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Above- and below-ground characteristics associated with wind toppling in a young *Populus* plantation

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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.

Key words Wind damage · Root morphology · Stem form · Thigmomorphogenesis · Clonal deployment

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Introduction

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 (c.f., Gratkowski 1956; Harris 1989; Hütte 1968; Miller 1986); 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 et al. 1982; Harris 1989; Lohmander and Helles 1987; Petty and Swain 1985; Quine et al. 1995; Somerville et al. 1989). 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 (Coutts 1986; Mason 1985; Quine et al. 1995) and planting techniques (Quine 1990) as well as choice of species or genotype (Eis 1978; Somerville et al. 1989) and initial spacing (Quine et al. 1995; Somerville et al. 1989).

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

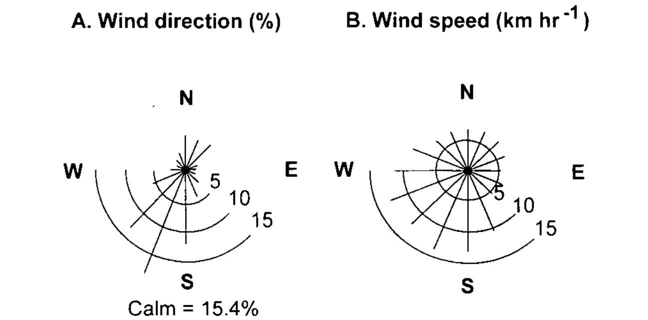

Fig. 1 A,B Summary of 20-year wind statistics from Olympia Airport (Meteorology Committee 1968). **A** Percentage of time winds come from each of 16 compass directions (or air is calm). **B** Mean wind speed by compass direction

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 in late March 1990, with 30-cm long unrooted cuttings placed vertically with approximately 25 cm below ground and 1–2 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 greater than 40 km h^{-1} originate almost exclusively from the south or southwest (Meteorology Committee 1968). On 20 January 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 h^{-1}, with a peak gust of 88 km h^{-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 1 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.

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 southern-most leaning tree was eligible for selection (since the wind came from the south, the southern-most 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,

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

Clone	Spacing	Degree of lean by clonal plot type							
		Monoclonal				Polyclonal			
		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	1	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

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 nine sectors: roots that originated between 0- and 15-cm below groundline divided into four 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 3 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,

$$\text{transformed lean} = \text{Ln}\ [(\text{plean} + 0.5)/(1.5 - \text{plean})]$$

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 ($\text{RtNum}_{\text{Total}}$); and cross-sectional root area (CSRA) by sector (e.g., CSRAN_{15} = CSRA of roots in north quadrant of 0–15 cm layer), layer (e.g., CSRA_{15}), or in total ($\text{CSRA}_{\text{Total}}$). In addition, a measure of root system balance was calculated for different portions of the root system as follows:

$$\text{Uneven}_{15} = \left|\frac{\text{CSRA}_{\text{N}15}}{\text{CSRA}_{15}} - 0.25\right| + \left|\frac{\text{CSRA}_{\text{E}15}}{\text{CSRA}_{15}} - 0.25\right| + \left|\frac{\text{CSRA}_{\text{S}15}}{\text{CSRA}_{15}} - 0.25\right| + \left|\frac{\text{CSRA}_{\text{W}15}}{\text{CSRA}_{15}} - 0.25\right|$$

A similar equation was used for $\text{Uneven}_{\text{All}}$ where all nine root sectors were utilized and the subtraction factor was 0.12 for the eight 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).

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*

Source of variation	*df*	Prob >*F*-value	
		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	0.14	0.01
Clone * Spacing * Plot type	6	0.39	0.09

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, 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 two 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.

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

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)

Spacing	Clone	HT/PHT			D13/PD13			HT/D13		
		No lean	Lean	Prob >*t*	No lean	Lean	Prob >*t*	No lean	Lean	Prob >*t*
0.5 m	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
1.0 m	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
1.5 m	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)

Variable	Clone			
	11–11	49–177	CL	47–174
$RtNum_{15}$ (number)	8.2a	7.8ab	5.6c	6.7bc
$RtNum_{30}$ (number)	10.8a	12.2a	11.1a	10.5a
$RtNum_{Down}$ (number)	4.3a	4.0a	4.2a	4.0a
$RtNum_{Total}$ (number)	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 (number)[a]	43b	38b	68a	25b
DBr (number)[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

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, 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 0–15 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 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 $P \leq 0.05$

Sector	Clone			
	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

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.

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

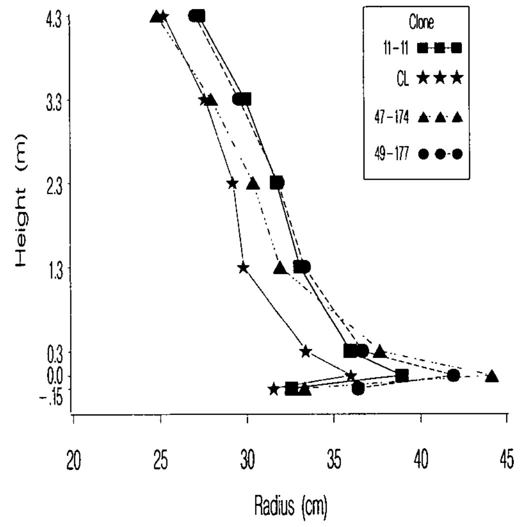

Fig. 2 Mean diameter by clone of tree boles from 0.15 cm below ground to 4.3 m above ground (1.0-m spacing)

also strongly tapered in its basal 30-cm section; it was less tapered than the other clones above 1.3 m.

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 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% vs 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 windward 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% vs 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., N15 in Fig. 3) nonleaning trees had significantly lower values for Unevèn$_{15}$ 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$_{15}$.

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)

Variable (units)	0.5-m spacing			1.5-m spacing		
	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$_{15}$ (number)	7.0	5.1	<0.01	7.9	6.1	0.09
RtNum$_{30}$ (number)	14.1	15.2	0.35	13.2	14.0	0.50
RtNum$_{down}$ (number)	1.8	1.5	0.58	2.2	2.6	0.31
RtNum$_{Total}$ (number)	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

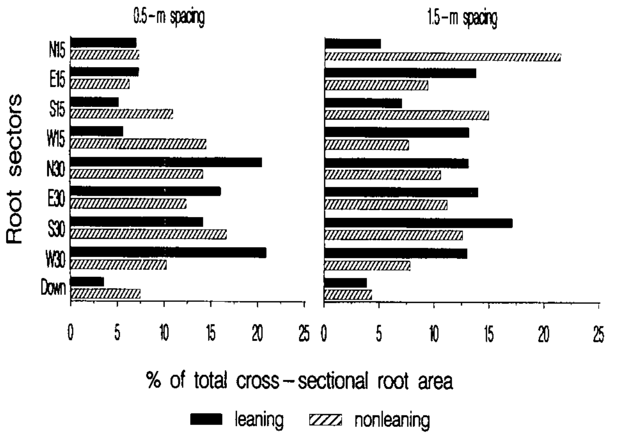

Fig. 3 Percentage of total root system cross-sectional area by root system sector for leaning and nonleaning trees in 0.5-m and 1.5-m spaced plots

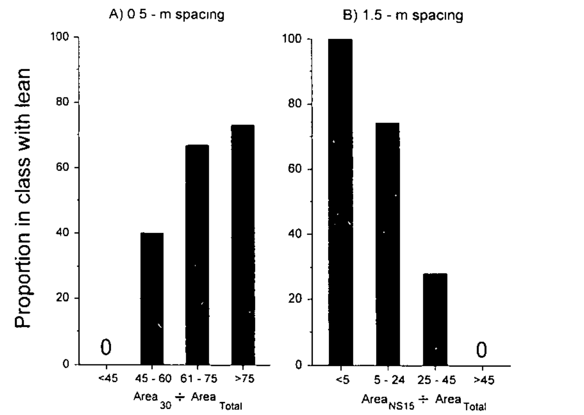

Fig. 4 Proportion of trees in each variable class that were leaning. Variables shown were first ones selected for each spacing by step-wise discriminant analyses with tree groups of leaning and nonleaning

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} quadrants 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 et al. 1982). On the other hand, trees in dense stands provide substantial mutual support which dampens the amplitude of the sway (Quine et al. 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 et al. 1982; Harris 1989; Somerville et al. 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 (Brünig 1973) and values above 1.0 have been suggested as associated with increasing susceptibility to wind damage in conifer stands (c.f., Sheehan et al. 1982; Cremer et al. 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 (c.f. Ceulemans 1990) rather than susceptibility to damage. Michael et al. (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 et al. 1994), root strength (Hathaway and Penny 1975), and branching characteristics (Weber et al. 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 (c.f., 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 – 15 cm layer than the other three clones but did not differ in numbers of roots in the 15 – 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 et al. 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.

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