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Intra-annual growth and mortality of four *Populus* clones in pure and mixed plantings

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Abstract Intra-annual growth rates were assessed during 3 years for four *Populus* clones grown in pure and mixed clonal stands at square spacings of 0.5, 1.0 and 1.5 m in western Washington, USA. Height growth rate peaked in August, except at the 0.5-m spacing where it peaked in July and June in years 2 and 3, respectively. Diameter growth rate generally peaked in June. Seasonal growth patterns in mixed clonal stands, relative to those in pure clonal stands, varied by clone. Following early season moisture stress in year 2, growth of a *P. balsamifera* ssp. *trichocarpa* clone declined significantly relative to three *P. balsamifera* ssp. *trichocarpa* x *P. deltoides* clones; this trend was most evident at the 0.5-mspacing. During this period of moisture stress, *P. balsamifera* ssp. *trichocarpa* had 11 and 36% mortality in pure and mixed stands, respectively, at the 0.5-m spacing; this clone had no mortality at wider spacings during the same period. Although height rankings among clones shifted during the first growing season, rankings at the end of year 1 were very similar to those at the end of year 3.

Keywords *Populus*· Biomass· Short-rotation· Clonal plantation

Introduction

There is little information available on the intra-annual growth patterns of woody crops under short-rotation intensive culture (SRIC). Owing to the very rapid growth rates of these plantations, quantification of stand development requires multiple measurements per growing season. Intra-annual assessments are particularly important for understanding the competitive interactions among clones in multi-clonal plantations.

Multi-clonal tree crops under SRIC have potential advantages over pure clonal plantations in that they offer the possibilities of increased productivity and reduced risk of widespread loss to disease or other damage (DeBell and Harrington 1993; McCracken et al.

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2005; Sennerby-Forsse 1995; Verwijst 1990). Potential disadvantages of mixed clonal plantations are increased operational expenses and reduced product uniformity, Mixed clonal stands have been established as a result of social pressures opposing establishment of large-scale, pure clonal plantations (DeBell and Harrington 1993; Stelzer 1997). Mixed clonal stands may be achieved through a mosaic of small, pure clonal blocks or through integration of multiple clones by row or at the individual tree level (Stettler et al. 1992).

Productivity of mixed clonal SRIC stands may be greater than or less than that of pure stands, depending on the clonal mixture, the site, and other factors (Benbrahim et al. 2000; Foster et al. 1998). Mixed clonal stands may be advantageous when demand for site resources differs temporally or spatially among clones; in a pure clonal plantation, simultaneous peaks in demand reduce stand-level efficiency of resource utilization (Lindgren 1993). Establishing poplar *(Populus* spp.) in a clonal mixture may result in overcompensatory growth, undercompensatory growth, or no effect on growth, depending on which clones are combined (Tauer 1975). Among 14 different combinations of poplar clones established in 3:1 clonal ratios, 4-year volume yields were as much as 29% greater or 10% less than that of an equal number of trees of the same clones grown on pure clonal plots (Foster et al. 1998). In that study, greater yields in mixed plots were suspected to have resulted from differences in crown or root architecture among clones that led to complementary, and thus more efficient, resource utilization. Eight-year productivity of mixed clonal poplar in central France did not differ from that of pure clonal stands, a finding attributed to the wide spacing (3.5 x 1.5 m) and similar growth patterns among clones (Benbrahim et al. 2000). In the study reported here, four poplar clones grown in mixed plots (1:1:1:1 clonal ratio) had a 3-year biomass yield similar to that of an equal area of pure plantings of the same four clones; however, the relative contribution of each clone to the total yield on the mixed plots varied dramatically (DeBell and Harrington 1997).

As trees grown in single-aged stands compete with one another, they inevitably differentiate into multiple crown classes over time (Kraft 1884). For SRIC tree crops in pure clonal stands, such differentiation among trees is held at a low level owing to uniform soil resources, genetic uniformity of trees, a, short rotation length, and a spacing selected for optimum yield. This uniform competitive environment is impacted by the diversity of genetic material in mixed clonal stands. For example, in a mixed stand, clones exhibiting slightly later budburst or clones with slower early season growth rates may be at a competitive disadvantage (Jonsson and Oskarsson 2007; Willebrand and Verwijst 1993).

Our objective was to compare intra-annual growth and mortality patterns in four poplar clones during the first 3 years after establishment in pure and mixed clonal stands. Three spacings were included to assess how competition between trees influenced intra-annual growth patterns. Previous studies reported tree morphology and cumulative biomass production in this experiment at the end of the third growing season (DeBell and Harrington 1997) and evaluated various competition indices (Brodie and DeBell 2004), but these studies did not assess inter- or intra-annual growth patterns.

Methods

Study site

The study site was located 12 km east of Olympia, WA at the Washington State Department of Natural Resources Meridian Seed Orchard. The site is in the Puget Trough physiographic province at an elevation of ~50 m (46°59' N, 122°45' W). The climate is

maritime, with mild, dry summers and cool, wet winters. Mean January and July temperatures are 7 and 17° C, respectively. Mean annual precipitation in Olympia is 1,293 mm, although total precipitation during the months of April through September averages only 277 mm. The site is a level glacial outwash plain, formed following the Vashon Glaciation 14,000 years ago. The soil is a very deep, somewhat excessively drained Indianola loamy sand (isotic, mesic Dystric Xeropsamment), which contains a minor amount of volcanic ash. Soil in a portion of the study area differs in that it contains gravel (20-30% by volume) in the surface horizons.

Prior to this study, the site was occupied by a Douglas-fir *(Pseudotsuga menziesii)* forest. Trees were harvested, stumps were removed, and logging slash was piled and burned. The site was then disked, and 900 kg ha^{-1} lime and 100 kg ha^{-1} each of N, P_2O_5, and K_2O were applied to the soil surface 1 month before planting. Following the second growing season of this study, 100 kg ha^{-1} N was applied as ammonium nitrate. Trees were irrigated using drip lines spaced 2.0 m apart with emitters (2.3 L h^{-1}) at a 1.0-m spacing. Irrigation was applied based on seasonal conditions and ranged from 75 to 100 cm per year. In year 2, the irrigation system malfunctioned, and the study was not irrigated until mid-July. Weeds were controlled all years using pre- and post-planting herbicides and hoeing.

Study design and installation

A detailed description of the study design and experimental materials is presented in DeBell and Harrington (1997). The study followed a randomized, complete-block design with a factorial combination of clonal treatments ($n = 5$) and spacings ($n = 3$) assigned to three experimental blocks. Blocking was based on soil properties (e.g., presence of gravel). Clonal treatments consisted of four poplar clones planted in square, pure plots and a fifth square plot where all four clones were uniformly represented in a mixture (Table 1). Mixed plots consisted of even-numbered rows with alternating CL and 49-177 clones and odd-numbered rows with alternating 11-11 and 47-174 clones. Spacings were 0.5-, 1.0-, and 1.5-m square grids (40,000, 10,000, and 4,444 trees ha^{-1}, respectively). Each plot consisted of at least 256 trees, with a minimum of three buffer rows around the interior measurement plot. Measurement plot size was 25 trees (5 rows x 5 columns) for pure clonal plots and 100 trees for mixed clonal plots (25 trees per clone). The study consisted of a total of 1,800 measurement trees (25 per plot x 4 clones x 2 plot types x 3 spacings x 3 blocks). Unrooted cuttings, 30 cm in length and >1 cm diameter, were planted the last week of March 1990 (study year 1). Secondary or multiple stems were pruned after the first growing season (1990), leaving each tree with a single stem. Measurement plot boundaries on two adjacent study plots planted with clone 47-174 were shifted prior to the third growing season because portions of those two plots suffered abnormally high rates of dieback and mortality caused by an unidentified shoot blight. The damage on parts of those plots was not representative of that clone's performance on the site.

Data collection and analysis

Height of each tree (nearest 5 cm) was measured 6 times during year 1 and 5 times during years 2 and 3. In all years, the initial measurement was between 12 May and 7 June and the final measurement was in November after the end of the growing season. Measurements occurred at 3- to 5-week intervals through September. Stem diameter (measured at a height of 1.3 m) was measured to the nearest millimeter on the same dates as height in years 2 and

Table 1 Description of four poplar clones planted in pure and mixed stands

Clone	Parentage	Characteristics
CL	*P. balsamifera* ssp. *trichocarpa*	Parent trees from western WA; '*Capitol Lake*' performed well in small trials; forms many sylleptic branches
11–11	*P. balsamifera* ssp. *trichocarpa* × *P. deltoides*	Parent trees from western WA and MS; tested extensively in the Pacific Northwest; forms many sylleptic branches
47–174	*P. balsamifera* ssp. *trichocarpa* × *P. deltoides*	Parent trees from western WA and MO; forms few sylleptic branches
49–177	*P. balsamifera* ssp. *trichocarpa* × *P. deltoides*	Parent trees from western WA and TX; forms a moderate number of sylleptic branches

Note: The three hybrid clones were developed by the University of Washington—Washington State University poplar breeding program. Clone CL was produced by the USDA Forest Service Pacific Northwest Research Station

Data on sylleptic branching are from this study (DeBell and Harrington 1997) and Cline and Dong-Il (2002)

3 and on one additional date in year 3. At each measurement, mortality, presence of insects or disease, and physical damage were noted.

To create an index of the aboveground competitive environment of each clone in the mixed clonal stands, relative height was calculated. Relative height was defined as the ratio of the mean height of living trees of the subject clone to the mean height of the other three clones on each plot. Dead trees of the three non-subject clones were assigned heights of zero because they provided no competition to the subject clone.

Our primary interest in this study was to determine, at inter- and intra-annual scales, when clonal differences in growth rate occurred. Thus, we used analysis of variance (ANOVA) models that included clone, year, and date within year as treatment effects (Proc Mixed; SAS Institute 2005). Because dates differed by year, a nested treatment arrangement was used for these two variables. Each plot type (i.e., pure or mixed) by spacing combination was analyzed in a separate model. Block was a random effect in all models. For each ANOVA model, we tested assumptions of homoscedasticity and normality of residuals (Zar 1999). Mean separations were performed using the Tukey HSD test (Zar 1999). Significance was judged at an alpha level of 0.05.

Results

Mortality

At the 0.5-m spacing, no mortality occurred until after the year-1 growing season (Fig. 1). However, clone CL incurred 17% mortality in pure stands and 41% mortality in mixed stands during the year-2 growing season. The majority of this year-2 mortality occurred between late June and late July, during the period when the irrigation system was not functioning. Most of the remaining mortality of clone CL at the 0.5-m spacing occurred during September-November of year 3; of this group, nearly 70% had experienced top dieback during the year-3 growing season. **In** contrast to the 0.5-m spacing, mortality rates at the 1.0- and 1.5-m spacings were extremely low for clone CL.

At the 0.5-m spacing, clones 11-11,47-174, and 49-177 incurred between 2 and 11% mortality during the year-2 growing season across pure and mixed stands. **In** approximately half of these trees, top dieback preceded mortality by 1-2 months. Because most of the

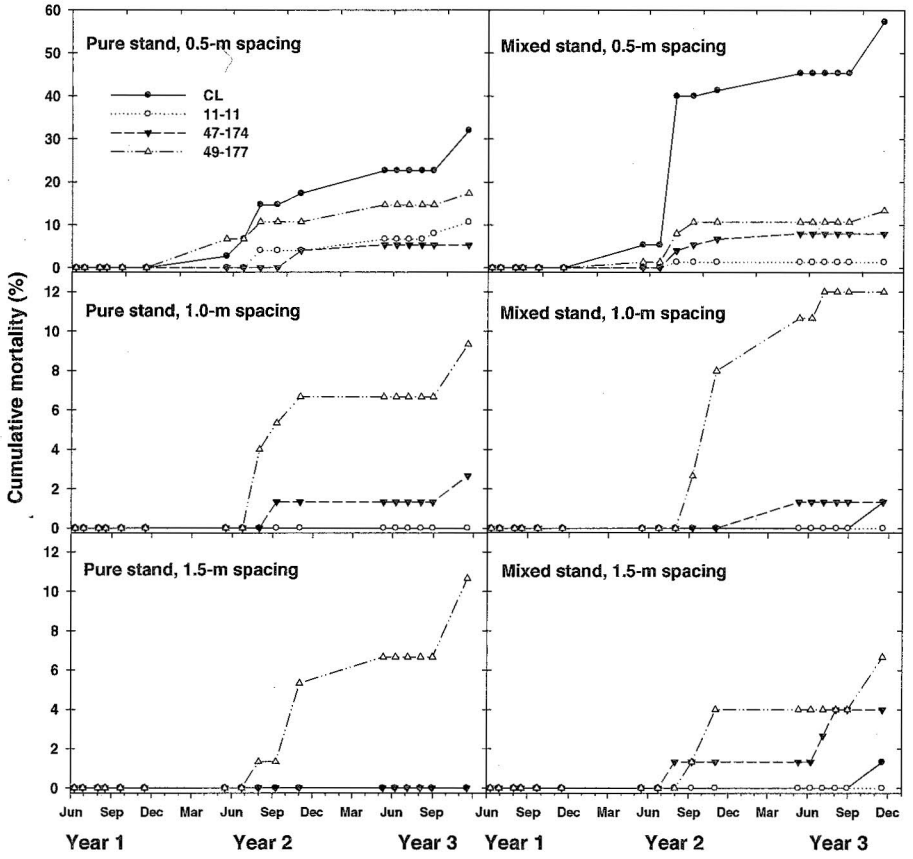

Fig. 1 Cumulative mortality of four poplar clones planted in pure and mixed clonal stands at three spacings in western Washington, USA

trees in this group had already experienced dieback or mortality in Mayor June, prior to the month of July when soils were driest as a result of irrigation system failure, drought was apparently not the sole cause of this mortality.

At the 1.0- and l.5-m spacings, cumulative mortality was 4% or less for all clones except clone 49-177. In both pure and mixed stands, clone 49-177 suffered 4-8% mortality during year 2, primarily between August and November. Most of the remaining mortality of clone 49-177 occurred between September and November of year 3; half of this mortality was associated with trees that had stem breakage (likely due to wind damage) or top dieback, while the other half was associated with an unidentified shoot blight.

Periodic height growth

Periodic height growth at all spacings in pure and mixed stands was significantly affected by the clone-by-date-within-year interaction (Table 2), indicating that clones followed different intra-annual trends and that these trends also differed by year. In year **1**, periodic height growth in pure stands was similar among clones, with the exception of clone CL which had a later growth rate peak and significantly less growth than the other clones in

July and August at 1.0- and ISm spacings (Fig. 2). Year-I growth in mixed stands followed a similar trend except that the inferiority of clone CL, relative to the other clones, was more pronounced at the O.5-m spacing rather than at the two wider spacings (Fig. 3). Also, the year-I growth rate peak of clone CL was not delayed, relative to the other clones, as it was in the pure stands. At the 1.5.m spacing, growth of clone CL was greater in mixed stands than in pure stands.

In year 2, clone CL had greater growth in May, compared to the other clones, at the 1.0- and l.5-m spacings. June growth rate in year 2 was low for all clones and spacings because the irrigation system was not functional. July and August growth for clone CL remained low at the narrower spacings, especially in mixed stands. At all spacings, late-season growth of clone CL was less in mixed stands than in pure stands, while late-season growth rates of clones 11-11 and 49-177 were greater in mixed stands than in pure stands.

In year 3, periodic growth rates were similar among clones, with two exceptions. Clone CL growth peaked early but was inferior to the other clones in mixed stands at all spacings. Mid-summer growth of clone 47-174 was superior to the other clones in pure stands at 1.0- and l.5-m spacings.

Periodic diameter growth

Periodic diameter growth at all spacings in pure and mixed stands was significantly influenced by the clone-by-date-within-year interaction: clones had different intra-annual trends and these trends also differed by year. Year-Z periodic diameter growth trends differed by spacing: at OS and 1.0-m spacings, growth rates were highest in June and then generally declined over the course of the growing season (Fig. 4). At the 1.5-m spacing, growth rates reached a maximum during the months of July and August and then decreased. In mixed stands, growth of clone CL was inferior to the other clones, although this trend occurred earlier in the growing season at closer spacings. At the widest spacing, growth of clone 47-174 was less in mixed stands than in pure stands.

In year 3, growth rates were generally lower at the first measurement relative to those of year 2; this produced a year-5 growth pattern with a more pronounced peak. Early growing-season diameter growth was greatest for clone 47-174 at the two wider spacings

Table 2 Analysis of variance results (Pr > *F*) from periodic growth analysis of four poplar clones in pure and mixed stands at three spacings

Variable	Source	Num. *df*	Pure stands			Mixed stands		
			0.5 m	1.0 m	1.5 m	0.5 m	1.0 m	1.5 m
Height	Clone	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Year	2	<0.001	<0.001	0.004	<0.001	<0.001	0.233
	Clone × year	6	0.014	<0.001	<0.001	0.038	<0.001	0.100
	Year (date)	13	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Clone × year (date)	39	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Diameter	Clone	3	<0.001	<0.001	0.004	<0.001	<0.001	<0.001
	Year	1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Clone × year	3	<0.001	0.008	<0.001	<0.001	0.006	0.247
	Year (date)	9	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Clone × year (date)	27	0.020	<0.001	0.001	<0.001	<0.001	0.006

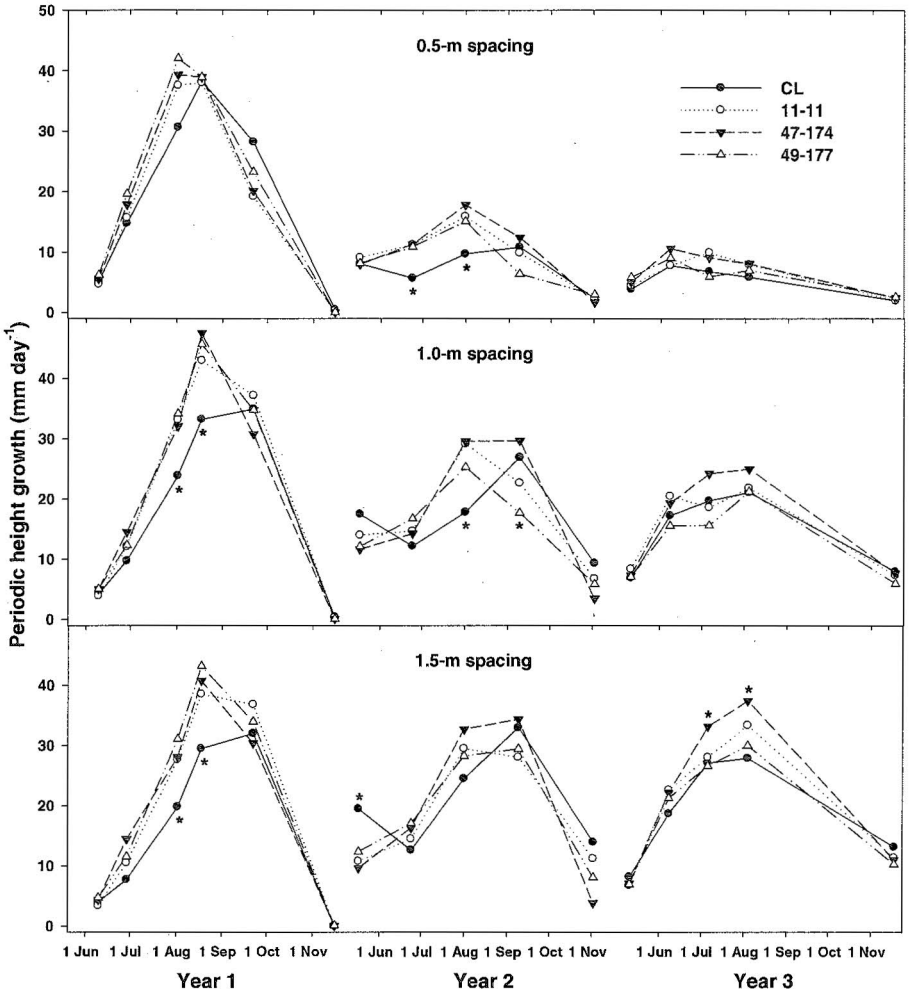

Fig. 2 Periodic height growth of four poplar clones in pure clonal stands at three spacings in western Washington, USA. *Plotted points* represent the end of each measurement interval. *Asterisk-marked points* differ significantly from the other three points on the same date

in pure stands. **In** mixed stands, May growth rates for clone CL were only slightly less than those of other clones, but beginning in June, clone CL growth became much inferior to the other clones. Growth of clone 47-174 in mixed stands was less than that in pure stands.

Relative height in mixed stands

At the *0.5-m* spacing, clone CL began to decline in relative height early in year 1, already 10% smaller than its mean neighbor height at the first measurement on 10 June (Fig. 5). Relative height of clone CL declined throughout all three growing seasons at this spacing. At the 1.0-m spacing, clone CL recovered some of its relative height in the second half of year 1 and at the beginning of year 2, but it subsequently declined throughout years 2 and

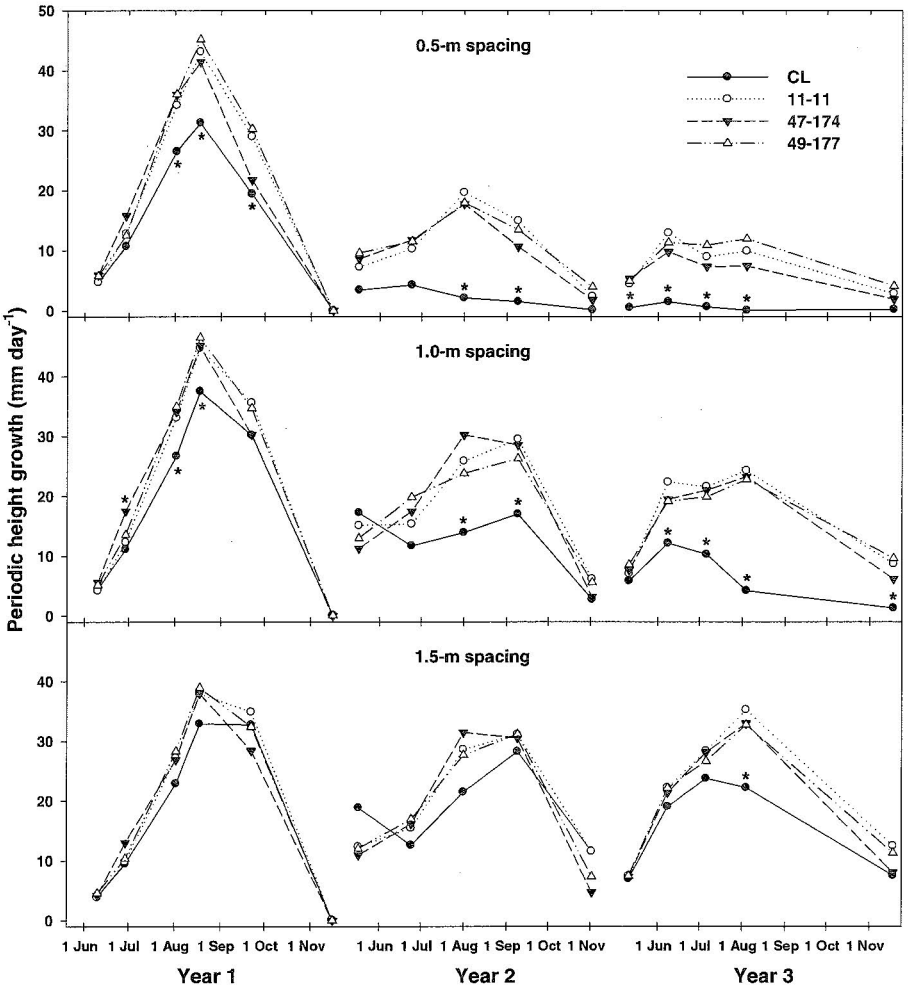

Fig. 3 Periodic height growth of four poplar clones in mixed clonal stands at three spacings in western Washington, USA. *Plotted points* represent the end of each measurement interval. *Asterisk-marked points* differ significantly from the other three points on the same date

3. At the 1.5-m spacing, clone CL was able to recover some of its relative height late in years 1 and 2 but not in year 3.

Clone 11-11 had the smallest relative height at all spacings on 10 June of year 1 but increased in relative height throughout all three growing seasons at all three spacings, with the greatest increases occurring in years 1 and 2. Clone 47-174 had a relative height advantage over the other clones by late June of year 1 at all spacings; however, clone 47-174 finished year **1,** as well as year 3, shorter than clones 11-11 and 49-177. At a 1.5-m spacing, clone 49-177 had a relative height advantage at the beginning of the first growing season, but ended the year similar to clone 11-11 in relative height. Clones 49-177 and 11-11 remained very similar in relative height throughout years 2 and 3 at all spacings.

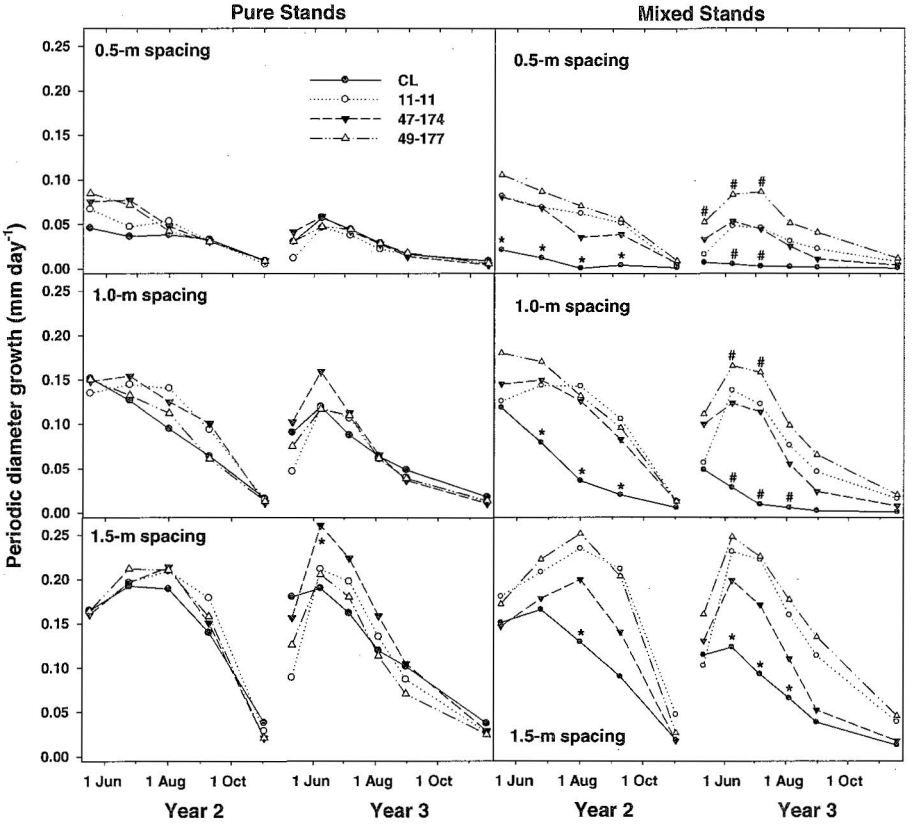

Fig. 4 Periodic diameter growth of four poplar clones in pure and mixed clonal stands at three spacings in western Washington, USA. *Plotted points* represent the end of each measurement interval. *Asterisk-marked points* differ significantly from the other three points on the same date. *#-marked points* differ significantly from the two median points on the same date

Discussion

Three-year analysis of periodic growth rates in pure and mixed clonal stands yielded several major trends: (i) clonal mixing affected the seasonal growth patterns of clones to different degrees, (ii) although height ranking changed during year 1, rankings at the end of year 1 were similar to those after three years, (iii) seasonal growth patterns were influenced by spacing, (iv) diameter growth rate peaked earlier in the growing season than height growth rate, and (v) growth rate and survival of clone CL, which were slightly less than that of the three hybrids in pure stands, were substantially reduced in mixed stands following early season moisture stress. The fact that clonal differences in growth rates were, overall, greater in mixed clonal stands than in pure stands is in agreement with earlier multi-clonal research that reported clonal growth differences were reduced when clones were planted in separate blocks (Ceulemans et a1. 1992).

Intra-annual height growth patterns differed by clone and between pure and mixed stands. Clones 11-11 and 49-177 showed a late-summer growth benefit of clonal mixing during year 3 at all spacings and during years 1 and 2 at 0.5- and 1.0-m spacings. This

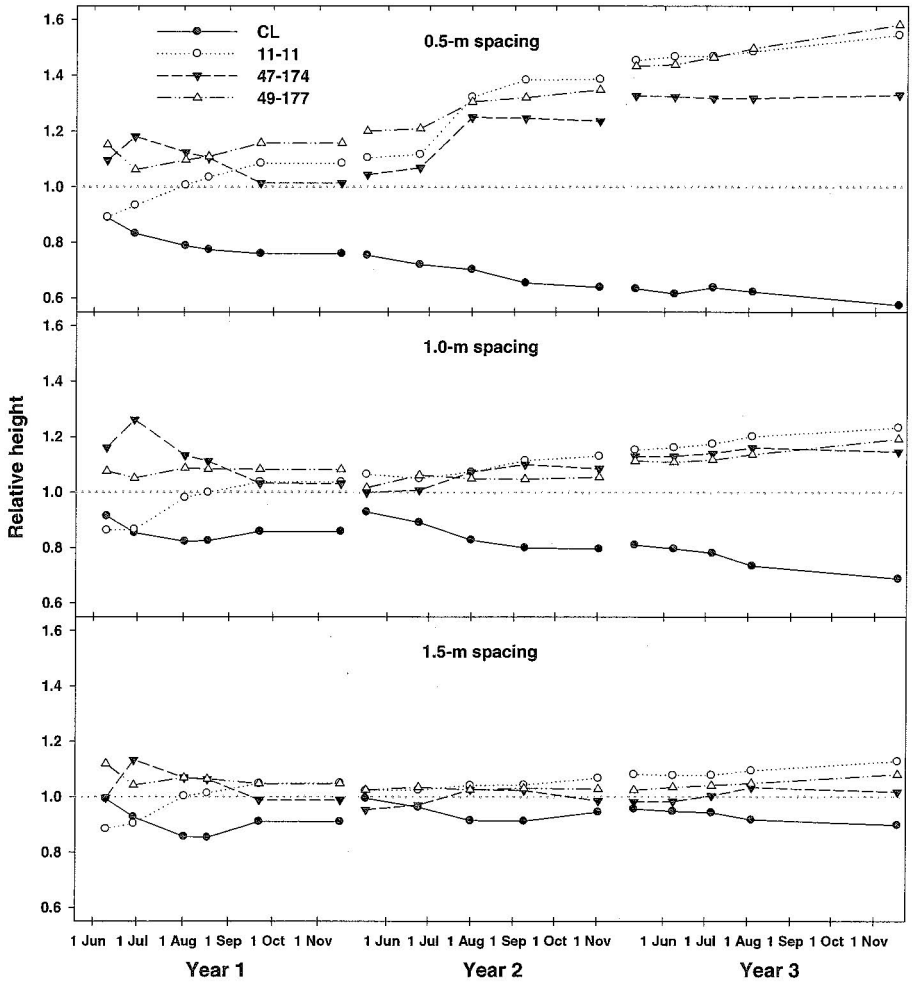

Fig. 5 Relative height (i.e., clone height: mean height of the other clones on the same plot) of four poplar clones in mixed clonal stands at three spacings in western Washington, USA. *Plotted points* represent the end of each measurement interval

suggests that, in mixed stands, clones 11-11 and 49-177 held some form of competitive advantage over the other two clones, especially at close spacings. The fact that the third hybrid clone (47-174) did not show a late-summer benefit of clonal mixing may have been due in part to its virtual lack of sylleptic branching (DeBell and Harrington 1997). In contrast to proleptic branches which originate from buds formed prior to the growing season, sylleptic branches originate from buds formed during the growing season (Ceulemans et al. 1990). The additional leaf area that sylleptic branches create benefits growth in poplar (Hinckley et al. 1989; Scarascia-Mugnozza et al. 1999), and the late summer height growth of clones 11-11 and 49-177 in mixed stands may have benefited from their abundant sylleptic branching in the upper crown (DeBell and Harrington 1997). Clone CL also formed many sylleptic branches, but in mixed stands, its relative height was much shorter than that of the other clones (Fig. 5). Thus, in mixed stands, the size and

crown architecture of clones CL and 47-174, respectively, apparently resulted in greater access to sunlight for clones 11-11 and 49-177.

In a pattern similar to that of height growth, stem diameter growth of clones 11-11 and 49-177 benefited from clonal mixing. At the 1.5-m spacing, increased diameter growth of clones 11-11 and 49-177 was associated with a concurrent decrease in diameter growth of clones CL and 47-174. Whilethese stem diameter growth trends may have been related to differences in photosynthate production associated with the aforementioned crown differences, they also were likely influenced by below ground interactions among clones, which were not quantified in this study.

Across treatments, diameter growth rate generally peaked earlier in the season than height growth rate. For most spacings and clones, diameter growth rate peaked around June. Height growth rate peaked in August, except at the 0.5-m spacing where it peaked in July and June in years 2 and 3, respectively, probably owing to the intensity of competition at that narrow spacing. The height growth rate of *P. deltoides* planted at a 3.0-m spacing in southern Illinois peaked during the second half of July (Minckler and Woerheide 1968). For all clones and spacings, we observed an increase in height-to-diameter ratio from June through the end of each growing season.

During the first growing season, the relative heights of clones in mixed stands shifted substantially over time. However, by the end of the first year, the four clones had established a relative height ranking very similar to that at the end of the third year, with minor differences occurring only among clones at the l.0-m spacing. In mixed stands, the year-1 patterns in relative height growth appeared to be largely under genetic control rather than a result of interclonal competition, as distinguishing growth patterns, such as the relatively high early season growth rate of clone 47-174 and the poor early season growth rate of clone CL, also were evident in pure stands. The clonal differences in relative height, however, were apparently magnified by competition, as evidenced by the spacing effects. In year 1, clonal growth differences were greatest at the 0.5-m spacing where clones 11-11 and 49-177 had superior late-season growth. This greater late-season growth may be attributed to the sylleptic branching and crown architecture of clones 11-11 and 49-177 which apparently allowed these clones to out-compete clone CL for sunlight. For example, clone 11-11 has branches that curve upward steeply, resulting in a narrow, compact crown that is believed to be particularly well-suited to narrower plantation spacings (Ceulemans et al. 1990; Hinckley et al. 1992). Not only does the crown architecture of clone 11-11 produce a comparatively high rate of solar radiation interception, it is also efficient in converting this radiation to biomass (Scarascia-Mugnozza et al. 1989).

While irrigation presumably minimized moisture stress through most of this study, the irrigation failure prior to mid-July in year 2 revealed the relative responses of the clones to temporary water limitation. At the 0.5-m spacing, cumulative mortality of clone CL increased from 3 to 15% in pure stands and from 5 to 40% in mixed stands between May and July. In mid-July of year 2, upper leaves of clone CL showed visible dessication; root growth and fine root survival also may have been negatively affected by this drought event (Pregitzer et al. 1993). After July of year 2, height growth rate of clone CL in mixed stands dropped well below that of pure stands and well below the other clones in mixed stands for the remainder of the study. Apparently clone CL fell below a relative size threshold after which it was no longer competitive with the other clones in mixed stands. It is unclear how competitive clone CL would have been if the drought had not occurred. The poor performance of clone CL during drought may have been a result of lower water use efficiency relative to that of the hybrid clones. Stomata of *P. balsamifera* ssp. *trichocarpa* are less responsive to water status, and remain open longer on a diurnal basis, compared to

P. balsamifera ssp. *trichocarpa* x *P. deltoides* (Ceulemans et al. 1988). Midday water potentials were measured on 16 August of year 2 (data not shown), after the irrigation system had been intentionally turned off for 7 days to accumulate a moderate amount of moisture stress. Water potentials for the *P. balsamifera* ssp. *trichocarpa* clone were higher than those of the hybrid clones, suggesting differences in stomatal response to droughty conditions.

Most of the mortality for all clones at the 0.5-m spacing occurred during the drought event resulting from the irrigation system failure in summer of year 2. However, earlier in year 2, an unidentified shoot blight was observed on clones 47-174 and 49-177, resulting in some leaf wilt and top dieback and 4-8% mortality of clone 49-177 at the 1.0- and 1.5-m spacings during that year. Rust *(Melampsora* sp.) and leaf curl *(Taphrina* sp.) also were observed in the study, particularly on the CL clone; stress resulting from these pathogens may have increased susceptibility of this clone to mortality during the year-2 drought event. Aside from the mortality of clone CL at the 0.5-m spacing that was associated with the year-2 drought event, mortality rates were similar between mixed and pure clonal stands. Mixed clonal SRIC crops elsewhere have shown differences in rates of pathogen infection and frost damage among clones (Verwijst 1990). Plots planted with a mix of three *Poplar* clones had a lower overall rust infection rate, but no difference in growth, compared to pure clonal plots (Miot et al. 1999). Similarly, rate of rust infection in *Salix* clones was reduced when clones were planted in a mixture (McCracken et al. 2005). The present study was established on relatively small, intermixed treatment plots rather than on a production scale, and therefore it was not possible to test whether clonal mixing affected pathogen infection.

In summation, we found that the negative impact of an individual clone's shortcomings, such as drought intolerance, is rapidly exaggerated in a mixed clonal planting. Performance of clone CL was substantially affected by a short period of drought that had much less effect on the other clones. Thus, physiological responses to potential environmental stressors or resource limitiations must be considered in selection of a clonal mixture. We also found that, despite different seasonal height growth patterns during year **1,** the relative clonal height rankings at the end of that year were similar to those after year 3. For the individual clones planted in mixed clonal stands, total annual growth was more important than intra-annual growth pattern in determining the relative performance of each clone. This supports the idea that clones exhibiting differing seasonal phenologies may be compatible in a clonal mixture.

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