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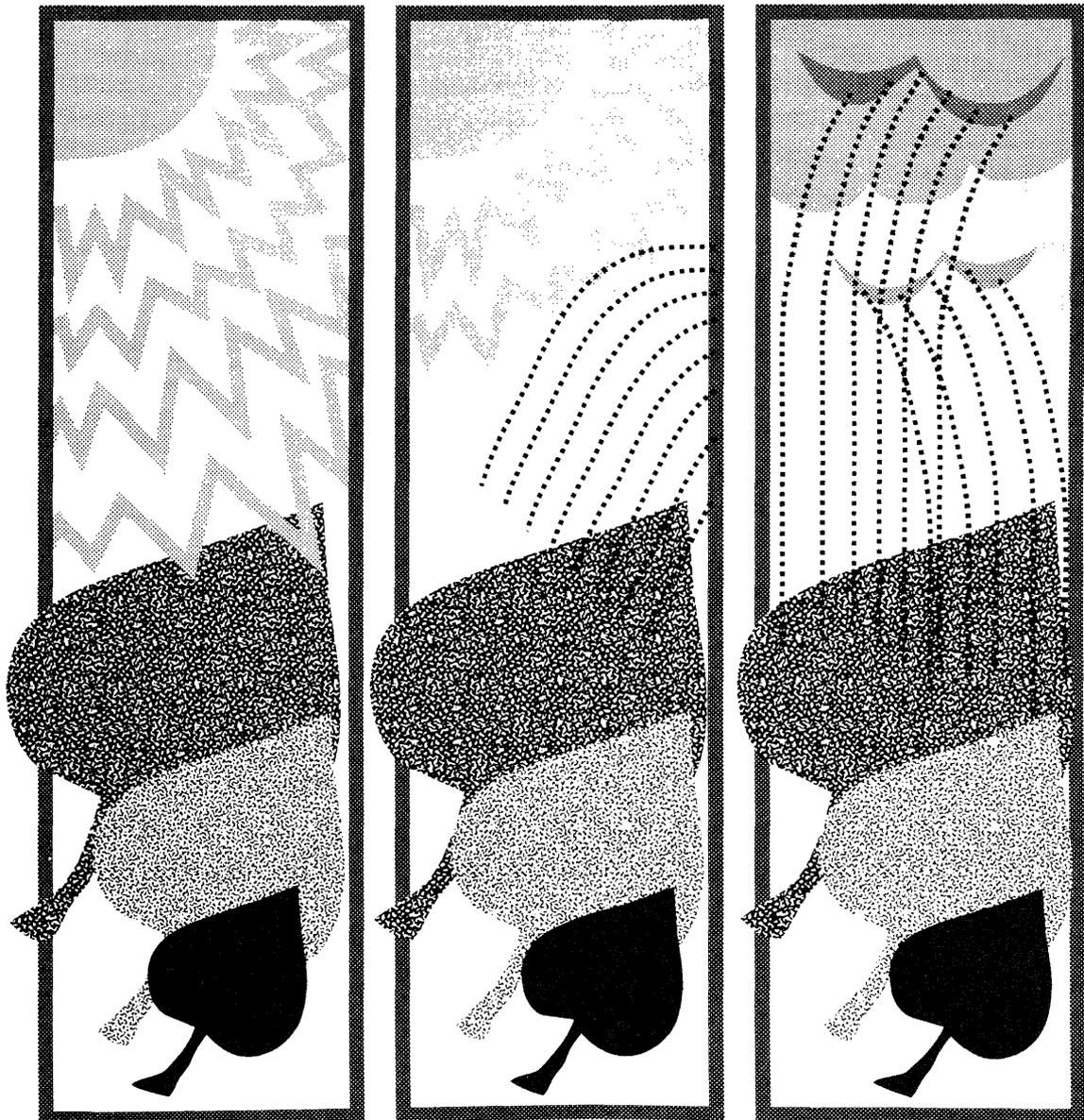
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Response of Three *Populus* Species to Drought

Terry Strong and Edward A. Hansen



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Species and hybrids in the *Populus* genus have great potential for short rotation intensive culture (SRIC). However, these species require abundant moisture through the growing season to maximize growth. Irrigation may not be necessary to maximize yields on sites with ample available soil moisture and frequent growing-season precipitation. However, soil moisture in the Lake States is seldom adequate. For example, soil moisture deficits generally limit tree growth 1 or more weeks every year and severe droughts occur about once every 10 years. Studies in northern Wisconsin have shown irrigation is necessary to maximize yields of *Populus* hybrids grown in SRIC plantations on productive agricultural land (Hansen 1988). However, irrigation of SRIC plantations is generally not economical (Rose *et al.* 1981, Lothner *et al.* 1981).

To maximize yield of SRIC *Populus* plantations without irrigation, species or hybrids need to be identified that grow well during moisture stress. Yield gains in agricultural breeding programs have been shown to result almost totally from inadvertent selection for moisture stress tolerant plants (Boyer 1982). Boyer stated that faster and larger yield gains would have been attained had the selection been made specifically for some characteristic that allowed the plant to tolerate moisture stress. Response to moisture stress has been shown to vary both within and

between tree species (Albertson and Weaver 1945, Cannell *et al.* 1978, Parker and Pallardy 1985, and Hennessey *et al.* 1988). The literature includes some information on water relations of *Populus* and field and growth room responses of *Populus* to moisture stress, but limited data showing variation between and within *Populus* species of field growth response to moisture stress (Pallardy and Kozlowski 1981, Pezeshki and Hinckley 1982, and Ridge *et al.* 1986).

We designed a study to identify traits that correlate well with *Populus* growth under different soil moisture conditions. Such traits might be useful for selecting parents and progeny in *Populus* breeding programs to increase yields on sites that have periodic soil moisture deficits. This report describes the field design and methodology of the study and growth patterns observed the first 3 years.

METHODS

Site

The study was located on the Harshaw Forestry Research Farm 15 km west of Rhineland, Wisconsin. The soil is a well-drained Pence formed in loamy surface deposits and underlying gravelly sand glacial outwash. It contains numerous pockets of cemented gravelly sand to clay loam at depths to 2 m.

The growing season is about 120 days (mid-May to mid-September). Precipitation during this period averages 43 cm, and temperature averages 17°C (table 1). Monthly average temperature ranges from 12.8°C for the last half of May to 18.9°C for July. Maximum temperatures are

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seldom greater than 35°C. Freezing temperatures can occur anytime during the growing season. Rainfall from June through August generally results from thunderstorms and consequently varies greatly. Because of rain-free periods, dry soils are not uncommon for 1 to 2 weeks during the summer.

Table 1.—Average monthly temperature and precipitation during the growing seasons of the study period

	May (15-31)	June	July	August	September (1-15)	Mean
<i>Temperature (°C)</i>						
1986	13.7	14.7	18.8	15.3	11.4	15.3
1987	15.5	17.8	20.3	17.3	14.3	17.6
1988	14.5	16.7	20.6	19.7	13.7	17.8
30-year Mean	12.8	16.4	18.9	17.7	14.1	16.6
<i>Precipitation (cm)</i>						
						Total
1986	1.1	10.5	16.5	5.8	9.4	43.3
1987	5.8	5.8	12.6	3.9	1.7	29.8
1988	2.2	5.0	9.5	9.9	3.9	30.5
30-year Mean	4.9	10.4	10.0	12.4	5.0	42.7

Experimental Design

The experimental design was a split plot with three irrigation treatments in the main plot and four replications. The three irrigation treatments included an unirrigated control, irrigation when soil water potential reached -0.15 MPa, and irrigation when soil water potential reached -0.05 MPa. Each main plot was planted with 20-cm-long hardwood cuttings of 36 *Populus* clones (12 clones each of three species: *P. balsamifera*, *P. trichocarpa*, and *P. deltoides*) (table 2). A single cutting of each clone was planted in a randomized location in each main plot. Tree spacing was 2.0 x 2.0 m with a two-row border of *P. tristis* ‘#1’ planted between each main plot and around the outside edge of the entire study.

Table 2.—Origin of *Populus balsamifera*, *P. trichocarpa*, and *P. deltoides* clones used in the study

Species	Clone #	Clonal origin
<i>Balsamifera</i>		
B01	LU002	Thunder Bay, Ontario, Canada
B02	LU039	Kakaboka Falls, Ontario, Canada
B03	LU112	Central Patricia, Ontario, Canada
B04	LU152	Pickle Lake, Ontario, Canada
B05	LU205	Eagle River, Wisconsin
B06	LU235	Crandon, Wisconsin
B07	LU253	Long Lake, Wisconsin
B08	LU258	Summit Lake, Wisconsin
B09	LU259	Pelican Lake, Wisconsin
B10	LU264	Rhineland, Wisconsin
B11	LU272	Lily, Wisconsin
B12	LU273	Lily, Wisconsin
<i>Trichocarpa</i>		
T01	2-3-5	Clark Fork, Idaho
T02	3-2-4	Coeur D'Alene River, Idaho
T03	4-3-5	Urquhart, Idaho
T04	4-4-4	Calder, Idaho
T05	4-6-4	Erlmo, Idaho
T06	5-1-5	Myrtle, Idaho
T07	5-2-5	Peck, Idaho
T08	0-6-1	Barriere, British Columbia, Canada
T09	0-6-5	Barriere, British Columbia, Canada
T10	0-9-2	Lumby, British Columbia, Canada
T11	0-10-2	Vernon, British Columbia, Canada
T12	0-13-1	Merritt, British Columbia, Canada
<i>Deltoides</i>		
D01	41-3	Indiana
D02	41-6	Indiana
D03	44-4	Indiana
D04	264-4	Illinois
D05	269-4	Illinois
D06	291-5	Illinois
D07	170-3	Minnesota
D08	171-6	Minnesota
D09	175-2	Minnesota
D10	180-6	Minnesota
D11	189-3	Minnesota
D12	192-4	Minnesota

Plantation Culture

The site was sprayed with 2.2 kg active ingredient (a.i.) ha⁻¹ of glyphosphate in the fall of 1985 to kill the quackgrass, and then it was disked. Linuron (1.7 kg a.i. ha⁻¹) was applied in the spring of 1986, just before planting. Weeds were controlled after planting by hoeing and dormant season overspraying with glyphosphate. Granular NH₃NO₃ 112 kg N ha⁻¹ was hand spread on the site each June. The treated plots were irrigated for 24 hours by a trickle system when the soil reached the designated soil water potential.

Measurements

Total height (mm) was measured each fall. Current annual height growth (CAHG) was calculated by subtracting the previous year's total height from the current year's total height. On trees with winter dieback, CAHG was calculated as the height of origin of the current growth subtracted from the current year's total height. In the second year, basal stem diameter was measured 10 cm above the ground. In the third year, diameter was measured at 1.37 m above the ground (d.b.h.). Stem volume (d²h) was calculated from the diameter and height measurements.

We recorded soil moisture daily in the wettest plots (-0.05 MPa) using tensiometers placed 20 cm below the surface. In the other plots, soil moisture was measured weekly 18 cm below the surface with a neutron probe. Temperature, precipitation, and humidity were recorded at a weather station 0.8 km from the study area.

Data Analysis

Data were analyzed by split-plot analysis of variance. Mean differences were calculated with least significant difference (LSD) techniques when the F-test was significant at the 0.05 probability level.

RESULTS AND DISCUSSION

Soil Moisture

The growing season was cooler and wetter than normal the establishment year (1986) but was warmer and drier than normal the second and third years of the study (table 1). In 1987, one significant drought period occurred from August 15 to August 29 (Julian dates 227 and 241) when only 0.25 cm of rain fell. Soil water potential in the driest plots decreased to nearly -0.15 MPa (fig. 1A).

In 1988 two significant drought periods occurred. From June 1 to June 27 only about 3 cm of rain fell (normal for this period is about 10 cm). In addition, daytime maximum temperatures were consistently 30 to 35°C (about 5 to 10°C above normal). Soil water potential in the unirrigated plots began to decrease in comparison to the soil water potential in the irrigated plots on about June 13 (Julian date 165, fig. 1B). Soil water potential slowly decreased during the next two weeks to a minimum of -0.26 MPa on June 27 (Julian date 179). During this 2-week period, both the -0.05 and -0.15 MPa plots were irrigated twice. Rainfall during the next 2 weeks was near normal, and soil water potential in the unirrigated plots increased to about the same water potential as in the irrigated plots.

In mid-July of 1988, another drought period began. From July 18 to August 1 (Julian dates 200 and 214), precipitation was only 0.75 cm (normal for this period is about 5 cm). Again maximum temperatures were well above normal and humidities were low. Soil water potential decreased rapidly to an average minimum of -0.54 MPa on July 28 (Julian date 210) on the unirrigated plots and -0.31 MPa just before irrigation on the -0.15 MPa treatment plots. Soil water potential in one individual unirrigated plot on this date was -1.35 MPa. During this period the -0.05 MPa plots were irrigated twice and the -0.15 MPa plots were irrigated once. Soil water potential increased during the rest of the growing season in the unirrigated plots under normal rainfall. The -0.05 MPa plots were irrigated only one more time.

Species Results

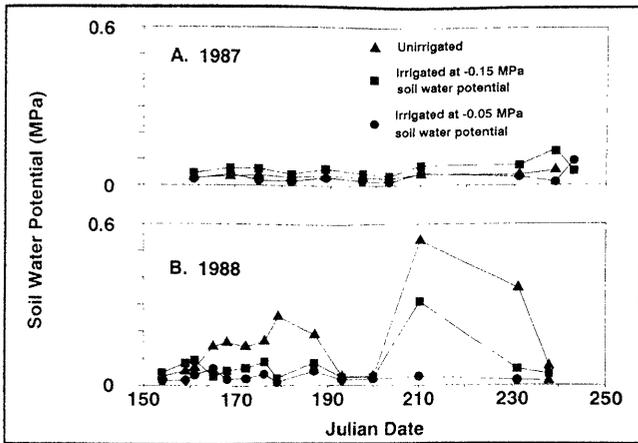


Figure 1.—Soil water potential trends during the 1987 and 1988 growing seasons under three irrigation levels.

The purpose of this study was to emphasize within-species rather than between-species clonal variation. Because the number of selections per species is limited, extrapolation of species differences from this data set to the population must be done with caution. However, some observations of variation between species are worth noting. There were significant differences between species in height, height growth, and diameter each of the 3 years. However, irrigation treatment was significant only in 1988 (table 3). Generally, the *P. deltooides* clones were the largest, the *P. trichocarpa* clones were intermediate, and the *P. balsamifera* clones were the smallest (table 4).

Table 3.—Significant treatment differences for selected variables within and between species

	1986	1987	1988	1987	1988	1987	1988	1988
	Height	Height	Height	Height growth	Height growth	Diameter	D.b.h.	D ² h
Between species								
Irrigation			*		**		*	*
Species	**	**	**	**	**	**	**	**
I x S								
Within species								
<i>P. balsamifera</i>								
Irrigation			**		**		**	**
Clone	**	**	**	**	**	**	**	**
I x C							*	**
<i>P. trichocarpa</i>								
Irrigation					**		**	
Clone	**	**	**	**	**	**	**	**
I x C								*
<i>P. deltooides</i>								
Irrigation			**		**		*	*
Clone	**	**	**	**	**	**	**	**
I x C								

* Denotes significance at the 0.05 probability level.

** Denotes significance at the 0.01 probability level.

Table 4.—Third-year total height (cm), d.b.h. (cm), stem volume (cm³), and height growth (cm) for three *Populus* species grown under three irrigation treatments for 3 years

Growth variable	Irrigation treatment	<i>P. balsamifera</i>	<i>P. trichocarpa</i>	<i>P. deltoides</i>
Height	None	295 (31) ¹	371 (30)	377 (42)
	-0.15 MPa ³	377 (18)	417 (30)	455 (40)
	-0.05 MPa ³	411 (26)	431 (50)	477 (32)
	Mean	361 (56) a ²	406 (43) b	436 (57) c
1988 Height Growth	None	76 (16)	120 (18)	111 (17)
	-0.15 MPa	146 (15)	177 (15)	189 (14)
	-0.05 MPa	178 (20)	182 (9)	206 (16)
	Mean	133 (47) a	160 (32) b	169 (45) b
D.b.h.	None	1.8 (0.2)	2.6 (0.3)	2.9 (0.6)
	-0.15 MPa	2.6 (0.2)	2.9 (0.3)	3.6 (0.5)
	-0.05 MPa	3.0 (0.3)	3.4 (0.8)	3.9 (0.5)
	Mean	2.5 (0.6) a	3.0 (0.6) b	3.5 (0.7) c
D ² h	None	1,189 (378)	3,613 (1,070)	4,184 (1,342)
	-0.15 MPa	2,804 (559)	5,166 (1,738)	6,750 (2,553)
	-0.05 MPa	4,523 (1,192)	6,962 (2,783)	8,537 (2,062)
	Mean	2,839 (1,592) a	5,247 (2,300) b	6,490 (2,629) c

¹ Number in parentheses is the standard deviation.

² Means followed by the same letter horizontally are not significantly different at the 0.05 probability level.

³ Irrigated when soil water potential reached this level.

Irrigation increased total and 1988 height growth, and d.b.h. in all three species (table 4). Because most drought impact was limited to 1988, the 1988 height growth was selected as the most sensitive indicator of species response to drought. The d.b.h. data are the accumulated diameters for the duration of the study. Comparing 1988 height growth between the wettest and driest treatments shows a range of 62 cm for *P. trichocarpa*, but 102 and 95 cm for *P. balsamifera* and *P. deltoides*, respectively. Also, the difference in 1988 height growth between the two wetter irrigation treatments (-0.05 and -0.15 MPa) was not significant for *P. trichocarpa* but was significant for the other two species.

We interpret this as an indication that *P. trichocarpa* clones have less growth loss on dry soils than do *P. deltoides* and *P. balsamifera* clones. *P. trichocarpa* was found to be less drought tolerant than *P. deltoides* in Washington (Schulte *et al.* 1987). However, the *P. trichocarpa* clones used in their study were collected west of the Cascade Mountains. The clones we used were collected from a drier climate in the Rocky Mountains and may be better adapted to drought conditions (table 1). Bassman and Zwier (in press) recently found that an eastern Washington clone of *P. trichocarpa* used water more efficiently than a western Washington clone of the same species because of adaptation to its native environment.

Clonal Results

Clonal differences in growth were observed in each of the species all 3 years (table 3). Irrigation growth differences were not detected until 1988. Before that, the range in clonal growth was similar for all species (table 5). For example, the range between the shortest and tallest clones in 1987 averaged over all irrigation treatments was 159 cm for *P. balsamifera*, 168 cm for *P. trichocarpa*, and 137 cm for *P. deltoides*. While the *P. balsamifera* clones were generally smaller than the *P. trichocarpa* and *P. deltoides* clones the tallest clones of each species were similar in size. Significant clonal variation within *Populus* species is not uncommon. Indeed, provenance tests have shown significant clonal variation in growth for each of the species used in this study (Weber *et al.* 1985, Heilman and Stettler 1985 for *P. trichocarpa*; Farmer 1970, Mohn and Randall 1973 for *P. deltoides*; and Farmer *et al.* 1986 for *P. balsamifera*).

A significant clone x irrigation interaction occurred in the 1988 growing season d.b.h. for *P. balsamifera* and d²h for *P. balsamifera* and *P. trichocarpa* (table 3). The presence of interactions in genotype studies is common and is well documented in the literature (Morgenstern 1982). Interactions are due to changes in either scale or ranking between treatments. In this case we would expect a change in scale, because we have found trees grow better with irrigation in these soils (Hansen 1988). In this study, we were looking for clones that have similar growth under all soil moisture regimes (drought tolerant). Drought "tolerance" as used in this study refers to the overall plant response to drought and does not refer to the biological mechanism involved as is the case when the two terms "tolerance" and "avoidance" are used (Kramer 1983).

After analyzing the data, we attributed these interactions to a change in scale between irrigation treatments rather than to a change in rankings. For example, the range in average d²h between the largest and smallest *P. balsamifera* clones was nearly twice as much in the wettest plots as compared to the unirrigated plots (table 6).

Table 5.—Pre-drought growth parameters of 12 *P. balsamifera* and *P. trichocarpa* clones and 7 *P. deltoides* clones ranked on basis of 1987 height¹

Clone	1986 Height	1987 Height	1987 Height growth	1987 Basal diameter
----- Centimeters -----				
<i>P. balsamifera</i>				
B09	101 ² a	296 a	195 a	4.1 bc
B10	102 a	274 b	172 b	3.9 c
B05	96 ab	262 bc	166 bc	4.0 c
B08	94 ab	251 cd	157 cd	3.6 d
B06	93 ab	245 cd	152 cd	4.6 a
B12	93 ab	242 cd	150 de	4.4 ab
B03	95 ab	240 de	145 de	3.4 d
B07	99 a	219 ef	120 g	3.5 d
B11	79 bc	200 fg	121 fg	3.5 d
B02	61 cd	196 g	135 ef	2.6 e
B01	61 cd	186 g	125 fg	2.8 e
B04	43 d	137 i	94 h	2.2 f
<i>P. trichocarpa</i>				
T08	135 a	335 a	200 a	5.1 ab
T09	144 a	326 a	182 a	5.5 a
T03	132 ab	316 a	181 a	5.1 ab
T11	125 ab	312 a	187 a	5.6 a
T10	128 ab	273 b	146 cd	4.3 d
T02	94 cd	265 bc	175 ab	5.4 a
T12	98 cd	257 bc	153 bc	4.2 d
T01	100 cd	244 bcd	144 cd	5.0 abc
T05	114 ab	237 cd	123 d	5.5 a
T04	99 cd	223 d	124 d	4.5 bcd
T07	92 d	181 e	90 e	3.0 e
T06	89 d	167 e	77 e	2.8 e
<i>P. deltoides</i>				
D07	142 a	330 a	188 a	5.4 a
D12	128 a	321 a	193 a	4.8 ab
D11	121 a	315 a	194 a	4.4 bc
D09	88 b	264 b	176 a	3.5 de
D05	69 bc	258 b	190 a	4.1 cd
D02	63 cd	249 b	186 a	3.6 de
D01	45 d	193 c	148 b	3.0 a

¹ Mean of all irrigation treatments (n=12).

² Means followed by the same letter in a column are not significantly different at the 0.05 probability level.

Table 6.—Stem volumes after the drought year for three *Populus* species by irrigation and clone.

Clones are ranked on the basis of stem volume in the -0.05 MPa irrigation treatment. Also shown is the ratio of stem volume in the driest treatment to stem volume in the wettest treatment.

Clone	Stem volume (d ² h)			Ratio
	None	-0.15	-0.05	
<i>P. balsamifera</i>				
a B10 b	2,781	4,657	9,049	0.31
B05 c	1,707	5,370	8,941	0.19
B06 c	832	2,841	6,102	0.14
a B08 b	2,223	4,287	5,858	0.38
B12	1,281	2,075	4,921	0.26
B03 b	1,471	2,187	4,281	0.34
B09	885	3,156	3,177	0.28
B07 b	1,511	2,782	3,144	0.48
B11 c	482	2,825	3,007	0.16
B01 c	479	1,534	2,482	0.19
B02	465	1,583	1,922	0.24
B04 b	148	353	430	0.34
<i>P. trichocarpa</i>				
T09	6,272	12,570	15,839	0.40
T11	5,502	5,136	14,348	0.38
a T08 b	7,092	15,977	13,561	0.52
T02 c	3,090	2,607	10,673	0.29
a T10 b	5,932	7,862	5,402	1.10
T03 b	4,776	6,028	5,130	0.93
T01 b	4,398	3,488	4,296	1.02
T12 b	3,703	2,607	3,991	0.93
T04 c	925	3,609	3,731	0.25
T05	788	656	2,196	0.36
T06	516	1,539	1,804	0.29
T07	355	529	898	0.40
<i>P. deltoides</i>				
D07	5,831	10,313	13,903	0.42
a D12 b	6,274	6,709	12,581	0.50
D02 c	1,605	6,823	12,170	0.13
a D11 b	8,408	11,587	8,780	0.96
D05 c	1,815	5,916	7,692	0.24
D09	3,478	6,270	7,088	0.49
D01 b	2,470	4,113	4,445	0.56

a Clones that are drought tolerant and exhibit good growth.

b Clones that are drought tolerant (dry to wet volume ratio > 0.50, 0.30 for *P. balsamifera*).

c Clones that are drought sensitive (dry to wet volume ratio < 0.30, 0.20 for *P. balsamifera*).

If we assume that each clone reached its genetic potential in the wettest treatment, we can determine a relative response to irrigation by determining the stem volume ratio of the driest to the wettest treatment. Clones with a higher ratio are considered unresponsive to irrigation (drought tolerant), and those with a low ratio are considered drought sensitive.

Many of the clones that have high ratios tend to grow poorly at all irrigation levels, such as clones B04, B07, T01, T06, T07, and T12 (table 6). However, a few clones with high ratios (drought tolerant) such as B08, T08, and T10 tend to grow well under all irrigated conditions (see a's in table 6). Other clones such as B06 and D02 are drought sensitive; they grow well only when irrigated (b's in table 6). Selected responsive and unresponsive clones in each of the species are compared in figure 2. The clone x irrigation interaction illustrated is significant for *P. balsamifera* and *P. trichocarpa* (table 3), but not significant ($p = 0.15$) for *P. deltoides* although a similar trend is noticeable.

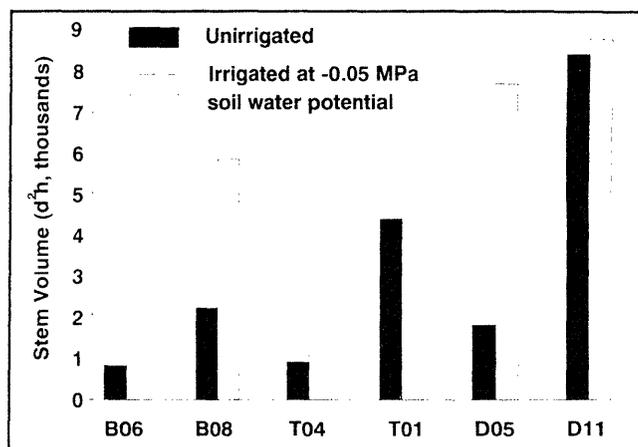


Figure 2.—Stem volumes of six *Populus* clones grown under two irrigation levels. A drought sensitive clone (B06, T04, and D05) and a drought tolerant clone (B08, T01, and D11) from each of the species are shown.

CONCLUSIONS

Substantial clonal variation in height, height growth, d.b.h., and stem volume occurred within each of the species.

Irrigation significantly increased growth in all species and most clones during a drought year (third year of the study).

P. trichocarpa responded less to irrigation than either *P. balsamifera* or *P. deltoides*.

All species contained clones that could be classified into one of three groups: good growth under all irrigation regimes, poor growth under all irrigation regimes, and good growth only when irrigated.

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