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Competitive effects of conspecific and herbaceous (weeds) plants on growth and branch architecture of *Populus* ×*euramericana* cv. Eugenei[1]

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Abstract: The influence of tree density (2×3, 1×2, and 0.5×1 m) and weed control (weedy vs. weed free) on the growth and branching architecture of *Populus* ×*euramericana* cv. Eugenei was examined in an experimental plantation in southwestern Michigan, U.S.A. In the presence of weeds, poplars were shorter ($p < 0.0001$), had a smaller basal diameter ($p < 0.0001$), initiated fewer branches ($p = 0.0004$), and had fewer living branches ($p = 0.002$), shorter branches ($p < 0.0001$), and branches that spread outward ($p < 0.0001$). Increasing tree density decreased poplar height ($p < 0.0001$), basal diameter ($p < 0.0001$), branch length ($p = 0.0062$), and the number of living branches ($p < 0.0001$). At high densities, branches spread outward at their origin ($p = 0.0015$) and then curved sharply upward ($p = 0.002$). At the highest planting density there was no difference in branching in plots with and without weed control. However, poplars in the weedy treatment were smaller than those in the weed-free treatment ($p < 0.0001$). Our results demonstrate that poplar growth and architecture can be influenced by competitors of very different stature. Weeds, in fact, have a greater effect on growth than conspecifics. As a result, poplars grown in the presence of weeds are stunted relative to poplars grown in the absence of weeds, even at the highest tree density where the competitive effects of poplars reduced weed biomass.

Résumé : L'influence de la densité des arbres (2×3, 1×2 et $0{,}5 \times 1$ m) et du contrôle des mauvaises herbes (avec ou sans mauvaises herbes) sur la croissance et l'architecture des branches de *Populus* ×*euramericana* cv. Eugenei a été examinée dans une plantation expérimentale située dans le sud-ouest du Michigan, aux États-Unis. En présence de mauvaises herbes, les peupliers étaient plus courts ($p < 0{,}0001$), avaient un plus petit diamètre à la base ($p < 0{,}0001$), formaient moins de branches ($p = 0{,}0004$), avaient moins de branches vivantes ($p = 0{,}002$), avaient des branches plus courtes ($p < 0{,}0001$) qui s'étendaient vers l'extérieur ($p < 0{,}0001$). Le fait d'augmenter la densité des arbres réduisait la hauteur du peuplier ($p < 0{,}0001$), le diamètre à la base ($p < 0{,}0001$), la longueur des branches ($p = 0{,}0062$) et le nombre de branches vivantes ($p < 0{,}0001$). Aux densités élevées, les branches s'étendaient de leur point d'origine vers l'extérieur ($p = 0{,}0015$) et se recourbaient par la suite fortement vers le haut ($p = 0{,}002$). À la plus forte densité, il n'y avait pas de différence dans l'architecture des branches entre les parcelles avec ou sans contrôle des mauvaises herbes. Cependant, les peupliers étaient plus petits dans le traitement sans contrôle des mauvaises herbes que dans le traitement avec contrôle des mauvaises herbes ($p < 0{,}0001$). Les résultats démontrent que la croissance et l'architecture du peuplier peuvent être influencées par des compétiteurs de stature fort différente. En fait, les mauvaises herbes ont un effet plus important sur la croissance que les compétiteurs de la même espèce. En conséquence, les peupliers cultivés en présence de mauvaises herbes sont rabougris comparativement aux peupliers cultivés en l'absence de mauvaises herbes, même à la plus forte densité où les effets compétitifs des peupliers réduisent la biomasse des mauvaises herbes.
[Traduit par la Rédaction]

Introduction

Competitive influences of neighbors on the architecture, size, survival, and reproductive output of plants have been shown to vary in relation to the abundance, size, and growth form of neighbors (e.g., Weiner et al. 1990). Therefore, neighbors of differing growth form or size should affect target plants in different ways. Most studies of plant competition have focused on the competitive interactions between conspecifics, or between plants of similar growth form. Comparatively few studies have examined the relative impact of neighbors with different growth forms (e.g., herbaceous plants vs. trees or shrubs) on the same target plant species (but see Rejmánek and Messina 1989).

In silvicultural systems, competitive effects on growth and architecture are expected from conspecifics. For example, increasing the density of conspecifics in tree plantations reduces tree growth (Zsuffa et al. 1977; Cannell 1980) and alters branching architecture (Kohyama 1980; Cannell 1980; Nelson et al. 1981*b*). The presence of herbaceous weeds also reduces tree growth (Zsuffa et al. 1977; Nelson et al. 1981*a*; Kennedy

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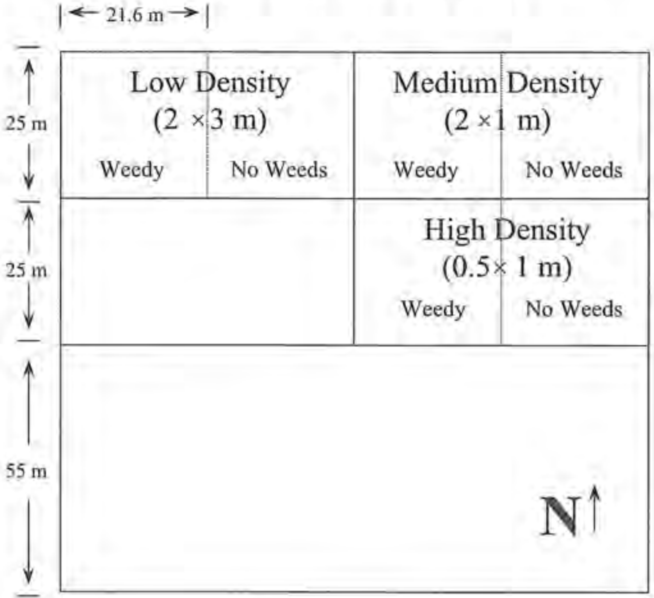


Fig. 1. Diagram of poplar research plots on the Kellogg Biological Station's Long-term Ecological Research (KBS–LTER) site. Position of density – weed treatment subplots are labeled. Poplars in the remainder of the plot were planted at a 2 × 1 m density.

1984; Knowe et al. 1985; Allen and Wentworth 1993; Lauer et al. 1993), but only few studies have examined the impact of weeds on tree architecture (Allen and Wentworth 1993).

In short-rotation silvicultural systems, high yield of woody biomass per unit area is the main objective and crown architecture and canopy density are major factors involved in silvicultural productivity (Farmer 1976). Crown architecture and canopy density are determined by branch angle, size, number, and distribution (Nelson et al. 1981*a*, 1981*b*; Burk et al. 1983) and leaf orientation, area, distribution, and morphology (Isebrands and Nelson 1982; Isebrands et al. 1983). Differences in branch characteristics result in major differences in crown form and leaf display, distribution, and density, which have been shown to influence light interception (Norman and Jarvis 1974; Smith et al. 1991; Smith 1993; Smith et al. 1993) and photosynthetic capacity (Hinckley et al. 1992). Because tree architecture has direct productivity consequences, factors affecting tree architecture either independently or in interaction are important in understanding productivity in silvicultural systems.

The focus of this study was to explore the effect of tree density and herbaceous weeds on the growth and branching architecture of *Populus* ×*euramericana* cv. Eugenei in a plantation setting. Poplar branching architecture and growth were measured to determine the plasticity of response to competitive stress and the effects of neighbors with very different growth forms (conspecific trees vs. herbaceous weeds). We predicted that tree density would have a relatively greater influence on architecture than herbaceous weeds because of their differences in stature and consequent effects on light. Weeds were expected to have a relatively greater influence on growth through their exploitation of soil resources. We also examined the interaction between tree density and herbaceous weeds on poplar growth and architecture because weed community structure is influenced by tree density. Maas (1992) has shown that weed biomass declines as tree density is increased in these plantations.

Methods

The Kellogg biological station long term ecological research site

This study was conducted at Michigan State University's W.K. Kellogg Biological Station, Long Term Ecological Research (KBS–LTER) site in southwestern Michigan. The KBS–LTER site was established in 1989 on a site with a history of agricultural cropping. The soil, primarily Kalamazoo silt loam (Typic Hapludalf, sandy to silty clay loam), is well drained and of moderate fertility (10.8 mg N/kg; Robertson et al. 1997). The mean annual temperature is 9°C (30-year mean) and annual precipitation is 860 mm/year, with about half falling as snow in the winter months. Within this area, seven cropping systems (till and no-till corn–soybean rotation, low-input and no-input corn–soybean–wheat rotation, a perennial herbaceous crop (alfalfa), a perennial woody crop (the poplar plots examined in this study), and a native successional community) with six replicates per cropping system were established in a randomized block design of 0.9-ha blocks

The poplar plots were established in late April – early May 1989. The plots were plowed and disked in late April and planted with unrooted hardwood cuttings (≈30 cm tall) of the clone *Populus* ×*euramericana* cv. Eugenei. Three planting densities were established in each of six replicate 0.9-ha plots: low, 2 × 3 m spacing; medium, 1 × 2 m spacing; high, 0.5 × 1 m spacing. However, only three of these replicate plots (1, 2, and 4) were used in this study. We omitted replicates 3 and 6 because trees in these replicates had a scale infestation; plot 5 was omitted because it had been invaded by black locust (*Robinia pseudoacacia* L.), which we felt would confound the analysis of the effects of herbaceous weed and conspecific effects on growth and branching architecture. Each density treatment was split on weed control (weeds vs. no weeds); weeds present in the plots emerged from the soil seed bank and dispersing propagules. The area of each density treatment was 50 × 23.2 and 25 × 21.6 m for each weed (or no weed) subplot within density treatments. The density – weed control treatments described above occupied less than half of each main plot (Fig. 1).

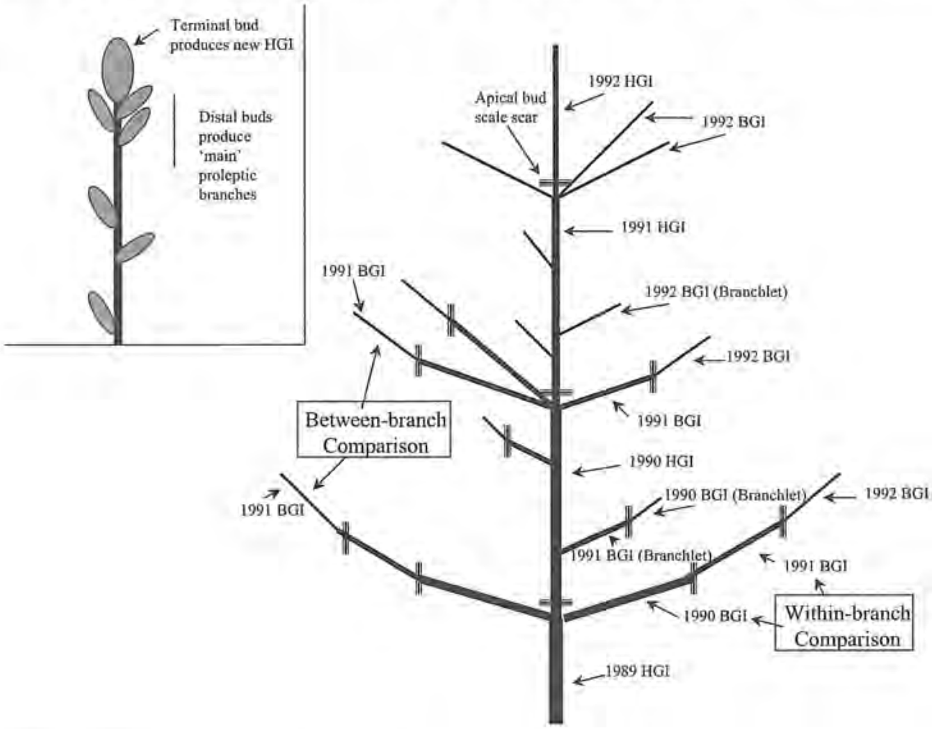
The weed-free subplots were established by applying a herbicide treatment shortly after planting. The herbicide mixture was 2.34 L/ha of oxyfluorfen; 3.5 L/ha of linuron; and 3.5 L/ha of simazine and was applied at a rate of 187 L/ha. Subsequent weed control was maintained in the weed-free plots by a combination of mowing, hand-hoeing, and herbicide (Glyphosate) application. All the plots were fertilized in the first year within early June with 110 kg N/ha as ammonium nitrate. Plots were not fertilized again.

In 1989 a set of trees in the center of each subplot was marked for annual monitoring of height and stem diameter (measured at 15 cm above ground). Twelve trees were marked in the low tree density and 28 trees in the medium and high tree density subplots of each treatment. In the subplots of all density treatments, 10 of these trees from three replicates (1, 2, and 4) were randomly selected for measures of branching architecture.

Architectural measurements

Branch architecture measurements were taken in the summer of 1992 on growth that occurred in 1990 and 1991. Under our conditions, this poplar hybrid produced three to five (mostly three) vigorous proleptic (main) branches each year on the main trunk in axils of lateral buds near the apex of the previous year's height growth increment. Basipetal to the main branches many small branchlets are produced, most of which die and abscise in the fall (Fig. 2). Measurements were made on the three most distal main branches produced from growth in 1990 and 1991 (total six/tree). On branches produced in 1990, separate measurements were made for growth in 1990 and 1991.

Fig. 2. Generalized poplar height (HGI, height growth increment) and branch growth showing branch growth increments (BGI) of main proleptic branches and smaller proleptic branchlets. Inset describes the fate of terminal and distal buds.



Branch architecture was characterized following the methods used by Polk (1974; and as adapted to poplars by Nelson et al. (1981*b*)) and included the following (Fig. 3):

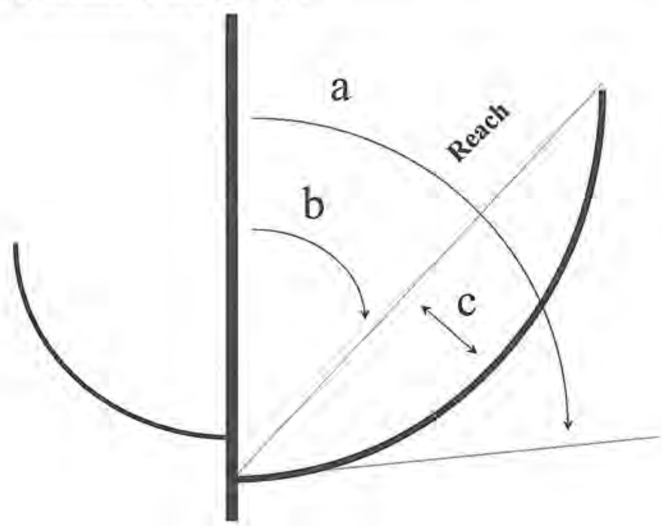
(1) Angle of origin: the angle formed by a branch at the point of insertion with the center line along the main stem axis at that point.
(2) Angle of termination: angle formed by a straight line from a branch tip to its point of origin and the center line along the bole axis.
(3) Reach: straight-line distance from the point of a branch origin to the tip of that branch.
(4) Maximum branch curvature: greatest departure (in cm) of a branch from a straight line extending from the point of origin to the tip of that branch. As in Polk (1974), upward curvature would have a positive value and downward curvature, a negative value.
(5) Number of branches: the total number of branches (alive, dead, or abscised) on each year's growth.
(6) Number of living branches: the total number of living branches on each year's growth.
(7) Basal diameter: basal stem diameter in 1992 (measured 15 cm above ground level).
(8) Height: tree height in 1991.

All the above measurements were nondestructive.

Branch angle was measured with a 30.5 cm 90° protractor fashioned from plywood similar to that described in Polk (1974). In measuring branch angle, the 0° line was parallel to the trunk of the tree (i.e., narrow branches that angled strongly upward have small branch angles and wide branches that spread out from the trunk have large branch angles; branches that are perpendicular to the trunk have a branch angle of 90°).

A split split plot ANOVA (SAS procedure GLM; SAS Institute Inc. 1989) was used to examine treatment effects (weed vs. no weed and tree density) on all measurements except total reach, height, and basal diameter. In the first split, the three densities were split on weed control. The second split (a repeated measures analysis) was on years. To compare within and between branch growth produced in the

Fig. 3. Measures used to describe branching traits in poplars following Polk (1974): (*a*) angle of origin, (*b*) angle of termination, (*c*) maximum branch curvature.



2 years, we first compared main branches produced in 1991 with the 1990 growth on the branches produced in 1990 (between-branch comparisons). For branches produced in 1990, we could compare growth in 1990 and 1991 (within-branch comparisons; Fig. 2). A split-plot ANOVA was used to examine treatment effects on the total reach (length of 1990 + 1991 growth on 1990 main branches), basal stem diameter in 1992, and height in 1992. All data were examined for normality prior to analysis, and distributions were consistent with the assumption of normality. Also, homogeneity of variance was tested using Bartlett's test (SAS Institute Inc. 1989). The variance across groups was found to be equal. Because these analyses involved

Table 1. Summary of split-plot ANOVA examining the effects of replicate, planting density, and weed control on *Populus* growth and size: (*a*) total reach (1990 + 1991 growth on 1990 main branches), (*b*) basal tree diameter (1992), and (*c*) tree height (1992).

		(*a*) Total reach			(*b*) Basal diam.			(*c*) Height		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Replicate	2	335.9	0.19	0.8290	741.9	1.15	0.3194	3.6	2.97	0.0542
Density	2	8 428.4	23.44	**0.0062**	12 277.4	19.02	**0.0001**	89.3	73.49	**0.0001**
Replicate × density	4	719.0	0.21	0.9235	1 901.4	1.47	0.2127	8.7	3.59	**0.0007**
Weed	1	75 220.8	86.65	**0.0001**	23 206.2	71.89	**0.0001**	305.2	502.52	**0.0001**
Density × weed	2	13 072.9	7.53	0.0231	9 595.6	14.86	**0.0001**	99.5	81.87	**0.0001**

Note: With Bonferroni corrections for multiple comparisons, the probability (*P*) value for a significant effect must be 0.01. Significant differences are noted in bold.

a large number of comparisons we calculated table-wide significance levels using the sequential Bonferroni technique (Rice 1989) to protect against group-wide type-I error. Main effects were interpreted only when there were no significant higher level interactions involving that variable. Also, although "replicate" was included in the analyses and in several analyses it was a significant "interactive" factor, for clarity and simplicity we did not presenting this level of analysis.

Results

Total reach, basal diameter, and height

Total reach of branches was influenced by both tree density and weed control (Table 1*a*). For all planting densities, the total reach of branches produced in 1990 was significantly longer in the weed-free than in the weedy treatments. However, the difference in total reach between weedy and weed-free treatments was less pronounced in the high-density treatment (Fig. 4*a*). Basal diameter and height of trees were influenced by an interaction between tree density and weed control (Tables 1*b*, 1*c*). Basal diameter and height decreased with increasing tree density in the weed-free treatment (Figs. 4*b*, 4*c*). In the weedy treatment, basal diameter was not affected by tree density (Fig. 4*b*) but height increased with increasing tree density (Fig. 4*c*).

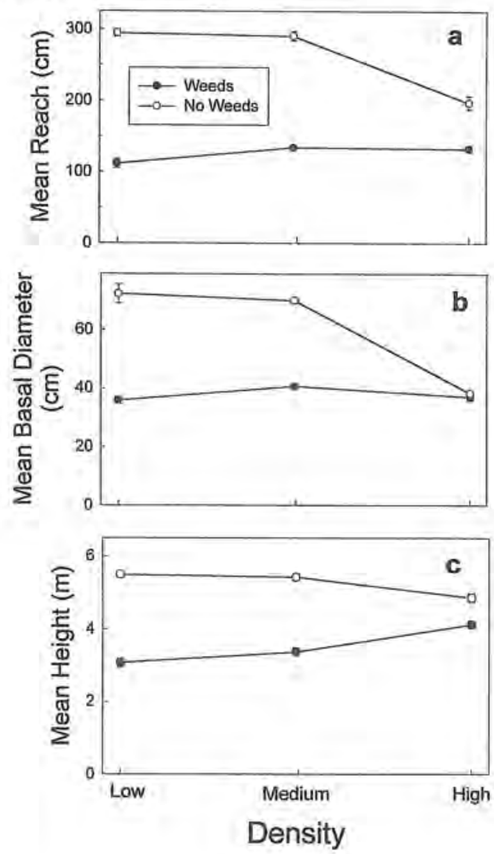
Between-branch comparisons

Interactions

Angle of origin, angle of termination, and the number of living branches were significantly influenced by tree density in interaction with year (Tables 2*a*, 2*b*, and 2*f*, respectively). On branches produced in 1990, the angle of origin was lower (branches had a more upward curvature) at higher tree densities; however, for branches produced in 1991, the angle of origin did not differ with tree density (Fig. 5*a*). Angles of termination on branches produced in 1990 and 1991 decreased (branches had a more upward curvature) with increasing tree density. The magnitude of the decrease was more pronounced on branches produced in 1990 than on branches produced in 1991 (Fig. 5*b*). The number of live branches in 1992 decreased with tree density and was especially pronounced at the high tree density in 1990 (Fig. 5*f*).

Branch number was significantly influenced by weed control in interaction with year (Table 2*e*). The poplars grown in weed-free conditions produced more branches per year than those grown with weeds, and this effect was especially pronounced in 1991 (Fig. 5*e*). Reach was significantly influenced

Fig. 4. The mean (±1 SD) (*a*) total reach of branches, (*b*) basal tree diameter, and (*c*) tree height as influenced by tree density and weed control. Differences among replicate blocks are not shown so as to simplify the presentation of the results.



by weed control in interaction with density (Table 2*c*). Branches were longer in the weed-free than in the weedy plots at low and medium planting densities. However, this effect was either decreased (1990) or nonexistent (1991) at the high tree density (Fig. 5*c*).

Main effects

Both year and weed control had significant independent main effects. Maximum curvature was the only measure of branching architecture in which year had a significant main effect (Table 2*d*). Branches produced in 1991 were more curved than were branches produced in 1990 (Fig. 5*d*). Maximum curvature and the number of live branches were influenced by weed control (Tables 2*d* and 2*f*, respectively). In both years, and for all densities, poplars in the weed-free treatment had branches that were far more curved than poplars in the weedy treatment (Fig. 5*d*). There also were more live branches on trees grown in the weed-free treatment than on those grown in the weedy treatments (Table 2*f*; Fig. 5*f*).

Within-branch comparisons

Interactions

The angle of termination was influenced by both tree density and weed control (Table 3*a*). In the weedy and weed-free treatment, the angle of termination decreased (i.e., branches had a more upward curvature) with increasing tree density and at medium and high planting densities, angles of termination were lower in the weed-free than in the weedy treatment (Fig. 6*a*). At low planting densities, angles of termination did not differ between weedy and weed-free treatments. Branch curvature was influenced by interactions between density, weed, and year (Table 3*c*). A three-way interaction occurred as a result of (1) branch growth being more curved in 1991 than 1990 and (2) branch growth being more curved in the weed-free treatment than in the weedy treatment in the low and medium planting densities (Fig. 6*c*).

Main effects

Within branches there were significant main effects of year on angle of termination and weed control on reach. The angles of termination were higher (i.e., branches wider) on branch growth produced in1990 than on branch growth produced in 1991 (Table 3*a*; Fig. 6*a*). Also, for both 1990 and 1991 growth, poplars grown in the weed-free treatment had longer branches at all planting densities than did poplars grown in the weedy treatments (Table 2*b*; Fig. 5*b*).

Discussion

Herbaceous weeds and the density of conspecifics appear to have a complex competitive effect on *Populus* in that both the density of conspecifics (trees) and herbaceous weeds interacted to influence poplar growth and branch architecture in these plots. However, conspecifics and herbaceous weeds were not equivalent in the degree or manner in which they suppressed growth and influenced branch architecture. The presence of herbaceous competition primarily affected poplar growth. At low and medium tree density, the presence of weeds decreased the height and basal diameter of the trees, and the branches were shorter and had more outward spread. The number of branches initiated and alive also was lower relative to weed-free treatments at these tree densities.

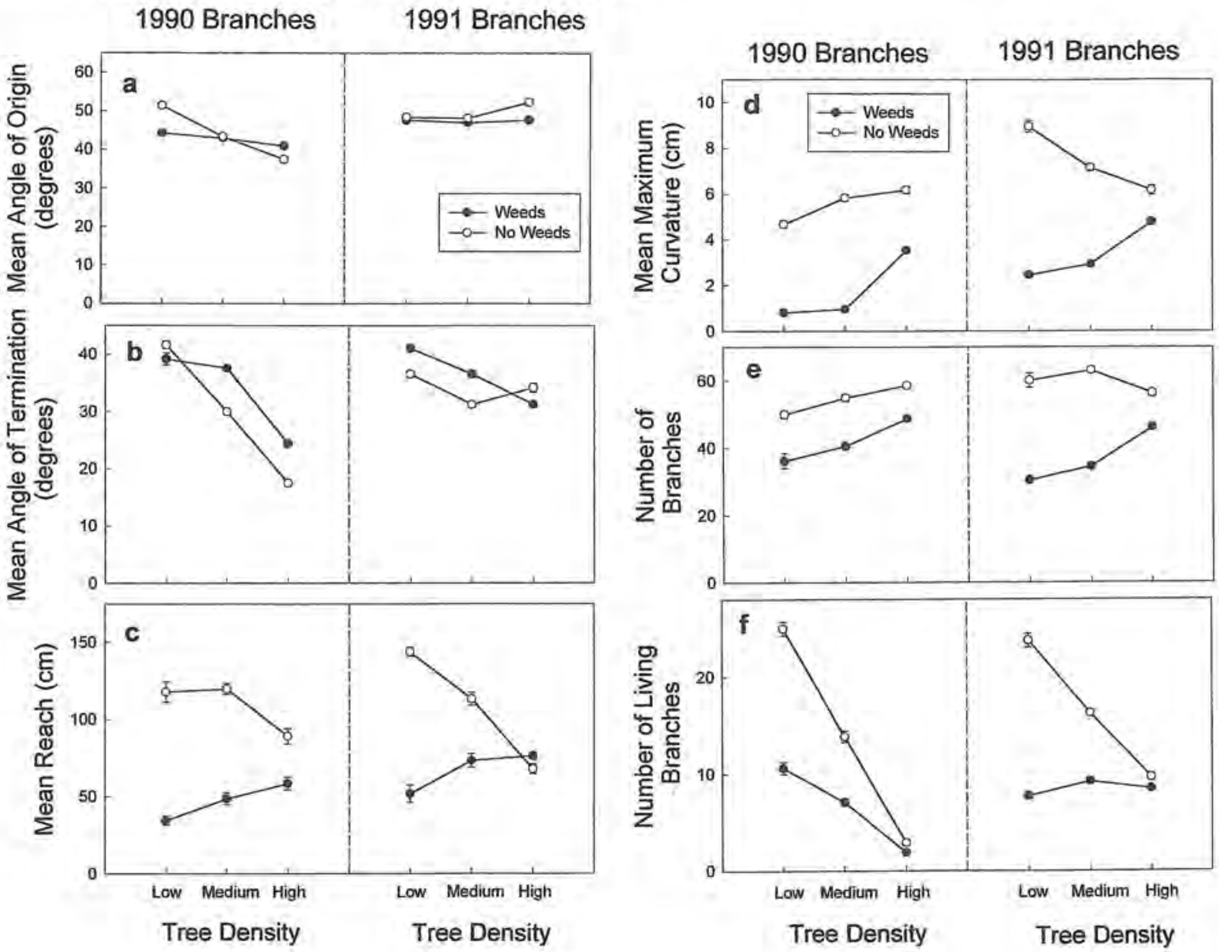
Weeds are well recognized as having a profound influence on the growth and production of plantation trees. Control of weeds has been shown to increase survival (Kennedy 1984; Lauer et al. 1993), tree height and diameter (Fitzgerald et al. 1975; Zsuffa et al. 1977; Nelson et al. 1981*a*; Rejmánek and Messina 1989; Kennedy 1984; Glover et al. 1989; Haywood and Tiarks 1990; Lauer et al. 1993), and branch length (Allen and Wentworth 1993), and result in earlier crown closure (Knowe et al. 1985) in plantations. The negative effect of

Table 2. Summary of split split plot ANOVA examining the effects of replicate, planting density, weed control, and year on between-branch comparisons in *Populus*: (*a*) angle of origin, (*b*) angle of termination, (*c*) reach, (*d*) maximum curvature, (*e*) number of branches, and (*f*) number of living branches.

		(*a*) Angle of origin			(*b*) Angle of termination			(*c*) Reach			(*d*) Max. curvature			(*e*) Branch no.			(*f*) Branches alive		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	F	P	SS	F	P
Replicate	2	14.9	1.38	0.3507	72.7	9.04	0.0328	6.5	0.01	0.9854	7.7	9.49	0.0303	316.8	9.01	0.0330	29.3	7.27	0.0466
Density	2	74.2	6.86	0.0509	1014.8	126.23	**0.0002**	1 741.5	3.96	0.1124	6.9	8.57	0.0358	381.8	10.97	0.0242	730.6	181.0	**0.0001**
Replicate × density	4	21.6	0.75	0.5791	16.1	0.51	0.7328	878.5	1.62	0.2316	1.6	0.59	0.6785	70.3	1.05	0.4240	8.1	0.37	0.8254
Weed	1	29.3	2.41	0.1713	96.9	13.93	0.0097	23 186.6	119.49	**0.0001**	138.2	74.55	**0.0001**	2865.4	49.62	**0.0004**	537.3	27.3	**0.0020**
Density × weed	2	20.9	0.86	0.4685	46.9	3.37	0.1044	8 430.3	21.72	**0.0018**	17.2	4.63	0.0608	274.6	2.38	0.1736	301.9	7.67	0.0222
Replicate × weed(density)	6	72.9	1.67	0.2105	41.7	0.88	0.5407	1 164.3	1.44	0.2793	11.1	2.69	0.0682	346.5	3.44	0.0327	118.1	3.61	0.0278
Year	1	239.3	33.0	0.0001	162.5	20.43	**0.0007**	708.1	5.24	0.0410	27.5	39.87	**0.0001**	12.2	0.13	0.7257	47.2	8.66	0.0123
Density × year	2	169.7	11.7	**0.0015**	289.3	18.19	**0.0002**	684.8	2.53	0.1209	8.2	5.94	0.0161	37.3	1.11	0.3613	114.3	10.49	**0.0023**
Weed × year	1	1.4	0.20	0.6660	19.2	2.41	0.1464	1 021.0	7.55	0.0177	0.1	0.21	0.6539	239.6	14.26	**0.0026**	1.1	0.21	0.6567
Density × weed × year	2	78.1	5.39	0.0214	110.2	6.93	0.0100	890.1	3.29	0.0725	6.6	4.76	0.0301	113.6	3.38	0.0684	1.0	0.09	0.9104

Note: With Bonferroni corrections for multiple comparisons, the probability (*P*) value for a significant effect must be 0.006 25. Significant differences are noted in bold.

Fig. 5. Between-branch comparisons showing the mean (±1 SD) of the (*a*) angle of origin, (*b*) angle of termination, (*c*) reach, (*d*) maximum curvature, (*e*) number of branches, and (*f*) number of living branches as influenced by tree density, weed control, and year. Differences among replicate blocks are not shown so as to simplify the presentation of the results.



herbaceous weeds on growth of plantation trees is thought to result from their depletion of soil moisture (Nelson et al. 1981*a*; McLaughlin et al. 1987; Carter et al. 1984; Petersen and Maxwell 1987) and nitrogen (Hansen et al. 1988; Maas 1992). However, the effects of weeds on branch architecture observed in our study also suggest that weeds may have more complex competitive effects on trees.

Part of this complexity arises from the interaction between poplar planting density and weed biomass. In our study, poplar planting density had a large impact on the assemblage of herbaceous weeds. In 1991, mean weed biomass was 397.1 ± 251.5, 281.2 ± 163.0, and 94.25 ± 71.51 g/m^2 for low, medium, and high poplar planting density plots, respectively. Dominant species, with respect to biomass, over all density treatments included *Apocynum cannabinum*, *Conyza canadensis*, *Hypericum perforatum*, and *Taraxacum officinale*. However, several species composing a large proportion of weedy biomass in low poplar density plots were not abundant in high poplar density plots (e.g., *Erigeron annuus* and *Aster pilosus*) and vice versa (e.g., *Dactylis glomerata* and *Elytrigia repens*; Maas 1992). As such, our results suggest that poplar growth and branching architecture were influenced both by weed control directly and by the interaction between weed biomass and poplar planting density.

Overall, weed control had a slight influence on poplar branching architecture. On branches initiated in 1990, at medium and high planting densities, the angle of termination was higher (i.e., branches wider) in the weedy than in the weed-free treatment on 1990 and 1991 growth. Also, branches were less curved (lower maximum curvature) on all branches in the weedy than in the weed-free treatment. A possible explanation for this pattern is that weeds reduced tree growth enough so that there was less aboveground interference between conspecifics, and consequently these smaller poplars produced under weedy conditions had branches that spread outward more than did poplars grown without weeds (Fig. 4).

Tree density had a smaller effect than the presence of weeds on tree growth and a larger effect on branch architecture. This result likely reflects the effects of both above- and belowground competition. In the weed-free treatments, increased tree density decreased basal stem diameter, tree height, branch length, and the number of live branches. Similar effects of conspecific tree density on growth have been observed in *Populus trichocarpa* Torr. & Gray in Britain (Cannell 1980) and in *Populus* in Wisconsin (Nelson et al. 1981*b*). However, in our study, increasing tree density had relatively smaller effects than weeds on tree height (i.e., no difference between low and medium density plantings with only a small reduction at

Table 3. Summary of split split plot ANOVA examining the effects of replicate, planting density, weed control, and year on within-branch comparisons (1990 vs. 1991) in *Populus*: (*a*) angle of termination, (*b*) reach, and (*c*) maximum curvature.

Source of variation	df	(*a*) Angle of termination			(*b*) Reach			(*c*) Max. curvature		
		SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Replicate	2	121.9	3.75	0.1211	174.9	0.96	0.4568	7.0	1.77	0.2817
Density	2	2268.2	69.72	**0.0008**	3 388.9	18.58	0.0094	6.7	1.69	0.2930
Replicate × density	4	65.1	13.00	**0.0003**	364.7	4.89	0.0143	7.9	8.60	**0.0016**
Weed	2	130.0	7.85	0.0311	37 347.1	91.67	**0.0001**	179.4	72.22	**0.0001**
Density × weed	2	174.6	5.27	0.0477	6 562.2	8.05	0.0200	33.6	6.67	0.0291
Replicate × weed(density)	6	99.4	13.24	**0.0001**	2 444.4	21.85	**0.0001**	14.9	10.83	**0.0003**
Year	1	172.4	137.78	**0.0001**	11 949.3	640.78	**0.0001**	160.1	697.78	**0.0001**
Density × year	2	1.5	0.60	0.5660	1 634.7	43.83	**0.0001**	8.3	17.99	**0.0002**
Weed × year	1	8.0	6.36	0.0268	81.5	4.37	0.0585	4.1	17.76	**0.0012**
Density × weed × year	2	1.4	0.57	0.5809	219.0	5.87	0.0167	14.8	32.22	**0.0001**

Note: With Bonferonni corrections for multiple comparisons, the probability (*P*) value for a significant effect must be 0.0125 (angle of termination), 0.0056 (reach), and 0.0167 (maximum curvature). Significant differences are noted in bold type.

high planting densities) and had no influence on the total number of branches. Numerous studies of tree plantations have shown that tree density has little influence on tree height (Gascon and Krinard 1976; Wood et al. 1976; Zsuffa et al. 1977; Cannell 1980). It is not clear why increased tree density, unlike the presence of weeds, has no influence on total branch number.

Changes in branch architecture were more affected by tree density than the presence of weeds, suggesting that growth and branching in poplars was due to competition for light. A number of studies have documented density effects on plant architecture in both trees (Faulkner 1970; Franco 1986; Jones and Harper 1987) and herbaceous plants (Maillette 1986; Schmitt et al. 1987; Geber 1989; Weiner et al. 1990; Weiner and Thomas 1992). In our study, increased tree density resulted in decreasing angles of origin for branch growth (i.e., branches angled upward) and an increased upward curvature of branches (i.e., decreased angles of termination and increased branch curvature). The magnitude of these effects differed among years; however, there was no tree density influence on the angle of origin for 1991 growth and branch curvature decreased with increasing tree density on 1991 growth in the weed-free treatment. A possible explanation for the decrease in branch curvature with increasing tree density for 1991 growth on 1990 main branches is that the 1991 growth was already coming off upwardly curved 1990 growth; therefore, even by growing straight, the 1991 growth is still curving upward. It is not clear why 1991 main branches in the weed-free treatment are not more curved with increasing tree density or why the angle of origin did not decrease with increased tree density on 1991 main branches.

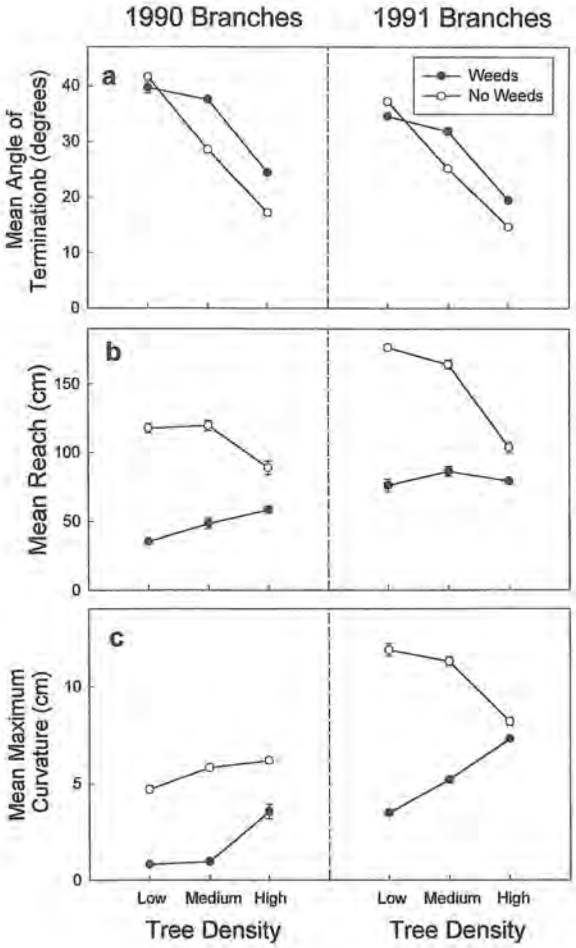
Our general result that at higher densities the angles of branch origin and termination of poplars decreased (became more curved upward) differs from the results found by (Nelson et al. 1981*b*), in which they compared nine different *Populus* clones, including 'Eugenei', in a plantation setting in Wisconsin. Nelson et al. (1981*b*) found, as we did, that the angle of branch origin decreased at higher planting densities. However, in our study the angle of termination decreased with increasing tree density (branches curved upward), whereas in Nelson et al.'s (1981*b*) study, the angle changed little with spacing. Nelson et al. (1981*b*) compared treatments where trees were grown for 4 years at higher densities (i.e., closer spacing) than in our study: 0.3 × 0.3, 0.6 × 0.6, 1.2 × 1.2 m; this study: 0.5 × 1, 1 × 2, 2 × 3 m). However, it is unclear how the closer spacing in Nelson et al.'s (1981*b*) study would result in branches that did not change or spread more outward with increasing tree density.

At high tree density, weed biomass was reduced in these stands, and therefore we expected that growth and branching traits would be influenced by an interaction between weed control and tree density (Pregitzer et al. 1992). We expected that this interaction would influence both below- and aboveground competition. At low planting densities, there was little aboveground intraspecific competition but presumably belowground interspecific competition between weeds and poplars; the most stunted poplars were in the low tree density weedy treatment. This interaction between weed control and tree density resulted in the convergence in growth patterns and branch architecture; mean reach, total reach, basal diameter, height, total branch number, number of living branches, and maximum curvature converge at high-density weedy and weed-free treatments.

The fact that convergence in growth patterns and branch architecture was not complete suggests that the reduction of weed biomass even under high poplar densities may have been insufficient to completely reduce the direct and indirect effects of weeds on poplar growth and branch architecture. Indeed, one of the more striking results of this study was the relatively larger influence of herbaceous competition than conspecifics on poplar growth. Comparing poplars at all densities in weedy versus weed-free treatments, herbaceous weeds clearly decreased poplar growth. For example, despite the decreased weed biomass at high planting densities, poplars in the high-density weedy treatment remained 15.2% shorter, had a 6.5% smaller basal diameter, 29.5% shorter branches, 17.3% fewer total branches, and 16.8% fewer living branches than poplars in the high-density weed-free treatment.

This influence of herbaceous competitors on poplar growth and architecture was likely a consequence of belowground competition for water and (or) soil nutrients. Smith and Huston (1989) have theorized that when water and nutrients are plentiful relative to light (e.g., the low and medium planting density – weed-free treatment), plants limit energy investment in roots

Fig. 6. Within-branch comparisons showing the mean (±1 SD) of the (*a*) angle of termination, (*b*) reach, and (*c*) maximum curvature as influenced by tree density, weed control, and year. Differences among replicate blocks are not shown so as to simplify the presentation of the results.



and concentrate on aboveground production to capture light. As water and nutrients become more limiting relative to light (e.g., the weedy treatments), additional carbon should be allocated to root growth. Maas (1992) has demonstrated that weeds reduce soil nitrogen in these plots. However, weather records from the KBS–LTER site (http://lter.kbs.msu.edu/weather/data/annualprecip.html) indicate that growing season precipitation was near or above the 30-year mean during this study, suggesting that competition between poplars and herbaceous weeds for water may not have limited poplar growth. On the other hand, because soils at the site are well-drained sandy to silty clay loam (Robertson et al. 1997), water stress during periodic growing season dry spells cannot be ruled out. As such, the greater growth and branch production found in the weed-free treatments support the carbon allocation theory of Smith and Huston (1989) given that nitrogen and perhaps also water were limited due to competition with herbaceous weeds.

Because herbaceous weeds and planting density interact to influence poplar growth and canopy architecture, they also will likely interact to affect yield of woody biomass per unit area in poplar plantations. Stand productivity is directly related to the size and structure of the canopy (Farmer 1976). Canopy architecture, in turn, influences leaf display, distribution, and density, which have been shown to influence light interception (Norman and Jarvis 1974; Smith et al. 1991; Smith 1993; Smith et al. 1993) and photosynthetic capacity (Hinkley et al. 1992). Thus, because our study has demonstrated that poplar branching architecture can respond to the presence of herbaceous weeds, it may be necessary to explore how herbaceous weeds influence branching architecture of other genetic stocks so that stand productivity in the presence of weeds can be maximized. For example, a genetic stock that is highly plastic in terms of shifting carbon allocation from root to stem production may be preferred under stressful conditions (i.e., as may occur as a result of competition from herbaceous weeds) because it exhibits relatively high growth rates (Laurence et al. 1994). Also, if stemwood is desired over branchwood, a narrow crown form with short upwardly angled branches with secondary branching would likely be most desirable. Thus, the extent to which the branching architecture of different genetic stocks having this growth form responds to the presence of weeds may affect the choice of stock and (or) planting density. In summary, our study has shown that competition by herbaceous weeds can be intense, profoundly influence the growth, architecture, and productivity of plantation trees, and is mediated by the planting density of the plantation trees.

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