed sylleptic branches. The combined effect of these two growth characteristics resulted in greater numbers of vigorous buds (axillary and suppressed) on the rootstocks of D-01 than on H-11; such buds play a significant role in sprout development. The number of sprouts initiated increased

Table 2. Effects of clone and spacing on initiation (total number) and survival (living at harvest) of sprouts during each growing season.

Clone	Spacing	Sprout variable	Year 1	2	3	4	5
			- Sprouts per rootstock* -				
D-01	0.18 m	Total	1	5	8	12	9
		Living	1	3	2	4	4
	0.30 m	Total	1	10	18	22	20
		Living	1	7	9	12	8
H-11	0.18 m	Total	1	4	4	5	6
		Living	1	1	1	1	2
	0.30 m	Total	1	5	5	8	8
		Living	1	1	1	2	2

* Sprout is used in a general sense: nearly all stems developed from axillary buds during year 1; most stems developed from suppressed buds during subsequent years, but some developed from axillary buds.

in the third and fourth year, more so on D-01 than on H-11. In number of sprouts living at harvest (and thus included in yield), even greater differences existed between the clones ($p < 0.01$). Such differences were especially evident in the 0.3-m spacing where clone D-01 averaged 7 to 12 living sprouts per rootstock each year and clone H-11 had only 1 or 2.

Rootstock survival also accounted for some of the trends in sprout development and thus in yield. Survival declined overall, but the mortality differed greatly by clone ($p < 0.01$) and spacing ($p < 0.01$) (Fig. 1a). By year 5, only 3% of clone D-01 rootstocks planted at 0.3-m spacing had died; rootstock mortality increased to 23%, however, at 0.18-m spacing. Such losses were much greater for clone H-11; more than two-thirds of the rootstocks planted at 0.18-m and about one-half of those planted at 0.3-m were dead after 5 years.

These mortality losses were accompanied by enhanced growth of sprouts on surviving rootstocks of clone H-11 and similar or slightly declining growth on surviving D-01 rootstocks. Heights of dominant sprouts were rather similar for the two clones in the first harvest, and both increased at the second harvest (Fig. 1b). Thereafter, height growth of clone H-11 tended to increase with successive harvests, and growth of clone D-01 remained constant or declined. The major aberration in the latter general trend is an improvement of growth of clone D-01 spaced at 0.3-m in the fifth year, when it equaled that attained in the second season. Diameter growth of dominant sprouts followed the same general pattern as height growth, including the exception (Fig. 1c). Overall, the clonal differences in sprout growth tended to balance differences in root stock survival, leading to similar production.

Total 5-year production in the woodgrass treatments ranged from 32.0 to 35.0 Mg ha^{-1} (Table 1). All treatments attained their highest current annual yield in the second harvest (first coppice harvest). Mean annual increment, however, peaked in both spacings of clone D-01 in the third year, and in both spacings of clone H-11 in the fourth year. At age 5, mean annual increment ranged from 6.4 to 7.0 Mg ha^{-1}. Although annual production averaged about 0.5 Mg ha^{-1} more in the denser (0.18-m) spacing, yields of the two spacings were not significantly different ($p = 0.16$). Cumulative 5-year yields of the two clones were essentially equal, averaging 33.4 Mg ha^{-1}.

Wider Spacings

Tree growth in the wider spacings (0.5-, 1.0-, and 2.0-m) also accelerated during the second year, and even more so in the third year in some of the wider spacings (Fig. 2). Height and diameter growth slowed in all clonal and spacing treatments in the fourth year. At age 5, trees of clone H-11 were substantially larger in height (32%, $p < 0.01$) and diameter (14%, $p < 0.01$), and greater in woody biomass (91%, $p < 0.01$) than those of clone D-01 (Fig. 2). Tree size increased with increasing spacing, with differences becoming greater with time (Fig. 2). Clonal and spacing differences were also observed in branch retention; clone D-01 retained its branches much longer than clone H-11, and trees of both clones retained their branches longer in the wider spacings.

Effects of spacing and clone × spacing interactions were evident beginning in the second growing season (Fig. 2). In the first two seasons, diameter growth of both clones increased with spacing, and the improvement in growth was substantially greater for clone H-11. By the third year, however, height and diameter increment

of the two clones were rather similar. During the fifth year, height and diameter increment of clone D-01 was equal to or better than clone H-11 in the widest two spacings. This change in relative clonal performance appears related primarily to differences in previous growth rate and resulting changes in intensity of competition in the plots. Clone H-11 has superior growth potential, but the realization of that potential is dependent upon adequate growing space and other growth factors. During years 4 and 5, competition intensified greatly; because of past

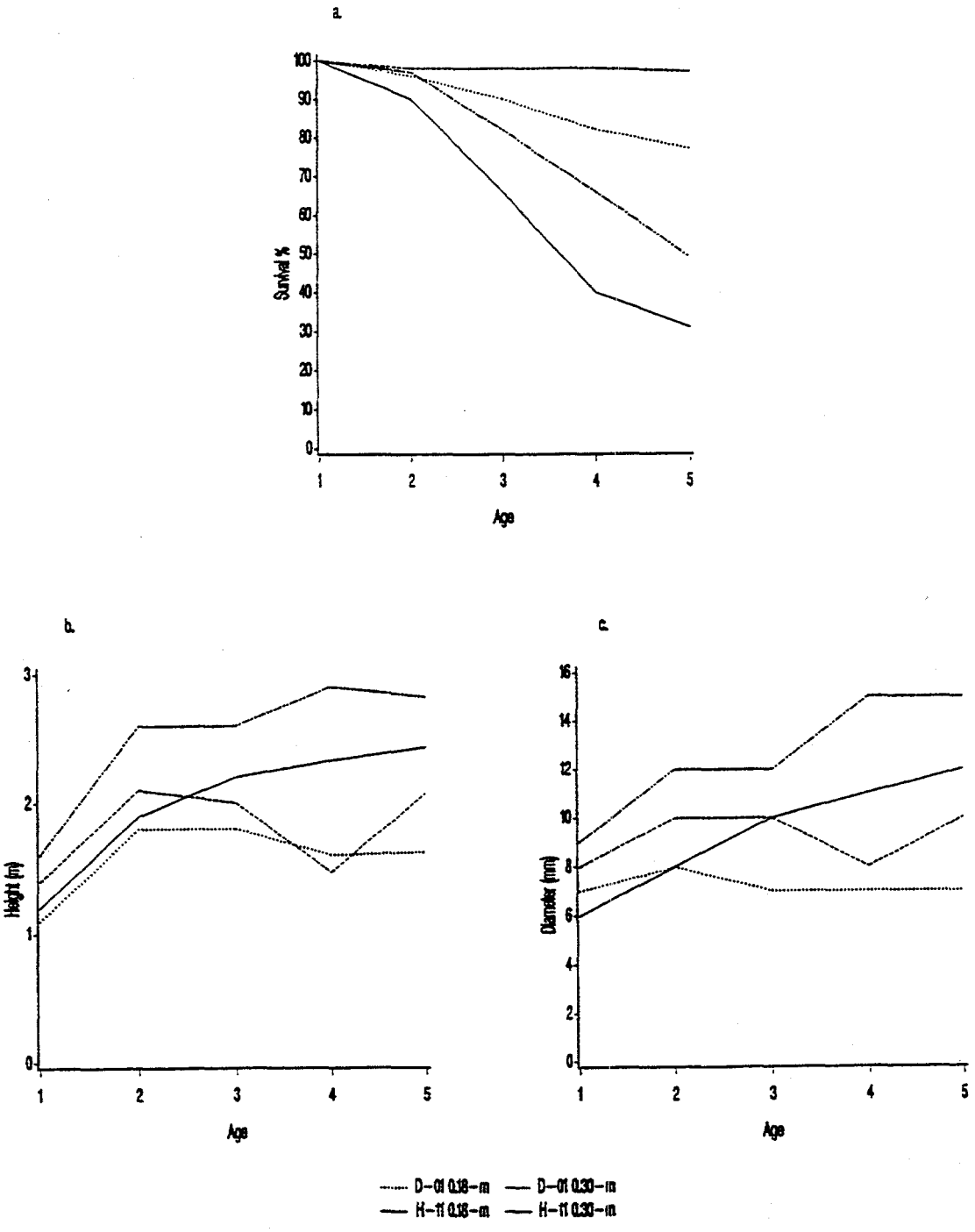


Figure 1. Cumulative five-year a) survival of rootstocks, and b) height and c) diameter of tallest sprout of two *Populus* clones (D-01 and H-11) in woodgrass.

growth trends, trees were larger and competition was greater in plots of clone H-11. Survival remained at 100% in all spacings of clone D-01, but 11% and 2% of the trees in 0.5- and 1.0-m spacings, respectively, of clone H-11 died and many more were suppressed. Even the 2.0-m spacing provided less than adequate growing space for maximum individual tree growth at this size and age, as indicated by our observations of superior growth of trees in the border (non-measured) rows of the plots.

Woody biomass accumulation per tree did not decline as did height and diameter growth (Fig. 2c). Mean tree woody biomass continued to increase substantially with spacing, and at age 5 was about 12 times greater in the 2.0-m spacing than in the 0.5-m spacing. As a result, biomass accumulation per hectare was much more similar among spacings (Fig. 3). Biomass accumulations in the 0.5-m and 1.0-m spacings are essentially equal, with those in the 2.0-m spacing being about 25% lower for clone D-01 and 16% lower for H-11. Relative amounts of stems and branches differed greatly by clone and spacing ($p < 0.01$); the proportion of woody biomass comprised of branches ranged from 5% in the 0.5-m spacing of clone H-11 to 28% in the 2.0-m spacing of clone D-01. Branch weights in the two densest spacings also differed significantly ($p < 0.01$) by clone, averaging 8.0 and 5.7 Mg ha^{-1} for clone D-01 and clone H-11, respectively. At 2.0-m spacing, however, branch biomass of the two clones was nearly identical (11.3 and 11.4 Mg ha^{-1}).

Woodgrass vs. Wider Spacings

Cumulative 5-year woody biomass production is shown in Figure 3 for all treatments. Yields for woodgrass spacings (0.18- and 0.3-m) include live woody biomass from five harvests; values for the 0.5-, 1.0-, and 2.0-m spacings represent estimates of live woody biomass standing after each growing season. Production increased in the woodgrass treatments with the second (coppice) harvest; yields in subsequent harvests tended to be equal to or lower than those of the second harvest. Cumulative yields for woodgrass over the 5-year period were 32 to 35 Mg ha^{-1}. Woody biomass production was significantly greater ($p < 0.01$) in the wider spacings than in the woodgrass spacings, regardless of clone. Cumulative yield of the *least* productive treatment in the wider spacings (clone D-01 at 2.0-m) was 41 Mg ha^{-1}. Yields of that clone in the 0.5- and 1.0-m spacing averaged 55 Mg ha^{-1}, or 50 to 60% greater than woodgrass yields. Cumulative yields of clone H-11 at the three wider spacings were two to three times greater than those of woodgrass treatments, ranging from 78 to 94 Mg ha^{-1}.

In terms of mean annual increment, production of woodgrass over the 5-year period was similar for both spacings and both clones—6.4 to 7.0 Mg ha^{-1}. Mean annual production of clone D-01 in the wider spacings ranged from 8.1 to 10.9 Mg ha^{-1}, and mean annual production of clone H-11 was from 15.7 to 18.8 Mg ha^{-1}. For years 3 to 5, annual woody biomass accumulation in the wider spacings of clone H-11 averaged nearly 25 Mg ha^{-1} per year; fifth-year increment in all three spacings (0.5-, 1.0- and 2.0-m) exceeded 30 Mg ha^{-1}. Current annual increment of clone H-11 did not decline; thus, mean annual production in the wider spacings of this clone would likely increase for at least another 2 to 3 years. Moreover, cumulative production in the widest (2.0-m) spacings of both clones presumably would approach that in the 0.5- and 1.0-m spacings.

IMPLICATIONS AND CONCLUSIONS

General plantation performance

Growth and development of trees and stands during the 5-year period of this study were excellent. Height and diameter were equal to or greater than growth for comparable spacings at other locations in the Pacific Northwest. This successful performance presumably resulted from a favorable irrigation and fertilizer regime as well as excellent weed control imposed uniformly on all treatments.

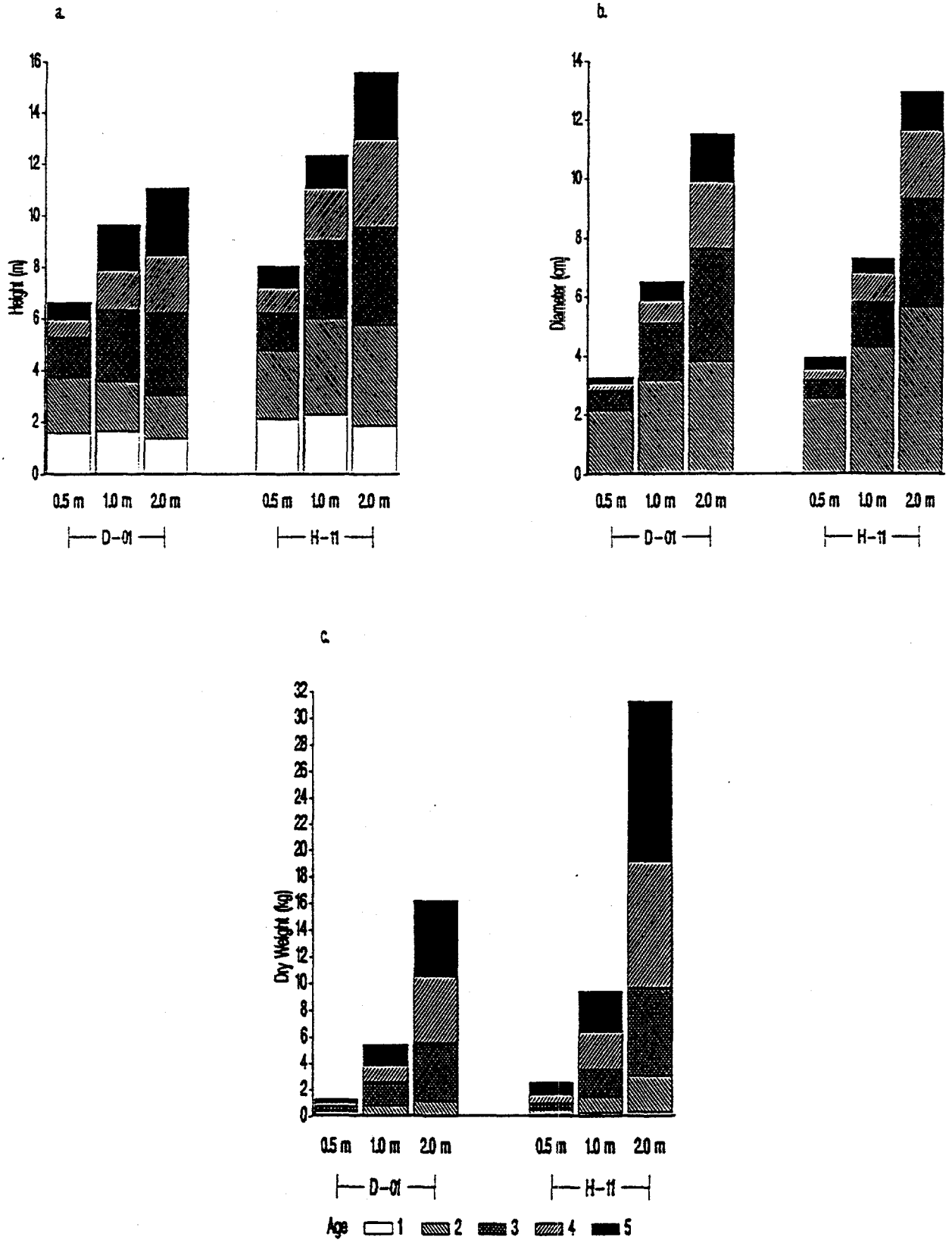


Figure 2. Cumulative five-year a) height growth, b) diameter growth, and c) mean tree yield growth of two *Populus* clones (D-01 and H-11) in wider-spaced treatments.

Comparison of woodgrass yields

Because interest in the woodgrass concept was stimulated by the promise of much higher yields than had been attained with more conventional culture, it is appropriate to compare our experiment yields with purported yields. To make such a comparison, one must first place the yields suggested by Dula (1984) or Vyas and Shen (1982) on a common basis with those determined in our study. The report by Dula (1984) suggests that *at least* 112 wet Mg ha^{-1} (50 wet tons per acre) per year of total aboveground yield (including leaves) can be expected. His sample contained 37% leaves; thus, stems and branches weighed 71 Mg. Moisture content of the stems and branches was 71%; therefore, dry woody biomass weighed about 20 Mg. Dula's yield was measured in a nursery environment in which long, narrow beds occupied only two-thirds of the total land dedicated to woodgrass production. To be comparable to "solid" plantings, which occupy the total land area, the woodgrass yield should therefore be reduced by one-third. Thus, the woodgrass yield indicated by Dula is equivalent to about 14 Mg of dry woody biomass per hectare per year. Our best coppice yields (i.e., the second harvest) were about 9 to 10 Mg for D-01 and about 8 Mg for H-11, and thereafter declined. It is possible, however, that other clones and other locations may lead to somewhat higher annual yields.

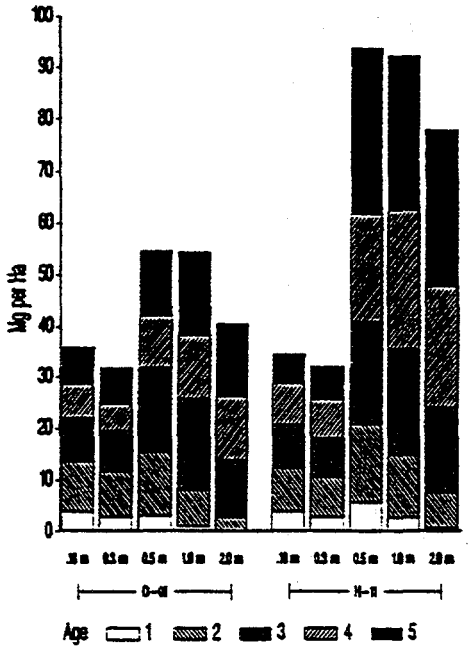


Figure 3. Cumulative five-year biomass production of two *Populus* clones (D-01 and H-11).

We therefore believe that the minimal woodgrass yield suggested by Dula is not unreasonable, provided that it is expressed on a basis comparable to that conventionally used to report short rotation yields—above-ground, leafless, dry matter. But, neither is it particularly high. When compared on a common basis, the woodgrass yield of 112 wet Mg of total aboveground biomass per hectare annually is similar to rates of production measured in many short-rotation intensive culture trials. Mean annual production in the 1.0-m spacing of clone H-11 was about one-third greater than Dula's estimated annual woodgrass yield.

Comparison of woodgrass with wider spacings

Per-hectare production during the first season was closely related to spacing, with the dense woodgrass treatments greatly outproducing the wider spacings. Leaf canopy closure occurred in all spacings during the second year, and growth per tree and per hectare accelerated—especially in the wider spacings. By the end of the second year, cumulative production of both clones in the 0.5-m spacing and of H-11 in the 1.0-m spacing equaled or exceeded that of woodgrass. The growth advantages of wider spacings became even greater in subsequent years. The wider spacings were therefore much superior to woodgrass for growing woody biomass with both *Populus* clones. Because the growth attributes of these two clones are so different, superiority of the wider spacings is likely to be characteristic of *Populus* in general. Although yield of woodgrass plantings of *Salix* is more productive than those of *Populus* (White and others, in press), preliminary results from trials in New York State and Sweden indicate the higher productivity of wider spacings and longer rotations in this genus also (Personal communication with L. P. Abrahamson, 1993).

Potential of *Populus* woodgrass in bioenergy production

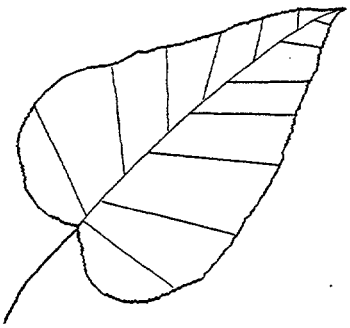
If yield and cost of production are the primary criteria for selection of a short-rotation density regime, spacings other than woodgrass are overwhelmingly superior. Yields of clone H-11 in the wider spacings are two to three times greater than those of woodgrass. Perhaps even more important are establishment costs which are substantially higher for woodgrass. Differences in cutting costs alone are tremendous; at 10¢ per cutting, such costs would be $31,000 and $11,000 per hectare for the two woodgrass spacings. This compares to $1000 per hectare for the 1.0-m spacing and $250 per hectare for the 2.0-m spacing. Even if cuttings were only 1¢ each, total cutting costs per hectare for the woodgrass spacings would be $3100 and $1100 versus only $100 per hectare for the 1.0-m spacing and $25 per hectare for the 2.0-m spacing—differences still amounting to at least $1000 per hectare. In order to overcome such differences in establishment costs, considerable savings would therefore be needed in other management, maintenance, harvest, or interest costs. Savings of sufficient magnitude are unlikely to be achieved.

Despite the disadvantages of woodgrass in terms of yield and production costs, the system could be desirable if characteristics of the produced biomass were superior in value to those of biomass grown by the wider-spaced, short-rotation systems. Because of its younger age and smaller size, woodgrass will have higher contents of bark, extractives, nutrients, and moisture and a lower content of cellulose than an equal biomass produced in a wider spacing on a somewhat longer rotation (Blankenhorn and others 1985a,b). Many of these differences would have negative value in various systems of energy conversion (Butler and others 1987), but they might be beneficial for some uses. Even so, the characteristics would have to be superior by many, many fold and the advantages derived therefrom reflected in raw material prices paid by the processing or conversion industry.

CONCLUSIONS

Our experiment, coupled with other current knowledge, indicates that woodgrass has little promise as a viable system for growing *Populus* biomass for energy. Other wider-spaced, short-rotation density regimes, especially those involving clone H-11 (and other *P. trichocarpa* × *P. deltoides* hybrids) appear superior in nearly all respects. They are producing higher yields than expected, and possibilities for commercial application of these systems seem much brighter.

Although the experiment was limited to *Populus* as are the above specific conclusions, the "woodgrass experience" has some implications with regard to other genera, clones, and biomass production systems. That is, a range of alternatives should be examined before any biomass production system is selected. The costs of—and the time required for—such evaluations are minimal when compared with unnecessary costs that may be incurred or productivity that may be foregone if decisions or commitments are made in the absence of such assessments.



Chapter 3

Tree Growth and Stand Development in Short-Rotation *Populus* Plantings: 7-Year Results for Two Clones at Three Spacings[1]

Dean S. DeBell, Gary W. Clendenen, Constance A. Harrington, and John C. Zasada

Abstract: Two *Populus* hybrids (11-11 and D-01) were planted in monoclonal block plantings at three spacings (0.5-, 1.0-, and 2.0-m) near Olympia, Washington, and evaluated over a 7-year period for individual tree growth rates and above-ground stand productivity. Differences were substantial between clones and among spacings in both individual tree characteristics (height and diameter growth) and stand productivity (leaf area, basal area, or biomass production). Relative differences in growth between the clones tended to increase with spacing. Woody biomass production of clone 11-11 averaged 18.2 Mg $ha^{-1}yr^{-1}$ at the 1.0-m spacing, whereas clone D-01 averaged only 10.1 Mg $ha^{-1}yr^{-1}$ at that spacing. The clones differed in phenology of height and diameter growth, maximum rate of periodic height growth, tendency to produce sylleptic branches, partitioning of woody biomass, and sensitivity of growth rates to competition. All of these characteristics have important influences on the productivity of short-rotation plantations.

Keywords: Poplar, cottonwood, stand density, yield, bioenergy, intensive culture, stem form, phenology, leaf area, sylleptic branching

Interest in growing short-rotation, intensively cultured poplar plantations as a source of fiber and biomass energy has accelerated during the past decade (Ranney and others 1987; Miner 1990; Hansen 1991). Research on genetic variation, breeding, selection, and whole-tree physiology has produced some very productive hybrid *Populus* clones (Stettler and others 1988; Hinckley and others 1989), and information and techniques have been developed for site preparation, plantation establishment, harvest and utilization (Heilman and others 1991). Thousands of hectares of clonal poplar plantations have been established by industrial owners in the northwestern USA and additional plantings are being considered in that region and elsewhere.

Usable yields, product values, and net returns from such plantations will be strongly influenced by tree spacing and rotation length. Knowledge of general principles and trends in tree growth and stand development is needed to make sound decisions on these matters, but stand-level research to provide information specific to short-rotation clonal poplar plantations is limited (Strong and Hansen 1993). This paper presents tree and stand characteristics for two clones planted at three spacings, describes some of the dynamics of tree and stand growth from establishment to age 7 years, and discusses implications of the findings for research and management of short-rotation plantations of poplar clones.

MATERIALS AND METHODS

Our research plantings were established in cooperation with the Washington State Department of Natural Resources at the Meridian Seed Orchard, located 12 km east of Olympia, Washington. Climate is mild with an average growing season of 190 frost-free days and a mean July temperature of 16° C. Precipitation averages 1290 mm per year, falling mostly as rain from October through May; summers are periodically dry. The soil is Nisqually loamy fine sand (a sandy, mixed, mesic Pachic Xerumbrept); it is a

[1] Published in *Biomass and Bioenergy* 11(4): 253-269 (1996).

deep, somewhat excessively drained, medium acid (pH 5.6) soil formed in glacial outwashes and would not be considered suitable for *Populus* growth without irrigation. Nearby unmanaged land is occupied by either prairie vegetation or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and several hardwood trees and shrubs, depending on fire history. The study site was previously farmed for strawberry and hay crops, and topography is relatively level. The land was prepared for planting by plowing and disking in winter 1985-86.

The study was established as a factorial design with two *Populus* clones and three spacing treatments, replicated in three blocks. One clone, D-01, was a *Populus* hybrid (taxonomic identity unknown, but suspected to be either *P. trichocarpa* × *P. nigra* or *P. trichocarpa* × *P. angustifolia*). This clone was selected from a Canadian planting by Dula's Nursery of Canby, Oregon (1984), and is believed to have been developed originally at the University of Idaho. The other clone, 11-11, was a *P. trichocarpa* × *P. deltoides* hybrid developed and tested by Heilman and Stettler (1985) of the University of Washington/Washington State University Poplar Research Program (Quinsey and others 1991). Square spacings were 0.5, 1.0, and 2.0 m. Corresponding numbers of trees per hectare were 40,000, 10,000, and 2,500. Size of treatment plots varied with spacing; all plots were sufficiently large to provide 100 interior measurement trees and a border that consisted of eight, four, and three rows of similarly spaced trees for the 0.5-, 1.0-, and 2.0-m spacing treatments, respectively. The intent was to provide a border at least one-half as wide as the estimated height of measurement trees at harvest. Clone-spacing treatments were assigned randomly within each replicate block.

Both clones were planted by hand as unrooted, hardwood cuttings in late April 1986. All cuttings were 30 cm long and had a minimum upper diameter of 1 cm; they were planted 20 cm deep with at least two healthy axillary buds remaining above ground. Previous experience indicated establishment success (i.e., survival and early growth) was poor if cuttings did not have at least one healthy bud above ground (Radwan and others 1987). Requiring two above-ground buds resulted in a small additional increase in establishment success but also increased the prevalence of multiple stems. At the end of the first growing season, survival averaged 98%. All multiple-stemmed plants were pruned to one stem, and any positions occupied by dead trees were replanted with unrooted cuttings; this resulted in stands composed solely of single-stemmed trees and with all planting spots occupied.

Supplemental nutrients and water were provided uniformly in plots of all treatments. A pre-planting application of mixed fertilizer (16-16-16) provided the equivalent of 100 kg ha^{-1} nitrogen, 43 kg ha^{-1} phosphorus, and 83 kg ha^{-1} potassium. Additional nitrogen (N) fertilizer (ammonium nitrate) was applied at an elemental rate of 100 kg ha^{-1} in May 1988 and again in March 1992. Plots were irrigated throughout each summer by a drip system; amounts applied averaged 400-600 mm per growing season but varied from 260 to 1200 mm; differences were associated more with scheduling conflicts and malfunctioning of irrigation pumps than with differences in potential evapotranspiration. All plots were kept free of weeds during the first year by tilling and hoeing; in the second and third year, developing weed patches were controlled by spot applications of herbicides (oxyfluorfen, pronamide, and glyphosate) and hoeing.

Tree survival, total height, and stem diameter were evaluated at the end of each of 7 growing seasons on the central 100 trees in each plot, and any tree damage or unusual conditions were noted. Height and diameter were also measured periodically on 25 trees per plot to assess seasonal growth patterns. Information on basal diameter (measured at stem height of 0.3 m) was obtained for all years, and breast-high diameter (dbh) was also measured after mid-season in the second year. Figures presenting periodic growth utilize basal diameter as it is available for all periods. Furthermore, periodic growth data from trees with top damage or those which later became suppressed or died were excluded from such figures, thus eliminating the apparent anomalies associated with changes in sample size or condition, and facilitating comparison of phenological patterns across years.

Cumulative basal area over time and diameter at age 7 are presented based on measurement at breast height (1.3 m) to facilitate comparisons with standard forestry measurements. Breast-high diameters at the end of the first year were estimated from height measurements and dbh-height relationships derived from data collected in June of the second year.

Indices for lower-stem taper were calculated from basal and breast-high diameters (basal/dbh) and slenderness was characterized with the ratio of height/basal diameter. After the first, second, and third seasons, numbers of buds and branches were counted for each annual height increment. Such data provided information on initial bud populations, development of sylleptic and proleptic branches, and branch longevity. A branch is classified as sylleptic if it develops and elongates during the same growing season the bud is formed. If the bud does not develop into a branch until the following growing season, the branch is classified as proleptic.

Yields for ages 1 through 7 were estimated from oven-dry biomass component equations applied to basal diameter and height measurements of individual trees. The equations were developed based on destructive sampling of trees at the end of years 1 through 5 and year 7; selected trees were from buffer rows and were representative of the range of sizes for each clone. Equations of the form, Ln(Y) = f(basal diameter, height, and age), were fit independently for each clone. Stem weights, branch weights, leaf weights, and leaf areas were estimated by separate equations. Coefficients of determination (R^2) between predicted and measured values ranged from 0.951 to 0.998. Stem and live branch weights were summed to provide above-ground dry woody biomass. Above-ground biomass estimates for all live trees on each plot were summed, and the resulting plot sums were expanded to woody biomass yield per hectare.

Leaf area index was estimated by determining the projected area of a sub-sample of leaves from each sample tree using an area meter (LICOR 3100). Leaf area per tree was then estimated via area/leaf weight relationships; it was expanded to a per unit area basis by summing estimates for all trees on the plot; total leaf area (m^2) was then divided by ground surface area (m^2) to provide the dimensionless leaf area index (LAI).

Annual biomass growth per tree and per hectare were plotted against a competition index calculated as the cumulative woody biomass per hectare at the beginning of the growth year. This allowed comparison of clonal growth rates at similar levels of competition, even when the same competition level was reached in different years.

Plot means were calculated for each variable and displayed in tables or figures to illustrate trends in development of the plantings. Whenever appropriate, data were analyzed by standard ANOVA techniques, and treatment means were compared by Bonferroni's test (Miller 1989) using $P \leq 0.05$ as the level of significance.

RESULTS AND DISCUSSION

Characteristics of trees and stands at age 7 years

Differences between clones and among spacings were substantial at age 7 (Table 1). Height and basal diameter differed significantly among all clone-spacing treatments, and absolute differences between the clones increased with spacing. Clone 11-11 trees planted at 2.0-m spacing averaged about 50% taller, 25% larger in breast-high diameter, and 80% heavier in total woody biomass than clone D-01 trees at the same spacing. Woody biomass production per hectare of clone 11-11 averaged 1.7 times that of clone D-01. Tree size differences among spacings within clones were even greater: diameters increased 3- to 4-fold and height increased 80 to 100% as spacing widened from 0.5 to 2.0 m. Stand basal area decreased with increased spacing, but woody biomass yields per hectare were similar among spacings, differing by only 5% for clone D-01 and 14% for clone 11-11. Yields averaged slightly greater in the 1.0-m spacing than in the other spacings of both clones, but these differences were not statistically significant.

Competition-related mortality had become substantial in the 0.5-m spacing of clone 11-11,

Table 1. Characteristics of two hybrid poplar clones at three spacings at age 7 years.

Clone	Spacing	Survival	Mean tree size: Basal diameter	Mean tree size: Breast-high diameter	Mean tree size: Height	Mean tree size: Woody biomass	Stand basal area and biomass: Basal area	Stand basal area and biomass: Stem	Stand basal area and biomass: Live branches	Stand basal area and biomass: Total live woody
	m	%	----- cm -----		m	kg	m²/ha	-------- Mg/ha --------		
D-01	0.5	93	3.7 a*	3.2	7.2 a	1.8	34.4 ab	59.3 b	8.3a	67.5a
	1.0	99	7.0 c	6.0	10.6 c	7.1	30.8 ab	60.5 ab	10.5b	71.0a
	2.0	100	13.4 e	10.8	13.1 d	27.3	24.1 a	53.4 a	14.8c	68.2a
Mean		97	8.0	6.7	10.3	12.1	29.8	57.7	11.2	68.9
11-11	0.5	70	4.8 b	4.5	9.6 b	4.0	53.7 d	105.1 c	6.9a	111.9b
	1.0	95	8.2 d	7.7	14.1 e	13.4	47.7 cd	119.4 d	8.3a	127.7b
	2.0	100	14.7 f	13.5	19.2 f	47.8	36.7 bc	106.2c	13.2c	119.5b
Mean		88	9.2	8.6	14.3	21.7	46.0	110.2	9.5	119.7

* Clone-spacing means followed by the same letter do not differ significantly at the 5% level.

averaging 30% of all stems; it had begun to occur in the 0.5-m spacing of clone D-01 and in the 1.0-m spacing of clone 11-11 but averaged only 7 and 5%, respectively. Basal diameter of trees in the 2.0-m spacing of clone 11-11 averaged 14.7 cm, and thus approximated the size generally considered to be the minimum desired or acceptable with regard to harvest costs and product quality for some uses (Kluender 1980).

Tree and stand characteristics for the 1.0-m and 2.0-m spacings of clone 11-11 at age 7 are similar to data collected in 3.0-ft and 6.0-ft plantings of this clone at the same age in unirrigated bottomlands along the lower Columbia River [pers. comm. from William Schuette of James River Corporation, Camas, Washington (January 4, 1995)]. Growth and yield in the slightly wider but comparable spacing treatments of our study averaged about 10% greater for individual tree characteristics (height and diameter) and 2 to 5% greater for stand production (basal area and biomass). Thus, general patterns of tree growth and stand development defined by our study are probably similar to those of productive clonal poplar plantations established in other locations in western Washington and Oregon.

Patterns of height and diameter growth

Effects of clone and spacing on cumulative height, diameter, and basal area per tree increased with time (Fig. 1a, b, and c). Clone 11-11 surpassed clone D-01 in cumulative size at all spacings at all times. Annual increments in these measures of growth increased during the first two or three years, but since have generally declined with age, size, and increasing inter-tree competition. Nevertheless, relative as well as absolute differences among spacings within each clone have tended to increase. Differences among spacings were generally greater for clone 11-11 than clone D-01, and varied with the growth trait (height, diameter, or basal area).

Aside from the general trends in growth associated with spacing and age, smaller than expected increments occurred in the fourth (1989) and in the sixth (1991) year (Fig. 1a, b, and c). In several instances, growth in the seventh year (1992) was greater than that in the sixth (1991), especially in the wider spacings. And in the narrow (0.5-m) spacings, growth in fifth year (1990) sometimes surpassed that of fourth year (1989). Weather and irrigation records show that 1989 and 1991 were dry years, and irrigation during the early part of the growing season (March-June) was less than normal because of equipment problems. As a result, total input (rainfall plus irrigation) of water during the early growing season of 1989 and 1991 was 50% or more lower than that occurring during the first three years of growth (1986-1988) and in the fifth (1990) and seventh (1992) years. Differences in phenology probably account for the relatively greater decline in clone D-01; it leafs out earlier and produces a larger proportion of its annual growth increment during the March-June period than does clone 11-11

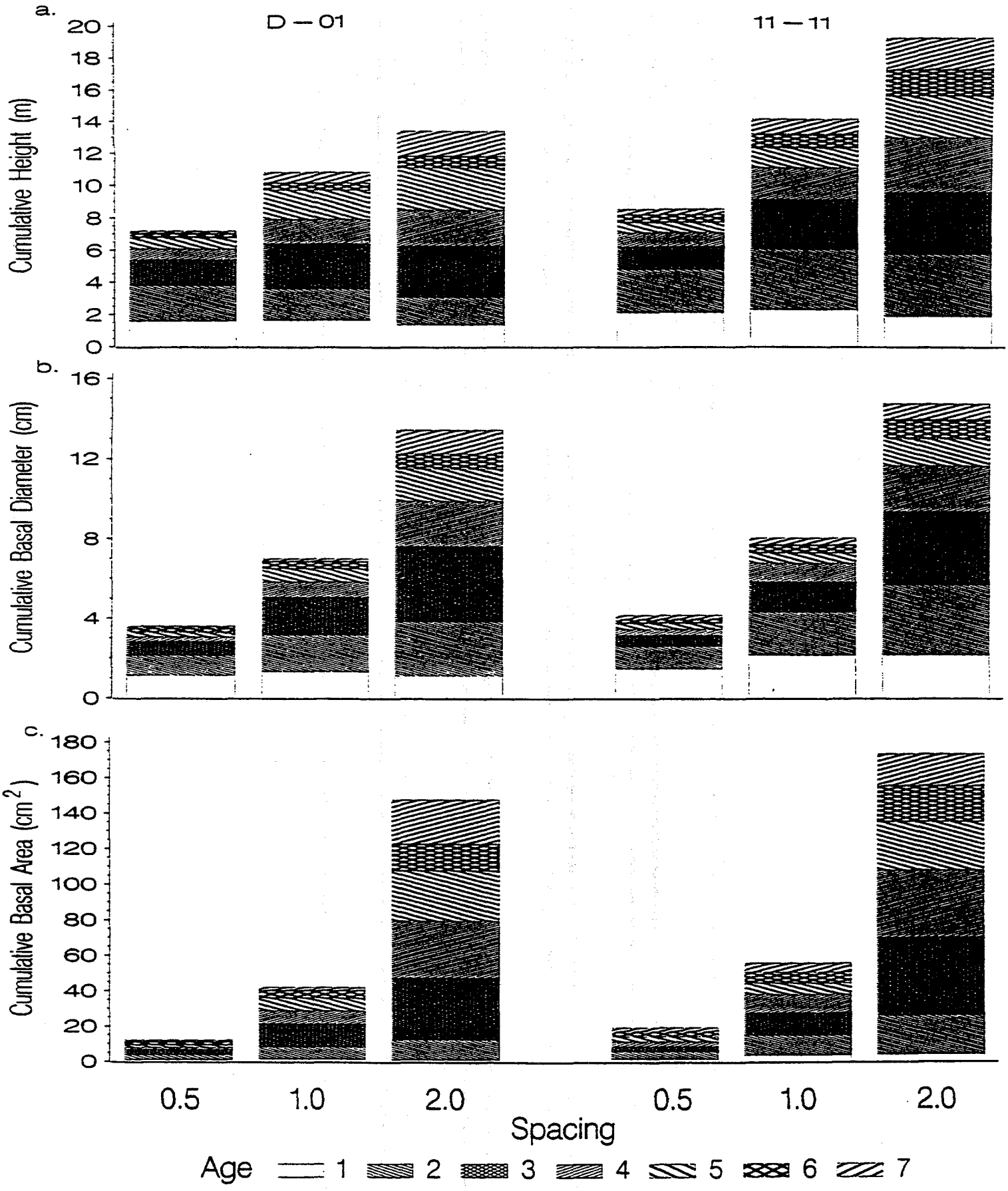


Fig. 1. Seven-year cumulative growth in height (a), basal diameter (b), and individual tree basal area (c) of two hybrid *Populus* clones planted at three spacings.

(DeBell and others 1996b). Thus, adverse conditions during the early growing season would have more detrimental impacts on clone D-01 than on clone 11-11 which produced most of its growth later in the season when conditions were more favorable.

Reductions in growth can be associated with factors other than moisture stress. Growth depressions have been observed during periods of low temperature and heavy cloud cover in plantations established in the lower Columbia River valley [pers. comm. from William Schuette of James River Corporation, Camas, Washington (January 4, 1995)]. Presumably such conditions may also affect growth differently in different clones.

Optimum spacing for height and diameter growth has changed with tree size and age. Although this can be inferred from annual growth increments displayed in Figures 1a and b, it is illustrated more specifically and in greater detail with the 25-tree periodic measurements in Figures 2a-d. Height growth of clone D-01 was little affected by spacing during most of the first growing season; from June of the second season (14 months) through June of the third season (26 months), however, height growth and attained height were greatest in the densest spacing (0.5-m) and declined with increased spacing (Fig. 2a). From mid-growing season of the third year until early in the fourth growing season, trees were tallest in the intermediate (1.0-m) spacing, though growth during much of the period increased with increased spacing. By the end of the fourth season (43 months) and thereafter, both height and height growth increased with increased spacing. Although changes occurred more rapidly for clone 11-11, similar trends are apparent (Fig. 2b); that is, greatest height growth and tallest trees initially occurred in the 0.5-m spacing but with time best growth and tallest trees developed in progressively wider (1.0- and 2.0-m) spacings.

Such height growth patterns can be generalized by considering the influence of spacing on relative height growth of both clones in relation to tree height. Height growth was at least as good in 0.5-m spacings as in the wider spacings for tree heights up to 3 m, and growth was slightly better in the 1.0-m spacing than in the 2.0-m spacing for heights up to nearly 6 m. Ratios of spacing to tree height have been used by European foresters as measures of stand density for decades (Braathe 1957), and Wilson (1946) proposed maintaining uniform stand densities in Lake States forests by thinning to spacings as a percentage of height. If data for the two *Populus* clones are examined in terms of a spacing/tree height ratio, the best height growth has occurred in the densest spacings in which the ratio was greater than 15%. When the spacing/tree height ratio dropped below 15%, the best growth occurred in the next wider spacing.

General growth patterns for basal diameter are similar to those for height in that advantages associated with wider spacings increase with tree size and stand age. During the first 2 to 3 months after planting, diameters taken 1 cm above the developing shoots were largest in the closest spacing. By the end of the first season, however, clone D-01 and clone 11-11 had the largest diameters in the intermediate (1.0-m) and widest (2.0-m) spacings, respectively (data not shown). Late in the second growing season (16 months) (Fig. 2c and d), attained diameters and diameter growth of both clones increased with spacing from 0.5 to 2.0 m; such differences among spacings increased over time.

Phenology as well as magnitude of height and diameter growth differed by clone and spacing (Fig. 3). Throughout most of the first season and into the middle of the second growing season (1987), height growth of clone D-01 was greater at 0.5-m than at 1.0-m spacings (Fig. 3a). During the first year, height growth peaked in July for all spacings at rates of 2.5 cm day^{-1} for the 0.5-m and 1.0-m spacings and about 1.8 cm day^{-1} for the 2.0-m spacing. Growth in August was only slightly less than that in July. Growth in the 1.0-m and 2.0-m spacings peaked in August of the second year at nearly 4 cm day^{-1}, and thereafter to the end of the year, growth in the 2.0-m spacing exceeded that in the 1.0-m spacing and the 0.5-m spacing. During the third season, height growth peaked in early August in all spacings, but the amount of growth increased with increased spacing, excepting the first growth period when growth in the 2.0-m spacing was slightly less than that in the two

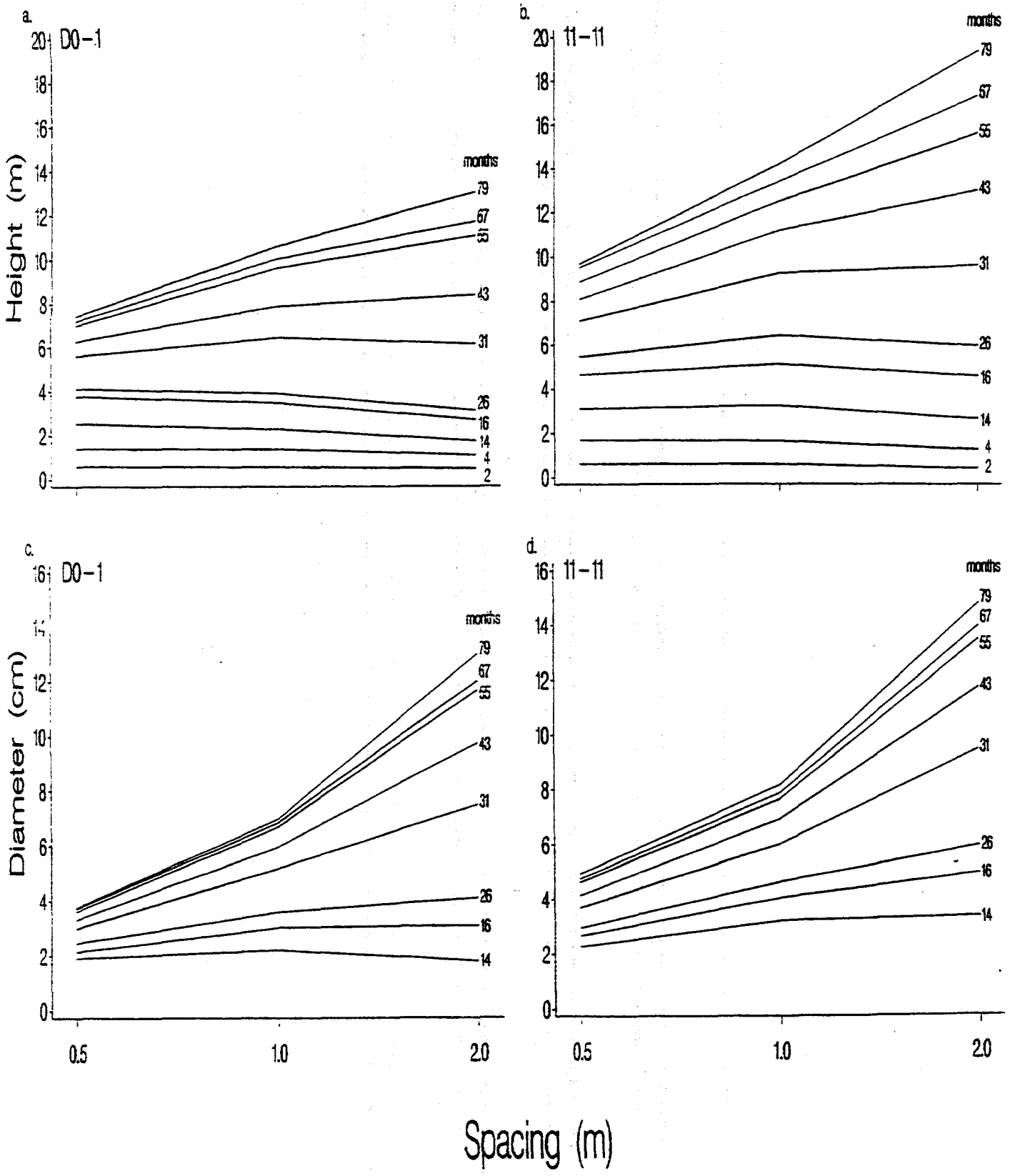


Fig. 2. Size of two hybrid *Populus* clones as related to spacing and months since planting —height of D-01 (a), height of 11-11 (b), diameter of D-01 (c), and diameter of 11-11 (d).

narrower spacings. Height growth of clone 11-11 followed similar patterns, but peak rates were 3 to 4 cm day^{-1} (Fig. 3b). Height growth was best in the denser spacings early in the first season, and it peaked in July. By the July of the second season, however, periodic growth increased with increased spacing and it peaked in early August at all spacings. Growth remained high into September, particularly in the two wider spacings.

Patterns of periodic diameter growth are shown for the second through the fourth year (1987 to 1989) in Figures 3c and d. Except for the first measurement period for clone D-01, the amount of growth in each period increased with increased growing space for both clones. In most years, peak growth period occurred 4 to 6 weeks later in the 2.0-m spacing than in the 1.0-m and 0.5-m spacings. In the fifth season (not shown in Fig. 3, but total annual growth can be seen in Fig. 1b), diameter growth of clone D-01 was greater than that of clone 11-11 in all spacings, presumably because trees were considerably larger and competition was much more intense in stands of clone 11-11. For both height and diameter growth, clone D-01 and clone 11-11 attained peak growth at similar times, but growth of clone D-01 declined more precipitously than clone 11-11. Thus, one of the traits that enables clone 11-11 to be more productive than clone D-01 is its ability to produce substantial amounts of growth later in the season.

Development of buds, primary branches, and leaf area

Height, diameter, and biomass growth of the clones may also be heavily influenced by the dynamics of bud and primary branch populations and associated effects on development of leaf area. Detailed measurements were obtained on bud and branch populations on current terminals during the first three years and leaf area was measured for the first 5 years. Some of these data are summarized in Table 2. Numbers of buds produced during the establishment year were similar among all clone and spacing treatments, but differences occurred between clones in the extent of sylleptic branching. Nearly one-third of buds in the two wider spacings of clone 11-11 developed into branches during the first growing season, resulting in per tree leaf areas averaging three or more times greater than those in other treatments. Sylleptic branching of clone D-01 was negligible compared with clone

Table 2. Height growth, bud populations, primary branching characteristics, and leaf area per tree during the first three growing seasons as related to clone and spacing.

	Clone D-01 by spacing			Clone 11-11 by spacing		
	0.5 m	1.0 m	2.0 m	0.5 m	1.0 m	2.0 m
			First year			
Height (cm)	159	165	137	212	228	188
Buds (no.)	46	48	43	45	47	45
Sylleptic branches (no.)		2	1	3	14	14
Leaf area (m^2)	0.4	0.5	0.4	0.5	1.7	2.8
			Second year			
Proleptic branches (no.)*	29	41	37	1	6	20
Terminal growth (cm)	239	194	174	275	380	393
Buds (no.)	42	43	45	49	60	62
Sylleptic branches (no.)	0	0	0	10	48	52
Leaf area (m^2)	1.2	2.4	4.8	1.6	5.4	14.9
			Third year			
Terminal growth (cm)	157	278	319	140	306	381
Sylleptic branches (no.)		1	6	2	12	16
Leaf area (m^2)	1.8	4.9	15.1	2.4	7.8	30.6

* Developed in year indicated but occur on previous year's height increment.

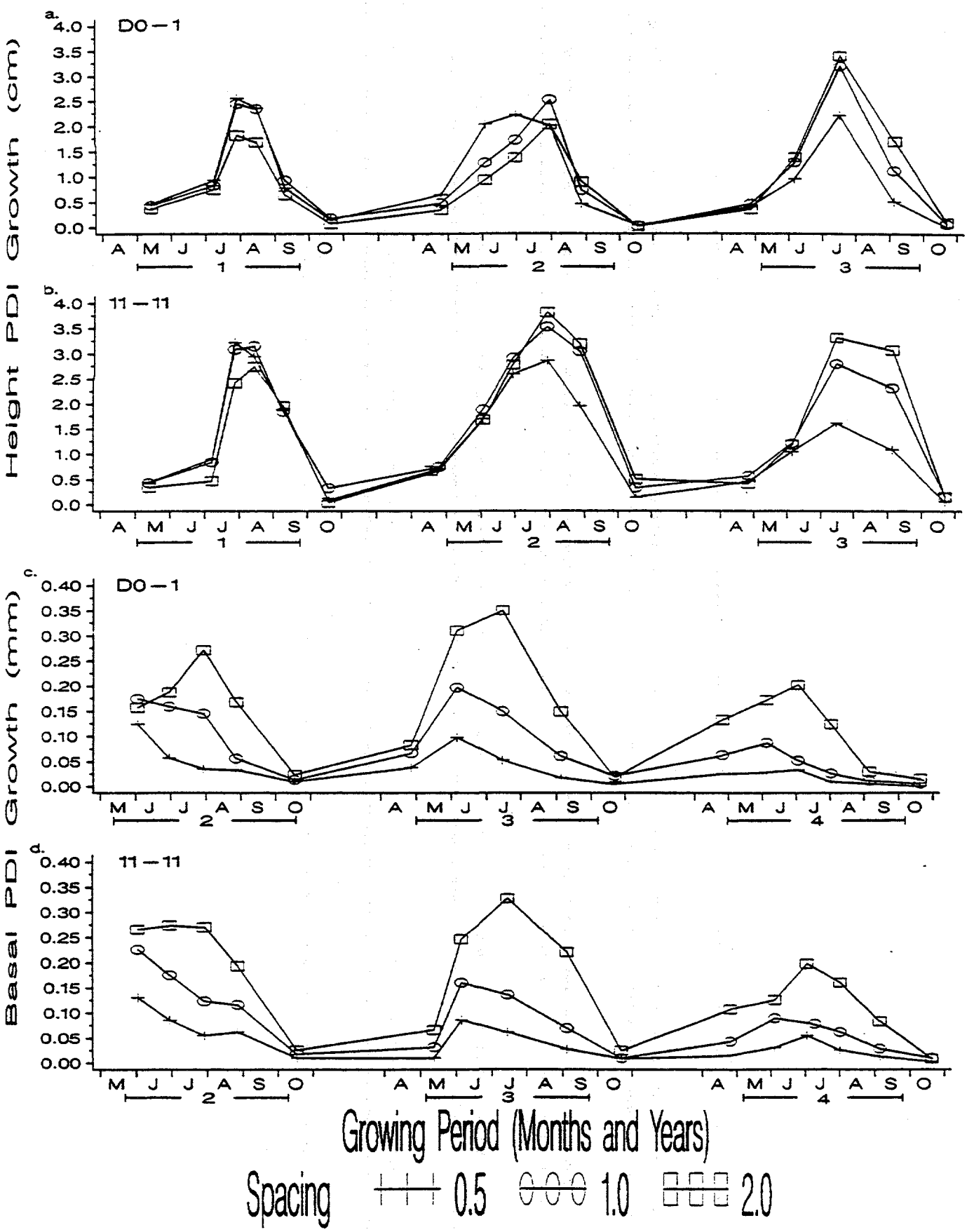


Fig. 3. Growth phenology of two hybrid *Populus* clones at three spacings: periodic daily increment (PDI) for height during the first through the third years (a and b) and periodic daily increment (PDI) for diameter during the second through the fifth year (c and d).

11-11; its branching habit was almost exclusively proleptic. Bud numbers and leaf areas per tree increased with increased spacing during the second year. For clone 11-11, proleptic branches (on the first year stem increment), terminal growth, and sylleptic branches also increased with increased spacing. By the end of the third year, it became apparent that syllepsis varied considerably in different years, even in clone 11-11. Nevertheless, the advantages of increased spacing were reflected in sylleptic branch and leaf area traits of both clones; terminal growth of the two clones was more similar and increased with increased spacing. Leaf areas, however, continued to be substantially greater for clone 11-11, averaging 33% to 102% greater than leaf areas of clone D-01 at the same spacings. Continued effects are associated with the fact that syllepsis is common on primary and secondary branches as well as terminals in young trees. Such differences in branching and leaf area were highly correlated with subsequent stand development and differences among clones in biomass productivity per hectare.

Although syllepsis is associated with higher production in established stands, it can create a problem for nursery managers and other producers of poplar cuttings because vigorous axillary buds are needed at the top of each cutting for successful plantation establishment (Radwan and others 1987). For many clones with a high degree of sylleptic branching, suitable cuttings can be made from only about one-third of the total length of shoots grown on orchard stools (or stumps). Mechanization is more difficult because much greater selectivity is needed in processing.

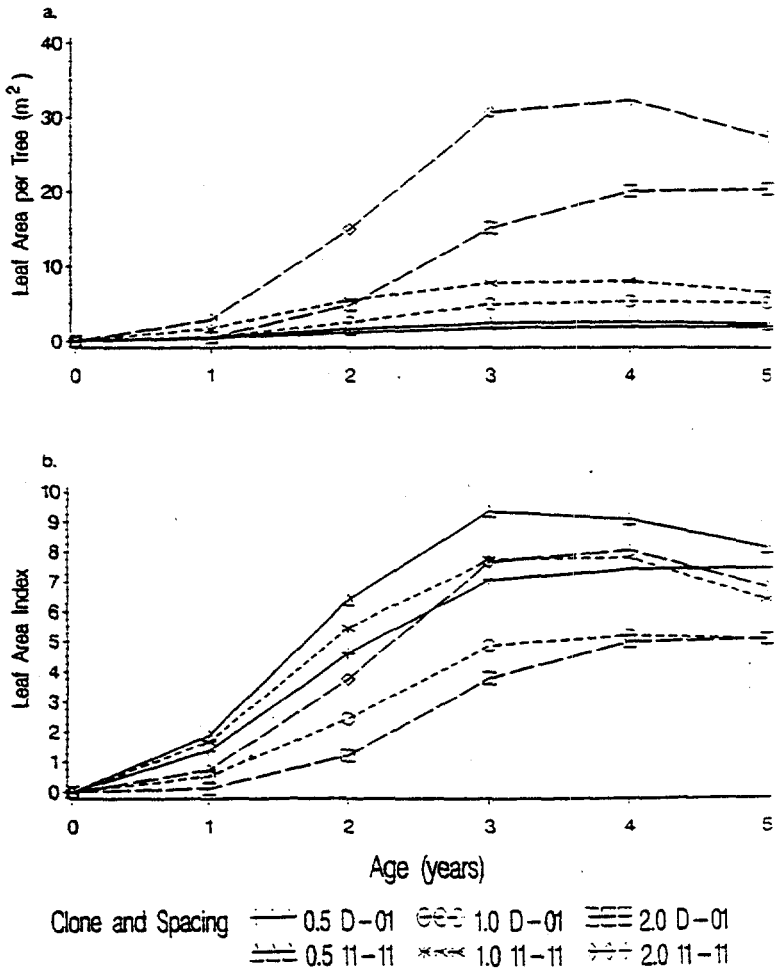


Fig. 4. Leaf area per tree (a) and per hectare (b) as related to clone, spacing, and age.

Branch population dynamics differed substantially between clones because of differences in syllepsis and changing stand conditions in the various spacings. Branches produced on the first year's height increment were traced over a 4-year period (Table 3). All sylleptic and proleptic branches produced by clone 11-11 at the 0.5-m and 1.0-m spacing had died by the end of the second growing season; branches produced on clone 11-11 trees at 2.0-m spacing remained alive through the second season, but all had died by the end of the third season. Branches remained alive much longer on clone D-01; 8, 13, and 77% of all branches produced on the first year's height increment in the three spacings were still alive after four growing seasons.

Leaf area per tree and per hectare (leaf area index) expanded rapidly during the second and third growing season (Fig. 4a and b). By the end of the third year, most clone and spacing treatments had attained a peak or near-peak leaf area index, beyond which it declined or was maintained at the same level. For clone 11-11, leaf area index peaked at 9.3 in the 0.5-m spacing; and at nearly 8.0 for the intermediate (1.0-m) and wide (2.0-m) spacings. Highest leaf area indices attained for clone D-01 were 7.5 in the 0.5-m spacing and 5.1 to 5.2 for the intermediate and wide spacings. Leaf area index did not decline substantially by age 5 for clone D-01, but leaf area index values for clone 11-11 averaged about 15% lower than those at peak levels for the spacings. The sustainable level of leaf area of several tree species is commonly 20% lower than the peak levels (Kozlowski and others 1991); thus, leaf area indices of 7 to 8 might be maintained by hybrid *Populus* stands on this site.

Table 3. Population trends of branches produced on first year's height increment as related to clone and spacing.

	Spacing (no. of branches)		
Year and clone	0.5 m	1.0 m	2.0 m
	First year		
11-11	3	14	14
D-01	<1	2	1
	Second year		
11-11	32*	42*	35
D-01	29	41	38
	Third year		
11-11	0	0†	0†
D-01	12	36	33
	Fourth year		
11-11	0	0	0†
D-01	2	6	26

* Sylleptic and proleptic branches formed in years 1 and 2, and all were dead by end of year 2. Branches in 2.0-m spacing were alive at end of year 2, but all died by end of the third growing season.

† Small amount of branch production from suppressed buds; these branches were all short shoots and died in year formed.

Accumulation of basal area and woody biomass per hectare

Basal area accumulation also accelerated during the second and third growing seasons (Fig. 5a); annual growth peaked during the third year in all clone and spacing treatments, excepting the 0.5-m spacing of clone 11-11 which peaked during the second year. By the end of the second year, the 0.5-m spacings had produced three to four times the basal area of the 2.0-m spacing; by year 7, however, basal areas of the 0.5-m spacings averaged only about 40% greater than those in the 2.0-m spacings.

Accumulation of woody biomass (wood and bark of stem and branches) followed a pattern similar to that of basal area, but peak growth occurred about one year later and was sustained longer. Moreover, by age 7 the two wider spacings of both clones had accumulated woody biomass in amounts equal to or more than that of the densest spacing (Fig. 5b). Such differences between patterns of basal area and woody biomass accumulation can be attributed to continued height growth and substantial differences in annual height increment (with corresponding influences on biomass increment) among spacings.

Current annual woody biomass production per tree and per hectare in the spacing treatments of each clone are illustrated in Figures 6a and 6b. Greatest production occurred during the third through the fifth season for the 0.5-m and 1.0-m spacings of both clones. Highest production occurred later (fourth through the seventh seasons) for the widest (2.0-m) spacing, however. The very dry conditions early in the fourth

and sixth seasons (1989 and 1991) resulted in temporary declines in growth of several treatments, thus making it difficult to determine the timing and magnitude of peak current annual growth. Growth during these periods of peak growth averaged 24.0 Mg ha^{-1} yr^{-1} for clone 11-11 and 14.0 Mg ha^{-1} yr^{-1} for clone D-01. Mean annual woody biomass production over the 7-year period for the most productive spacing (1.0-m) of clones 11-11 and D-01 was 18.2 and 10.1 Mg ha^{-1} yr^{-1}, respectively. In clone D-01, mean annual biomass growth peaked at age 5 in the 0.5-m and 1.0-m spacing at 10.6 and 11.2 Mg $ha^{-1}yr^{-1}$, respectively; in clone 11-11, at age 5 in the 0.5-m spacing at 17.6 Mg $ha^{-1}yr^{-1}$ and at age 6 in the 1.0-m spacing 18.4 Mg $ha^{-1}yr^{-1}$. Mean annual woody biomass production in the 2.0-m spacing at age 7 was 9.7 Mg $ha^{-1}yr^{-1}$ for clone D-01 and 17.1 Mg $ha^{-1}yr^{-1}$ for clone 11, and it had not begun to decline for either clone. Such levels of production for clone 11-11 substantially exceeded the "working maximum" yields of 10-12 Mg $ha^{-1}yr^{-1}$ suggested in a synthesis of earlier studies of closely-spaced hardwood plantations grown on 4- to 5-year rotations (Cannell and Smith 1980).

Partitioning of woody dry matter

The partitioning of above-ground woody biomass differed substantially in the two genotypes. Clone D-01 accumulated more branch biomass at each spacing than did clone 11-11 (Fig. 7). Such differences in accumulation do not reflect differences in branch production because branch retention differed greatly between the clones (Table 3). Clone 11-11 produced 50 to 100% more stem biomass than clone D-01 and

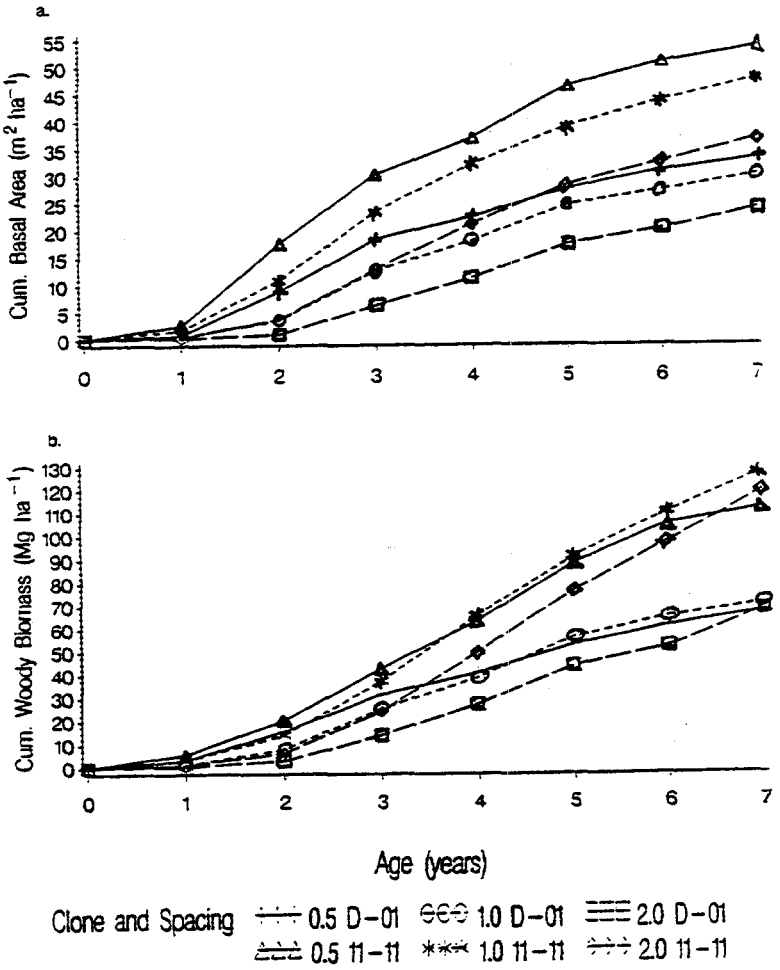


Fig. 5. Cumulative basal area (a) and live woody biomass (b) per hectare as related to clone, spacing, and age.

had much higher overall productivity. The proportion of above-ground woody biomass in branches generally diminished from age 1 or 2 to age 5, after which it remained relatively stable (Fig. 8). At age 7, the proportions of biomass associated with branching varied by clone and spacing. Clone D-01 had partitioned 11% of the woody biomass produced at the densest spacing to branches and 24% at the widest spacing to branches whereas clone 11-11 partitioned 7 and 13% to branches at the same spacings, respectively.

Table 4. Stem form characteristics of two clones at three spacings at age 7 and at similar heights. Slenderness ratio = height ÷ basal diameter (m/cm). Lower-stem taper = basal diameter ÷ breast-high diameter (cm/cm).

		Age 7		Similar height	
Clone	Spacing	Slenderness	Taper	Slenderness	Taper
D-01	0.5	1.95	1.16	1.95	1.16
	1.0	1.51	1.17	1.51	1.17
	2.0	0.98	1.24	0.98	1.24
11-11	0.5	1.99	1.05	2.05	1.06
	1.0	1.73	1.06	1.62	1.06
	2.0	1.31	1.09	1.11	1.10

Stem form

Slenderness and lower-stem taper were influenced markedly by spacing and differed somewhat between clones (Table 4). At age 7, height-basal diameter ratios were nearly 200 in the 0.5-m spacings of both clones and diminished with increased spacing, much more so for clone D-01 than clone 11-11. Lower-stem taper was similar in the 0.5-m and 1.0-m spacings but slightly greater at 2.0-m spacing; clone D-01 had

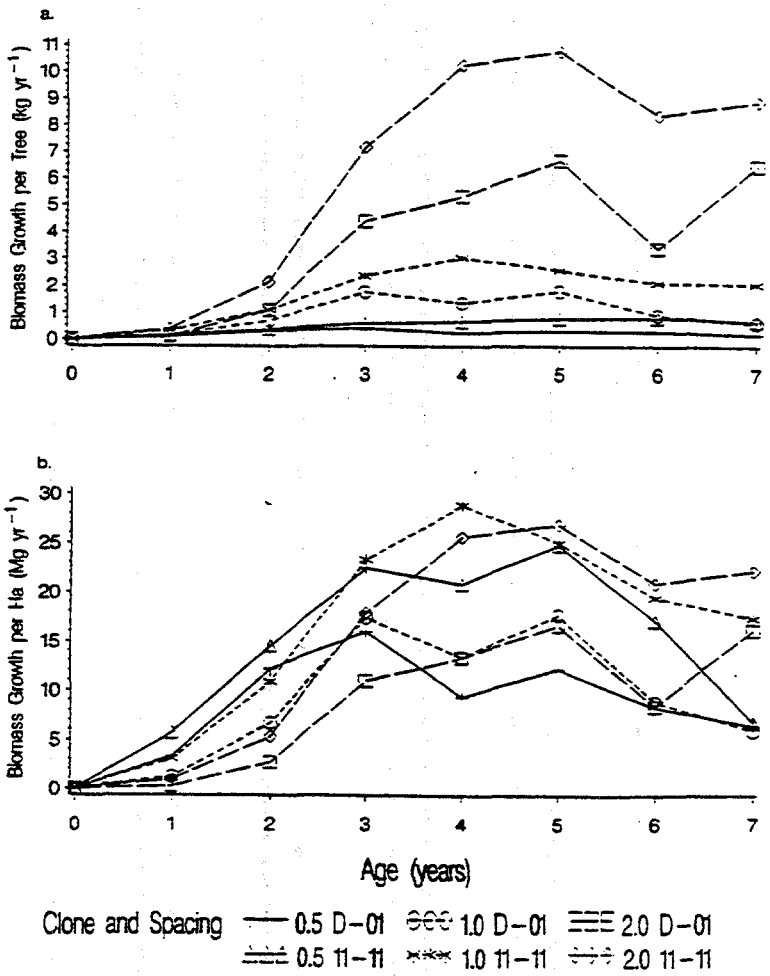


Fig. 6. Current annual woody biomass growth per tree (a) and per hectare as related to clone, spacing, and age.

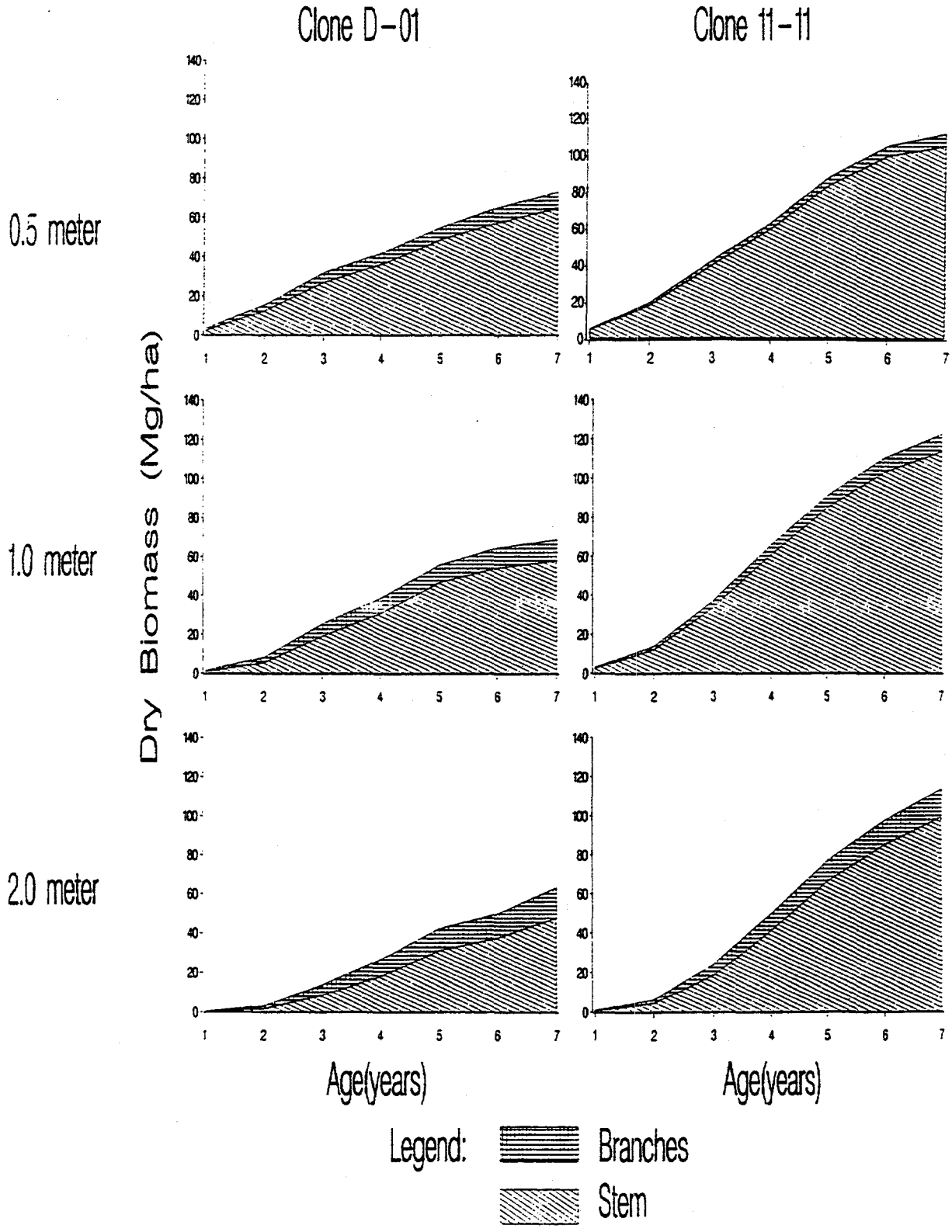


Fig. 7. Seven-year cumulative biomass of live stems and branches of two hybrid *Populus* clones at three spacings.

greater taper than clone 11-11. Because tree size (especially height) differed greatly between the clones at age 7, slenderness and taper ratios were also compared at similar tree heights (Table 4); heights used for clone D-01 were attained at 7 years whereas clone 11-11 had attained the same height at 4 years. The marked difference between the clones in slenderness (height ÷ basal diameter) was much reduced when comparisons were made at similar tree heights. General trends among spacings for slenderness and lower stem taper and among clones for lower-stem taper, however, resulted in essentially the same relationships described above. Clone 11-11 has considerably less taper than clone D-01, and the difference between these two clones in taper appears to be linked strongly to differences in branching characteristics (syllepsis and retention).

Crown closure, competition, and differentiation

Crown closure occurred in all spacing treatments before or during the third growing season; closure was observed visually in terms of touching or overlapping crowns and also was reflected in the attainment of peak or near peak leaf area index. Competition thereafter intensified, and incremental growth in many traits began to decline, especially in the 0.5-m spacing (Fig. 1a, b, and c). In natural stands and most plantations, differences among trees in leaf area and current growth become larger, soon leading to differences in tree sizes and thus to stand differentiation. Such differentiation has occurred in the 0.5-m spacings of the clonal poplar plantings, as evidenced by coefficients of variation in tree diameter at age 7 of about 40% for both clones. Variation in the intermediate (1.0-m) and wide (2.0-m) spacings, however, was much lower. It averaged about 30% for each clone in the 1.0-m spacing but was higher for clone D-01 (22%) than clone 11-11 (14%) in the 2.0-m spacing. Coefficients of variation in two clone 11-11 spacings (0.5-m and 2.0-m, the most and least differentiated clonal poplar plantings) were compared with plantings of intermixed red alder families at the same spacings on the same site. Variation within the densest spacing was similar (~40%) for the two genera, suggesting that microsite differences have equal or greater influence than genetic differences on stand differentiation in very dense stands. Much less differentiation, however, occurred in the clonal poplar plantations than in the red alder plantings at the widest spacing (coefficient of variations were 14 and 26%, respectively). Low differentiation poses no problem (actually uniformity is a desirable quality) when target sizes and spacings needed to attain them are known and well defined. If such information is not known or is not used to design clonal plantations, however, slow differentiation of trees in over-dense plantings can result in reduced growth of all trees and thus will require noncommercial thinning or a longer wait before trees attain minimum usable size.

Mortality and stockability

Differentiation among trees in stands of shade-intolerant species, such as *Populus* spp., leads subsequently to death of the smaller trees. Although most managed *Populus* plantations will be harvested before competition-related mortality (self-thinning) occurs to any significant degree, research plantings in the self-thinning stage are of interest because they provide data for developing guidelines for stand density management (Reukema and Bruce 1977; Drew and Flewelling 1979; Puettmann and others 1993). With such information, plantation spacings can be selected so that, on average, trees will attain a specific target size before growth is drastically reduced and competition-related mortality occurs. Although such mortality began at different times in the 0.5-m spacings of clone D-01 (year 6) and clone 11-11 (year 3), tree sizes were approximately the same at its onset; i.e., basal diameter, dbh, and height were approaching 3.5 cm, 3.0 cm, and 7.0 m, respectively.

It is possible that optimal spacings may differ with clone and cultural treatments; i.e., the stockability (or tolerance to crowding) may be manipulated genetically or culturally, thus increasing productivity of the system (DeBell and others 1989a). Substantial mortality has occurred in only the 0.5-m spacing of clone 11-11, but mean tree and stand growth have declined

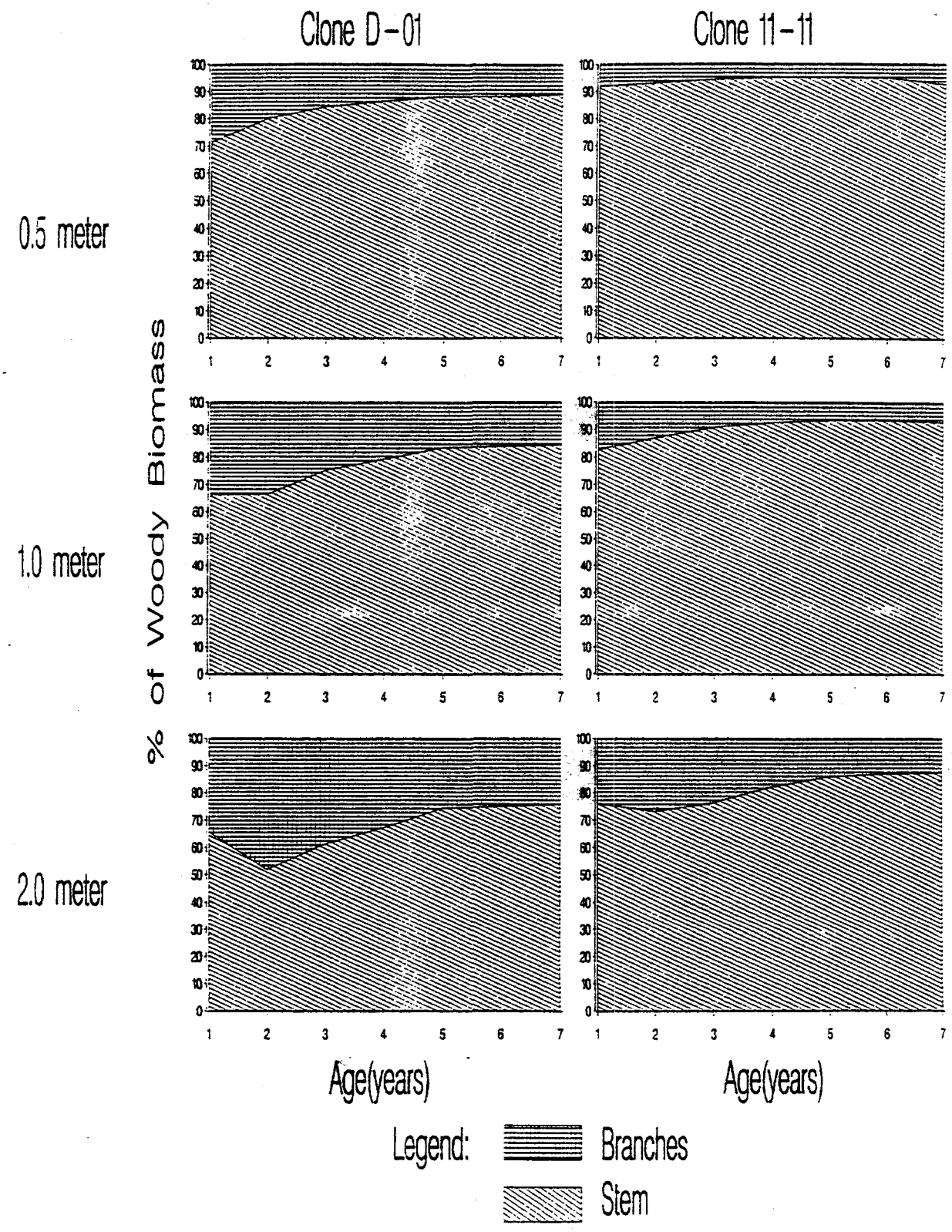


Fig. 8. Relative proportions of live stems and branches of two *Populus* clones as related to spacing and age.

considerably in all spacings. Various measures of annual mean tree and per hectare growth were plotted in relation to various measures of stand development or competition. In nearly every instance (growth measures and competition indices), growth of hybrid clone 11-11 exceeded that of clone D-01 at similar levels of competition. Annual biomass growth (per tree and per hectare) is evaluated in relation to cumulative woody biomass at the beginning of the growing season in Figures 9a and 9b, respectively. There is an **acceleration phase** when *annual* growth increases with the accumulation of biomass, a **maximum growth phase** which may appear as a plateau with or without a pronounced peak, and a **declining growth phase**. The two clones behave rather similarly during much of the acceleration phase (approximately 0 to 20 Mg/ha of accumulated biomass); clone 11-11, however, attains a higher maximum growth rate at all spacings in the latter part of the phase than does clone D-01. The phase of maximum growth appears to continue over a wider range of standing biomass (20 to 70 Mg ha^{-1}) for clone 11-11 than for clone D-01 (20 to 50 Mg ha^{-1}). Furthermore, clone 11-11 produced considerably more biomass per annum during most of the declining growth phase than did clone D-01. Thus, clone 11-11 not only grew more rapidly than did clone D-01; it also demonstrated a capacity to grow more rapidly at higher levels of competition.

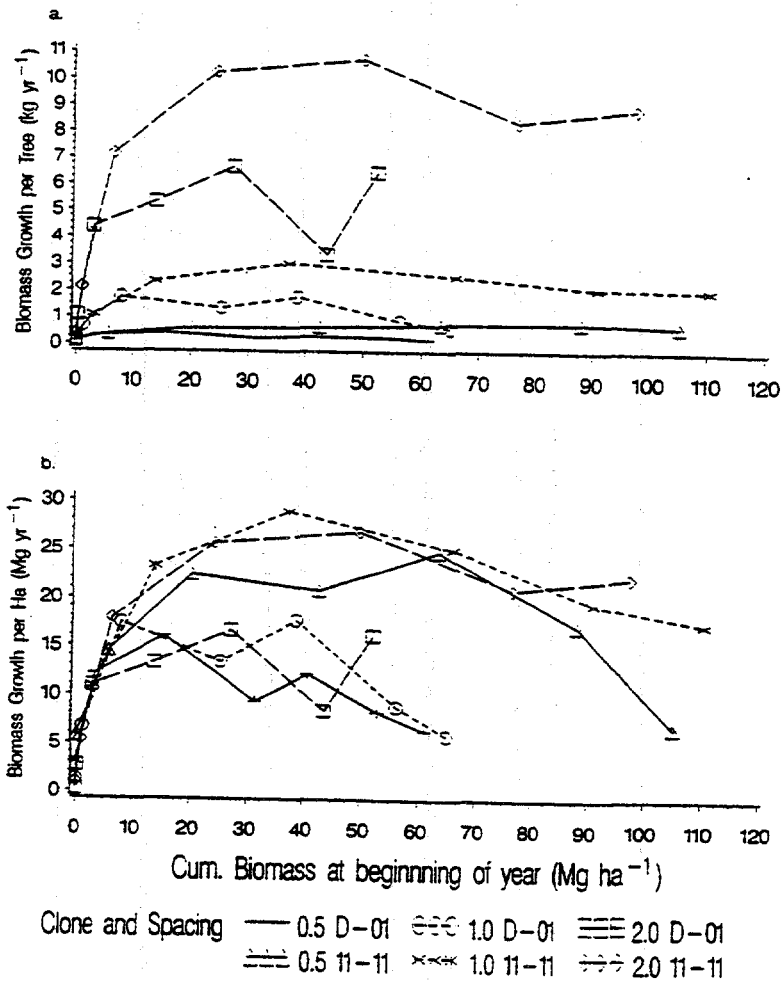


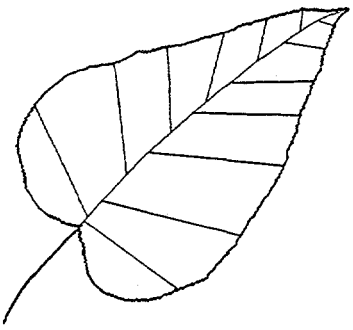
Fig. 9. Annual woody biomass growth per tree (a) and per hectare (b) as related to clone, spacing, and cumulative woody biomass at the beginning of each growth year.

SUMMARY AND CONCLUSIONS

The two hybrid *Populus* clones differed markedly in growth rate, phenology, partitioning of woody biomass, and stockability. Clone 11-11 produced nearly 75% more woody biomass on average than clone D-01, and less biomass (in both relative and absolute terms) was accumulated in branches. Such superiority in productivity of clone 11-11 was associated with greater sylleptic branching, a longer and later period of growth during the growing season, and the capacity to continue to grow well at high levels of competition. Cumulative 7-year production of clone 11-11 in the best treatments attained 54 m^2 ha^{-1} of basal area and 128 Mg ha^{-1} of woody biomass. Production in the best treatments of clone D-01 totaled only 34 m^2 of basal area and 71 Mg ha^{-1} of woody biomass.

The most favorable growth environment changed over time from the closest to the widest spacing for each of the clones. Patterns as well as magnitude of growth were influenced by spacing; that is, trees in wide spacings produced more growth later in the season than did those in dense spacings, and they accumulated a larger proportion of biomass to branches. At age 7, trees of clone 11-11 in the widest spacing averaged nearly 15 cm in basal diameter and 19 m in height, and total woody production at 120 Mg ha^{-1} was not significantly different than that of the two denser treatments. Despite such excellent growth and stem yield, it was obvious that individual tree growth had slowed considerably (Fig. 1a,b,c) and would have been greater at yet wider spacing as evidenced by the fact that outside border trees were already larger than 15 cm in basal diameter at age 4.

Differences between the clones increased with spacing, thus indicating that the growth capacity of clone 11-11 is more fully realized at wider spacing. Nevertheless, our examination of relationships between current annual growth and levels of stand density or competition revealed that peak growth of clone 11-11 was not only higher than clone D-01, but it also continued to higher levels of stand density before declining. Such differences in stockability merit further testing with other clones, perhaps using the crown competition factor concept recently suggested by Hall (1994). Morphological and physiological studies have contributed substantially to understanding the productivity of *Populus* clones at the individual tree level (Isebrands and others 1988; Hinckley and others 1989; Ceulemans and others 1990); related stand-level research that links morphological and physiological characteristics to the ability of trees (and stands) to grow well at high levels of competition is also needed. Both traits — individual tree growth and stockability — are important in the productivity of short-rotation biomass plantations.



Chapter 4

Tree Growth and Stand Development of Four *Populus* Clones in Large Monoclonal Plots[1]

Dean S. DeBell, Constance A. Harrington, Gary W. Clendenen, John C. Zasada

Abstract: Four clones of *Populus* were planted in replicated monoclonal plots near Olympia, Washington, to evaluate their suitability for use in short-rotation culture. All clones were easily established and had minimal problems from damaging agents during the first five years. Observed differences among clones in pattern and amount of growth appeared to be associated with differences in number and density of buds, sylleptic branching, and phenology. In addition, differences in drought tolerance and stockability may also have influenced clonal differences in annual growth and stand productivity. Individual tree growth was limited by the dense 1.0-m spacing, but the best-growing clones averaged 13 to 16 m tall, 7 to 9 cm in breast-high diameter (1.3 m), and produced stand basal areas exceeding 38 m^2 ha^{-1} at 8 years. Mortality was negligible for 7 years, after which various combined effects of competition, stem borer damage (*Cryptorhyncus lapathi*), and a severe windstorm caused mortality ranging from 18 to 36% in the three fastest growing clones.

Keywords: Tree improvement, short rotation, intensive culture, biomass, productivity, stockability

Interest in short-rotation production of native cottonwoods and various *Populus* L. hybrids for fiber and energy has accelerated greatly during the past decade (Ranney and others 1987; Miner 1990; Heilman and others 1991). Several large forest products corporations have made or are considering substantial investments in poplar tree farms in the Pacific Northwest. Farmers and other landowners are assessing opportunities for producing and marketing cottonwood from their smaller acreage (Associated Forest Products Consultants, Inc. 1990). Productivity can be very high, provided that suitable clones are planted on proper sites and appropriate cultural techniques are applied. Many clones have been selected for planting based on performance in small evaluation plots, but few comparative data have been published on growth and yield in larger monoclonal plots where competition from neighboring clones had little or no influence on absolute or relative form, structure, and growth of the individual clones. This report describes survival, growth, stem characteristics, and stand development to age 8 of four *Populus* clones planted at 1.0-m spacing in monoclonal plots having sufficient size and borders to limit effects from trees growing in adjacent plots. To aid in interpreting clonal differences in stand productivity, detailed measurements were taken in some years to assess leaf area, bud populations, branching characteristics, and the phenology of height and diameter growth.

[1] In press in *New Forests* (1997)

APPLICATION

Productivity was high and differed substantially among four *Populus* clones, ranging from 11 to 18 Mg $ha^{-1}yr^{-1}$. Findings of interest to managers of clonal plantations include:

- Clonal rankings in height, diameter, and stand productivity were firmly established by age 3,
- Stem form differed markedly among clones and was correlated with differences in bud and branch characteristics,
- Differences in tree growth and stand productivity among clones were much

less in our large monoclonal plots than had been previously reported from smaller plots, and

- Clones appeared to differ in stockability (tolerance to crowding or competition). This implies that optimal management regimes may differ among clones with respect to one or more of the following: target diameter, stand density, or rotation age.

METHODS

The study was established in cooperation with the Washington State Department of Natural Resources at the Meridian Seed Orchard located 12 km east (lat. 47° 0' N, long. 122° 45' W) of Olympia, Washington. The low-elevation site (50 m) has a mild climate with an average growing season of 190 frost-free days and a mean July temperature of 16° C. Annual precipitation is approximately 1290 mm, falling mostly as rain from October through May; summers are periodically dry. The soil is Nisqually loamy fine sand (a sandy, mixed, mesic Pachic Xerumbrept); it is a deep, somewhat excessively drained, medium acid (pH 5.6) soil formed in glacial outwash, and would not be considered suitable for *Populus* growth without irrigation. Nearby unmanaged land is occupied by either prairie vegetation or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and several hardwood shrubs, depending on fire history. The land is level and was previously farmed for strawberry and hay crops. It was prepared for planting by plowing and disking in winter 1985-86.

The study compared four *Populus* clones planted in monoclonal plots at 1.0-m square spacing; all four clones were under consideration for use in biomass plantations. Two clones were collected by Stettler and his colleagues (Weber and others 1985; Quinsey and others 1991) in wild stands of native black cottonwood (*P. trichocarpa* Torr. & Gray); clone 7-75 was collected at 91-m elevation along the Puyallup River near Orting, Washington, and clone 8-81 was obtained at 7-m elevation in the Nisqually River Delta which is near the study site. Early growth of the Orting and Nisqually clones was above average for black cottonwood clones in initial screening trials (Heilman and Stettler 1985). The other two clones were *Populus* hybrids; clone 11-11 was a *P. trichocarpa* × *P. deltoides* Bartr. ex Marsh. var. deltoides hybrid developed and tested by the University of Washington/Washington State University Poplar Research Program (Heilman and Stettler 1985; Quinsey and others 1991); clone D-01 was a *Populus* hybrid (taxonomic identity unknown, but suspected to be either *P. trichocarpa* × *P. nigra* L. or *P. trichocarpa* × *P. angustifolia* James) developed originally at the University of Idaho and subsequently selected from a Canadian planting by Dula's Nursery of Canby, Oregon (Dula 1984).

Each clone was tested in three plots of 100 measurement trees planted at 1.0-m × 1.0-m spacing, surrounded on all sides by at least four rows of similarly spaced trees. Plots of the two hybrid clones (11-11 and D-01) were randomly located within three blocks of a larger study that compared "woodgrass" (i.e., < 0.3-m spacing, coppiced annually) and wider-spaced systems (square spacings of 0.5-, 1.0-, and 2.0-m) for biomass production (DeBell and others 1993). Plots of the two native black cottonwood clones (7-75 and 8-81) were randomly positioned within a satellite block immediately adjacent to the larger study. An additional 20 cuttings of clone 11-11 also were planted in the satellite block. Conditions of the soil and other environmental characteristics, however, were very uniform among all blocks and plots.

The clones were established by hand planting unrooted, hardwood cuttings in late April 1986. All cuttings were 30-cm long and had a minimum upper diameter of 1 cm; they were planted 20-cm deep with at least two healthy axillary buds remaining above ground. Previous experience indicated establishment success (i.e., survival and early growth) was poor if cuttings did not have at least one healthy bud above ground (Radwan and others 1987). Requiring two above-ground buds resulted in a small additional increase in establishment success but also increased the prevalence of multiple stems. At the end of the first growing season, all multiple-stemmed plants were pruned to one stem and any positions occupied by dead trees were replanted with unrooted cuttings; this re-

sulted in stands composed solely of single-stemmed trees and with all planting spots occupied.

Supplemental nutrients and water were provided uniformly in plots of all treatments to enhance survival and growth. A preplanting application of mixed or complete fertilizer (16-16-16) provided the equivalent of 100 kg ha^{-1} nitrogen, 43 kg ha^{-1} phosphorus, and 83 kg ha^{-1} potassium. Additional nitrogen fertilizer (ammonium nitrate) was applied at 100 kg N ha^{-1} in May 1988 and again in March 1992. Plots were irrigated throughout each summer by a drip system; amounts applied averaged 400-600 mm per growing season but varied from 260 to 1200 mm; yearly differences were associated more with scheduling conflicts and malfunctioning of irrigation pumps than with differences in potential evapotranspiration. All plots were kept free of weeds during the first year by tilling and hoeing; in the second and third year, sporadic weed patches were controlled by spot applications of herbicides and hoeing.

Tree survival, total height, and stem diameter were evaluated at the end of each of 8 growing seasons on the central 100 trees in each plot, and any tree damage or unusual conditions were noted. Height and diameter were also measured periodically on 25 trees per plot to assess seasonal growth patterns. Information on basal diameter (measured at stem height of 0.3m) was obtained for all years, and breast-high diameter (dbh) was also measured after mid-season in the second year. Figures presenting periodic growth utilize basal diameter as it is available for all periods. Cumulative basal area over time and diameter at age 8 are presented based on measurement at breast height (1.3 m) to facilitate comparisons with standard forestry measurements. Breast-high diameters at the end of the first year were estimated from height measurements and dbh-height relationships derived from data collected in June of the second year.

Indices for lower-stem taper were calculated from basal and breast-high diameters (basal/dbh) and slenderness was characterized with the ratio of height/basal diameter. After the first, second, and third seasons, numbers of buds and branches were counted for each annual height increment. Such data provided information on initial bud populations, development of syllleptic and proleptic branches, and branch longevity. Observations were recorded on leaf phenology, insect and disease problems, and wind damage.

Yields for ages 1 through 5 were estimated from oven-dry biomass component equations applied to basal diameter and height measurements of individual trees. The equations were developed via destructive sampling of trees at the end of years 1 through 5; selected trees were from buffer rows and were representative of the range of sizes for each clone. Equations of the form, Ln(Y) = f(basal diameter, height, and age), were fit independently for each clone. Dry weights of stems and branches were estimated by separate equations. Coefficients of determination (R^2) between predicted and measured values ranged from 0.906 for branch weight of clone 8-81 to 0.999 for stem weight of clone 7-75. Stem, branch, and leaf weights were estimated by separate equations; stem and branch weights were summed to provide above-ground dry woody biomass. Above-ground woody biomass estimates for all trees on each plot were summed, and the resulting plot sums were expanded to woody biomass yield per hectare. Destructive sampling of all clones did not occur after year 5; thus, stand growth parameters beyond age 5 are limited to height, diameter, and basal area.

Leaf area index was estimated by determining the projected area of a sub-sample of leaves from each biomass sample tree using an area meter (LICOR 3100). Leaf area per tree was then estimated via area/leaf weight relationships; it was expanded to a per unit area basis by summing estimates for all trees on the plot; total leaf area (m^2) was then divided by ground surface area (m^2) to provide the dimensionless leaf area index (LAI).

Annual diameter growth (per tree) and basal area growth (per hectare) were plotted against a competition index calculated by summing the product of basal diameter (m^2) × height (m) (both measured at the beginning of the growth year) for all trees on the plot and expanding it to a per hectare value. This allowed comparison of clonal growth rates at similar levels of com-

petition, even when the same competition level was reached in different years.

Statistical comparisons required special consideration because the four clones had been assigned to plots randomly as components of two adjacent experimental plantings rather than as one experiment. We first examined the data for differences in growth performance among blocks and concluded that there were none. Two approaches were used to arrive at that determination: (1) analyses of variance for height and diameter of clones 11-11 and D-01 indicated that block effects were non-significant for both height ($p = 0.66$) and diameter ($p = 0.53$); and (2) graphic comparisons revealed that early growth of 20 trees of clone 11-11 in the satellite block (composed primarily of replicated plots of clones 7-75 and 8-81) was essentially identical to mean growth of clone 11-11 in the other three blocks. Given the lack of evidence for environmental or growth differences among blocks, we examined mean tree and plot data via standard analysis of variance procedures assuming a completely randomized design (i.e., block was not considered as a source of variation). Where appropriate, clonal treatment means were compared by the Ryan-Einot-Gabriel-Welsch multiple-stage test (Ramsey 1978) (using $p \leq 0.05$ to judge significance) and standard deviations were calculated. These data are displayed in tables or figures to illustrate trends in development of the clonal plantings.

RESULTS AND DISCUSSION

Survival and growth during the establishment year

Cuttings of all four clones produced roots and shoots very well, and survival at the end of the first growing season and prior to replacement planting was 96% or higher. The two black cottonwood clones (7-75 and 8-81) averaged 2.4 m in height and 2.2 cm in basal diameter; hybrid clone 11-11 was 2.3-m tall and 2.2 cm in basal diameter, but hybrid clone D-01 was considerably shorter in height (1.7 m) and smaller in basal diameter (1.3 cm). Above-ground dry woody biomass averaged 2.9 Mg ha^{-1} for the two black cottonwood clones and hybrid 11-11; whereas, clone D-01 produced only 1.2 Mg ha^{-1}.

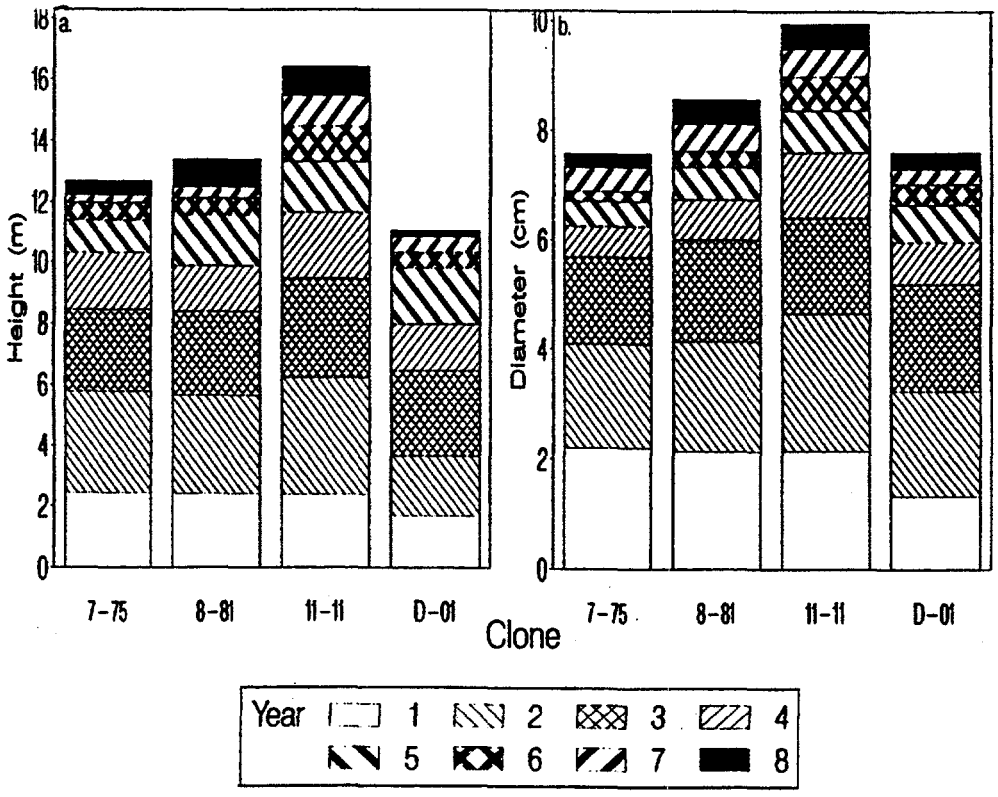


Fig. 1. Eight-year cumulative growth in height and basal diameter of trees surviving to year 8 by clone.

Patterns of height and diameter growth

Annual increments of height and diameter growth are shown by clone in Figure 1 for all trees that survived through age 8. By the end of the second year, height and diameter of hybrid clone 11-11 were greater than either of the black cottonwood clones, which in turn were larger than hybrid clone D-01. Ranking by size thereafter remained similar through age 8 years, except that clone 7-75 was surpassed eventually by clone 8-81 in both height and diameter and was equaled by clone D-01 in diameter. Annual growth of all clones declined as trees became older and larger and inter-tree competition became more intense, but growth of the black cottonwood clones accelerated somewhat for diameter during the seventh year and for height in the eighth year, presumably in response to increased crown differentiation within the stands. Relative growth of the different clones differed among years and over time as follows. During the third through the seventh years, annual growth of hybrid clone D-01 was equal to or greater than either black cottonwood clone (7-75 or 8-81) in both height and diameter, and its growth during the fifth year (1990) was slightly greater than that of clone 11-11. Diameter growth of clone 8-81 was equal to or greater than clone 11-11 in the first, third, seventh, and eighth years.

Differences among clones in magnitude and trends in annual growth can be attributed in part to differences in leaf and growth phenology and prevailing weather conditions. Clones D-01 and 7-75 commonly broke bud in early March; clone 8-81, by mid-March; and clone 11-11, at the end of March or in early April. Terminal bud-set occurred in early to mid-September in clone D-01, and foliage soon yellowed and dropped. Terminal growth continued into October for the two black cottonwood clones and hybrid 11-11, and green foliage sometimes remained on the latter clone into early November. Such differences in shoot and leaf development are reflected in seasonal patterns of periodic daily height and diameter growth of dominant and co-dominant trees as shown in Figure 2 for the third growing season — a year of average temperature and moisture conditions. By mid-May, height growth of all clones had accelerated; all attained maximum height growth of 2 to 3 mm per day in July. Height growth of clone D-01 then declined rapidly whereas growth of the two black cottonwood clones and hybrid clone 11-11 continued at a near maximum rate

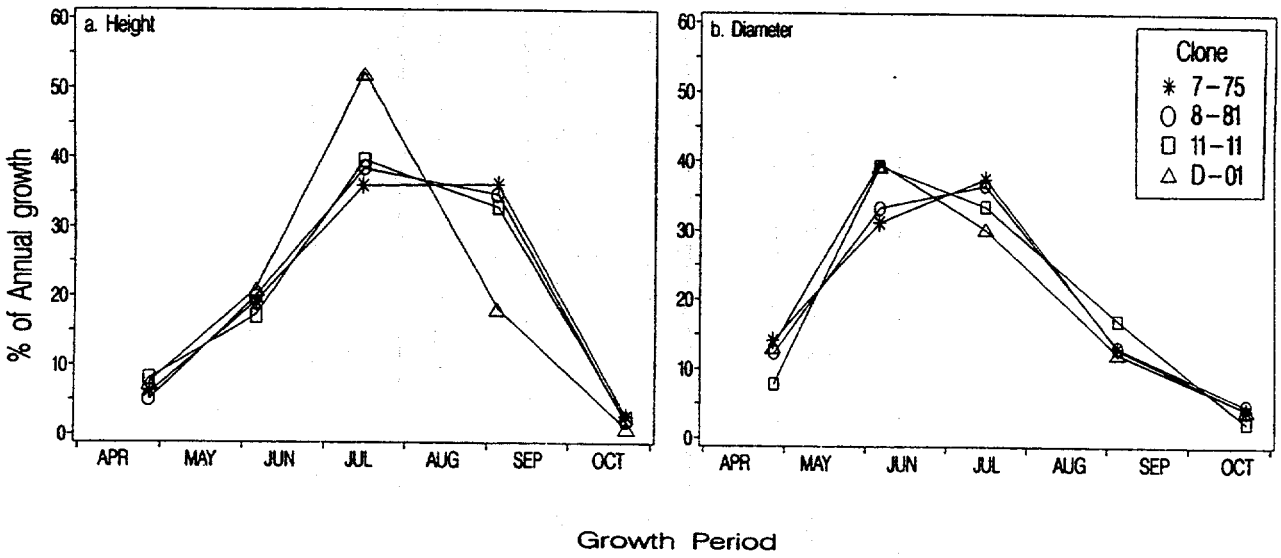


Fig. 2. Phenology of height and basal diameter growth of four *Populus* clones planted at 1.0-m spacing.

into September. In general, diameter growth of the *Populus* clones peaked earlier than height growth. Although this finding may run counter to phenological trends commonly found for other conifers and hardwoods in temperate zones, it is consistent with the pattern for red alder (*Alnus rubra* Bong.), another species with a "sustained growth" habit (Zimmerman and Brown 1971), growing at the study site and other locations (DeBell and Giordano 1994).

There were also differences in diameter growth patterns among clones. Diameter growth of clone D-01 peaked earlier than that of the two black cottonwood clones. Diameter growth of the two black cottonwood clones and, to a lesser extent, hybrid clone 11-11 remained at a high level later into the season whereas clone D-01 declined rapidly after its peak in mid-May. When moisture was abundant and temperatures were warm early in the growing season and conditions later in the season were unfavorable (i.e., dry or unusually cool), growth of clone D-01 was relatively better than growth of the other clones. Conversely, adverse growing conditions during the early season followed by more favorable late season temperature and moisture conditions favored growth of the other clones. Similar though less pronounced differences existed between the two black cottonwood clones and hybrid clone 11-11, but relative growth performance probably is more specifically influenced by the duration of drought stress as the hybrids of *P. trichocarpa* and *P. deltoides* have greater stomatal control and drought resistance than black cottonwood (*P. trichocarpa)* clones (Schulte and others 1987).

Although general declines were expected with age, growth was less than expected in the fourth (1989) and sixth (1991) years (Fig. 1a and b), with the apparent reduction being greater for the two black cottonwood clones and clone D-01 than for clone 11-11. Weather and irrigation records show that during the March-June period in both 1989 and 1991, precipitation was below normal and irrigation inputs were very low because of equipment problems. Total input of water during the early growing season of

Table 1. Tree height, axillary buds on the current terminal shoot, branching characteristics, and leaf area per tree during first and second year growth of four *Populus* clones.

	Clone			
Characteristic	7-75	8-81	11-11	D-01
	First year			
Height (m)	2.4a	2.4a	2.3a	1.7b
Buds (no.)	44.8a	46.4a	47.2a	48.0a
Sylleptic branches (no.)	20.6a	20.0a	14.2a	1.6b
Leaf area (m^2)	1.7a	1.6a	1.7a	0.5b
	Second year			
Proleptic branches (no.)	15.7b	21.3b	5.8c	40.9a
Terminal growth (m)	3.4ab	3.0b	3.8a	1.9c
Buds or current terminal (no.)	44.3b	47.2b	59.5a	42.7b
Buds producing sylleptic branches				
(no.)	4.7b	9.9b	22.3a	0.0c
(%)	10.6	21.0	37.5	0.0
Leaf area (m^2)	3.4bc	3.7b	5.4a	2.4c
	Branch retention			
Total branches on first year height increment at end of				
2nd year	35.0a	38.7a	6.7b	40.7a
3rd year	1.0b	2.0b	0.0b	36.1a

Note: Values in a row followed by the same letter did not differ at $p \leq 0.05$.

1989 and 1991 was at least 50% less than that occurring during the first three years of growth (1986-1988) and in the fifth (1990) and seventh (1992) years.

Development of buds, branches, and leaf area

Height and diameter growth of the clones prior to the onset of intertree competition were strongly influenced by the dynamics of bud and branch populations and associated effects on the development of leaf area (Table 1). Although the clones produced similar numbers of buds on the main stem during the establishment year, substantial differences occurred in the extent of sylleptic branching and development of leaf area. A branch is classified as sylleptic if it develops and elongates during the same growing season the bud is formed. If the bud does not develop into a branch until the following growing season, the branch is classified as proleptic. The two black cottonwood clones and clone 11-11 had many more sylleptic branches and at least three times the leaf area of clone D-01 by the end of the first growing season. The total number of branches per tree produced by clone D-01 during the first two years was comparable to those produced by the other clones; however, since almost all of its branches were proleptic, they did not contribute to the development of leaf area until the second year. In addition, proleptic branches have been shown to export a lower percentage of photosynthate than sylleptic branches (Scarascia-Mugnozza 1991; Hinckley and others 1992). The combination of the differences in pattern of leaf area development and the carbon export behavior of the two branch types has been suggested as conferring a potential productivity advantage to clones with greater production of sylleptic branches (Hinckley and others 1992). Although the degree of syllepsis may not be the only contributing factor, differences in second-year sylleptic branching and leaf area were consistent with subsequent growth rankings among the four clones (Table 1, Fig. 1). For example, clone 11-11 produced more buds and more sylleptic branches than any other clone; it produced 39 to 124% more leaf area and maintained its size ranking. A shift in rank occurred between the two native clones. Clone 7-75 outgrew clone 8-81 during the first two seasons, but by the end of the second year the greater sylleptic branching of clone 8-81 resulted in greater leaf area. By the end of the third season, these two black cottonwood clones were very similar in height but clone 8-81 was slightly larger in diameter. By the fifth season, clone 8-81 had surpassed clone 7-75 in both height and diameter. Number of branches retained on the first year's height increment was greater for clone D-01 than for the other three clones. After the third growing season, little branch mortality had occurred on the lower portion (first year's growth) of clone D-01 whereas, essentially all branches had died on the other clones.

Table 2. Slenderness ratio and lower stem taper by clone at ages 2 and 8. Slenderness ratio = height in meters ÷ diameter at 0.3 m in centimeters. Lower stem taper = diameter at 0.3 m ÷ diameter at 1.3 m.

	Slenderness ratio		Lower stem taper	
Clone	Age 2	Age 8	Age 2	Age 8
7-75	1.46a	1.70a	1.35bc	1.13b
8-81	1.41a	1.59b	1.39b	1.18a
11-11	1.41a	1.72a	1.18c	1.06c
D-01	1.17b	1.51c	1.66a	1.20a

Note: Values in a column followed by the same letter do not differ at $p \leq 0.05$.

Stem form

The clones also differed in slenderness ratio (height/basal diameter) and lower-stem taper (basal diameter/dbh) (Table 2). At age 2, clones 7-75, 8-81, and 11-11 had smaller values for lower stem taper and higher slenderness ratios than D-01. The values for lower stem taper at age 2 were negatively correlated ($r = -0.92$; $p=0.07$) to the percentage of buds producing sylleptic branches. Thus, the higher the percentage of buds becoming sylleptic branches, the less tapered the tree bole. This effect is consistent with the previously mentioned observation that sylleptic branches export a higher percentage of photosynthate than proleptic branches (Scarascia-Mugnozza 1991; Hinckley and others

1992). Such differences among clones were reduced over time as the live crowns lifted and lower stem growth was influenced by more complex interactions of branch type, age, and crown position, including clonal differences in branch retention. Slenderness ratios have increased over time as would be expected at this dense spacing. Clone 8-81 grew proportionately more in diameter than in height between years 2 and 8 than 11-11 and thus shifted in rank from first to third in relative slenderness.

Leaf area indices and accumulation of woody biomass and basal area

Leaf area expanded rapidly in the second and third growing seasons, nearing or reaching a peak in all clones during the third year (Fig. 3a). Leaf area index attained maxima of 7.7 and 7.8 for hybrid clone 11-11 at age 3 and 4 and then declined to 6.4 at age 5. Maximum leaf area indices for the other three clones ranged from 5.0 to 5.7. Leaf area indices for clones 11-11, 7-75, and 8-81 had declined by age 5, averaging about 20% lower than the maxima. Leaf area index of clone D-01, however, changed relatively little after attaining a plateau of about 5.0 at age 3.

Above-ground woody biomass production accelerated markedly during the third season, and rates were more or less maintained through the fifth year (Fig. 3b). At 5 years, total production was 56 Mg ha^{-1} for D-01, 63 and 66 Mg ha^{-1} for 7-75 and 8-81, and 91 Mg ha^{-1} for 11-11. Mean annual increments through age 5 were 11 Mg ha^{-1} for D-01, 13 Mg ha^{-1} for 7-75 and 8-81, and 18 Mg ha^{-1} for 11-11. Subsequent evaluations of biomass production of clones 11-11 and D-01 through year 7 in adjacent spacing trials revealed that current annual biomass increment had peaked in the 1.0-m spacings in the 4th year for clone 11-11 and in the 5th year for clone D-01. The decline was so great in clone D-01 that mean annual increment also culminated in the 5th year; mean annual biomass increment did not peak in clone 11-11, however, until the 6th year. Because height and diameter increment patterns of the two black cottonwood clones were intermediate between those of the two hybrids, we suspect that similar biomass growth trends occurred and that mean annual biomass increments at 5 years represented a near maxima for all four clones in the study environment. Moreover, our measured rates of production for clone 11-11 are very similar to those obtained in 7-year-old research trials (17 Mg ha^{-1} yr^{-1}) and operational plantings (12 to 17 Mg ha^{-1} yr^{-1}) by James River Corporation in the lower Columbia

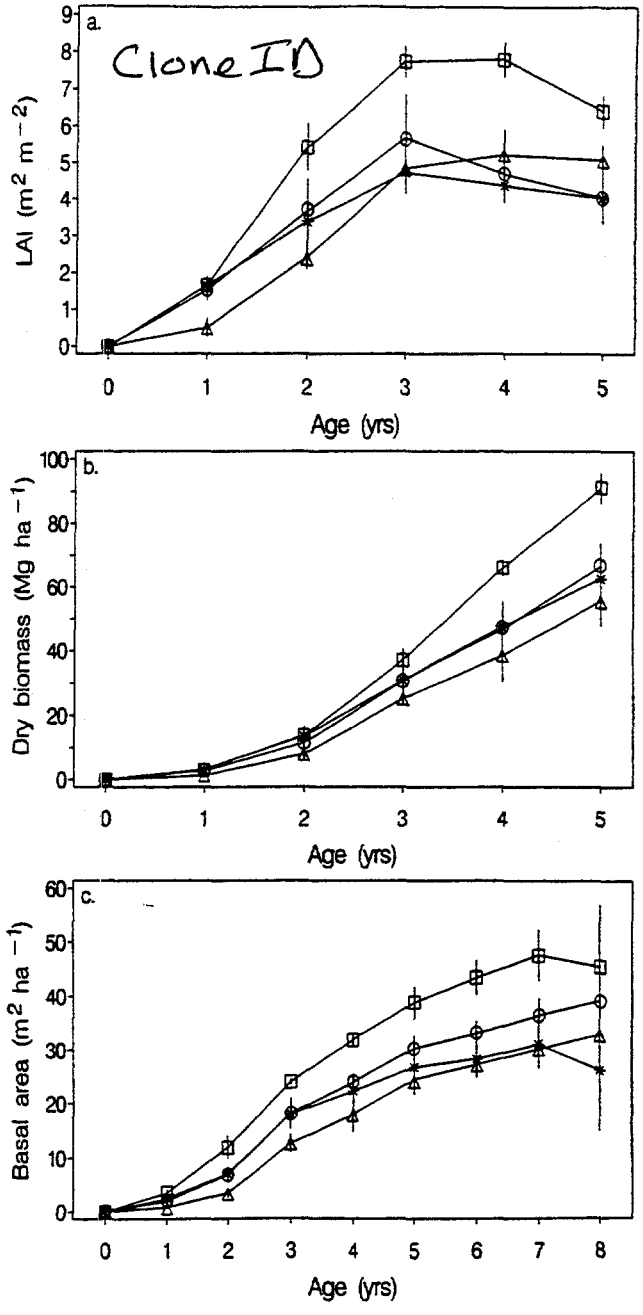


Fig. 3. Accumulation of leaf area (a), above-ground woody biomass (b), and basal area (c) in stands of four *Populus* clones (legend as in Fig. 2b). Basal area based on diameter at 1.3 m. Standard errors shown as vertical lines.

River Valley [pers. comm. from William Schuette of James River Corporation, Camas, Washington (January 4, 1995)].

The clones also differed in the amount and proportion of branches in the woody biomass yields. Clone D-01 had the most branches (~10 Mg ha^{-1}), and they comprised about 18% of the woody biomass. Branch weights for other clones were 5 to 7 Mg ha^{-1} and accounted for only 7 to 10% of the woody biomass.

Basal area growth accelerated during the second and third season (Fig. 3c). Rate of accumulation declined slightly thereafter, but basal area of all clones continued to increase through the seventh season. Accumulated basal area of two clones, however, was lower for different reasons at the end of the eighth season. Losses in basal area of hybrid clone 11-11 were caused by combined effects of borer damage and a severe windstorm; losses for clone 7-75 were associated primarily with competition-related mortality. Highest basal areas per hectare attained at age 7 for clones 11-11 and 7-75 were 48 m^2 and 31 m^2, respectively, whereas highest basal areas attained at year 8 for clones 8-81 and D-01 were 38 m^2 and 33 m^2.

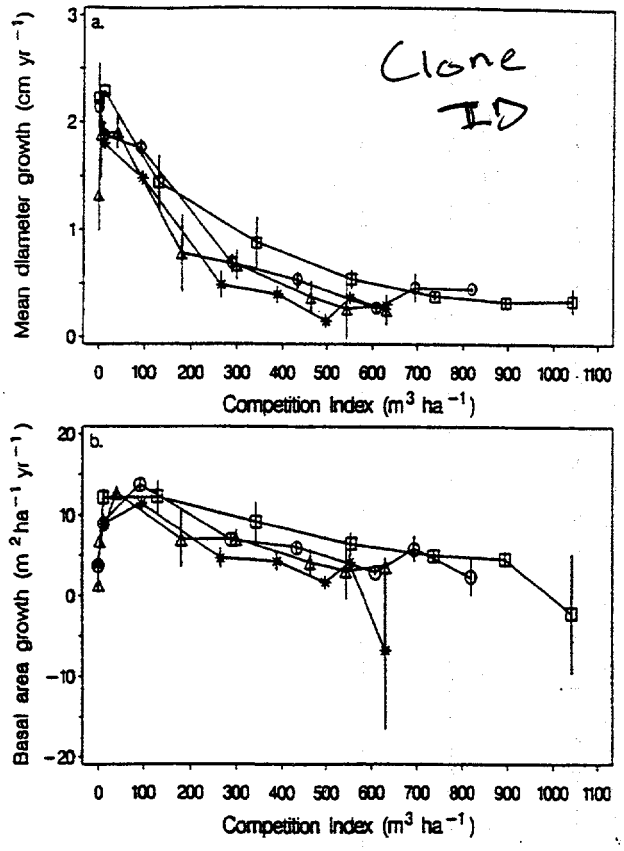


Fig. 4. Current annual diameter growth per tree (a) and basal area growth per hectare (b) in relation to an index of stand competition (Σ D^2H in m^3ha^{-1}) at the beginning of the growing season for four *Populus* clones (legend as Fig. 2b). Standard errors shown as vertical lines.

Relative tolerance to intertree competition

Mean tree growth in height and diameter peaked in the second or third year, and, in general, annual basal area and, presumably, woody biomass growth per hectare had begun to decline by the fifth year for all clones planted at the 1.0-m spacing. Such declines in mean tree and per hectare growth in these young plantings are largely due to the development of stress associated with intense intertree competition. In order to determine whether differences existed among clones in tolerance to competition or "stockability" (DeBell and others 1989a), measures of annual mean tree (diameter) and per hectare (basal area) growth were plotted against a stand competition index (Figure 4a and 4b). With the exception of clone 8-81 in year 7 or 8, growth of hybrid clone 11-11 exceeded that of other clones at similar levels of competition. For other clones, annual basal diameter growth per tree began to decline at lower levels of competition index, and the decline was more abrupt than for hybrid 11-11 (Fig. 4a); the same is true of basal area growth per hectare (Fig. 4b). The sharp decline in apparent basal area growth during the last period (year 8) for clones 11-11 and 7-75 is due to mortality discussed in the previous section on basal area accumulation. Thus, clone 11-11 not only grows more rapidly than other clones, it also has the capacity to tolerate and grow more rapidly at higher levels of stand density. Both traits — individual tree growth and stockability — are important to stand productivity.

Tree and stand characteristics at 8 years

Current annual increment in basal area and above-ground woody biomass peaked in all clones, and total accumulation in basal area

(and presumably biomass) has declined in two clones. Tree survival at the end of the eighth year ranged from 68 to 95% (Table 3). Little mortality had occurred in any clone through age 7 years, but the two native clones and hybrid clone 11-11 suffered considerable mortality during the eighth growing season. Clone 11-11 was clearly superior to all other clones in height and diameter. The sizable differences among clones in mean basal area at age 8 were not statistically significant (Table 3), primarily because the values are strongly influenced by recent mortality and this was not distributed uniformly among the replicate plots of individual clones.

Damaging agents

During the first eight growing seasons, insect and disease problems were generally minimal. Aphids appeared on all clones but soon were controlled by an expanding population of ladybugs. *Melampsora* rust developed during late summer on the two native clones (7-75 and 8-81) and may partially account for their poorer subsequent growth in comparison to clone 11-11 which remained essentially free of rust. Some lateral buds were destroyed on all clones by eriophyd mites (*Eriophyes parapopuli*). This damage occurred primarily on the ends of lower lateral branches and was roughly proportional to the timing of budset (damage greatest on D-01, intermediate on 7-75 and 8-81, and least on 11-11).

Heavy infestations of the poplar-and-willow borers (*Cryptorhynchus lapathi*) were observed after the fifth year, especially in clone 11-11. Observations made in adjoining plots of other spacings suggested that infestations were greater in stands having higher density or more intense competition. By the end of the seventh growing season, 27 and 16% of the trees in clones 11-11 and 7-75 had been attacked, respectively, whereas only 8 and 5% of clones D-01 and 8-81 were affected.

After trees were measured at the end of the seventh growing season, a severe windstorm occurred in the area and resulting damage varied significantly among clones. Hybrid clone D-01 and the two native clones (7-75 and 8-81) were basically unaffected; although some trees of these clones had broken branches or tops, none were windthrown or seriously broken. Clone 11-11, however, suffered substantial damage; some stems were windthrown or "lodged", but most damaged stems were broken at 0.2 to 1.0 m above ground. About 7% of all measurement trees of clone 11-11 in the 1.0-m spacing suffered such breakage, which occurred primarily in stem segments with evidence of considerable borer activity, and thus considerably weakened structure.

Table 3. Survival, height, diameter, and stand basal area of four *Populus* clones planted at 1.0-m spacing at age 8 years.

Clone	Survival	Height	Diameter 0.3 m	Diameter 1.3 m	Basal area
	%-	m	---- cm ----		m^2ha^{-1}
7-75	68a	12.8bc	7.6b	6.8b	26.2a
8-81	85a	13.4b	8.6ab	7.3b	38.1a
11-11	79a	16.1a	9.5a	9.0a	45.5a
D-01	95a	11.1c	7.6b	6.4b	32.9a

Note: Values in a column followed by the same letter do not differ at $p \leq 0.05$.

CONCLUSIONS AND IMPLICATIONS

All four clones were easy to establish with unrooted hardwood cuttings at the experimental site under the imposed management regime and survival was excellent. Growth differences, however, were manifested early and clonal rankings were established by age 3. Bud and branching characteristics were closely related to leaf area development, tree growth rates, and stem form of the four clones tested.

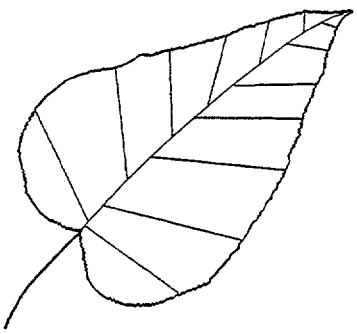
Competition in these 1.0-m spaced plantings was such that growth in height and diameter of all clones declined substantially by the fourth growing season. Subsequent work in adjacent spacing trials involving clones 11-11 and D-01 only indicated that mean annual increment peaked during the sixth season for clone 11-11 and during the fifth year for clone D-01. Given that declines in height and diameter increment of the two black cottonwood clones were intermediate between clones 11-11 and D-01, it seems reasonable to rank the clones based on

productivity attained through year 5. Thus, clone 11-11 with 18 Mg ha^{-1} yr^{-1} was about 40% more productive than the two black cottonwood clones and more than 60% more productive than clone D-01.

Other research (DeBell and others 1996a) and operational experience [pers. comm. from William Schuette of James River Corporation, Camas, Washington (January 4, 1995)] suggest that these productivity values are indicative of the levels of mean annual production that may be obtained at wider spacings with slightly longer rotation ages. Our productivity values, however, are lower and differences among clones are less than values reported previously. Mean annual production values determined at age 5 by Heilman and Stettler (1985) for clone 11-11 and the population sources from which clones 7-75 and 8-81 were derived were about 28 and 16 Mg ha^{-1}, respectively. These authors appropriately acknowledged that clonal interactions among adjacent 9-tree plots exaggerated differences between high and low producers. Although the small plots established in most genetic trials are necessary (and useful) for screening large numbers of clones, they do not provide adequate information on per hectare productivity or on relative productivity differences among clones selected as appropriate for operational use. More accurate definition of such differences may be important when other factors, such as susceptibility to damaging agents or wood quality, may be significant considerations.

Plottings of annual growth in relation to stand competition indices suggested that stockability differences (tolerance of crowding or competition) exist among the clones. The potential importance of such differences to stand productivity merits additional investigation over longer time periods and with additional clones. Any finding of substantial differences in stockability implies that optimal management regimes may differ among clones with respect to one or more of the following: target diameter, stand density, or rotation age. Moreover, given the same management regime, clones having higher stockability offer greater flexibility for extending rotation length because yield reductions due to mortality or growth deceleration will be lower than for clones having lower stockability.

Pests and weather conditions had differential influences on the four clones despite the short time involved in our evaluation. The most productive clone (11-11) was resistant to the native *Melampsora* rust and least affected by drought, but was the most susceptible to borer infestation and wind damage. Such differences could attain considerable importance in some locations, particularly with longer rotations.



Chapter 5

Productivity of *Populus* in Monoclonal and Polyclonal Blocks at Three Spacings[1]

Dean S. DeBell and Constance A. Harrington

Abstract: Four *Populus* clones were grown at three spacings (0.5 m, 1.0 m, and 1.5 m) in monoclonal and polyclonal plots in western Washington. After the third year, many individual tree and stand traits differed significantly by clone, spacing, deployment method, and their interactions. Differences among clones in growth and form were greater in polyclonal than in monoclonal plots, and differences in performance between deployment methods were greater in the denser spacings. Monoclonal stands had greater uniformity in tree size than polyclonal stands. Total woody yield decreased with increased spacing. Some clones differed in yield from other clones in both monoclonal and polyclonal plots. Assuming equal numbers of plants from the same clones were planted, the manner of deployment had no effect on productivity; that is, although there were clonal differences in yield, mean yield of the four clones in monoclonal plots did not differ from the yield of polyclonal plots. Comparative yields (polyclonal ÷ monoclonal) of the clones in polyclonal plantings differed substantially, however, and the increases or decreases in comparative yield differed with spacing. As a result, production and inventory was less evenly balanced among clones with polyclonal than monoclonal deployment.

Short-rotation intensive culture (SRIC) of clonal poplar and willow plantations has advanced from a theoretical concept to a viable fiber and biomass production system through strong research and development efforts in North America (Ranney and others 1987; Richardson 1989) and Europe (Christersson and others 1993). In the northwestern USA, research on genetics and physiology has produced several hybrid poplar clones (Stettler and others 1988; Hinckley and others 1989) that are very productive when planted on suitable sites using appropriate cultural techniques (Heilman and others 1991). SRIC is becoming an important component of the rapidly changing forest products economy of the Pacific Northwest (Miner 1990) where several companies have established large farms to produce poplar fiber.

Although current knowledge is sufficient to establish productive *Populus* plantations, significant questions remain concerning effects of spacing and genotype deployment on growth and yield. Most clones have been selected based on growth performance in small, monoclonal evaluation plots of a single spacing. Few data have been collected to evaluate or compare growth and yield of clones in larger plots or in plots of different spacings. One European study has shown that relative growth of clones may differ by spacing (Panetsos 1980), but experimental environment (i.e., different clones planted on adjacent spokes in a Nelder's design) consisted of inter-clonal as well as intra-clonal competition. There is little information concerning the degree to which relative clonal performance in monoclonal planting changes with spacing. Several reviews have considered factors to be considered in decisions about clonal deployment (DeBell and Harrington 1993; Lindgren 1993; Zsuffa and others 1993; Foster and Knowe 1995). There is a paucity of experimental data that address specific questions related to monoclonal vs. polyclonal deployment. Preliminary reports exist for a small test in Yugoslavia (Markovic and Herpka 1986) and one in Oregon (Shuren 1994, 1996); in addition, diameter distributions have been modeled using data from several combinations of two clone mixtures of eastern cottonwood (*Populus deltoides* Bartr.) (Knowe and others 1994). Do clones grow similarly (in absolute terms and

[1] In press in *Canadian Journal of Forest Research* (1997).

relative to each other) in monoclonal and polyclonal plots? Are there differences in yield between monoclonal and polyclonal plots? Do the answers to these questions concerning deployment differ with spacing?

To help answer the above questions, we established monoclonal and polyclonal plantings of four *Populus* clones at three spacings. This paper reports 3-year results for survival, height, diameter, tree form, stand uniformity, and yield as affected by spacing in monoclonal and polyclonal plots.

MATERIALS AND METHODS

Site description

The research plantings for our study were established in spring 1990 at the Washington State Department of Natural Resources Meridian Seed Orchard, located 12 km east of Olympia, Washington. Elevation is about 50 m. Climate is mild with an average growing season of 190 frost-free days and a mean July temperature of 16° C. Precipitation averages 1290 mm per year, falling mostly as rain from October through May; summers are periodically dry. Prior to installation of this study, the immediate area was in native forest occupied by Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and several hardwood species and shrubs. The trees were felled, merchantable stems removed, stumps pushed out of the ground, and the non-merchantable material was burned in piles. The topography is level and is occupied by two distinct soil types, both derived from glacial outwash. Most of the area contains a very deep, somewhat excessively drained, loamy sand (soil series Indianola, classified as mixed, mesic Dystric Xeropsamment). A minor portion of the area had gravel contents of 20 to 30% in the loamy sand surface soil, but does not drain as rapidly as the formerly mentioned soil type. Because of low rainfall during the growing season, neither soil would be considered suitable for commercial *Populus* plantations without irrigation.

The site was disked after harvest and burning, and a mix of N-P-K fertilizers was applied one month prior to planting to provide the equivalent of approximately 100 kg each of N, P, and K per hectare. In addition, 900 kg lime ha^{-1} was applied as a mixture of limestone and dolomite. Between the second and third growing season, 100 kg N ha^{-1} was applied as ammonium nitrate. Both the preplant and subsequent fertilizer applications (including lime) were spread on the soil surface but not incorporated. Preplanting and post-planting herbicide applications and hoeing were used as necessary to maintain the plots in a weed-free condition. Irrigation was provided by drip lines laid down 2 m apart; emitters (2.3 liters per hour) were spaced at 1-m intervals along each line. Amounts of water applied varied by year and weather conditions, ranging from 75 cm to 100 cm $ha^{-1}yr^{-1}$.

Experimental design and treatments

The study was established as a factorial design with five clonal treatments (four clones planted in monoclonal plots and one polyclonal plot with all clones in intimate mixture) and three square spacings, replicated in three blocks.

The four *Populus* clones were selected for use based on availability of stock, contrasting branching characteristics, and superior growth. Three of the clones were *P. trichocarpa* × *P. deltoides* hybrids developed in the University of Washington -Washington State University poplar breeding program (Heilman and Stettler 1985; Quinsey and others 1991); they have been used in many commerical plantations, and cuttings were provided by James River Corporation:

- Clone 11-11 is one of the first hybrids developed in the program, and it has been planted extensively throughout the Northwest; it grows rapidly and produces many sylleptic branches (i.e., branches that develop and elongate during the same growing season in which the bud is formed).
- Clone 47-174 grows very rapidly but produces very few sylleptic branches.
- Clone 49-177 grows very rapidly and produces many sylleptic branches.
- The fourth clone is a local selection of *P. trichocarpa* named Capitol Lake (CL) that had demonstrated excellent growth in

small research plantings. It produces many sylleptic branches.

The three square spacings (0.5-m, 1.0-m, and 1.5-m) were selected to provide a range of stand density conditions; the two wider spacings have been commonly used in research plantings and in operational bioenergy plantations. The narrowest planting (0.5-m) provided a treatment in which competition developed more rapidly and to a higher degree.

Plot installation

Plot size varied by spacing; each treatment plot consisted of a 100-tree interior measurement plot (ten rows by ten columns) surrounded by three to eight buffer rows. Areas where debris piles had been burned were delineated and excluded from use in the study. Two blocks of plots were located on the major soil type; the third block was placed on the gravelly, less rapidly draining soil type.

The plots were established with unrooted woody cuttings which were $\geq$ 1 cm in diameter, 30 cm long, and had several healthy buds present. Cuttings were soaked in water overnight and then firmed into holes created with metal rods. The goal was to insert approximately 25 cm of the cutting length into the ground, but two healthy axillary buds were to remain above ground. Previous experience indicated establishment success (i.e., survival and early growth) was poor if cuttings did not have at least one healthy bud above ground (Radwan and others 1987). Requiring two buds above-ground ensured that a high percentage of cuttings sprouted but necessitated a later pruning to remove secondary or multiple stems. Planting was done during the last week of March 1990; stem pruning was done in autumn 1990.

Polyclonal plots were planted with 49-177 and CL alternating in even-numbered rows and 11-11 and 47-174 alternating in odd-numbered rows. Thus, the eight trees surrounding any individual subject tree represented a consistent composition of three clones, all of which differed from the subject tree.

Data collection and analyses

In both monoclonal and polyclonal plots, the 100-tree interior plot was used to measure tree dimensions and estimate standing biomass at the end of the third growing season. Tree diameter and height were recorded, and any unusual conditions (stem characteristics, stress or damage due to weather, insects, or diseases) were noted. Tree diameters were measured at 0.3 and 1.3 m above ground with metal diameter tapes and were recorded to the nearest 0.1 cm. Heights were measured with telescoping fiberglass poles and recorded to the nearest 5 cm.

Indices for lower-stem taper (0.3 m diameter/dbh × 100) and slenderness (ht/dbh × 100) were calculated from measurements of diameter and height. Coefficients of variation for diameter and height were calculated for each 100-tree measurement plot, and the three plot values were averaged to provide a mean coefficient of variation for each treatment.

To estimate standing biomass at age 3, five trees were selected from the buffer rows surrounding the interior measurement plot in each monoclonal plot. Trees in the outermost buffer row and in the buffer row immediately adjacent to the measurement plot were excluded. In total, 180 trees were selected to cover the range of tree sizes present in the study (i.e., 15 trees for each clone and spacing). Biomass-estimation trees were measured for height and stem diameter at 0.3 and 1.3 m, felled, and the number of live and dead branches counted. Live branches were classified as either sylleptic or proleptic. The trees were then divided into component parts (stem and live branches) and fresh weights of the components were determined. Subsamples of each were selected for determination of moisture content and dried to constant weight at 105° C.

Branching traits of the clones were examined using data from the two largest trees of the five trees sampled for biomass in each plot. Such trees were representative of trees in the stand's canopy. An index of branchiness was calculated as the percentage of total live woody weight

associated with live branches. In addition, mean tree values were determined for numbers of live and dead branches, live branches only, and sylleptic branches formed in 1992.

Regression equations to predict dry biomass by component (stem or branches) were developed for each clone using logarithms of tree diameter at 0.3 m and height as forced independent variables. Coefficients of determination (R^2) ranged from 0.957 (live branches of clone 49-177) to 0.997 (stems of clone 47-174). Spacing was also evaluated for inclusion as an additional variable, but it contributed significantly to only two equations (stem biomass of clone 49-177 and branch biomass of clone 47-174). Partial R^2 for spacing in such instances was only 0.01. The equations were adjusted for log bias and then used to predict biomass components of individual trees in each permanent measurement plot. Stem and live branch weights were summed by component for each plot, and the sum was expanded to provide estimates of biomass per hectare.

Relative performance of each clone in polyclonal and monoclonal plantings was also evaluated by comparing the yield of the clone in polyclonal plots to its yield in pure culture, assuming an equal area occupied (or equal number of stems at time of planting). Thus, "comparative yields" of each of the four clones in polyclonal plantings were calculated for each spacing by dividing the yield of the clone in polyclonal plots by one-fourth of the yield it attained in monoclonal plots.

Three types of setups were used for analysis of variance (ANOVA). To answer most questions associated with individual trees, e.g., "Are there differences among clones, spacings, and deployment in mean tree size and stem form?", the first-order sources of variation (with their degrees of freedom) were: blocks (2), clone (3), deployment (1), and spacing (2). Some branch data, however, were collected only in monoclonal plots; in these instances, the first-order sources of variation for the analyses were blocks (2), clone (3), and spacing (2). Both of these analyses used mean tree values by plot and clone as response variables. To answer the questions associated with plots, "Are there differences in yield or stand uniformity between monoclonal and polyclonal blocks?", we used plot yield (i.e., the sum of the individual tree values converted to a per hectare basis) and coefficients of variation as response variables. For such analyses, there were five clonal deployment options or treatments (four monoclonal and one polyclonal). The ANOVA setup had clonal treatment (4), block (2), and spacing (2) as the first-order sources of variation. Survival data were analyzed using the *logit* transformation (Sabin and Stafford 1990).

Treatment effects were judged as significant when the probability of a greater F value was ≤ 0.05; however, the actual probability values are provided for readers to make judgements based on other values. Means were separated by Ryan-Einot-Gabriel-Welsh multiple F test procedures (SAS Institute Inc. 1988).

RESULTS

The experimental design provided a sensitive assessment of treatment effects because tree growth was very rapid (2-4 m height increment per year) and environmental conditions within and among treatment plots and within blocks were extremely uniform. The main effects of clone and spacing were significant for all traits, deployment was significant for tree size and lower-stem taper, and interactions between two or three main effects were significant for most individual tree characteristics but not for stand characteristics such as yield and size variation (Table 1). Effects of block were significant for all tree and stand traits related to growth or productivity (but not to stem form, branching habit, or tree size variation); as expected, the third block on the gravelly, more poorly drained soil had smaller trees and lower yields than the other two blocks which were similar.

Survival

Initial establishment success (i.e., root and shoot development of cuttings) was excellent. All planting positions were occupied with vigorous trees by early summer and all had a surviving tree at the end of the first growing season. Competition-related mortality began to occur in the 0.5-m spacing during the second

Table 1. Results of analyses of variance for various tree and stand characteristics

A. Tree characteristics

	Source of variation					
Trait	Clone	Spacing	Deployment	C × S	C × D	C × S × D
Survival	**	**	0.18	**	0.07	*
Height	**	**	**	**	**	**
Dbh	**	**	**	**	**	0.09
Lower-stem taper	**	**	**	**	**	**
Slenderness	**	**	0.07	**	**	**
Branch index	*	**	NA	*	NA	NA
Live & dead branches	**	**	NA	0.59	NA	NA
Live branches	**	**	NA	0.28	NA	NA
1992 Sylleptic branches	**	**	NA	0.10	NA	NA

B. Stand characteristics

Trait	Spacing	Clonal treatment	S × CT
Stem yield	**	**	0.93
Branch yield	**	**	0.09
Total woody yield	**	**	0.90
Coefficient of variation:			
- height	**	**	0.12
- dbh	**	**	0.51

NOTE: ** = significant at $P < 0.01$; * = significant at $P < .05$; actual values shown for $P > 0.05$.

NA = not analyzed because specific data collected only in monoclonal plantings.

year, most of which occurred in the CL clone planted in the polyclonal plots. In other clones, at least one tree died at this spacing in both monoclonal and polyclonal plots. Clones 47-174 and 49-177 suffered some mortality at all spacings due to an unidentified shoot blight. By the end of the third-growing season, survival averaged 92% and differed significantly by clone, spacing, and their interaction with deployment. The vast majority of the mortality, however, occurred in the CL clone planted at 0.5-m spacing in polyclonal blocks; only 43% of trees remained (Table 2). The other combinations of clone and deployment in the 0.5-m spacing had much higher survival (81 to 97%). At the 1.0-m and 1.5-m spacings, CL, 11-11, and 47-174 had 96 to 100% survival. Clone 49-177 had slightly lower survival (88 to 93%) at these spacings, and all of the mortality was associated with an unidentified shoot blight.

Tree size

Height and diameter varied significantly with spacing, clone, manner of deployment, and interactions thereof (Table 3). Averaged over all clones in monoclonal plantings, height increased from 6.8 to 11.0 m, and diameter increased from 3.3 to 7.5 cm as spacing widened from 0.5 to 1.5 m. Mean heights and diameters for each clone averaged over all spacings in monoclonal plots were 9.2 m and 5.5 cm for 11-11; 9.3 m and 5.4 cm for 47-174; 9.3 m and 5.8 cm for 49-177; and 8.8 m and 5.2 cm for CL. Size differences among the clones in the monoclonal plots increased as spacing increased; the range in height increased from 0.3 m at 0.5-m spacing to 0.7 m at 1.5-m spacing, whereas the range of diameters increased from 0.3 cm to 1.0 cm over the same spacings. Although actual rankings of clones in terms of mean height and diameter varied only minimally with spacing in

Table 2. Survival of *Populus* clones at the end of the third growing season by clone, spacing, and type of deployment.

	Survival by clone %			
Block type	11-11	47-174	49-177	CL
	0.5-m spacing			
Monoclonal	94a	94a	81a	82a
Polyclonal	97a	92a	88a	43b
	1.0-m spacing			
Monoclonal	100a	98a	91a	100a
Polyclonal	100a	99a	88a	99a
	1.5-m spacing			
Monoclonal	100a	100a	91a	100a
Polyclonal	100a	96a	93a	99a

NOTE: Means followed by the same subscript letter do not differ significantly at P = 0.05.

the monoclonal plantings, absolute and relative differences among clones were substantial in polyclonal plantings, and a shift in ranking by height occurred between clones 11-11 and 47-174. In monoclonal plantings, clone 47-174 was slightly taller than clone 11-11, whereas the latter clone was slightly larger in diameter. In polyclonal plantings, however, clone 11-11 was larger than clone 47-174 in both height and diameter, and differences between the clones became significant as spacing widened to 1.5 m (Table 3). Clone CL was the smallest clone in all monoclonal plantings, and its size relative to the other clones was diminished dramatically in polyclonal plantings.

Tree form

Lower stem taper and slenderness differed among clones and spacings, and these traits differed in some clones and some spacings between monoclonal and polyclonal plots (Table 4). At age 3, clone 11-11 had the least taper; its taper did not change significantly with spacing and did not differ in monoclonal vs. polyclonal plantings. Clone 47-174 had the greatest lower stem taper in monoclonal plots and differed significantly from other clones at the two widest spacings, but its taper did not differ between polyclonal and monoclonal plantings. The taper of clones 49-177 and CL tended to be intermediate between the other two clones. Taper of clone CL did not differ significantly with spacing in monoclonal plots, but it decreased with increased spacing in polyclonal plots. Moreover, the taper of clone CL was significantly greater in polyclonal than in monoclonal plantings at the two closest spacings. Taper of clone 49-177 was unaffected by either spacing or deployment.

Slenderness differed minimally among clones in monoclonal plantings, but clonal differences were substantial in polyclonal plantings where slenderness of clone CL was significantly greater and that of clone 49-177 was substantially less than the other two clones. Slenderness decreased with increased spacing as expected because diameter growth is enhanced to a greater degree than height growth by increased growing space. Deployment had only minor effects on slenderness of clones 11-11 and 47-174; effects on the other two clones were more substantial and occurred in opposite directions for each. Slenderness of clone 49-177 was lower in polyclonal plots than

Table 3. Mean diameter and height at age 3 by type of clonal deployment, clone, and spacing.

	Dbh (cm)		Height (m)	
Clone	Mono	Poly	Mono	Poly
	0.5-m spacing			
11-11	3.2_{j}	3.4_{ij}	6.7_{i}	7.0_{i}
47-174	3.2_{j}	3.1_{j}	6.9_{i}	6.6_{i}
49-177	3.5_{ij}	4.2_{i}	6.9_{i}	7.8_{h}
CL	3.2_{j}	1.5_{k}	6.6_{i}	3.9_{j}
$\bar{x}$	3.3	3.2	6.8	6.3
	1.0-m spacing			
11-11	5.7_{gh}	6.0_{f-h}	9.9_{e-g}	10.3_{b-f}
47-174	5.6_{h}	5.4_{h}	10.0_{d-g}	9.9_{e-g}
49-177	5.9_{gh}	6.9_{d-f}	9.8_{e-g}	10.9_{a-d}
CL	5.2_{h}	3.2_{j}	9.2_{g}	6.6_{i}
$\bar{x}$	5.6	5.4	9.7	9.4
	1.5-m spacing			
11-11	7.6_{b-d}	8.3_{ab}	11.0_{a-c}	11.2_{ab}
47-174	7.4_{b-e}	6.6_{e-g}	11.0_{a-c}	10.3_{c-f}
49-177	8.0_{a-c}	8.9_{a}	11.3_{a}	11.2_{a}
CL	7.0_{c-e}	5.6_{gh}	10.6_{a-e}	9.5_{fg}
$\bar{x}$	7.5	7.3	11.0	10.6

NOTE: Within a column, means followed by the same subscript letter do not differ significantly at P = 0.05.

Table 4. Stem form and branching characteristics of four *Populus* clones.

	All trees				Dominant trees in monoclonal plots			
	Lower stem taper		Slenderness index		Branchiness	Live and dead	Live	1992 sylleptic
Clone	Mono	Poly	Mono	Poly	index	branches (#)	branches (#)	branches (#)
				0.5-m spacing				
11-11	109_{hi}	110_{g-i}	193_{bc}	193_{bc}	5.0	91	29	13
47-174	114_{e-h}	120_{bc}	195_{b}	183_{c-e}	4.6	38	13	0
49-177	112_{f-i}	113_{f-i}	180_{de}	168_{fg}	6.8	96	30	8
CL	113_{f-i}	121_{ab}	187_{b-d}	216_{a}	4.5	97	36	14
				1.0-m spacing				
11-11	110_{g-i}	109_{i}	160_{gh}	159_{gh}	5.2	128	43	25
47-174	120_{a-c}	118_{b-e}	150_{h-j}	156_{hi}	4.2	76	25	1
49-177	112_{f-i}	111_{g-i}	151_{h-j}	142_{j}	7.1	115	38	15
CL	113_{f-i}	119_{b-d}	158_{g-i}	173_{ef}	9.8	128	68	29
				1.5-m spacing				
11-11	112_{f-i}	113_{f-i}	130_{k}	121_{lm}	9.6	129	54	28
47-174	124_{a}	122_{ab}	122_{k-m}	132_{k}	12.1	87	40	1
49-177	111_{f-i}	112_{f-i}	130_{kl}	115_{m}	10.4	128	58	24
CL	116_{e-f}	115_{d-g}	130_{k}	149_{ij}	12.6	132	72	32

NOTE: Stem Taper Index = 0.3 diam./dbh × 100; Slenderness Index = ht(m)/dbh(cm) × 100; within a column, means followed by the same subscript letter do not differ significantly at P = 0.05. Branchiness Index = Live branch weight/Total Live Woody weight × 100.

monoclonal plots, whereas that of clone CL was significantly greater in polyclonal plots.

Branchiness as defined by the percentage of total live woody weight due to live branches differed significantly by clone, spacing, and their interaction. On average, clone CL had the highest branch index which was significantly greater than that of clone 11-11; branchiness of other clones was intermediate and did not differ from either clone CL or clone 11-11. Branch biomass index increased with increased spacing, being significantly greater at 1.5-m spacing (11%) than at the two closest spacings (5 and 7%). Ranking of the clones, however, changed markedly and clonal differences were greater for numbers of branches (Table 4). Total branches (live and dead) increased significantly as spacing widened from 0.5 m (80 branches) to 1.0 m (112 branches) and further increased, though to a lesser, non-significant extent, in the 1.5-m spacing (119 branches). Clone 47-174 produced significantly fewer branches (67) than any other clone, and CL had the most branches (119). Differences among clones were even greater for live branches and 1992 sylleptic branches. Capitol Lake had the greatest number of live branches (59) and clone 47-174 the least (26 branches), with the other two hybrid clones (11-11 and 49-177) having similar amounts (42 branches each). Live branch numbers increased with increased spacing, with the number in each spacing differing significantly from the other two spacings. Number of sylleptic branches was reduced at close spacing and differed more among clones than other branch traits. Clones 11-11 and CL produced similar numbers of sylleptic branches (24 and 28, respectively); 47-174 had none in the closest spacing and averaged only one branch per tree in the two wider spacings; and clone 49-177 produced intermediate numbers ranging from 8 in the closest spacing to 24 in the widest spacing.

Stand uniformity

Clonal plantations established on intensively prepared sites are relatively uniform compared with most naturally regenerated forests. Nevertheless, stand differentiation does occur; at the end of the third year in this study, there were significant differences in height and diameter differentiation (as measured by coefficient of

variation) across spacings and among clonal treatments. On average, the 0.5-m spacing exhibited the greatest within-plot variability in heights and diameters and the 1.5-m spacing showed the least (Table 5). The hybrid clones were somewhat more variable than clone CL in the monoclonal plantings; among the hybrids, clone 49-177 tended to be the most variable, especially at the two wider spacings. Coefficients of variation for various traits in polyclonal plots were higher than the mean for the monoclonal plots at the same spacing, and with the exception of the height variation of clone 49-177 in 1.5-m spacing, they were significantly higher than for any clone in corresponding monoclonal plots (Table 5). Although coefficients of variation for all clonal treatments were greatest in the 0.5-m spacing, *relative* differences between polyclonal and monoclonal plots in within-plot variation were smallest for diameter and height at that spacing and increased with increased spacing. For example, coefficients of variation for diameters in the 1.0-m and 1.5-m polyclonal plots were more than 60% higher than the mean of coefficients of variation for the corresponding monoclonal plots, whereas they were only 22% higher at the 0.5-m spacing. Similarly, polyclonal plantings had coefficients of variation for diameter that were 33 to 41% higher than those for the most variable clone (49-177) in monoclonal blocks at 1.0- and 1.5-m spacing and only 13% higher than the most variable monoclonal plantings (11-11) at 0.5-m spacing. In general, trends for variation in height are similar (though less striking) to those for variation in diameter.

Stand yield at age 3

Above-ground yields differed significantly among clones and spacings (Table 6). Three-year total live woody yields ranged from a low of 35.2 Mg ha^{-1} for clone CL at 1.5-m spacing to a high of 54.9 Mg ha^{-1} for clone 49-177 at 0.5-m spacing. Averaged over all spacings, total live woody yields in Mg ha^{-1} at age 3 in monoclonal plantings were 48.7 for 49-177, 45.9 for 11-11, 45.3 for 47-174, and 37.3 for CL. Total woody yields of polyclonal plots (43.1 Mg ha^{-1}) were significantly higher than yields from monoclonal plots of CL. Total woody yields of all clonal treatments decreased as spacing increased, with yield at 1.5-m spacing being significantly lower than yields at the two closer spacings. Stem yield patterns were similar to patterns for total live woody yields as they constituted more than 90% of total yield (Table 6). Branch yield, however, increased with increased spacing and was significantly greater at 1.5-m spacing than at the other two spacings. Clonal rankings in branch yield also differed from rankings in stem and total woody yield; overall, clone 49-177 had significantly higher branch yield than the other three clones in monoclonal plots. At the widest spacing, however, branch yields of clones 47-174 and CL were slightly higher than those of

Table 5. Coefficients of variation (%) in height and diameter for *Populus* clones in mono- and polyclonal plantings at three spacings.

		Clonal treatment					
Trait	Spacing	11-11	47-174	49-177	CL	Polyclonal	Mean
		---------- % ----------					
Height	0.5 m	30.9	25.7	28.1	24.4	31.4	28.1_A
dbh		36.4	32.7	34.0	32.5	41.2	35.3_X
Height	1.0 m	14.8	12.5	18.1	11.0	22.1	15.7_B
dbh		20.2	17.2	21.8	17.2	30.8	21.4_Y
Height	1.5 m	6.8	9.3	13.9	8.1	12.4	10.1_C
dbh		12.3	15.8	18.3	13.4	24.4	16.8_Z
Height	Mean	17.5_{bc}	15.8_c	20.0_{ab}	14.5_c	22.0_a	
dbh		22.9_b	21.9_b	24.7_b	21.0_b	32.1_a	

NOTE: In the column, spacing means followed by the same subscript do not differ significantly at P = 0.05. Within a row, clonal treatment means followed by the same subscript do not differ significantly at P = 0.05.

Table 6. Characteristics of stand yield in *Populus* plantings at 3 years.

Clonal treatment	Yield: Stem	Live branches	Total live woody
	Mg ha^{-1}		
0.5-spacing			
Monoclonal			
11-11	47.4	2.5	49.9
47-174	47.2	2.3	49.5
49-177	51.2	3.7	54.9
CL	36.8	2.1	38.9
Average	45.6	2.6	48.2
Polyclonal	44.2	2.8	47.0
Average for spacing	45.4_A	2.7_B	48.0_A
1.0-spacing			
Monoclonal			
11-11	45.6	2.6	48.2
47-174	43.5	2.8	46.3
49-177	44.7	3.6	48.3
CL	34.9	2.8	37.7
Average	42.2	3.0	45.1
Polyclonal	41.5	2.9	44.4
Average for spacing	42.1_A	2.9_B	45.0_A
1.5-m spacing			
Monoclonal			
11-11	36.2	3.2	39.4
47-174	35.5	4.6	40.1
49-177	38.8	4.3	43.1
CL	30.8	4.4	35.2
Average	35.3	4.1	39.4
Polyclonal	33.7	4.2	37.9
Average for spacing	35.0_B	4.1_A	39.1_B
All spacings			
Monoclonal			
11-11	43.1_a	2.8_b	45.9_a
47-174	42.0_a	3.2_b	45.3_a
49-177	44.9_a	3.9_a	48.7_a
CL	34.2_b	3.1_b	37.3_b
Average	41.0_a	3.2_b	44.3_a
Polyclonal	39.8_a	3.3_{ab}	43.1_a

NOTE: Within a column, spacing means followed by the same upper case subscript and clonal means followed by the same lower case subscript do not differ significantly at P = 0.05.

clone 49-177, a striking reversal of the clonal rankings of branch yield at the 0.5-m spacing.

Both stem and total woody yield of polyclonal plots tended to be slightly lower than those of the average of monoclonal plots but not significantly so (Fig. 1, Table 6). Averaged over all clones and spacings, monoclonal plots yielded 44.3 Mg ha^{-1} of live woody biomass whereas polyclonal plots yielded 43.1 Mg ha^{-1}. There were substantial differences, however, between monoclonal and polyclonal deployment in the contribution of each clone to total yield (Fig. 1). Moreover, the magnitude of such differences varied by spacing. The clones made rather similar contributions (22 to 27%) to total yield in monoclonal plantings at the widest (1.5-m) spacing. For polyclonal plantings at that spacing, clone 49-177 and clone 11-11 provided 35% and 31% of total yield, respectively, whereas clones 47-174 and CL provided only 20% and 14%. The disparity among clones in polyclonal plots was much greater as spacing decreased. At 0.5-m spacing, clone CL provided only 1%, whereas clone 49-177 provided 46% of the total yield.

Comparative yield

Comparative yield — that is, clonal yield values in polyclonal plots expressed as a fraction of those obtained in monoclonal plots, assuming equal area is occupied by the clone — provides additional clarification of clonal interactions in mixed plantings. Whether one looks at total live woody biomass or stem (not shown), it is apparent that each clone manifested a different response to mixture and spacing treatments (Fig. 2). Clone 11-11 yielded slightly more in polyclonal than in monoclonal plantings with the greatest difference (+18%) occurring at the widest spacing. Clone 49-177, on the other hand, grew markedly better (+58%) in polyclonal plantings than in monoclonal plantings at 0.5-m spacing. But as spacing widened, the superiority of its growth in polyclonal plots relative to monoclonal diminished and was only 26% better at 1.5-m spacing. In contrast to the above two clones which had enhanced growth in polyclonal plots, yields of clones 47-174 and CL were lower in polyclonal than in monoclonal plots; the extent of the decreases and trends with spacing differed markedly, however, between the latter two clones. Clone 47-174 was less affected and the relationship with spacing was nonlinear. Mild detrimental effects of the mixture on relative yield at 0.5-m spacing (12% lower than in monoclonal plots) became nearly negligible (about 3% lower) at 1.0-m spacing and then increased at 1.5-m spacing (-22 to -25%). Yield of clone CL was severely depressed

in polyclonal plantings at 0.5-m spacing, providing less than one-tenth the yield in monoclonal plots. Detrimental effects, however, became less severe with increased spacing (about 40% lower at 1.5-m spacing).

DISCUSSION AND CONCLUSIONS

By age 3, wider spacings produced trees that were taller and had larger diameters than were produced in closer spacings. Due to fewer number of trees per unit area, however, narrow spacings maximize biomass production during the initial years after planting. The wider the spacing, the more uniform were tree diameters and heights. There were only minor changes in clonal rankings for most tree and stand characteristics across spacings in monoclonal plots, but the advantage in yield associated with being the *top* ranked clone decreased substantially with increasing spacing. Thus, if evaluations were made at a narrower spacing than would be used operationally, the yield advantage could be substantially overestimated. Differences in relative performance of clones across spacings can be attributed to: (1) clonal branching habits and the effects of spacing on the expression thereof and (2) other clonal differences in physiological responses to self-shading and other aspects of intra-clonal competition.

Clonal differences and spacing by clone interactions were enhanced in polyclonal plantings. Moreover, differences in relative performance of clones in polyclonal vs. monoclonal plantings increased with time. Clones such as CL that grew more slowly than others in monoclonal plots would be expected to grow even more slowly in polyclonal plots once competition reached levels detrimental to growth. In polyclonal plantings, the good clones tend to get better and the poor clones get poorer. But even clones that are superior in monoclonal plots (such as 47-174) may be placed at a competitive disadvantage when faced with neighbors of differing physiological or morphological attributes. Such relative differences among clones in polyclonal vs. monoclonal plantings also generally increased with stand density (i.e., they were greater at 0.5-m than at wider spacings). Interactions between density and deployment strategy were very striking for clones CL and 49-177. On the other hand, the

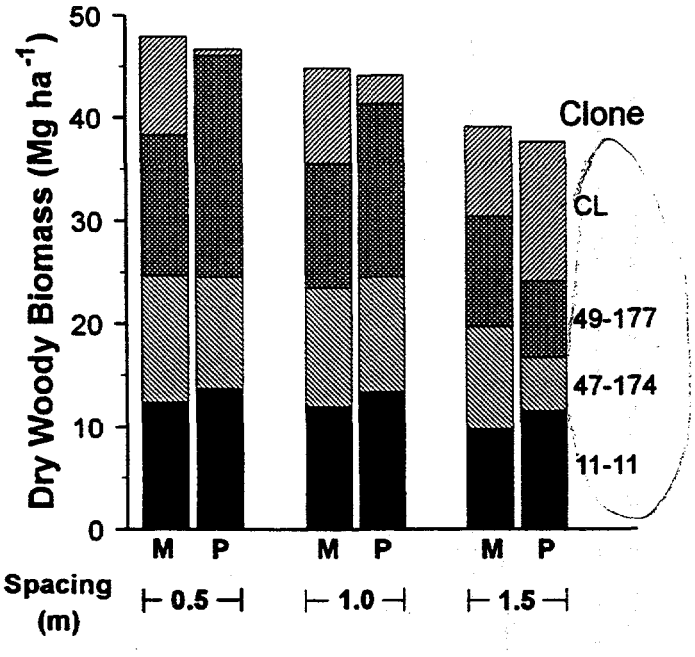


Fig. 1. Total biomass per hectare at age 3 produced by four *Populus* clones deployed in monoclonal and polyclonal planting at three spacings; assuming equal numbers of trees were initially planted for each clone in both methods of deployment.

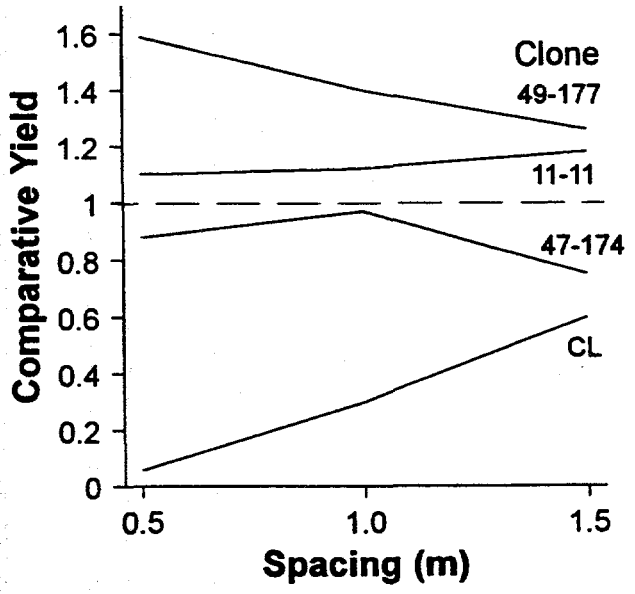
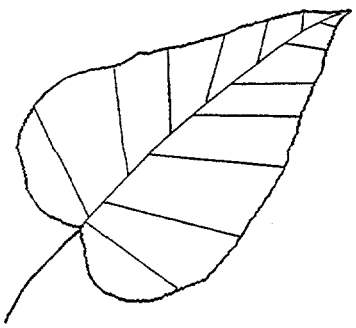


Fig. 2. Comparative yields (polyclonal ÷ monoclonal) of four *Populus* clones in polyclonal plantings as related to spacing. Values exceeding 1.0 indicate higher productivity of the clone in polyclonal plantings; values lower than 1.0 indicate reduced productivity.

performance of clone 11-11 was little affected by deployment strategy or its interaction with spacing. And clone 47-174 again provides an exception to the generality for some traits; for example, its yields in polyclonal and monoclonal plantings were more similar at 0.5-m than at 1.5-m spacings. The latter reversal probably was related to the branching habit of 47-174; reduced sylleptic branching was not as great a disadvantage at close spacing where syllepticity of all clones was minimal. At the wider spacing, however, where syllepticity was fully expressed, clone 47-174 was at a much greater competitive disadvantage relative to other clones such as 11-11 and 49-177 which grew rapidly and produced many sylleptic branches.

Some people argue on theoretical grounds that yield in polyclonal plantings may be higher and that deployment in more diverse plantings may reduce risks by protecting populations from catastrophic losses. Our study failed to show any yield advantage of polyclonal plantings. Monoclonal yields of some individual clones exceeded polyclonal yields, but not significantly so; moreover, on average, polyclonal yields were slightly (though not significantly) lower than the 4-clone average of monoclonal yields. Hazards that may hinder tree survival and growth are many as are the mechanisms through which they enter, affect, and spread through a plantation. Such differences in damaging agents are obviously important considerations in deployment strategies. Other things being equal, however, the theoretical risk-spreading advantages may be less than one might otherwise assume if relative yield of individual clones changes markedly in polyclonal plantings. In 0.5-m spacings, for example, 46% of inventory was tied up in just one clone (49-177) and another 29% in a second clone (11-11); the remaining two clones accounted for only 25% of inventory. When the same four clones were deployed in monoclonal plantings, however, their relative contribution to overall production and inventory was much more similar, ranging from 20% for clone CL to 28% for clone 49-177. In our plantings, risks were spread over a less balanced inventory — in effect, relying on a less diverse population — when the same four clones were deployed in polyclonal plantings than in monoclonal plantings. Although this effect might be reduced with inclusion of additional or different clones, the same principle may apply. It therefore seems important to understand and consider the effect of deployment strategies on the distribution and balance of inventory among clones.



Chapter 6

Above- and Below-Ground Characteristics Associated with Wind Toppling in a Young *Populus* Plantation[1]

Constance A. Harrington and Dean S. DeBell

Abstract: Damage from a dormant-season windstorm in a 3-year-old *Populus* research trial differed among four clones and three spacings and between monoclonal and polyclonal plots. Clonal differences in susceptibility to toppling (or leaning) were associated with both above- and below-ground characteristics. Susceptible clones had less taper in the lower stem and more weight in branches on the upper stem. The most susceptible clone also had the most above-ground biomass per unit of cross-sectional root area. The other susceptible clone had the least root system development in the windward quadrants. Wind toppling was least at the closest spacing. Apparently, mutual support was more important than individual tree characteristics from which the most damage would be expected at the closest spacing. Differences between paired trees of the same clone and spacing which did or did not topple were primarily associated with distribution of root systems by compass quadrant or depth. At the closest spacing where crown sway would have been minimized, trees which did not topple had greater cross-sectional root area in the windward direction than trees which did topple. At the widest spacing where crown sway would have been greatest, windfirm trees had greater cross-sectional root area than non-windfirm trees in both the windward and leeward directions. Toppling was reduced in polyclonal plots; this reduction may have been the result of more rapid stand differentiation in the polyclonal plots or reduction in the "domino effect" by inclusion of more windfirm clones in the mixture.

Keywords: Wind damage, root morphology, stem form, thigmomorphogenesis, clonal deployment

[1] Published in *Trees — Structure and Function* 11(2): 109-118 (1996)

Forest damage associated with high velocity winds is an important risk factor in production forestry but is often dismissed as being unpredictable and beyond management control (Somerville 1989). Influences of edaphic and topographic characteristics on susceptibility to wind damage have been documented and modeled for many forest regions (cf. Gratkowski 1956; Hütte 1968; Miller 1986; Harris 1989); these influences should be considered in land allocation or scheduling decisions but cannot usually be altered. On the other hand, individual tree and forest stand characteristics also influence susceptibility to wind damage, and many of these are clearly under management control. Above-ground characteristics that may serve as predictors of wind damage include crown and bole form, stand age, tree height, plant density and species composition (Cremer and others 1982; Petty and Swain 1985; Lohmander and Helles 1987; Harris 1989; Somerville and others 1989; Quine and others 1995). Recent stand history, such as thinning operations, may result in major changes in these characteristics. Below-ground characteristics associated with damage — such as root system extent and distribution — are affected by site preparation (Mason 1985; Coutts 1986; Quine and others 1995) and planting techniques (Quine 1990) as well as choice of species or genotype (Eis 1978; Somerville and others 1989) and initial spacing (Somerville and others 1989; Quine and others 1995).

It is usually very difficult to assess experimentally the specific characteristics that predispose trees to wind damage or to determine the relative importance of factors in specific situations because site, stand, and tree characteristics are extremely variable and major wind events occur irregularly and unpredictably. An unusual opportunity for critical evaluation,

however, was created by a severe windstorm in January 1993 that damaged many trees in a 3-year-old *Populus* research trial in western Washington (USA). This trial had been established on an agriculturally prepared site with uniform soil conditions and included replicated plots of four clones planted in monoclonal and polyclonal blocks at three spacings. A preliminary survey indicated that although there was spatial variability in the amount of damage, some clones and planting arrangements were clearly more susceptible to wind toppling (leaning or uprooting) than others. Since the research trial had been installed with randomized assignment of clones, spacing, and clonal block type, we were able to (1) document stand and tree characteristics associated with wind damage in a replicated trial, (2) compare selected above- and below-ground characteristics among four clones which differed in their susceptibility to toppling, and (3) contrast gross root system morphology and above-ground characteristics between paired trees which were or were not damaged.

MATERIALS AND METHODS

Plant materials and planting design

A research trial was installed in spring 1990 near Olympia, Washington, to examine differences in growth patterns and biomass yields of four *Populus* clones planted in monoclonal or polyclonal plots at three spacings. The study area is level (0-1% slope) and at low elevation (50 m); it had previously been in native forest cover and was cleared, root raked, burned, plowed, and treated with herbicide prior to planting. The soil is a very deep, somewhat excessively drained, loamy sand (with surface gravel in one block) and would not be considered suitable for growth of *Populus trichocarpa* Torr. and Gray without irrigation. During the study the plots were maintained in a weed-free condition and supplemental water was applied during each growing season with a drip-irrigation system. Nutrients and lime were applied prior to planting at dosages equivalent to 112 kg N ha^{-1}, 103 kg P ha^{-1}, 108 kg K ha^{-1}, and 900 kg lime ha^{-1}; between the second and third growing season, an additional 100 kg N ha^{-1} was applied.

Three of the clones used in the trial were *P. trichocarpa* × *P. deltoides* Bartr. ex Marsh hybrids: 11-11, 47-174, and 49-177 (clonal material developed by the University of Washington -Washington State University *Populus* breeding program). The fourth clone, named "Capitol Lake", was a local *P. trichocarpa* selection. The three square spacings used in the trial were 0.5 m, 1.0 m, and 1.5 m; the close spacings were selected to increase early competition and thus compress stand development into a short period. At each spacing, the clones were planted in monoclonal plots and in a four-clone mixture (polyclonal plots). Polyclonal plots alternated mixed rows of Capitol Lake and 49-177 with mixed rows of 11-11 and 47-174. The study was installed as a randomized complete block design with three adjacent blocks; the total experiment included 45 plots (5 clonal plot types, 3 spacings, and 3 blocks). Each treatment plot consisted of a 100-tree interior measurement plot surrounded by a minimum of three buffer rows planted and treated in the same manner as the measurement plots. Plots were planted late March 1990, with 30-cm long unrooted cuttings placed vertically with approximately 25 cm below ground and 1 to 2 buds above the soil line.

Total height and stem diameter at 0.3 and 1.3 m above ground were measured at the end of each growing season on all trees in each measurement plot. Ten to fifteen trees of each clone and spacing were removed at the end of the 1st, 2nd, and 3rd growing seasons from the middle buffer row (or rows) of monoclonal plots to develop biomass equations. Some trees of clones 47-174 and 49-177 were infected with an unknown shoot blight and were removed after the 2nd and 3rd year measurements to reduce future infection sources. Suppression-related mortality, primarily of Capitol Lake, occurred at the narrowest spacing and was not removed. At the end of the 3rd growing season, mean heights (and diameters) per clone in monoclonal plots ranged from 6.6 m (3.2 cm) at the 0.5-m spacing to 11.3 m (8.0 cm) at the 1.5-m spacing. Averaged over all clones, mean heights and diameters were similar between monoclonal and

polyclonal plots, but the within-plot variation was greater in polyclonal than monoclonal plots.

Wind History

The study area is located about 12.5 km from the U.S. Weather Bureau Station at Olympia, Washington. Elevation, topographic position, and slope percent are similar at both locations. Winds recorded over a 20-year period were mostly from the south or southwest and wind speeds are highest in those and associated directions (Fig. 1). Winds 40 km hr^{-1} originate almost exclusively from the south or southwest (Meteorology Committee 1968). On January 20, 1993, the western portion of Washington State (USA) experienced a storm with gale-force winds. The storm lasted only a few hours but due to the high speed and gusty nature of the winds, damage to trees was common. The Weather Bureau recorded a maximum 1-min wind speed of 56 km hr^{-1}, with a peak gust of 88 km hr^{-1}; this highest velocity wind originated from 210° (SSW) (U.S. Dept. of Commerce 1993).

Damage survey. All planted trees (including those in plot buffers) were surveyed for damage within one month of the windstorm. Each tree was assigned to a 5° lean class (i.e., lean of 0°, 5°, 10°,...), and if leaning, the direction of the lean was recorded. Comments on tree condition other than lean (e.g., stem breakage) were also recorded. Leaning trees occurred individually, in lines, and in groups.

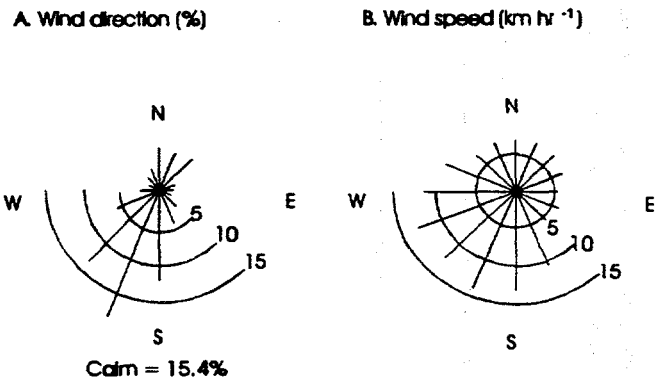


Fig. 1A,B. Summary of 20-year wind statistics from Olympia Airport (Meteorology Committee 1968). A. Percentage of time winds come from each of 16 compass directions (or air is calm). B. Mean wind speed by compass direction.

Clonal characteristic study. Because clones differed markedly in extent of damage, data were collected to describe each clone. Twenty trees per clone were randomly selected from monoclonal, 1.0-m spaced plots. Selected trees were excavated and measurements taken of above- and below-ground characteristics as described below.

Paired-tree study. For each clone, six pairs of trees in 0.5-m plots and six pairs in 1.5-m plots were identified (except for clone 47-174 as discussed below). The two trees in each pair were approximately the same diameter and, as much as possible, had the same exposure to the wind (i.e., were in same general area of the same plot); one tree in each pair was not leaning (lean class of 0) while the other was leaning. If several adjacent trees in a north-south line were leaning, only the southernmost leaning tree was eligible for selection (since the wind came from the south, the southernmost leaning tree could be considered to be least influenced by damage to other trees.) There was so little damage to 47-174 that it was only possible to identify four pairs of trees in the 1.5-m spacing (six were identified in 0.5-m spacing); for this clone two additional pairs of trees were selected in 1.0-m plots.

Detailed tree measurements. Selected trees were felled (severed at ground line) and the central portion of their root systems excavated to quantify gross root system morphology. Prior to excavation the cut surface was scribed to indicate its orientation in relationship to geographic north. Lateral roots were severed approximately 20 cm from the stem to facilitate transport to the laboratory. Stems were measured for total length, height to live crown, and diameter at 0.3 m, 1.3 m, 2.3 m, 3.3 m, and 4.3 m above groundline. The center of gravity of each stem with leafless branches attached was determined (by balancing).

For measurement purposes the root system was divided into 9 sectors: roots that originated between 0- and 15-cm below groundline divided into 4 geographic sectors (N, S, E, W); roots that originated between 15- and 30-cm

below groundline divided into 4 geographic sectors (N, S, E, W); and the downward-oriented sector composed of roots that formed from the callus tissues at the base of the cutting. In each sector, the diameter of all first-order roots 2 mm was measured with calipers. If a root was obviously elliptical, measurements were taken along the long and short axes and averaged. Diameter measurements were taken just exterior to the swelling associated with the intersection of the first-order root and the central axis of the root system (the below-ground portion of original stem cutting). The diameter of the central axis was also measured at groundline (0 cm) and 15 cm below ground.

Trees representative of each clone and spacing had been harvested three months before the storm and detailed measurements made of stem weight and number and weight of branches by type and year of origin. Some of these measurements are presented to provide additional information on the four clones.

Data analysis. The proportion of trees in a plot with lean 0° (plean) ranged from 0% to 100%; for analysis the data were transformed as recommended by Sabin and Stafford (1990) using the equation,

transformed lean = Ln [(plean +0.5)/(1.5-plean)].

Some plots had many trees with only a 5° lean; to determine if the results would differ when a higher cutoff value was used to classify a tree as "leaning", a separate analysis was run with trees having lean less than 15° classified as non-leaning. Analysis of variance was run on the transformed variables with clone, spacing, clonal plot type (monoclonal or polyclonal), and block as class variables in a randomized complete block design. Model effects were judged significant at $p \leq 0.05$; actual probability values are also provided.

Above-ground tree characteristics that may have been associated with tendency to lean were examined with a t-test which compared leaning and non-leaning trees by clone and spacing. These characteristics were tree height/mean plot height, tree diameter/mean plot diameter, and tree height/diameter at 1.3 m. Only observations from monoclonal plots were included in this analysis. If variances between groups were not equal, the t-test probabilities were calculated using the Cochran and Cox approximation (Cochran and Cox 1950).

Variables that were used to summarize root systems included number of roots by layer (e.g., $RtNum_{15}$ = number of roots 0-15 cm) and in total ($RtNum_{Total}$); and cross-sectional root area (CSRA) by sector (e.g., $CSRA_{N15}$ = CSRA of roots in north quadrant of 0-15 cm layer), layer (e.g., $CSRA_{15}$), or in total ($CSRA_{Total}$). In addition, a measure of root system balance was calculated for different portions of the root system as follows:

$$Uneven_{15} = \left|\frac{CSRA_{N15}}{CSRA_{15}} - 0.25\right| + \left|\frac{CSRA_{E15}}{CSRA_{15}} - 0.25\right| + \left|\frac{CSRA_{S15}}{CSRA_{15}} - 0.25\right| + \left|\frac{CSRA_{W15}}{CSRA_{15}} - 0.25\right|$$

A similar equation was used for $Uneven_{All}$ where all 9 root sectors were utilized and the subtraction factor was 0.12 for the 8 sectors in the 0-30 cm portion of the root system 0-30 and 0.04 for the downward sector.

Clonal differences among above- and below-ground characteristics were analyzed using analysis of variance. Both dimensionless variables (e.g., indices or proportions) and those which quantified above- and below-ground characteristics were examined.

In the paired-tree study, variables which differed between leaning and non-leaning trees were assessed with paired t-tests run for all trees combined, and separately by spacing. Discriminant analyses (Morrison 1967) were run for the entire paired-tree data set and separately by spacing (groups were lean and no-lean). Only dimensionless variables were used in these analyses to allow pooling data from trees of different sizes. Thus, paired-tree analyses did not include actual values, such as the cross-sectional root area in a sector, but did include relative values (e.g., sector root area divided by the total for the root system) or count variables (e.g., number of roots).

RESULTS

Survey study

Damage associated with the storm included leaning trees, broken stems, uprooted trees, and broken tops and branches. Stem snap (stems broken off below 2.0 m) was not common; in our study area and adjacent young *Populus* plantations, stem snap was observed only on stems previously weakened by tunneling by the poplar-and-willow borer (*Cryptorhynchus lapathi*). The most prevalent type of serious damage associated with the storm was toppling. The percentage of trees in interior measurement plots with stem lean equal to or greater than 5° ranged from 0% to 100% with an overall mean of 12%. Differences in amount and severity of wind toppling were clearly associated with clone, spacing, and clonal plot type (Tables 1 and 2). In monoclonal plots, the percentage of trees with stem lean equal to or greater than 5° averaged 26% for 49-177, 23% for 11-11, less than 1% for 47-174, and 4% for Capitol Lake. The two more susceptible clones (11-11 and 49-177) had more than 40% of trees in 1.0-m spaced monoclonal plots with lean equal to or greater than 5°. For these two susceptible clones, the widest spacing was intermediate in damage and the narrowest spacing had the least damage. The difference in damage among spacings was minor for the other 2 clones, resulting in a significant clone-by-spacing interaction. Averaged across clone and spacing, the percentage of trees with lean equal to or greater than 5° averaged 6.5% in polyclonal plots compared to 12.7% in monoclonal plots; this difference between clonal plot types was significant. Compared to monoclonal plots, damage in polyclonal plots at 1.0-m spacing was reduced, damage at 1.5-m was increased and the interaction between spacing and plot type was significant.

The analysis which used 15° as the cutoff to classify a tree as leaning also resulted in significant effects of clone, spacing, and spacing by plot type (Table 2). Under this classification, clone 49-177 had many fewer trees in the high lean categories than 11-11 (Table 1) and was intermediate between 11-11 and the two less susceptible clones in its level of damage. Damage was still greatest at the intermediate spacing in monoclonal plots and at the widest spacing in polyclonal plots. The effect of clonal plot types was nonsignificant using the higher cutoff value to classify a tree as leaning.

Table 1. Percentage of stems with varying degrees of departure from vertical (lean) by clone, spacing, and clonal plot type. Classes may not sum to 100 due to rounding.

		Degree of lean by clonal plot type							
		Monoclonal				Polyclonal			
Clone	Spacing	0°	5°	10°	≥ 15°	0°	5°	10°	≥ 15°
11-11	0.5 m	91	2	2	4	100	0	0	0
	1.0 m	56	7	12	25	81	7	9	3
	1.5 m	85	8	5	2	76	3	11	11
	All spacings	77	6	7	11	86	3	7	4
47-174	0.5 m	100	0	0	0	100	0	0	0
	1.0 m	100	0	0	0	99	1	0	0
	1.5 m	99	0	1	0	93	4	1	1
	All spacings	100	0	0	0	97	2	0	0
49-177	0.5 m	97	0	1	2	100	0	0	0
	1.0 m	52	26	12	11	89	2	6	3
	1.5 m	77	7	11	5	83	3	7	7
	All spacings	74	11	8	6	91	1	4	3
Capitol Lake	0.5 m	98	1	2	0	100	0	0	0
	1.0 m	95	2	1	2	100	0	0	0
	1.5 m	97	2	1	0	100	0	0	0
	All spacings	96	2	1	1	100	0	0	0
All clones	0.5 m	96	1	1	2	100	0	0	0
	1.0 m	76	8	6	9	92	2	4	1
	1.5 m	90	4	4	2	88	2	5	5

Table 2. Probabilities of ANOVA model components on proportion of trees in a plot with lean 0° or lean ≥15°. Variables were transformed as described in the text. The error term for the model had 46 df.

		Prob. F-value	
Source of variation	df	Lean 0°	Lean ≥ 15°
Block	2	0.68	0.76
Clone	3	<0.01	<0.01
Spacing	2	<0.01	0.03
Plot type	1	0.03	0.12
Clone * Spacing	6	0.03	0.26
Clone * Plot type	3	0.15	0.40
Spacing * Plot type	2	0.04	0.01
Clone * Spacing * Plot type	6	0.39	0.09

Mean plot values for above-ground tree characteristics — such as mean tree height or diameter — differed by clone and spacing but were not associated with tendency to lean. Many differences between leaning and nonleaning trees, however, were associated with relative size attributes. For example, the ratio of tree height to mean plot height or tree diameter to mean plot diameter differed significantly between leaning and nonleaning trees for many comparisons (Table 3). This tendency for leaning trees to be larger than the plot mean was particularly strong for the 0.5-m plots where *all* leaning trees had values for height and diameter greater than the mean values for the plot. The ratio of tree height to diameter at 1.3 m decreased as spacing increased; within a spacing the ratio was greatest for 47-174. Leaning trees had significantly lower ratios of height to diameter than nonleaning trees in the 0.5-m spacing; i.e., their diameters were proportionately further above the plot mean than their heights. Height-diameter ratios in the 1.0-m spacing were similar for leaning and nonleaning trees, but leaning trees tended to have higher height-diameter ratios in the 1.5-m spacing.

Clonal characteristic study

Some above- and below-ground characteristics differed among clones while others were very similar (Tables 4 and 5). Differences in numbers of roots and percent of root area by layer were small among the three hybrid clones (Table 4); however, Capitol Lake had fewer roots and a lower percentage of total cross-sectional root area in the 0- to 15-cm layer than the other clones. Capitol Lake and 47-174 had higher values for $CSRA_{W15}/CSRA_{15}$ and $CSRA_{N30}/CSRA_{30}$ and lower values for $CSRA_{NS15}/CSRA_{Total}$ than the other two clones, but only the largest of these differences were significant. Capitol Lake and 47-174 had significantly higher values for $Uneven_{ALL}$ than 11-11 and 49-177; that is, their root systems were less evenly balanced than those of the other two clones.

Table 3. Means and t-test probability values for ratios of tree height to mean plot height (HT/PHT), tree diameter to mean plot diameter (D13/PD13), and tree height to tree diameter (HT/D13) for leaning and nonleaning trees by spacing and clone (monoclonal plots only). NT = nontestable.

		HT/PHT			D13/PD13			HT/D13		
Spacing	Clone	No lean	Lean	Prob t	No lean	Lean	Prob t	No lean	Lean	Prob t
0.5m	11-11	0.97	1.40	<0.01	0.95	1.49	<0.01	2.12	1.98	<0.01
	47-174	1.00	—	NT	1.00	—	NT	2.22	—	NT
	49-177	0.99	1.32	<0.01	0.98	1.43	<0.01	2.01	1.80	<0.01
	CL	0.99	1.25	<0.01	0.99	1.30	<0.02	2.12	1.91	0.03
	All	0.99	1.36	<0.01	0.98	1.45	<0.01	2.10	1.93	<0.01
1.0m	11-11	0.93	1.09	<0.01	0.91	1.12	<0.01	1.80	1.70	<0.01
	47-174	1.00	—	NT	1.00	—	NT	1.81	—	NT
	49-177	0.98	1.02	0.10	0.98	1.02	0.14	1.69	1.67	0.48
	CL	1.00	1.08	<0.01	0.99	1.09	<0.01	1.77	1.75	0.16
	All	0.98	1.05	<0.01	0.98	1.07	<0.01	1.77	1.69	<0.01
1.5m	11-11	1.00	1.00	0.63	1.01	0.97	0.02	1.46	1.49	0.02
	47-174	1.00	1.00	0.98	1.00	0.89	0.23	1.51	1.60	0.33
	49-177	0.99	1.04	<0.01	1.00	1.01	0.62	1.43	1.46	0.10
	CL	1.00	0.96	0.14	1.00	0.95	0.21	1.51	1.53	0.65
	All	1.00	1.02	<0.01	1.00	0.99	0.14	1.48	1.48	0.85

Table 4. Mean values of selected above- and below-ground variables by clone. All trees from 1.0-m spaced monoclonal plots. Clones are arranged from left to right in decreasing order of susceptibility to wind toppling. Values in a row followed by the same letter did not differ at $p < 0.05$. Means based on 20 trees per clone unless indicated otherwise. ABGWoody = total above-ground weight of stems and branches; MRA = mean root area; LBr = live branches; DBr = dead branches; WBr = branch weight; WSt = stem weight; SBr_{92} = sylleptic branches on 1992 height increment. All weights on an oven-dry basis.

	Clone			
Variable	11-11	49-177	CL	47-174
$RtNum_{15}$ (#)	8.2a	7.8ab	5.6c	6.7bc
$RtNum_{30}$ (#)	10.8a	12.2a	11.1a	10.5a
$RtNum_{Down}$ (#)	4.3a	4.0a	4.2a	4.0a
$RtNum_{Total}$ (#)	23.3ab	24.0a	20.9b	21.2ab
$CSRA_{15}/CSRA_{Total}$ (%)	0.43a	0.45a	0.30b	0.43a
$CSRA_{30}/CSRA_{Total}$ (%)	0.46ab	0.41b	0.53a	0.43ab
$CSRA_{Down}/CSRA_{Total}$ (%)	0.11a	0.14a	0.17a	0.14a
$CSRA_{NS15}/CSRA_{Total}$ (%)	0.23ab	0.25a	0.15b	0.21ab
$CSRA_{W15}/CSRA_{15}$ (%)	0.28a	0.23a	0.34a	0.32a
$CSRA_{N30}/CSRA_{30}$ (%)	0.26ab	0.21b	0.35a	0.32ab
$Uneven_{All}$	0.65b	0.63b	0.77a	0.76a
HT/CG	0.35a	0.35a	0.35a	0.33a
HT (m)	10.0a	9.7a	9.2a	9.9a
DGL (cm)	7.0ab	7.4a	6.2b	7.8a
HT/D13 (m cm^{-1})	1.73b	1.68b	1.82a	1.83a
HT/DGL (m cm^{-1})	1.44b	1.32c	1.50a	1.28c
D13/DGL	0.83a	0.79b	0.83a	0.70c
$ABGWoody/CSRA_{Total}$	2.41a	1.72b	2.40a	1.48c
ABGWoody/MRA	56a	41b	50a	32c
LBr (#)[a]	43b	38b	68a	25b
DBr (#)[a]	86a	77ab	61bc	50c
WBr/WSt[a]	0.14b	0.15b	0.20a	0.09c
SBr_{92} (g)[a]	155a	164a	96a	7b

[a] Based on 6 trees per clone.

Mean root area by sector differed among clones (Table 5) with 47-174 having the largest mean root area and Capitol Lake the smallest. Clone 49-177 had greater mean root areas in the surface leeward quadrants (N_{15} and E_{15}) than in the windward ones (S_{15} and W_{15}), whereas the other three clones had greater mean root areas in the surface windward quadrants (S_{15} and W_{15}) than in leeward ones.

Table 5. Mean cross-sectional area (mm^2) per root by clone and root system sector. Clone order as in Table 4. Values in a row followed by the same letter did not differ at $p \leq 0.05$.

	Clone			
Sector	11-11	49-177	CL	47-174
N_{15}	102	226	92	202
E_{15}	88	210	91	201
S_{15}	143	177	97	205
W_{15}	117	174	100	260
N_{30}	78	105	94	145
E_{30}	106	105	92	121
S_{30}	143	98	100	101
W_{30}	95	102	110	143
Down	58	117	68	88
Mean (all sectors)	102bc	141ab	91c	157a

The two clones with greater resistance to wind damage (CL and 47-174) had higher slenderness ratios than the more susceptible clones (Table 4). The clones differed in their pattern of stem taper (Fig. 2) resulting in a major shift in clonal ranking if slenderness ratio was calculated using diameter at groundline rather than at 1.3 m. With the change from diameter at 1.3 m to diameter at groundline, clone 47-174 shifted from having the highest slenderness ratio of the four clones to having the lowest ratio. Although 47-174 had much greater taper than the other clones from groundline to 1.3 m, it did not differ markedly from 11-11 and Capitol Lake from 2.3 to 4.3 m. Clone 49-177 was also strongly tapered in its basal 30-cm section; it was less tapered than the other clones above 1.3 m.

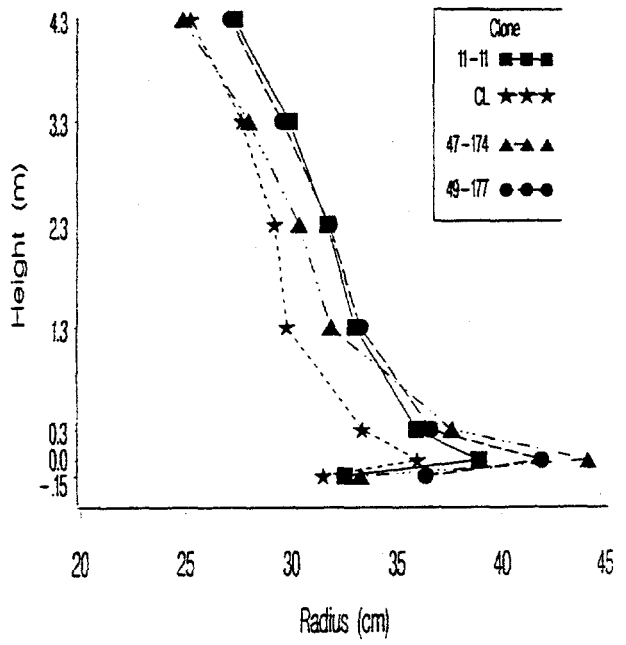


Fig. 2. Mean diameter by clone of tree boles from 0.15 cm below ground to 4.3 m above ground (1.0-m spacing).

Capitol Lake was somewhat shorter in height, smaller in diameter, and had a higher ratio of branch weight to stem weight than the other three clones (Table 4). Capitol Lake, 11-11, and 49-177 had a similar number of branches per tree, but a larger percentage of total number of branches per tree were dead on 11-11 and 49-177 than on Capitol Lake (Table 4). Clone 47-174 produced many fewer sylleptic branches than the other clones; this was reflected in the low value for branch weight on the previous year's stem section. Clone 47-174 supported the least above-ground woody weight per unit of root system cross-sectional area (ABG Woody/$CSRA_{Total}$); it also had the lowest value for woody weight per mean root area (ABG Woody/MRA).

Paired-tree study

There were no significant differences between paired leaning and nonleaning trees in above-ground characteristics; this was expected as the selected trees had been matched on their above-ground size and appearance. Many root-system characteristics differed between leaning and nonleaning trees. These included the relative amounts of CSRA in the nine measurement sectors (Fig. 3) and the distribution of CSRA into levels or quadrants (Table 6). There were clear differences between root systems from the two spacings so the results are summarized separately by spacing. Although there were important differences among clones in some root system characteristics (as described above), these clonal differences were minimized by the paired-tree approach and are not presented here.

At the 0.5-m spacing, leaning trees had less of their total root system area in the 0-15 cm layer than did nonleaning trees (25% versus 39%, $p < 0.01$). This increase in relative root area in the nonleaning trees was not evenly distributed (Fig. 3). Leaning and nonleaning trees had the same percentage of their total root system in the N_{15} ($p = 0.88$) and E_{15} quadrants ($p = 0.71$); however, nonleaning trees had much higher percentages in the S_{15} ($p = 0.02$) and W_{15} ($p = 0.05$) (i.e., higher percentages in the wind-

Table 6. Comparison of selected root-system characteristics by spacing and stem lean classification (all clones combined). Shown are probability values for paired-t test (n = 24 for 0.5-m spacing, n = 22 for 1.5-m spacing).

	0.5-m spacing			1.5-m spacing		
Variable (units)	Nonleaning	Leaning	Prob > t	Nonleaning	Leaning	Prob > t
$CSRA_{15}$ (cm^2)	7.1	4.0	<0.01	35.2	24.4	0.05
$CSRA_{30}$ (cm^2)	8.8	11.2	<0.01	25.0	28.1	0.19
$CSRA_{Down}$ (cm^2)	1.3	0.5	0.06	2.6	2.2	0.79
$CSRA_{total}$ (cm^2)	17.2	15.7	0.11	62.8	54.7	0.15
$RtNum_{15}$ (#)	7.0	5.1	<0.01	7.9	6.1	0.09
$RtNum_{30}$ (#)	14.1	15.2	0.35	13.2	14.0	0.50
$RtNum_{down}$ (#)	1.8	1.5	0.58	2.2	2.6	0.31
$RtNum_{Total}$ (#)	22.8	21.8	0.52	23.3	22.7	0.84
$Uneven_{15}$	0.9	1.0	0.06	0.7	0.9	0.03
$CSRA_{15}/Area_{DGL}$ (%)	23	13	<0.01	41	28	0.03
$CSRA_{15}/Area_{D13}$ (%)	35	20	<0.01	73	50	0.03

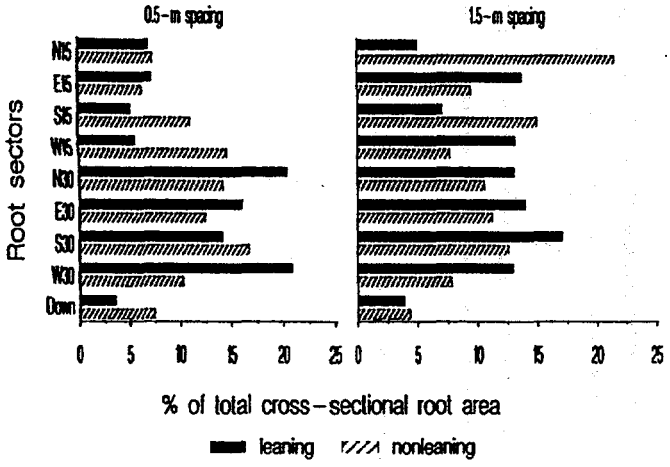


Fig. 3. Percentage of total root system cross-sectional area by root system sector for leaning and nonleaning trees in 0.5-m and 1.5-m spaced plots.

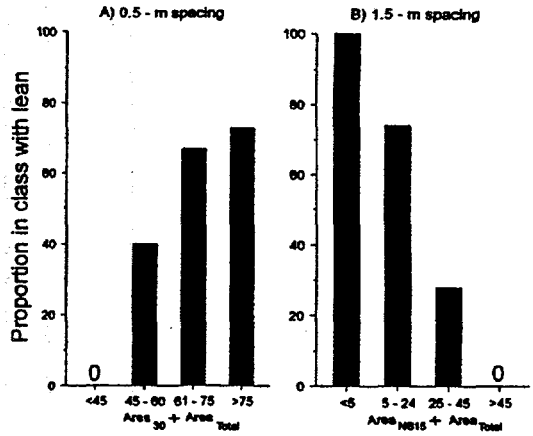


Fig. 4. Proportion of trees in each variable class that were leaning. Variables shown were first ones selected for each spacing by step-wise discriminant analyses with tree groups of leaning and nonleaning.

ward quadrants). Nonleaning trees also had a greater percentage of their total root system in downward oriented roots ($p = 0.05$). Total root area did not differ between leaning and nonleaning trees, nor did total number of roots (Table 6). Leaning trees did have fewer roots per tree in the 0-15 cm layer than nonleaning trees.

At the 1.5-m spacing, leaning trees again had proportionately less of their total root system area in the 0-15 cm layer than nonleaning trees (29% versus 53%, $p < 0.01$); for both leaning and nonleaning trees, these percentages were higher than at the narrower spacing. Major increases in relative amount of root area in the 0-15 cm layer of nonleaning trees at this spacing occurred in the N_{15} ($p < 0.01$) and S_{15} ($p = 0.02$) quadrants rather than in the S_{15} and W_{15} quadrants as was evident at the 0.5-m spacing. Although the visual difference in mean values might imply otherwise (e.g., N_{15} in Fig. 3), nonleaning trees had significantly lower values for $Uneven_{15}$ than nonleaning trees. This apparent discrepancy occurs because leaning trees more commonly had one or more quadrants with no or few roots, resulting in higher values for $Uneven_{15}$.

Root systems from trees in the wider spacing were substantially larger in total cross-sectional area than those from trees in the narrower spacing; however, the total number of roots per tree and the number per layer were very similar at both spacings. Total root system area is correlated with above-ground dimensions such as the cross-sectional stem area at groundline ($Area_{GL}$) or at 1.3 m ($Area_{D13}$). The percentage of root area in the 0-15 cm layer differed by tree lean classification and spacing, as did measures which related $CSRA_{15}$ to $Area_{GL}$ or $Area_{D13}$. Percentages and root area in relation to stem cross-sectional area at the root collar or at 1.3-m height were significantly lower for leaning trees than non-leaning trees, and lower at the 0.5-m spacing than the 1.5-m spacing.

Discriminant analyses identified variables which were effective in separating trees into leaning or nonleaning groups. For the 0.5-m spacing, the relative area in the 15-30 cm layer ($CSRA_{30}/CSRA_{Total}$) was the most effective variable to distinguish between leaning and nonleaning trees. The discriminant function using $CSRA_{30}/CSRA_{Total}$ correctly classified 75.0% of the trees from the 0.5-m spacing into the correct group; adding additional variables provided only marginal improvement. Examination of this variable revealed that the percentage of leaning trees increased with increasing values for $CSRA_{30}/CSRA_{Total}$ (Fig. 4A); clearly having a high proportion of the total CSRA in the 15-30 cm layer reduced windfirmness. Analysis of trees from the 1.5-m spacing selected relative CSRA in NS_{15} ($CSRA_{NS15}/CSRA_{Total}$) as the most effective classification variable; this variable correctly classified 81.8% of the trees. Increasing the proportion of the root system in the NS_{15} quad-

rants increased the likelihood that a tree would be windfirm (Fig. 4B). Combining observations from all spacings into one analysis reduced the percentage of trees correctly classified; however, both of the variables selected in the analyses by spacing were significant in a combined analysis.

DISCUSSION

Wind firmness in forest stands of the same age and species composition is influenced by stem form, crown form, stand density, and the smoothness of the upper canopy surface. These factors do not vary independently. Trees with high slenderness and low taper can sway more in wind and are more likely to be thrown or broken (Sheehan and others 1982). On the other hand, trees in dense stands provide substantial mutual support which dampens the amplitude of the sway (Quine and others 1995). These high-density stands are generally more windfirm than stands at lower density even though individual trees are more slender and have less lower-stem taper (Cremer and others 1982; Harris 1989; Somerville and others 1989). The importance of mutual support in minimizing damage was underscored in the current study by the fact that all leaning trees in the narrowest spacing were taller than mean plot height. In this study, the intermediate spacing had the highest rate of toppling; apparently the reduction in slenderness from the closest spacing was more than offset by the decreased mutual support among trees.

High values for stem slenderness (HT/D13) are considered to increase susceptibility to wind damage (von Brünig 1973), and values above 1.0 have been suggested as associated with increasing susceptibility to wind damage in conifer stands (cf. Cremer and others 1982; Sheehan and others 1982). Since all our plots had slenderness values above 1.4, it is apparent that a higher value would be more appropriate for these limber stems. In addition, due to major differences in lower stem taper among clones, slenderness calculated from groundline diameter rather than diameter at 1.3 m was more closely associated with clonal differences in susceptibility to toppling.

Spacing also affects below-ground characteristics important in wind firmness. Root systems in the narrowest spacing were not merely smaller versions of those in the wider spacings, they differed in several important characteristics. For example, the percentage of the total cross-sectional root area in the surface 15 cm ranged from 32% at the 0.5-m spacing to 46% in the 1.5-m spacing. Root system size is related to tree crown rather than bole size (McMinn 1963); thus, even if similar size trees were compared, they would have smaller crowns and thus smaller root systems in the closer spacing. Differences between spacings also existed in the distribution of root area by compass quadrant, possibly indicating that mechanical forces on the root systems differed by spacing.

Frequency of wind toppling was significantly less in polyclonal plots than monoclonal plots, particularly at the 1.0-m spacing. Separation of trees into different size classes (height or diameter) occurred more rapidly in polyclonal than in monoclonal stands. Thus, polyclonal plots were more variable in height which would have broken up the gusts and may have improved their stability (Gardiner 1995). The taller trees in the polyclonal plots also had larger crowns, however, which probably indicates they also had larger, better developed root systems than the average tree in the monoclonal plots. In addition, we presume that polyclonal plots reduced the opportunity for "domino effects"; that is, including clones with higher wind firmness reduced the probability that a primary leaning tree would topple onto another tree susceptible to toppling. There has been considerable debate on the probable susceptibility of monoclonal and polyclonal blocks to biotic or abiotic hazards but specific data have been limited (DeBell and Harrington 1993).

Numerous differences among *Populus* clones have been previously documented, but most reports related clonal differences to net productivity (cf. Ceulemans 1990) rather than susceptibility to damage. Michael and others (1988), in discussing differences in root:shoot biomass ratios between two *Populus* clones, did suggest that less extensive root development could make trees more susceptible to windthrow. They concluded, however, that the yield

advantages of less extensive root development were likely to be more important in irrigated, short-rotation, intensive-culture systems than the advantages of wind resistance and water and nutrient acquisition which would be associated with more extensive root development. Other reported differences among *Populus* clones that could influence susceptibility to toppling include root growth and development (Faulkner and Fayle 1979), root:shoot ratios, length and density of fine roots (Heilman and others 1994), root strength (Hathaway and Penny 1975), and branching characteristics (Weber and others 1985).

In our trial, clone 11-11 was the least resistant clone to toppling. It did not differ from the other two hybrids in number of roots or in root area in most sectors. Clone 11-11 did have the smallest mean root area of the three hybrids, the highest amount of above-ground biomass per unit of root area, and the highest ratio of above-ground biomass to cross-sectional area of the mean root. When stem slenderness was expressed as height divided by root-collar diameter, 11-11 had the highest value of the three hybrids; it also had the lowest rate of stem taper from groundline to 1.3 m. Clone 11-11 produced large numbers of sylleptic branches, and of the three hybrids, had the largest number of live and dead branches and the largest ratio of branch weight to stem weight.

Clone 49-177 was the second most damaged, but many of the leaning trees of this clone were inclined from vertical less than 15° and may recover. In comparison with 11-11, 49-177 had a significantly lower amount of above-ground woody biomass per unit of root area. Clone 49-177 had the highest amount of upper-stem branch weight; in comparison with 11-11, it was more tapered from groundline to 1.3 m and less tapered from 1.3 to 4.3 m. Clone 49-177 differed from the other three clones in having larger mean root area in the surface leeward quadrants as opposed to the windward sectors. Roots under tension are only about one-third as strong as roots under compression (Falk 1980). Thus, if less root development occurred in the windward quadrants (S and W in this case), trees could be more susceptible to toppling.

Clone 47-174 was clearly the most resistant clone to wind toppling. It did not differ from the other clones in total number of roots but did have the largest roots (especially in S_{15} and W_{15} sectors) and the lowest amount of above-ground biomass per unit of cross-sectional root area. It also had the highest rate of lower stem taper and the lowest number of branches and weight of upper-stem branches. In common with Capitol Lake, the other clone resistant to toppling, 47-174 had a higher mean value for $Uneven_{All}$; that is, its root systems were less evenly balanced than those of 11-11 or 49-177. Although root systems with major imbalances are unstable (cf. Harris 1989; Quine 1990; and Table 5), a small increase in $Uneven_{All}$ is apparently beneficial if tied to increased root development on the windward sectors of the root system.

Capitol Lake had fewer roots per tree and a lower percentage of total root system area in the 0- to 15-cm layer than the other three clones but did not differ in numbers of roots in the 15- to 30-cm or downward-oriented layers. Although wide-spreading surface roots can be associated with windfirmness, if these roots are too shallow, their small associated soil weight will inhibit stability (Coutts 1983); thus, having a lower percentage of total root system area in the surface layer may not always be a negative attribute. Capitol Lake was slightly shorter and smaller in groundline diameter (DGL) than the other clones; based on DGL, it had the highest slenderness ratio of the four clones. It had the highest number of live branches, but weight of upper-stem branches was fairly low. Based on the relatively high amount of above-ground biomass per unit of root area and the small mean root area, Capitol Lake would have been expected to have been less windfirm than it demonstrated in this storm. The greater mean root area of Capitol Lake root systems in the windward as opposed to leeward quadrants was probably a beneficial characteristic. Differences in root strength have been reported among *Populus* and *Salix* clones (Hathaway and Penny 1975); thus, it is possible that roots of Capitol Lake are stronger per unit of cross-sectional area than those of the three hybrid clones. Root system characteristics not assessed in this study

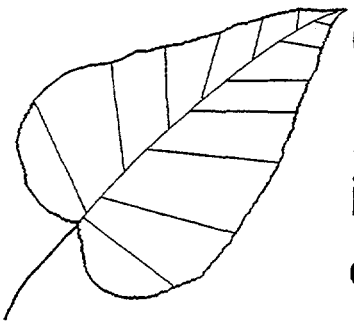
(e.g., root angle or branching) could also be contributing to the windfirmness of this clone.

Thigmomorphogenesis refers to developmental changes in growth caused by compressive and tensional forces, such as those induced by wind (Jaffe 1973). These responses result in anatomical or morphological changes which make plants more resistant to future perturbation. In this study there were differences in root system development by compass quadrant that appear to be associated with the direction of the prevailing winds, and the degree of thigmomorphogenetic response varied among the clones. Clonal differences in below-ground characteristics, apparently in response to perturbation, have not previously been reported. Subjecting young seedlings of Sitka spruce [*Picea sitchensis* Bong. (Carr.)] and European larch (*Larix decidua* Mill.) to unidirectional winds resulted in greater root development on the windward side for both species and greater development on both the windward and leeward sides for larch (Stokes and others 1995); thus, the role of wind in influencing root system development and species differences in root response to wind have been documented. In addition, thigmomorphogenetic differences in response among families of *Pinus taeda* have been reported for stem xylem anatomy (Telewski and Jaffe 1986) and ethylene production (Telewski 1990). Since these responses are hormone mediated (Roberts 1988, Telewski 1995), it might be possible to develop an early screening technique to predict the degree of response by clone. Most *Populus* plantations are established on former agricultural lands which are often unsheltered and windy. Clone 11-11 was widely planted in the Pacific Northwest for several years, and many plantings of this clone were damaged by the same windstorm that impacted our study area. Thus, selection among high-yielding clones for thigmomorphogenetic response in root system development could be desirable for exposed sites with consistent wind patterns.

In the paired-tree analyses, several root system characteristics differed between leaning and non-leaning trees. These characteristics were primarily those which quantified root system distribution among sectors or layers. When examined by spacing, one root system variable ($CSRA_{30}/CSRA_{Total}$ for 0.5 m and $CSRA_{NS15}/CSRA_{Total}$ for 1.5 m) could correctly classify at least 75% of the observations. Thus, even though clonal differences in root systems were important in determining susceptibility to toppling, there were characteristics which toppled trees of all clones shared.

Observers have long recognized inter-tree variability in root system characteristics to be high and have attributed that variability to differences in species, genotype, tree spacing, vigor, age, or soil and site characteristics (Sutton 1980). It is interesting to note that even for clonal plants of one age growing at the same spacing and under fairly uniform soil and site conditions, there existed substantial variation in some root system characteristics. Presumably even small differences in the original cutting or in microsite conditions can influence root system development.

This study indicates significant differences in wind damage among clones, among spacings, and between plot types; with some interacting effects of these factors. In situations where the probability of wind damage is high, the selection of clones resistant to wind damage may be an effective approach to reducing risks — and planting of resistant clones in monoclonal blocks would be a practical way to salvage damage when it does occur. In addition, it may be worthwhile to orient cultural practices such as disking or use of rectangular spacings to minimize any detrimental effects on root system development in the windward directions.



Chapter 7

Leaf Characteristics Reflect Growth Rates in 2-Year-Old *Populus* Trees[1]

Constance A. Harrington, M. A. Radwan, Dean S. DeBell

Abstract: We examined the relationships between biomass or growth rates and leaf characteristics of 2-year-old trees of two clones of *Populus*. Leaf characteristics were: total plant leaf area or leaf weight, mean size (or weight) of fully expanded terminal leaves, and foliar concentrations and contents of N, P, K, Ca, Mg, total chlorophyll and total available carbohydrates. Sample trees (n = 156) were chosen from two irrigation regimes and several fertilization treatments to provide a wide range in environmental conditions and growth rates for each clone. Total plant leaf area or weight were strongly correlated with total above-ground biomass (r = 0.98 - 0.99); however, mean size (area or weight) of the fully expanded terminal leaves was also quite strongly correlated with biomass (0.64 - 0.72), height growth (0.54 - 0.72) and diameter growth (0.53 - 0.73). With one exception (correlation between foliar K concentration and height growth of one clone, r = 0.67), leaf size characteristics were more strongly correlated with biomass or growth than were concentrations or contents of foliar chemicals. Since size of the terminal leaves is easy to measure, it may be useful as a simple indicator of potential productivity.

It has long been recognized that plants growing under substantial soil moisture or nutrient stress have smaller leaves and lower growth rates than plants of the same genotype growing under more favorable conditions. In addition, rapid production of leaf area appears to be an important attribute of fast-growing plants. Previous work on *Populus* has shown that: (1) mean leaf size per clone and clonal performance are correlated (Ridge and others 1986, Isebrands and others 1988, Ceulemans 1990), (2) mean leaf size per clone increases as ortet location becomes more mesic and the expression of this relationship is greater at a more mesic test site (Dunlap and others 1995) and (3) mean leaf size and leaf growth rates were greater in irrigated than non-irrigated trees (Roden and others 1990). This past work generally involved relatively few samples (2 to 5 trees) per clone and did not examine within-clone variation in leaf size and productivity.

In this study we examined the relationships between growth rates or attained size and leaf characteristics of 2-year-old trees of two *Populus* clones. We concentrated on evaluating the size, weight and selected chemical characteristics of the fully expanded leaves produced on the current terminal shoot. In young, fast-growing, short-rotation, intensively cultured plantings, leaves on the current terminal are considered to be the most important suppliers of photosynthate for height and diameter growth (Isebrands and Nelson 1983). In addition, we examined the relationship of total plant leaf area or weight to total above-ground biomass, diameter growth, and height growth.

MATERIALS AND METHODS

Unrooted cuttings of two Populus clones were planted at 2- x 2-m spacing in alternate rows in a 0.7 ha block near Olympia, Washington, USA. The clones were 11-11, a *Populus deltoides* Bartr. ex Marsh x *Populus trichocarpa* Torr. & Gray hybrid and 7-75, a *Populus trichocarpa* selection from a natural stand near Orting, WA (approximately 40 km from the study area). Both clones were developed (or selected) by the University of Washington/Washington State University Poplar Research Program (Quinsey and others 1991). The study area is relatively flat, elevation

[1] In press in *Canadian Journal of Forest Research* (1997).

is 50 m and the soil is Nisqually loamy fine sand (sandy, mixed, mesic Pachic Xerumbrepts), a very deep, somewhat excessively drained soil which formed in sandy glacial outwash (USDA Soil Conservation Service 1990). Four plots in each of three contiguous blocks were randomly assigned to an irrigation regime (low or high) and 4-tree subplots were assigned to a fertilization treatments which applied varying amounts of N (0 to 500 kg N ha^{-1} as ammonium nitrate), and P (0 to 1000 kg P ha^{-1} as triple superphosphate), K (0 to 1000 kg K ha^{-1} as muriate of potash), and 0 to 10 t lime ha^{-1}. The fertilization subplot treatments were laid out in a continuous function design (Shoulders and Tiarks 1983). Irrigation was applied with a drip system; during the 2nd growing season (May 1 through August 30), the low regime received 14 cm and the high regime 51 cm of rainfall plus irrigation.

Samples for this study were collected from selected fertilizer subplot treatments to represent the range of nutrient environments established in the plantation. Equal numbers of trees per clone and irrigation regime were sampled in each treatment to provide a balanced data set (n=156; 39 for each clone and irrigation regime). The data set also encompassed the range of tree sizes and current growth rates occurring in the plantation. Fully expanded terminal leaves (leaf plastochron index _ 6 per Larson and Isebrands 1971) were collected from 2-year-old trees during the last week of August. Most of the annual growth and nutrient uptake had occurred and the foliage had not yet deteriorated. Sampling was done in early morning and consisted of 3 to 4 leaves per sample tree.

Immediately after harvest, fresh weight, leaf area, and number of leaves per sample tree were determined. Chlorophyll a and b were extracted from the blade portions of a subsample of fresh leaves by maceration in 80% acetone, optical densities measured spectrophotometrically, and contents computed according to Arnon (1949). Remaining leaf samples (blades and petioles) were dried to constant weight at 65° C, ground to 40 mesh, then analyzed for total N (including nitrate) by the micro-Kjeldahl procedure (Bremner and Mulvaney 1982); P by the molybdenum-blue technique (Chapman and Pratt 1961); and K, calcium (Ca), and magnesium (Mg) by atomic absorption (Perkin-Elmer Corporation 1976). Determination of total available carbohydrates was done by extraction and hydrolysis in sulfuric acid (Smith and others 1964). Concentrations of total available carbohydrate were calculated as percent glucose in ovendried leaf tissue.

Tree height and basal diameter (0.15 m) were measured at the end of the first growing season and in the second growing season when the leaves were sampled. The plantation was thinned the same week the terminal leaves were collected and total above-ground biomass was determined for each tree by weighing the entire above-ground portion of the plant. In addition, half of these thinned trees were partitioned into stem, branches, and leaves, and component weights and leaf areas were determined. Subsamples were taken to determine moisture content and fresh weight/dry weight relationships. For the trees that were not partitioned, total plant leaf area and leaf weight were predicted from total plant weight using regression equations developed for each clone and irrigation regime.

DATA ANALYSIS

Analyses were done to explore relationships among leaf characteristics and tree productivity rather than to test specific models or determine significant differences among discrete fertilizer treatments. Lateral root development was rapid and roots of trees planted in one subplot treatment commonly extended into adjacent fertilizer and irrigation treatments. Thus, individual tree characteristics did not reflect responses to distinct treatments; however, the treatments provided an extensive variety of growing conditions that resulted in a wide range of tree sizes, growth rates, and leaf characteristics.

Plottings of tree biomass or growth (height and diameter growth during the second growing season) versus leaf characteristics were examined. Non-linear relationships between variables were not apparent and data transformations were assumed unnecessary for subsequent analyses. Simple correlation coefficients were determined between the biomass or growth variables and the leaf characteristics for

each clone and irrigation regime. If differences in the relationships observed between irrigation regimes or clones were non-significant or minimal, the data were pooled and the correlations determined for the combined observations. Only correlations for variable combinations for which at least one of the clones had an r value ≥ 0.60 are presented. Simple and multiple regression equations using leaf size and chemical characteristics were examined for their ability to predict 2nd year height growth. The biomass and growth variables were also examined using analysis of variance with clone, irrigation, and clone by irrigation as the model sources of variation.

RESULTS

Mean growth of both clones in the study plantation was good, but due to the imposed range in nutrient conditions, plant biomass and growth rates varied substantially within each clone and irrigation regime (Table 1). Mean total above-ground biomass, height growth and diameter growth were significantly greater for clone 11-11 than for clone 7-75 and greater for the high versus the low irrigation regime.

Clone 11-11 had greater mean area and weight of terminal leaves, and greater total plant leaf area (or weight) than clone 7-75 (Table 2). Leaf length was similar but shape of the leaves differed between clones with 11-11 having a broader leaf base and a more deltoid shape. Clone 7-75 had higher mean concentrations of N, P, K, and chlorophyll and lower concentrations of Ca than clone 11-11, but concentrations of Mg and total available carbohydrate were similar in both clones. On average, high irrigation increased mean area and weight of terminal leaves, total plant leaf area, and P concentrations, but decreased concentrations of most other nutrients and chlorophyll. Total available carbohydrates were essentially unaffected by irrigation regime. Potassium levels in clone 11-11 were also unaffected by irrigation; in clone 7-75, however, K levels were substantially increased in the high irrigation regime.

Mean area and weight of terminal leaves were positively correlated with total above-ground biomass, height growth and diameter growth of both clones (Table 3). The correlations between mean weight of terminal leaves and total biomass or growth variables were similar to those for mean terminal leaf area because area and weight of terminal leaves were very strongly correlated ($r = 0.97$ for clone 11-11; $r = 0.89$ for clone 7-75). Correlations between total plant leaf area or leaf weight and total biomass were stronger than those of terminal leaf traits with total biomass or diameter; however, correlations of total plant leaf traits with height growth were weaker than those of terminal leaf traits with height growth.

Foliar K concentrations were correlated with biomass and growth of clone 7-75, but not with biomass or growth of clone 11-11 (Table 3). Foliar concentration or content (i.e., concentration multiplied by mean leaf weight) of most

Table 1. Mean, range, and standard error of total above-ground biomass, and second-year height and diameter growth by clone and irrigation regime. In the analysis of variance, clone and irrigation were each significant but the clone x irrigation interaction was not.

		Clone 11 - 11		Clone 7 - 75	
		Irrigation regime			
Production trait	Parameter	Low	High	Low	High
Total above-ground biomass (kg)	Mean	2.8	4.2	2.4	3.2
	Range	0.1 - 6.9	2.0 - 6.4	0.1 - 5.4	1.1 - 5.3
	S.E.	0.21	0.18	0.19	0.18
Height growth (m)	Mean	2.2	2.8	1.9	2.6
	Range	1.2- 4.2	1.0 - 4.4	1.2 - 3.1	1.7 - 3.7
	S.E.	0.08	0.10	0.07	0.08
Diameter growth (cm)	Mean	2.7	3.5	2.5	3.1
	Range	1.3 - 1.4	2.6 - 4.6	1.2 - 3.4	2.1 - 4.0
	S.E.	0.10	0.09	0.09	0.08

Note: In the ANOVAs for these 3 traits, clone and irrigation were significant ($P<0.05$), but clone x irrigation was not.

Table 2. Means (and ranges) for selected leaf characteristics by clone and irrigation regime. N = 39 per clone/irrigation regime except for chlorophyll and total available carbohydrate where N = 12 per clone/irrigation regime.

	Clone 11 - 11		Clone 7 - 75	
	Irrigation Regime			
Characteristic	Low	High	Low	High
Terminal leaves				
Mean area (cm^2) †	314 (79 - 574)	434 (174 - 603)	221 (58 - 497)	349 (141 - 469)
Mean dry weight (g) †	4.1 (0.9 - 6.9)	5.4 (2.1 - 6.8)	2.6 (0.6 - 2.1)	3.9 (1.4 - 5.6)
Nutrient concentrations ($g\ kg^{-1}$)				
Nitrogen †	14.4 (7.4 - 19.8)	11.4 (8.4 - 14.8)	17.6 (12.1 - 20.8)	15.0 (11.1 - 17.3)
Phosphorus ‡	1.9 (1.0 - 2.4)	2.0 (1.3 - 2.6)	2.1 (1.4 - 2.9)	2.5 (1.4 - 3.8)
Potassium ‡	12.6 (7.4 - 17.9)	12.0 (8.8 - 19.4)	17.6 (12.4 - 22.4)	22.0 (15.6 - 27.3)
Calcium ‡	9.7 (5.9 - 14.6)	7.7 (6.1 - 10.8)	6.8 (4.1 - 10.0)	6.5 (4.7 - 10.2)
Magnesium	2.4 (1.8 - 3.0)	1.9 (1.6 - 2.2)	2.2 (1.6 - 3.4)	2.0 (1.7 - 2.8)
Other leaf components				
Total chlorophyll ($g\ kg^{-1}$) ‡	1.39 (1.05 - 1.70)	8.8 (0.76 - 1.05)	1.44 (1.18 - 1.62)	1.25 (1.02 - 1.45)
Total available carbohydrates (g glucose/kg tissue)	159 (117 - 236)	160 (128 - 193)	154 (131 - 193)	159 (144 - 196)
Total plant leaf area (m^2) ‡	10.9 (0.4 - 27.6)	16.1 (7.8 - 24.9)	7.5 (0.3 - 16.9)	9.6 (3.1 - 14.8)
Total plant leaf weight (kg) ‡	1.1 (0.1 - 2.7)	1.6 (0.8 - 2.5)	0.7 (0.1 - 1.6)	1.0 (0.3 - 1.5)

Note: In the ANOVA for these characterisitcs, † indicates clone and irrigation were significant (P<0.05), ‡ indicates clone, irrigation, and clone x irrigation were significant. For Mg, irrigation and clone x irrigation were significant.

nutrients, chlorophyll, and available carbohydrates were significantly correlated (P ~0.05) with total biomass and growth of both clones. In all cases except K concentration and height growth of clone 7-75, however, correlations between biomass or growth and mean area and weight of terminal leaves or total leaves were substantially higher than correlations with concentrations or contents of nutrients and chlorophyll. For clone 7-75, the multiple regression equation predicting height growth which included K concentration and mean terminal leaf area (R^2=0.53) accounted for substantially more variation than the equation using only mean terminal leaf area (R^2=0.39). For clone 11-11, none of the multiple regression equations which included additional foliar variables increased R^2 values more than 0.02 over the equation with mean terminal leaf area as the independent variable.

Relationships between mean terminal leaf area and height growth were similar for high irrigation and low irrigation regimes of clone 11-11, despite the fact that trees in the high irrigation regime generally had much larger leaves (Fig. 1). Moreover, the relationship between leaf area and height growth for trees of clone 7-75 in the low irrigation regime (Fig. 1)

Table 3. Correlations between size or growth variable and leaf characteristics. Included in the table are the variables for which at least one of the clones had a correlation coefficient ≥ 0.60. All coefficients in the table are significant at P = 0.0001 except correlations with K concentrations for 11-11 which are non-significant (n = 78 per clone.

	Size or growth variable and clone					
	Total above-ground biomass		Height growth		Diameter growth	
Leaf characteristic	11 - 11	7 - 75	11-11	7 - 75	11-11	7 - 75
	R value					
Terminal leaf area	0.68	0.72	0.72	0.63	0.73	0.64
Terminal leaf weight	0.64	0.70	0.71	0.54	0.70	0.53
Total leaf area	0.99	0.98	0.54	0.46	0.77	0.73
Total leaf weight	0.99	0.99	0.55	0.48	0.78	0.76
Terminal leaf K concentration	- 0.01	0.40	- 0.02	0.67	0.04	0.46

was essentially identical to the relationship for clone 11-11. The relationship for trees of clone 7-75 in the high irrigation regime, however, was not as strong (i.e., the slope of the line was not as steep). Maximum area per terminal leaf was clearly lower for clone 7-75 than for clone 11-11; none of the clone 7-75 trees had mean leaf areas 500 cm^2 whereas 14 percent of clone 11-11 had leaf areas exceeding that size.

DISCUSSION

A strong correlation between total leaf area or total leaf weight and tree productivity (size or growth) has been reported previously (Larson and Isebrands 1971, Larson and others 1976) as have high positive correlations between mean size of mature leaves and relative growth of various *Populus* clones (Ridge and others 1986, Isebrands and others 1988, Ceulemans 1990). The present study expands on these general relationships to demonstrate a very simple, yet strong correlation between mean size of the fully expanded terminal leaves and productivity of two *Populus* clones. Our findings apply to within clonal differences in productivity (size and growth) "created" by manipulating several growth factors — N, P, K, and lime amendments and water availability.

Despite the range of nutritional status affecting tree size and growth and significant correlations between production variables and chemical concentrations or contents, mean size of terminal leaves (area or weight) was more strongly correlated with productivity than concentration or content of any single chemical with the one exception of K concentration and height growth in clone 7-75. Thus, this simple, easy-to-measure characteristic may be a very useful indicator of potential productivity or future growth. It merits further testing as a possible tool to aid in site selection, matching clones to sites, or monitoring tree response to cultural treatments as well as providing an early indicator of the relative performance of various clones.

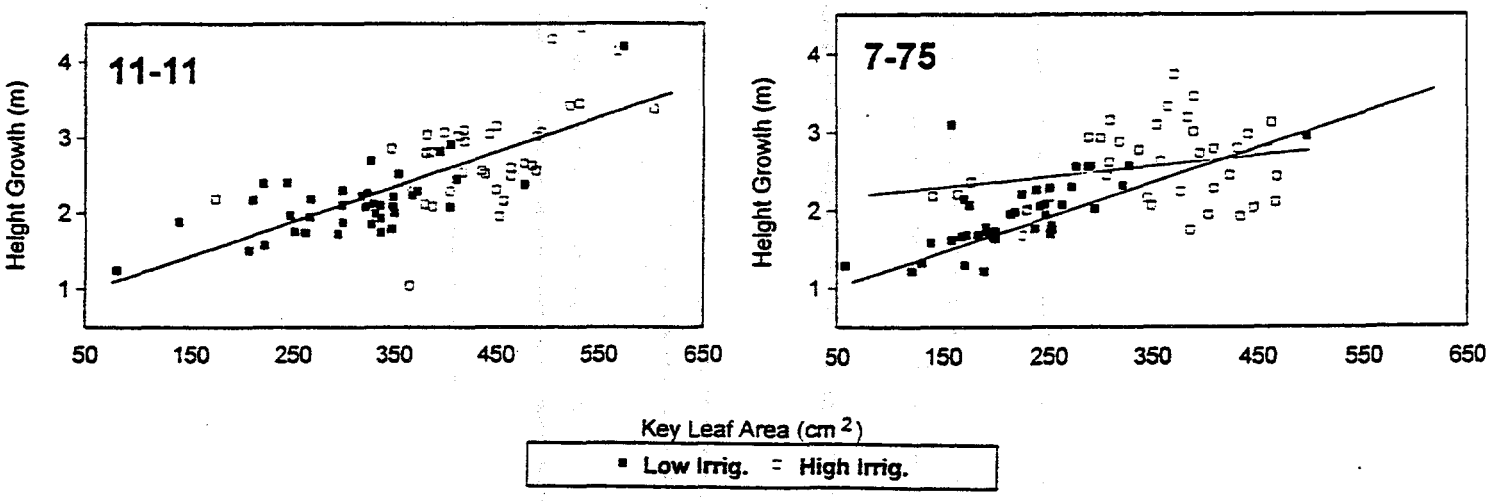
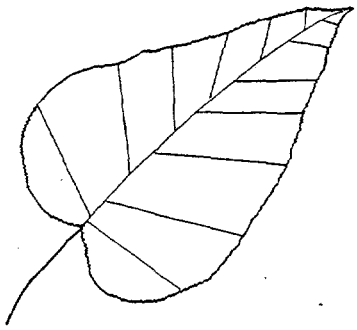


Fig. 1. The relationship between mean area of fully expanded terminal leaves and 2nd-year height growth for clone 11-11 and clone 7-75. For 11-11, one regression relationship was sufficient for both low and high irrigation regimes ($y = 0.0043 x + 0.8$). For 7-75, the low irrigation regime could be described by the same equation as for 11-11, but the high irrigation regime was best described by $y = 0.0014 x + 2.1$.



Chapter 8

Use of Harmonized Equations to Estimate Above-Ground Woody Biomass for Two Hybrid Poplar Clones in the Pacific Northwest[1]

Gary W. Clenenden

Abstract: Equations were developed to estimate components of above-ground woody biomass, as a function of diameter, height, spacing, and age for two hybrid poplar clones in western Washington. Independent and harmonized fitting techniques are compared. With the small sample sizes that are unavoidable in such experiments, harmonized equations provided more useful and consistent estimates of biomass increment than did independent equations by age and spacing. They were also better suited to interpolation and extrapolation of long term trends of biomass increment than those based on the independent fits.

Keywords: Biomass equations, *Populus*, cottonwood, spacing, stand density, yields.

Considerable interest has developed in short-rotation intensive culture of poplar and other species for energy and fiber products. Research to date has provided productive clones and successful establishment methods (Heilman and others 1991). Important questions remain about spacing, rotation age, and interrelationships with growth rate as affected by site, cultural treatment and genetic (clonal) interactions with site and cultural treatment. Answers to these questions and management decisions will vary with objectives but must be based on an understanding of growth patterns of trees and stands. Availability of equations to estimate biomass components based on more easily measured tree characteristics, such as diameter and height, are prerequisite to such understanding.

Many past attempts to characterize and understand tree and stand growth have involved applications of general allometric equations to estimate growth responses to treatment, including allocations of biomass among tree components, without examining differences in allometry among treatments. This has occurred in forestry applications and is especially prevalent in ecology and biomass research. Moreover, most available equations were developed independently for each year or growth period; each equation contains some unexplained variation and is influenced by sampling inadequacies, annual climatic fluctuations, and measurement errors. All of these influences become part of estimated changes and/or increments because such changes and increments are determined by differences between estimates from the independent equations.

Previous studies have developed biomass estimates across treatments and spacing but have not examined differences in allometry among treatments. Blankenhorn and others (1986) used diameter and height as predictor variables for separate equations for each treatment and year. Other recent examples are Dolan (1984), who used log-log equations for each spacing and year to estimate biomass with logarithms of diameter and height as predictor variables for the logarithm of biomass; Auclair and Bouvarel (1992), who estimated biomass for coppiced poplar using height of tallest shoot and number of dominant shoots as predictor variables in a nonlinear equation; and Blackwell and others (1992), who used the logarithm of diameter as a predictor of the logarithm of biomass for lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.). Baldwin (1987) presents a summary of biomass prediction equations for

[1] Accepted for publication in *Biomass and Bioenergy* (1996).

planted southern pines, but there is no reference to modeling density (spacing) or age effects. The same is true of Clark's (1987) summary of biomass equations for southern softwood and hardwood species. Several other papers on biomass studies and equations outside the United States also do not mention spacing or age effects (Auclair 1987; Kasile 1987; Pelz 1987; Singh 1987).

A particular problem arises in experiments that involve estimates of biomass and biomass increment over a series of years. Relationships are expected to change over time. Development of equations to estimate biomass components at each measurement date requires destructive sampling. Yet, extensive sampling at each measurement is not possible without destroying the experiment. Consequently, equations for estimating biomass components from readily measurable variables such as diameter and height must be developed from very small samples. Regressions fit to very small samples can be expected to be relatively inaccurate and may not produce consistent estimates for successive measurement dates.

Harmonization and constrained fitting techniques have had considerable use in forestry, particularly in estimation of height and stem volume. Growth estimates obtained by subtracting two successive independent estimates of height (or volume derived from these heights) are often erratic and sometimes impossible, because of the combination of small height samples and unavoidable errors in height measurement. Techniques have been developed for smoothing these trends over time that provide consistent estimates and reasonable interpolations and extrapolations for ages where measurements are not available. Curtis (1967) states that harmonized curves provide more reasonable estimates of change over time and a more consistent basis for estimating volumes and increments than independently fitted curves. Omule and MacDonald (1991) said essentially the same thing when they said that curves may cross illogically when fitted independently across measurement periods. Hyink and others (1988), Omule and MacDonald (1991), and Flewelling and DeJong (1994) developed procedures for fitting constrained, harmonized height/diameter curves for use with repeatedly measured plot data. Similar problems exist in biomass studies resulting from small sample size and measurement errors.

This paper reports one of the first attempts to develop individual prediction equations by clone and to harmonize curves over age and spacing as a means of overcoming the unavoidable limitations of small samples. It outlines procedures used for biomass sampling, development of harmonized equations, and their use to facilitate understanding of patterns and trends in above-ground woody biomass increment across time and among treatments. The results of independent fit and harmonized fit estimates are also contrasted.

METHODS

This study was conducted as an adjunct to an experiment established in 1986 in cooperation with the Washington State Department of Natural Resources in Olympia, Washington. The experiment was a factorial design with two poplar clones and three spacings arranged in three blocks. One clone, D-01, was a *Populus* hybrid (taxonomic identity unknown, but suspected to be either *P. trichocarpa* × *P. nigra* or *P. trichocarpa* × *P. angustifolia*) developed originally at the University of Idaho and subsequently selected from a Canadian planting by Dula's Nursery of Canby, Oregon (Dula 1984). The other clone, 11-11, was a *P. trichocarpa* × *P. deltoides* hybrid developed and tested by the University of Washington and Washington State University (Heilman and Stettler 1985). The clones were established as pure plantings at square spacings of 0.5, 1.0, and 2.0 m (corresponding to 40,000, 10,000, and 2,500 trees per hectare respectively). Size of plots varied with spacing such that each plot had 100 interior measurement trees and a buffer approximately one-half as wide as the projected height of the trees at five years (original anticipated time of harvest). Each buffer had a minimum width of three rows of trees spaced at the measurement plot spacing. Clone-spacing treatments were assigned randomly within each block. Yields were estimated by applying the oven-dry biomass component equations developed during this study to diameter and height

measurements taken on the 100 trees on each plot.

Field procedures

Trees were selected in the interior buffer rows of each plot for destructive sampling. Two trees were selected for each 1.0-m plot for year one because it was assumed that inter-tree competition (thus differences among spacings) were negligible and six trees per treatment (two per clone and spacing combination per block) were selected for years two through five and year seven to represent the distribution of diameters in each treatment. Trees were not sampled during the sixth year. A total of 192 trees were sampled. Sampling was done after the cessation of growth and bud set. The sample trees were felled, measured for diameter at 0.3 and 1.3 m and total height, and separated into stem and branch components. Each component was weighed in the field to obtain fresh weights. A subsample of each component was obtained from each tree; the subsamples were pooled by treatment and oven-dried to a constant weight at 105° C. The dry weight/fresh weight ratios so obtained were used to estimate dry weights of the components for individual sample trees.

Office procedures

Independent fits—Stem and branch biomass equations were developed independently for each clone and spacing combination at the end of each growing season. Equations were fit using stepwise linear regression procedures and the Statistical Analysis System, SAS/STAT (SAS Institute Inc. 1987) of the following form:

$$\mathbf{Ln(Y) = f[Ln(D), Ln(H), Ln(D)Ln(H)]}$$

where:

- Ln(Y) = natural logarithm of the component to be estimated, such as stem dry weight or branch dry weight,
- Ln(D) = natural logarithm of diameter at 0.3 meters above ground, and
- Ln(H) = natural logarithm of total tree height,

Harmonized fits—After several years' data were available, a harmonized model of the following form was also fit:

$$\mathbf{Ln(Y) = f[Ln(D), Ln(H), S, Ln(S), A, Ln(A)]}$$

where:

- Ln(Y) = natural logarithm of the component to be estimated such as stem dry weight or branch dry weight,
- Ln(D) = natural logarithm of diameter at 0.3 meters above ground,
- Ln(H) = natural logarithm of total tree height,
- S = spacing (0.5, 1.0, or 2.0 m),
- Ln(S) = natural logarithm of spacing,
- A = age (years since establishment), and
- Ln(A) = natural logarithm of age.

Spacing was considered a continuous variable; the actual value of 0.5 was used for the 0.5-meter spacing, 1.0 was used for the 1.0-meter spacing, and 2.0 was used for the 2.0-meter spacing.

The full model is represented by each of the above predictor variables in linear combination and all possible cross products of those single variables with the restriction that S and Ln(S) could not appear together and A and Ln(A) could not appear together in the same cross product. A single variable or cross product was allowed to enter the equation at each step if its coefficient was significant at the 0.05 probability level and was removed from the equation if its coefficient was not significant at the 0.05 probability level. Only variables with coefficients significant at a probability level less than 0.05 were allowed to remain in the final equations (Draper and Smith 1981).

Residuals analysis—Residuals were examined using Cook's distance to evaluate an observation's influence on the regression coefficients, and outliers were tested by using the Bonferroni t-test (Weisberg 1980). Three data points out of 378 were classified as outliers and were rejected from the data set at the 0.05 probability level. Standardized residuals of the rejected data points ranged from -3.9 to 5.8. Before rejection, these data points were carefully examined for possible reasons why they were different from other data points; no bio-

logical reason was found and the sampled material was not available for re-examination. Therefore, it was assumed that some type of measurement or recording error had occurred.

Logarithmic bias—Both the independently fit and the harmonized equations are logarithmic in form, thus a correction for logarithmic bias was needed. Guidelines given by Flewelling and Pienaar (1981) were used to select an appropriate log bias correction factor. Log bias correction factors were applied to each prediction equation which increased the estimated biomass by a small fixed percentage (less than 3% for woody biomass).

Application of tree level equations for stand estimates—The biomass equations were used with measured diameters and heights to estimate biomass of tree components for individual trees on the research plots. The individual tree estimates were summed over all trees on the plot and expanded to per hectare estimates. Biomass growth rates were estimated indirectly as differences between estimates for successive growth periods. Woody biomass was estimated as the sum of stem biomass and branch biomass.

RESULTS AND DISCUSSION

Independent fits

Initially, biomass was modeled using independent annual fits to provide information on allometry of component values relative to diameter and height and immediate short term estimates of yield. Independently fit equations may theoretically provide "best" estimates of cumulative growth (or size) at any given time, but unfortunately, "best" or even "good" estimates of annual growth cannot be derived therefrom because of year-to-year inconsistencies and variation associated with sampling, field measurements, or shifts in predictor variables. Moreover, independently fit annual equations cannot be interpolated or extrapolated reliably for periods for which measurements are not available. Maximum points are not easily identifiable because of fluctuations and inconsistencies in estimated growth rates.

Each year the same independent model was fit, but the same predictor variables did not always enter. This is a common occurrence when using stepwise regression procedures. This is accentuated by the small size (six trees) of the available samples for each clone and spacing combination for each year. The difference in equation forms from year-to-year was probably a major contributor to the inconsistencies observed when the independent annual fits were used to estimate increments by subtraction. Forcing consistent independent variables for each year, however, would have resulted in the inclusion of insignificant variables and/or exclusion of significant variables. Table 1 shows the regression coefficients for the independently fit stem dry weight equations for both clones and number of observations, R^2s, mean square errors (MSE), means for the transformed Y, and standard errors of estimate as a percent of the untransformed (geometric) mean for those fits by spacing and year. Variables entering the equations from year-to-year and spacing-to-spacing were most consistent in stem dry weight fits. Branch weights were much less consistent and fits were not as good as for stem dry weights.

Woody biomass—In the first three years the independently estimated increments (Fig. 1a) decreased with increased spacing for the D-01 clone, a result which was expected because the trees had not fully occupied the site. In the fourth year the trend of increment with spacing had reversed (i.e., growth increased with increased spacing); in the fifth year, however, the trend changed again with the 1-m spacing having the maximum increment. In years six and seven, the increments increased with increased spacing.

In the first year the trend in biomass increment for the 11-11 clone (Fig. 1b) decreased with increased spacing, but in years two and three the increment trend was mixed with the 1-m spacing having maximum increment. In year four the increment increased with increased spacing, but in year five an unexpected reversal occurred when the increment trend decreased with increased spacing. In years six and seven the trends again reversed and increased with increased spacing. In year six, the increment of the 0.5-m spacing was exception-

ally small, especially when compared to the extremely large increment the year before.

These inconsistent patterns in increment trends with spacing were disconcerting because they did not match expectations and current knowledge about general stand growth patterns. Once trees had fully occupied the site and biomass increments began to increase with spacing, the trend was expected to continue. Increment was expected to increase as spacing increased between trees. Current annual diameter and height increment trends (Fig. 2a, b, c, and d) did not show the inconsistent patterns observed for above-ground woody biomass (Fig. 1a and 1b), however. Moreover, no mortality occurred during the sixth and seventh growth periods to explain the inconsistencies in per hectare patterns and disparities with diameter and height growth trends. Subtracting the estimates from the independent equations was unreliable for estimating annual growth trends or patterns.

In year six, diameters and heights were measured but no trees were sampled for biomass; therefore, no equation could be developed. However, equations were available for years five and seven. An estimate of biomass (and corresponding increments) can be obtained from the independent estimates for the sixth growth period by either of two interpolation methods. The first is simple linear interpolation between year five and seven. This apportions increment, including mortality, equally between growth periods six and seven. The mortality assumption may or may not be correct. Differences in annual diameter and height increments are not accounted for. Figure 3a illustrates the results of using straight line

Table 1. Regression coefficients and associated fit statistics for independently fit stem dry weight equations by clone, spacing, and year

		Clone D-01						Clone 11-11					
		Year						Year					
Spacing		1	2	3	4	5	7	1	2	3	4	5	7
	Intercept		4.049	4.972	4.408	3.950	3.524		3.082	4.808	3.998	3.387	3.031
	Ln(D)				2.078	2.474	2.745				2.461	2.944	2.984
	Ln(H)								1.022				
	Ln(D) × Ln(H)		1.472	0.845					0.828	0.886			
0.5-m	n		6	6	6	6	6		6	6	6	6	6
	R^2		0.992	0.991	0.991	0.999	0.991		0.995	0.992	0.997	0.998	0.997
	MSE		0.003	0.004	0.008	0.001	0.028		0.001	0.011	0.005	0.002	0.013
	Mean Ln(Obs Y)		5.529	6.507	7.331	7.440	7.470		6.085	6.439	7.691	8.304	8.555
	% Error*		5.53	6.78	9.30	3.05	18.04		2.68	10.95	7.10	4.33	12.27
	Intercept	3.071	4.580	5.267	4.847	5.117	2.833	4.350	5.249	-2.447	3.912	3.767	3.673
	Ln(D)				1.738		1.799				2.432	2.587	2.640
	Ln(H)	2.471					0.969			4.825			
	Ln(D) × Ln(H)		1.060	0.716		0.731		1.832	0.677				
1.0-m	n	6	6	6	6	6	6	6	6	6	6	6	5
	R^2	0.965	0.988	0.899	0.997	0.999	1.000	0.992	0.975	0.987	0.988	0.997	0.997
	MSE	0.016	0.002	0.036	0.002	0.001	0.001	0.001	0.003	0.007	0.005	0.002	0.002
	Mean Ln(Obs Y)	4.195	6.202	7.345	8.189	8.270	6.699	5.580	7.039	7.752	8.953	9.261	8.994
	% Error	13.26	4.91	20.73	3.95	3.67	3.91	3.21	5.33	8.53	7.55	4.91	5.02
	Intercept		4.207	4.966	4.359	5.132	5.482		5.059	4.469	5.244	5.433	5.417
	Ln(D)											1.835	
	Ln(H)												
	Ln(D) × Ln(H)		1.442	0.844	0.927	0.718	0.658		0.796	0.904	0.710		0.653
2.0-m	n		5	6	6	5	6		6	6	5	6	6
	R^2		0.930	0.992	0.986	0.983	0.998		0.970	0.977	0.981	0.986	0.995
	MSE		0.016	0.005	0.009	0.006	0.003		0.002	0.004	0.004	0.002	0.007
	Mean Ln(Obs Y)		6.034	7.826	9.743	9.291	9.751		7.256	8.675	9.497	10.080	10.036
	% Error		13.44	7.02	10.12	8.26	5.53		5.02	6.44	6.78	4.57	8.53

* % Error = $e^{(\text{Mean (Ln(Obs Y))} + \text{sqrt(MSE)})} * e^{-(\text{Mean (Ln(Obs Y))})} * 100$

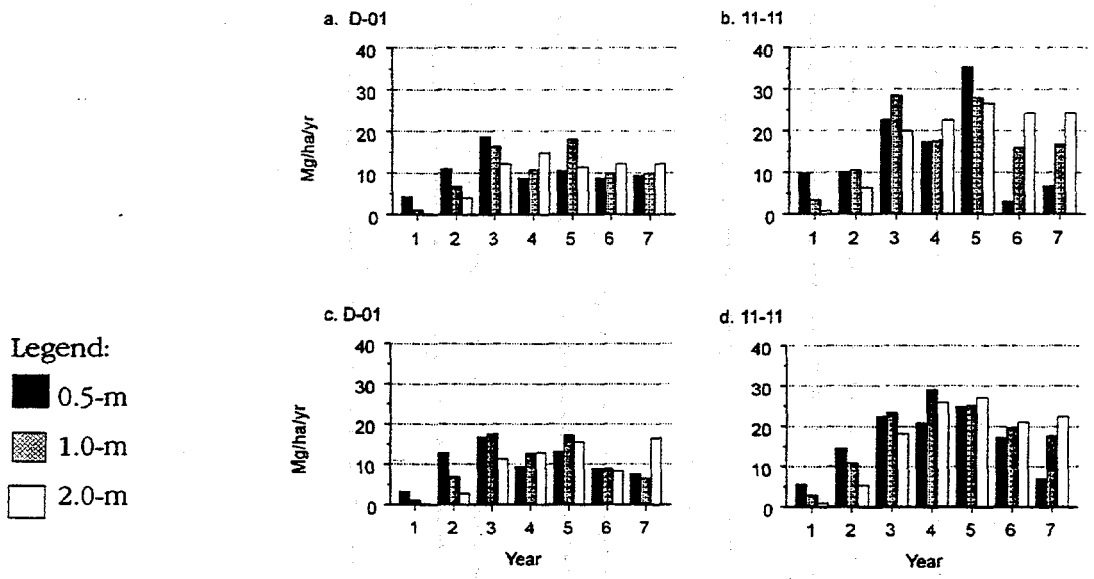


Fig. 1. Above-ground woody biomass (stem + branches) annual increments for independent fits (a and b) and harmonized fits (c and d) by clone, spacing, and year.

interpolation for clone D-01 at the 2-m spacing. Notice that the trend for year five to year seven for the independent fit does not follow the trend lines for diameter and height increments, thereby washing out the effects of the drought in the early growing season in year six. Figure 3b illustrates the results of using straight line interpolation for clone 11-11 at the 2-m spacing.

The second method of interpolation is to substitute the measured diameter and heights for year six into the year five and seven equations and then average the two estimates (substitution method). This procedure incorporates differences in mortality for the two growth periods plus differences in diameter and height increments. Figure 3c and 3d illustrates the results of using the substitution method for clone D-01 and 11-11, respectively, at the 2-m spacing. Intuition suggests that the substitution method should track the trends in diameter and height increment; however, in this case the results for clone 11-11 (Fig. 3d) are the opposite of those trends. In this instance the year five equation greatly overestimated the biomass when applied in year six, which included heights outside the range of those found in year five.

Table 2. Regression coefficients and associated fit statistics for harmonized stem dry weight equations by clone.

	Clone D-01	Clone 11-11
Intercept	3.212	4.957
LN(D)	1.265	1.540
Ln(H)	0.910	-0.566
A		-0.353
Ln(A)	-0.240	
S	0.211	
Ln(D) × Ln(H)	0.138	0.291
Ln(D) × A	0.026	
Ln(D) × Ln(A)		-0.351
Ln(H) × Ln(A)		0.926
Ln*H) × Ln(S)	-0.173	
Ln(D) × Ln(H) × Ln(S)		-0.029
n	94	92
R^2	0.996	0.998
MSE	0.012	0.006
Mean Ln(Obs Y)	7.407	8.114
% Error†	11.33	8.12

Harmonized fits

Because of inconsistencies between growth estimates from year-to-year when using the independent equations, especially year five increment in woody biomass trends across spacing, equations harmonized over age and spacing were fit to the combined data for each clone. The new harmonized equations resulted in more consistent estimates of annual yields and increments over age and spacing for each of the clones than did the independent equations. Table 2 shows the regression coefficients for the harmonized stem dry weight equations for both clones and number of observations, R^2s, MSEs,

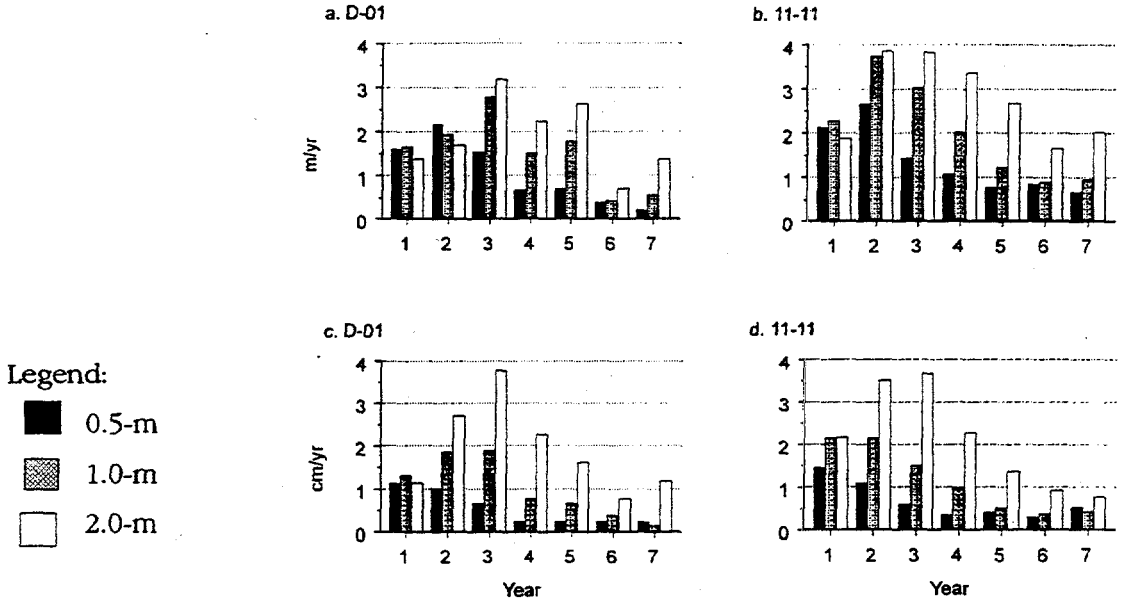


Fig. 2. Annual height increments (a and b) and diameter increments (c and d) by clone, spacing, and year.

means for the transformed Y, and standard errors of estimate as a percent of the untransformed (geometric) mean for those fits.

Harmonized fits across time require several successive measurements, and annual fluctuations in estimated growth rates, artifacts, and data collection biases tend to be reduced by the smoothing process. The harmonization process produces smoothed long-term trends in allometry and provides for interpolation for periods where samples were not taken. They also can be extrapolated more reliably than independent annual fits. Maximum points are more easily identified than with independent fits because of the smoother trends.

Woody biomass—Figures 1c and 1d illustrate the current annual above-ground woody increments per hectare using the harmonized prediction equations. The trends in annual increments decreased with increased spacing during the first two years and began to transition to increasing with increased spacing in year three. Clone D-01 remained in transition (Fig. 1c), increased from 0.5-m to 1-m, and decreased from 1-m to 2-m spacing, until year seven when the 2-m spacing increased above the 1-m spacing. The 11-11 clone was in transition (Fig. 1d) during years three and four and increased with increased spacing in year five and continued to show increased trends with increased spacing in years six and seven. The only apparent anomaly was in clone D-01 in year seven when the 1-m increment fell below the 0.5-m and there was a large increase in the 2-m spacing increment (Fig. 1c); however, this same pattern was also present in the measured diameter increments (Fig. 2c).

The harmonized fits proved to be superior to the independent fits when estimating biomass for year six when biomass was not sampled. Years four and six were both dry years and irrigation during the early spring was less than normal because of equipment failures, resulting in 50% less water input during the early growing season than other years. The diameter and height increment (Fig. 2) reflect this early water deficit, especially height increment for D-01. The interpolated values based on the independent fits (Fig. 1a, b) do not show a corresponding depression in the year-six growth rates, but the harmonized fits do reflect the reduced growth in a similar manner as the height and diameter increments illustrated in Figures 2a and 2b. The harmonized fit for clone D-01 shows the same depression in growth for the 2-m spacing as does height increment (Fig. 2a and 3a). Figure 3 illustrates that the harmonized fit can be used (interpolated) for measurements where no biomass samples were taken to estimate growth and that in fact the estimate reflects the real climatic effect which occurred as measured by the height and diameter increments for the same period.

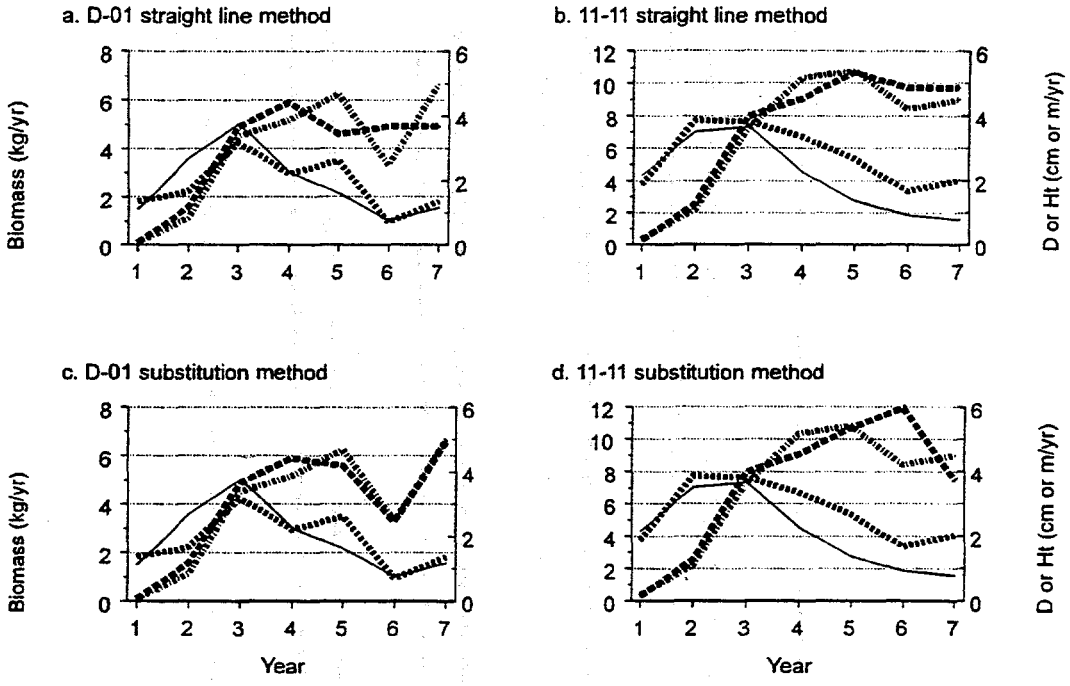
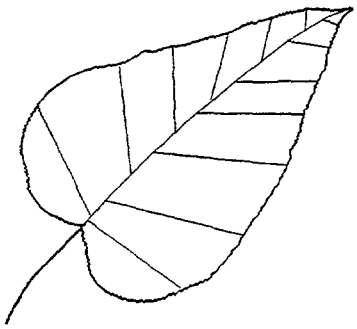


Fig. 3. Above-ground woody biomass (stem + branches) mean tree annual increment trends as estimated from harmonized and independent fits at 2-m spacing using two different interpolation methods to estimate increment in year six for the independently fit biomass equations. Diameter and height increment trends are included for comparison.

CONCLUSIONS

The anomalies that appear in biomass estimates based on independently fit equations are in large part a consequence of very small samples used in fitting the biomass equations. This is an unavoidable limitation in experiments that require estimates of biomass over a series of years, because only small numbers of trees can be destructively sampled to determine tree biomass, without destroying the overall experiment.

Because of the intrinsic unreliability of biomass regressions derived by independent fits to very small samples, results will generally be more consistent and more readily interpretable if regressions are harmonized over age and spacing, using all data combined, rather than fit as independent equations for each year and spacing. If fewer than three years of data from one spacing are available, harmonization across age is not reasonable; however, harmonization across three or more spacings is possible with fewer years of data. Harmonized fits will also provide more accurate estimates for years lacking biomass measurements than can interpolations based on independent fits.



Chapter 9

Summary and Conclusions

Studies conducted in the PNW-DNR plantations from 1986through 1996 provided much experimental data on response of *Populus* clones to silvicultural practices and management regimes. These data have been presented and discussed in Chapters 2 through 8, all of which have been published or accepted for publication in scientific journals. Other information derived from data collected in early phases of the studies was published previously (Radwan and others 1987; DeBell and others 1989b; DeBell and Clendenen 1991; DeBell and Harrington 1993). The purpose of this chapter is to summarize several of the principal findings in broad yet practical terms for those who are developing techniques and making decisions concerning the establishment and management of clonal poplar plantations. These major "take-home messages" are:

1. **Establishment success of unrooted stem cuttings of *Populus trichocarpa* and *Populus* hybrids requires the presence above-ground of at least one healthy axillary bud.** This finding arose from our first unsuccessful attempt to establish the Yelm plantings with stock provided by commercial firms in the region (Radwan and others 1987). The importance of bud characteristics is not stressed in many guidelines for propagation and production of *Populus* cuttings (e.g., FAO 1979; Dickmann and Stuart 1983), probably because absence of buds is rarely a problem with clones of other *Populus* species. The sylleptic branching habit of *P. trichocarpa* and many of its hybrids in the moderate, marine climate of western Washington and Oregon results in many "spent" buds; that is, sylleptic branches develop from buds in the leaf axils and high syllepticity results in few buds remaining on the main shoot. In most cases, only one-third of the current shoot has enough buds to make satisfactory cuttings, even though diameter and length of the shoot would otherwise permit the production of at least twice as many cuttings. Growing cutting stock in dense stool beds should result in adequate buds on a much greater proportion of the shoot, given that sylleptic branching is strongly influenced by stand density and was substantially reduced in the 0.5-m spacings in our trials (Chapter 3).

2. **The "woodgrass" system has little promise as a management regime for growing *Populus* biomass.** The coppice system, proposed by nurseryman Dula (1984) and promoted by some members of the bioenergy and political communities, involved establishing a *Populus* hybrid (clone D-01) at very high densities (100K to 600K rootstocks per hectare) and harvesting biomass annually. Our experimental tests resulted in "woodgrass" yields that were only 35 to 60% of the yields produced by wider spacings on 5-year rotations (Chapter 2; DeBell and others 1993). Moreover, costs of establishing "woodgrass" would be substantially higher and biomass characteristics would be less desirable for most products and conversion processes than those of more widely spaced, "high forest" systems. The "woodgrass experience" of the biomass community also has broader sociopolitical and scientific implications; that is, a range of alternatives should be examined before any short rotation biomass system is selected or highly promoted. The costs — and time required for — such evaluations are minimal when compared with unnecessary costs that may be incurred or productivity that may be foregone when decisions are made in the absence of such assessments.

3. **Decisions about spacing and rotation length are very important in short-ro-**

tation, intensively cultured *Populus* plantations, much more so than in traditional forest management. Spacing or stand density has strong effects on individual tree growth, stem form, and branching habits in *Populus* plantations; and, at the stand level, spacing exerts influence on growth phenology (especially late-season growth), yield, patterns of mean annual biomass increment (including the magnitude and culmination thereof), and optimal rotation length (Chapter 3, DeBell and others 1996). Moreover, the relationships of spacing to tree and stand performance change over time as the plantation develops. Relative differences among clones are affected by and tend to increase with growing space in monoclonal plots. Proper spacing in light of desired tree size at the intended harvest age is needed to capture the potential of many improved clones. In our plantations, there was a substantial infestation of poplar-and-willow borer after competition became intense. Infestation was first observed at the closest spacings, and percent of trees affected increased with time.

Factors such as desired tree size, biomass composition, yield, and subsequent flexibility in scheduling harvests must be considered and balanced in spacing-rotation length decisions. In most cases, optimal spacings will be wider and rotations longer than those envisioned in most earlier biomass research (cf. Ranney and others 1987), including the studies reported in this document. For example, syntheses of our work with other data suggest that spacing should on average provide approximately 70 ft^2 per tree (6.5 m^2 per tree) if mean tree diameter at harvest is targeted at the 6-inch (15-cm), the size believed to be the minimum for achieving reasonable harvesting costs. Even for this size, however, actual spacing may vary by clone and the stockability thereof [the latter concept is described in DeBell and others (1989) and evidence of clonal differences in stockability is presented in Chapters 3 and 4].

Some management organizations, such as James River Corporation, have chosen to use rectangular rather than square spacings for reasons of mechanical efficiency. Important effects on growth and yield may also exist. Our DOE-sponsored work with red alder suggested that stands planted in rectangular arrangements differentiate more readily, leading to more rapid tree growth and greater stand yield, than do stands planted in square spacings. Presumably, such differences arise because trees in the latter stands spend more time in a "quasi-stagnant" phase when competition intensifies (Chapter 4). Recent work in Finland with silver birch (Niemistö 1995a, b) and in Yugoslavia with clonal poplar (Markovic and Herpka 1986) also point to some probable benefits of rectangular spacing.

4. **Large plots are needed to accurately evaluate and define clonal differences in tree growth, biomass yield per hectare, and stockability.** Although short-term assessments on small plots are necessary and useful for initial screening of large numbers of clones, they do not provide adequate information on per hectare productivity or on relative productivity differences among clones selected as suitable for operational use. The plots used in our studies consisted of at least 100 measurement trees, surrounded by 3 to 8 rows of border trees; the intent was to provide a border at least one-half as wide as the estimated height of trees at rotation age. Tree height growth in our studies was equal to or better than growth reported by others, but stand growth and yield values were lower and differences among clones were less than previously reported. For example, mean annual production values determined at age 5 by Heilman and Stettler (1985) for clone 11-11 and for *P. trichocarpa* sources from which two clones used in our studies were derived were about 28 and 16 Mg ha^{-1}, respectively; whereas our tests provided yield estimates of 18 and 13 Mg ha^{-1} for clone 11-11 and the two native clones (Chapter 4, DeBell and otheres 1997). Our yield estimates, however, were similar to those achieved in pilot-scale and operational plantings of James River Corporation at the Lower Columbia River Fiber Farm [pers. comm. from William Schuette of James River Corporation, Camas, Washington (January 4, 1995)]. Large plots carried long enough for intense competition to develop, and preferably into the stage where competition-related mortality begins, are also needed to assess differences in stockability among clones and cultural prac-

tices. More accurate definition of differences in stockability and yield becomes particularly important when other matters, such as susceptibility to damaging agents or wood quality, become significant considerations in choosing among clones and cultural regimes.

5. **Deployment of clones in monoclonal plantings results in production at least equal to that obtained in polyclonal plantings. Moreover, monoclonal stands (and biomass components contained therein) are more uniform and inventory is more evenly balanced among clones.** Our test of monoclonal and polyclonal deployment of four clones at three spacings revealed that numerous tree and stand traits differed by clone, spacing, and deployment and many of the interactions of these factors (Chapter 5). Differences among clones in growth and form were greater in polyclonal than in monoclonal plots, and differences in performance between deployment methods were greater in the denser spacings. Total woody yield decreased with increased spacing, and yield differed among clones in both monoclonal and polyclonal plots. Assuming that clonal selections have been made and equal numbers of plants from the same clones will be planted, our results indicate that method of deployment will have little or no effect on overall productivity; that is, although there were clonal differences in yield, the mean yield of the four clones in monoclonal plots did not differ from the yield of polyclonal plots.

These results, coupled with other considerations, reinforce our opinion that deployment in mosaics of small monoclonal plots is at present the most effective and efficient approach for operational establishment of short-rotation poplar plantations and for the development and refinement of technology related thereto (DeBell and Harrington 1993).

6. **Stand damage associated with high winds may be an important factor in western Washington and Oregon, but risks can be minimized by selection of resistant clones.** The "Inaugural Day Storm" of January 1993 caused severe toppling, leaning, and breakage in several *Populus* plantations in the region, including some at James River Corporation's Lower Columbia River Fiber Farm and the PNW-DNR plantations near Olympia. Because the latter plantings were established in a replicated experimental design, an unusual opportunity existed to assess stand and tree characteristics associated with wind damage; such assessments included above- and below-ground morphology as well as stand treatments (Chapter 6). Wind damage differed significantly among clones, spacings, and deployment method. Susceptibility of individual trees was linked to minimum stem taper, high branch weight on the upper stem, and uneven root distribution (particularly if rooting was low in the windward direction). Clone 11-11 was the most susceptible clone, with 44% of stems in the 1.0-m spacing leaning; whereas clone 47-174 suffered no damage. Clone 49-177 also suffered high wind damage (48% of stems affected), but the degree of lean was less than for clone 11-11. Overall, most damage occurred in the 1.0-m spacing and least occurred in the 0.5-m spacing, and damage was markedly lower in polyclonal than in monoclonal plots.

In addition to avoiding location and topographic positions associated with high velocity winds, the most effective approach to reducing wind damage is probably the selection of wind-resistant clones. Furthermore, post-planting cultivation should be minimized in wind prone areas. Observations in our plantings indicated that damage was substantial at wider spacings (2.0-m) in older plantings of clone 11-11 where weeds had been controlled with a rotovator during the first growing season; the shallow lateral roots in the cultivated rows were bent or cut, resulting in root systems that were structurally weakened in the cultivated row. No damage, however, occurred in a similar aged, adjacent planting that had not been rotovated, despite the fact that the stand had been thinned recently. Finally, managers might also consider rectangular spacings oriented with the short side (i.e., least distance between trees) parallel with the prevailing direction of high winds.

7. **The size of the most recent, largest, fully expanded leaves on the current terminal is strongly related to biomass, height and diameter growth, and appears to be an excellent integrator of growing conditions and growth potential.** The design of one of

our plantations created microsites with a wide range of nutrient and moisture conditions. These conditions were reflected in the productivity of trees growing on the microsites. Despite such diverse conditions and performance, terminal leaf size (area or weight) was more strongly correlated with biomass productivity than any other single tree or leaf characteristic, including concentration or content of selected nutrients, chlorophyll, or total available carbohydrates. This simple characteristic is very easy to measure and may be a very useful indicator of potential productivity or future growth as it is influenced by different kinds and levels of growth factors. Thus, we believe that terminal leaf size merits further testing as an aid in site selection, matching clones to sites, or monitoring tree response to cultural treatments as well as provided an early indicator of the relative performance of various clones.

8. **Harmonized equations provide more useful and consistent estimates of biomass and biomass increment than do independent equations for each age and cultural treatment (e.g., spacing); harmonized equations also are better suited to interpolation and extrapolation of long-term trends in biomass accumulation.** The development and refinement of cultural practices and management regimes for clonal plantations require accurate estimates of biomass increment at various points in time prior to final harvest. In many instances, the allometry between biomass components and readily measured variables such as diameter and height differs by clone and cultural treatment and changes over time. Unfortunately, the development of equations to estimate biomass at each measurement date requires destructive sampling, yet sampling within each treatment cannot be extensive without destroying the experiment. Because of the small number of samples that can be obtained, independent fits are unreliable and may lead to inconsistent and unreasonable trends when annual or periodic increment is estimated by subtracting biomass estimated from independent equations for two points in time. Thus, they may also lead to invalid comparisons among stand treatments such as spacing and fertilizing. Comparisons of biomass estimates and growth trends based on equations developed from independent fits and harmonized fits demonstrated the clear superiority of the latter methods (Chapter 8).

9. **Much progress has occurred in short-rotation poplar technology during the past decade, but major needs for silvicultural information remain.** These unmet needs are particularly important for the more diverse sites and objectives of non-industrial landowners. The most important needs include (1) methods for evaluating site productivity and opportunities for enhancing site potential via cultural treatments, and (2) guidelines for management of stand density and selection of rotation length. We suspect that useful interim methods and guidelines could be developed via syntheses of data that are currently available or could be obtained by measurement of existing plantations, provided that scientists, managers, and landowners involved in poplar culture wish to share and cooperate in such an endeavor.

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