Adaptive growth of tree root systems in response to wind action and site conditions

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Summary   Soil-root plate dimensions and structural root architecture were examined on 46-year-old Sitka spruce (*Picea sitchensis* (Bong.) Carr.) trees that had been mechanically uprooted. Rooting depth was restricted by a water table, and root system morphology had adapted to resist the wind movement associated with shallow rooting. The spread of the root system and the ratio of root mass to shoot mass (root/shoot ratio) were both negatively related to soil-root plate depth. Root systems had more structural root mass on the leeward side than the windward side of the tree relative to the prevailing wind direction.

Cross sections of structural roots were obtained at distances of 0.5, 0.75, 1.0, and 1.25 m from the tree center. Buttressed parts of roots had greater lateral and vertical secondary thickening above rather than below the biological center. This uneven growth, which produced a shape similar in cross section to a T-beam, was greater on the leeward side of the tree, and was greatest at 0.5 m from the tree center of shallow rooted trees. Further from the tree, particularly on the windward side, many roots developed eccentric cross-sectional shapes comparable to I-beams, which would efficiently resist vertical flexing. Roots became more ovoid in shape with increasing distance from the tree, especially on deep rooted trees where lateral roots tapered rapidly to a small diameter.

We conclude that these forms of adaptive growth in response to wind movement improve the rigidity of the soil-root plate and counteract the increasing vulnerability to windthrow as the tree grows.

Keywords: buttress development, I-beam roots, root morphology, structural roots, thigmomorphogenesis, tree stability, windthrow.

Introduction

Resistance of forest trees to breakage or overturning in windy climates depends largely on structural modifications for mechanical strength. Plant growth responses to movement, termed thigmomorphogenesis by Jaffe (1973), include changes in branch and foliar development, stem shape and mass. In many tree species, leaf size, branch size and stem height are restricted by the mechanical action of the wind, whereas secondary thickening of the stem base is enhanced

(Telewski 1995). Additional resistance to wind bending can occur as a result of increased thickening of the lower stem along the axis of the prevailing wind direction (Jacobs 1953), and in conifers, this thickening is greater on the lee side of the stem (Robertson 1991). Development of stem shape is believed to maintain uniform stress over the stem surface during wind loading (Metzger 1893, Morgan and Cannell 1994). These aboveground developmental responses counteract increasing movement as the tree grows and reduce the risk of stem breakage in high winds.

Uneven secondary thickening between root and stem, resulting in the development of supporting buttresses, may also reflect growth to equalize mechanical stress during wind loading (Ennos 1995). The large tabular buttresses, characteristic of many tropical tree species, and the smaller more rounded buttresses, often observed on temperate trees, make a rigid connection between the stem and root system. Buttresses reduce bending and concentration of stress at the base of the tree (Mattheck 1993). These structures also increase the leverage required for overturning by moving the "hinge" point of the root system further from the base of the tree.

Trees continuously alter their morphology in response to changes in wind exposure. Wilson (1975) found increases in growth ring width both in the lower stem and at the base of structural roots of *Pinus strobus* L. trees in response to increased wind movement after stand thinning. Urban et al. (1994) reported that, after removal of neighboring trees, there was an immediate increase in thickening of structural roots of *Picea glauca* (Moench) Voss, but a 4-year delay before an increase in stem diameter growth occurred. Similar temporal differences between stem and root thickening of *Pinus resinosa* Ait. trees in response to thinning were reported by Fayle (1983). Allocation of assimilates to those parts of the tree under the greatest stress optimizes the use of available resources to stabilize the tree and to moderate increases in wind movement.

Coutts (1986) separated resistance to uprooting of shallow rooted trees into four components: resistance to bending of the leeward side "hinge" roots; anchorage of windward roots under tension; mass of the soil-root plate; and resistance of soil to breaking. Tree stability is improved by adaptive growth that increases the rigidity and size of the soil-root plate (Blackwell et al. 1990). For example, shallow rooted Sitka spruce (*Picea*

sitchensis (Bong.) Carr.) trees allocate more biomass to structural roots on their leeward side relative to the prevailing wind direction (Quine et al. 1991, Nicoll et al. 1995): a response that reduces bending in the soil-root plate and increases resistance to windthrow.

Resistance to bending may also occur through changes in the shape of structural roots. Rigg and Harrar (1931) reported that several North American conifer species growing in sphagnum moss above a shallow water table formed major roots with a cross-sectional shape comparable in appearance and function to that of an I-beam (or I-girder). Some roots had a shape more like a T-beam, and others had an oval shape. I-Beam shaped roots are also found on Scots pine (*Pinus sylvestris* L.), lodgepole pine (*Pinus contorta* Dougl.), birch (*Betula* spp.), oak (*Quercus* spp.), and Sitka spruce growing on waterlogged peat in the British uplands (Anon. 1964). This shape uses a minimum of material to maximize resistance to bending in the vertical plane (Wood 1995) and further increases rigidity of the soil-root plate.

In exposed upland conifer plantations of the U.K., rooting depth is often restricted by a water table that fluctuates close to the ground surface for much of the year (Ray et al. 1992). Sitka spruce, the most commonly planted species on these sites, has roots that are particularly intolerant of anoxia (Armstrong et al. 1976) and can survive only a few centimetres below the water table (Coutts and Nicoll 1990a, Ray and Schweizer 1994). As shallow rooted trees grow in height, their increasing mass and wind movement exaggerate the flexing of structural roots near the ground surface. We have examined the various mechanical modifications that occur during the development of root systems that limit this movement and resist overturning of the tree.

Methods

Site details

One hundred 46-year-old dominant and co-dominant Sitka spruce trees were selected by stratified random sampling from a 24-ha upland plantation at Crookburn in Kershope Forest, Cumbria, U.K. (200–245 m altitude, south-east aspect; latitude 55°06′ N, longitude 2°47′ W). The trees had been planted at 1.8 m spacing on manually spread turfs next to shallow furrows about 30 cm deep and 3.6 m apart. Part of the site was a former drainage experiment with drains at 10-, 20- and 40-m intervals. Other areas were outside the drainage experiment and were undrained. Soils varied from surface-water gley (stagno-orthic gley soil; Avery 1990) on the steep slopes (5–14°) to peaty-gley (humic stagno-orthic gley soil; Avery 1990) on gentle slopes (0–4°). The site has a mean yearly rainfall of approximately 1300 mm. Wind direction was not monitored on the site before extracting the trees, but mean wind direction monitored at Caplestone Fell, 7 km away, between January 1989 and July 1995, was 248° from North (B.A. Gardiner, Forestry Commision, Roslin, U.K., personal communication). Analysis of wind direction at the experiment site from February to the end of May 1996 confirmed that there

is a highly significant linear relationship ($P < 0.001$) with wind direction recorded simultaneously at Caplestone Fell.

Selection and extraction of study trees

Water table depth was monitored in a 1-m-deep borehole positioned 1 m from the center of each tree. Boreholes were lined with 55-mm-diameter rigid plastic tubes, perforated along their length to allow free water movement. The depth of the water table was measured and recorded at weekly intervals for 6 weeks in the winter of 1991 (November to December). These data were used to select 50 of the 100 trees to give a range of mean winter water table depths, and hence, a corresponding range of root plate depths.

In 1993–1994, the selected trees were felled, leaving a 3-m-high stump. Eleven trees were windblown during harvesting and were excluded from the study. Stem and crown dimensions were measured, and stem sections and branches were weighed. Study trees had a mean height of 24 m and a mean stem diameter of 0.32 m taken at a height of 1.3 m.

To extract the trees, a nylon sling was attached to the stump 2 m above the soil surface, and connected to the steel cable from a hydraulic winch on a tractor. All trees were pulled in a direction away from, and perpendicular to, the plough furrow at a constant pull rate of approximately 2 cm s^{-1}. Each tree was pulled over completely, and the stem anchored to the ground to allow safe measurement of the soil-root plate.

Soil-root plate measurement

Soil-root plate spread was measured by recording the distance from the center of the stem to the edge of the plate on each of eight cardinal radii. A sharpened steel rod (1 m long, 6 mm in diameter) was pushed through the plate at 0.5-m intervals along each cardinal radius until it emerged, and the thickness of the plate was measured from the rod. The soil surface level was marked on each stump. All soil was then removed from the root plate with a high pressure air jet from an "air-knife" (Briggs Technology Inc., Pittsburgh, PA), and the stem was cut from the root plate at the root collar. Root samples removed from two trees were weighed before and after drying for 7 days at 80 °C to determine water content.

Root system architecture measurements

Root system architecture was measured by a technique similar to that described by Quine et al. (1991) and Nicoll et al. (1995). The azimuth angle (horizontal direction) of all roots, including root branches, greater than 10 mm in diameter was recorded at 0.5 and 1.0 m from the stump center. These angles were measured at the geometric center of the stump, between a line to a reference point marked on the furrow side of the stump, and a line to the middle of each root. Diameters of the roots were measured in the horizontal and vertical planes at the same positions.

Root systems were weighed by suspending them from a load-cell under a tractor arm. During this operation, samples cut from two trees were weighed and dried at 80 °C for 7 days before recording dry weight. Root system dry mass was calculated for all trees, and fresh mass (i.e., weight at time of

extraction) was estimated by adding the water mass calculated from the original percentage water content.

Cross-sectional shape of structural roots

On each tree, cross-sectional samples were cut from the 10 largest roots at 0.5, 0.75, 1.0, and 1.25 m from the geometric center of the stump. Before cutting, a label was fixed to the top of the root section, the depth of this point was measured relative to the soil level mark on the stump, and its azimuth direction was recorded. When the root at the sample point was branching or fused to other roots, and therefore had more than one biological center, the section position was moved, if possible, up to 5 cm to allow a single centered part of the root to be sampled.

One face of each root cross section was sanded smooth to allow examination of the growth rings. Dimensions of all sections were measured in the manner shown in Figure 1a. Measurements were made relative to the biological center (bc) of the root, i.e., the original primary root position. Dimensions were recorded as follows: V_a = distance above bc to root edge, V_b = distance below bc to root base, H_a = width at $0.5V_a$, H_b = width at bc, H_c = width at $0.5V_b$. It was necessary to omit measurement of fused root sections, which had more than one biological center, from this analysis.

Three descriptors of root shape were calculated from the dimensions of structural root cross sections: "T-angle", "I-angle", and V_a/V_b ratio (see Figure 1b). The descriptors allowed comparison of root shapes even when the roots were not symmetrical around a vertical axis through the biological center (Figure 1). The T-angle describes the unevenness of lateral thickening between the upper and lower parts of the root, and hence, the tendency toward a T-beam shape. Angles greater than 90° indicate more lateral thickening in the upper part of the root (H_a) than the lower part of the root (H_c), whereas angles less than 90° indicate the reverse pattern: the further the

angle deviates from 90°, the more T-beam shaped the section. The I-angle describes the tendency toward an I-beam shaping of the root; angles greater than 180° indicate an I-beam shape and angles less than 180° indicate an ovoid shape. The V_a/V_b ratio compares thickening in the vertical plane above and below bc, i.e., a ratio of 1 indicates equal vertical thickening above and below the biological center, and the higher the ratio, the greater the upward relative to downward thickening.

Statistical analyses

Soil-root plate and root data were analyzed by regression analysis and analysis of variance, and differences between means were compared by the F-test. Descriptors of structural root cross-sectional shape were compared between quadrants of the root systems on the windward and leeward side relative to the prevailing wind direction, and between shallow rooted (< 0.6 m) and deep rooted (> 0.6 m) trees.

The center of root cross-sectional area (Nicoll et al. 1995) was calculated for each tree to examine the directional allocation of root biomass and allow comparison with previous root architecture studies. This is similar to the root system center of mass described by Coutts et al. (1990), and is based on the center of diameter calculation used by Quine et al. (1991), but gives most weighting to the largest roots (A.D. Milner, Forestry Commission, Roslin, U.K., personal communication) that have the greatest role in tree stability. The center of the cross-sectional area (CSA) of a root is the mean position of the structural root within the root system relative to the stem center, using measured azimuth angles and weighted by CSA (Nicoll et al. 1995). Root CSAs were calculated (as oval shape) using vertical and horizontal diameters measured at 0.5 m from the tree center. More accurate CSAs, calculated using measurements taken from the cut sections of roots, could not be used for this analysis because only 10 sections were cut at each
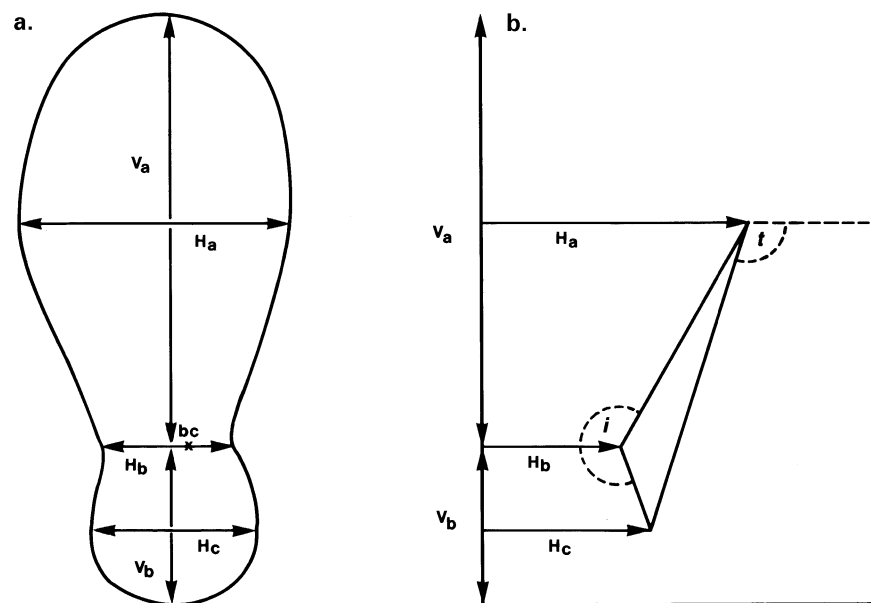

Figure 1. (a) Measurement of root cross section dimensions. (b) Calculation of root shape descriptors: T-angle (t), I-angle (i), and V_a/V_b ratio.

distance from the tree, and there was a large amount of missing data at 0.5 m because of fused roots.

The origin of the coordinate system is the center of the tree stem. If the center of the root CSA is at the origin, then root mass is evenly distributed around the tree, but displacement from the origin indicates uneven development of the root system. The center of the root CSA for an individual tree has co-ordinates:

$$X = \sum_{i=1}^{n} X_i \; ; \; Y = \sum_{i=1}^{n} Y_i,$$

where the Cartesian co-ordinates of the ith root ($i = 1...n$) weighted by CSA are:

$$X_i = D_i \sin\theta_i \; ; \; Y_i = D_i \cos\theta_i,$$

θ_i represents the azimuth angle,

$$D_i = \frac{d_i}{\sum_{i=1}^{n} d_i}$$

and d_i is the product of the vertical and horizontal diameters of the ith root. The distance (R) between the center of root CSA from the origin of the co-ordinate system and its orientation, θ, are given by:

$$R = (X^2 + Y^2)^{1/2} \; ; \; \theta = \tan^{-1}(X/Y).$$

Large values of R indicate that roots tend to cluster together in a preferred direction, θ, whereas small values imply uniformity around the tree stump. Both X_i and Y_i are independent normally distributed variables with common variance, σ^2; hence, the hypothesis of no clustering can be tested using the statistic, $R^2/n\sigma^2$, where σ^2 is an estimate of the variance. Under the hypothesis of no clustering, this statistic has an F-distribution with 2, $2(n-1)$ degrees of freedom. The hypothesis is rejected whenever $R^2/n\sigma^2$ is greater than $F(2, 2(n-1); \alpha)$, when testing at the $\alpha\%$ significance level (Nicoll et al. 1995).

Results

Soil-root plate shape

The mean winter water table depth under the study trees was 423 mm, and the mean soil-root plate depth was 559 mm. There was a direct relationship between soil-root plate spread and depth, with the shallowest plates having the widest spread. Figure 2a shows plate surface area (normalized for tree size by dividing by stem mass) plotted against plate depth. The linear regression line fitted to these points showed a significant negative relationship ($P < 0.001$) between depth and spread: normalized soil-root plate area = −17.19(soil-root plate depth) + 18.103.
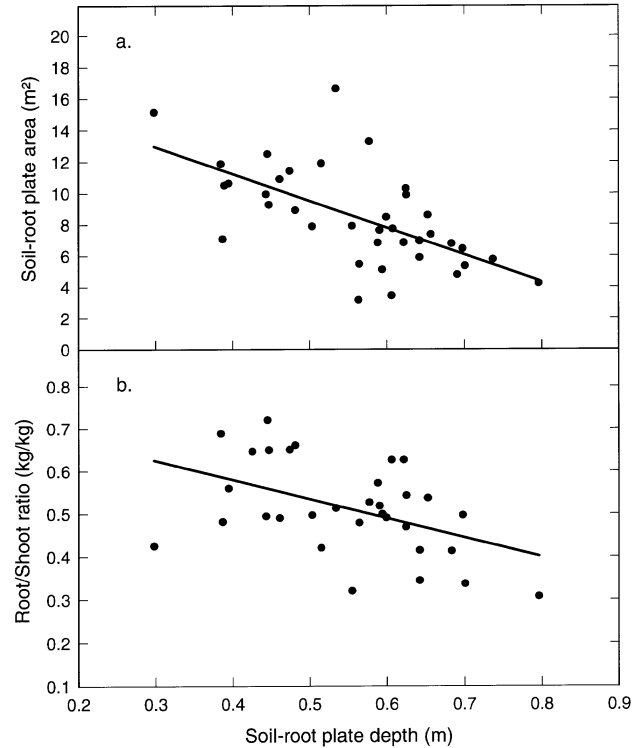

Figure 2. (a) Soil-root plate area (normalized for tree size by dividing by stem mass) against soil-root plate thickness. (b) Root/shoot fresh mass ratio plotted against soil-root plate thickness.

The root system mass (without soil) was smaller on shallow rooted trees than on deep rooted trees; however, shallow rooted trees also had smaller stems and crowns. Thus, the smaller the rooting depth, the larger the root/shoot ratio (Figure 2b); i.e., compared to deep rooted trees, shallow rooted trees allocated a larger proportion of biomass to belowground components. The regression: root/shoot mass = −0.45(root depth) + 0.7601 was significant at $P < 0.01$.

Root system architecture

The center of root CSA showed no significant clustering of root direction on any individual tree. However, for all trees combined (Figure 3), there was a significant clustering of centers of root CSA toward 50.5° from North ($P < 0.01$). This clustering was on the leeward side of the trees, at 162.5° from the prevailing wind direction.

Cross-sectional shape of structural roots

The buttressed part of the root (adjacent to the stem) was frequently made up of several roots fused together, but the overall cross-sectional shape was similar regardless of the number of constituent roots (see Figures 4a and 4b). Analysis of single centered roots (Figure 5) indicated that T-angles were largest (i.e., having a pronounced T-beam shape as in Figure 4a) at the 0.5 m and 0.75 m radii. The T-angle decreased from the 0.75 m radius to a minimum at the 1.25 m radius (Figure 5a). Leeward sector roots had significantly greater
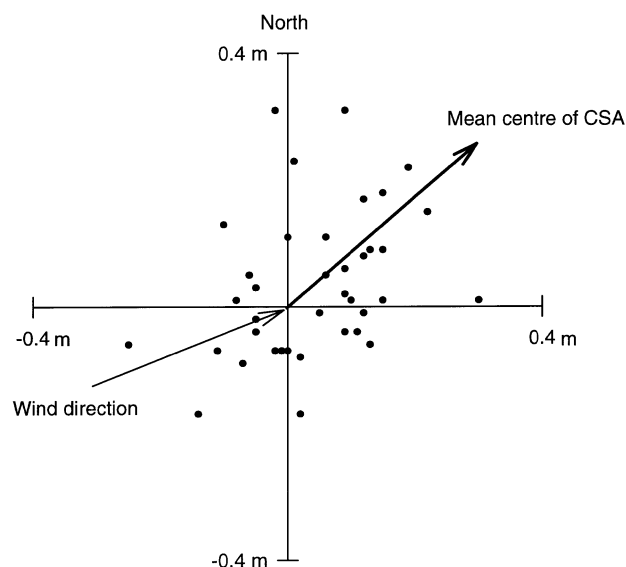
Figure 3. Mean centers of root cross-sectional areas (CSA) for all trees relative to North. Arrows indicate the prevailing wind direction (248° from North) and the direction of clustering of center of CSA for all trees. Axes show distance (m) from the tree stem center.

T-angles than windward sector roots at 0.75 and 1.0 m radii (both $P < 0.001$).

At 0.5 m from the tree center, i.e., within the most buttressed part of the root system, leeward roots of deep rooted trees had the largest mean I-angle, and windward roots of deep rooted trees had the smallest mean I-angle (Figure 5b). Further away from the tree at the 0.75 and 1.0 m radii, root I-angles were larger (more I-beam shaped) on windward roots than on leeward roots for both shallow and deep rooted trees. An example of a distinctive I-beam root, with a large I-angle, is shown in Figure 4c. Differences between mean I-angles were significant only at a radius of 1.25 m where windward roots of shallowly rooted trees had substantially greater I-angles than roots of other groups ($P < 0.05$), although differences at 0.5 m also approached significance ($P = 0.06$). Root diameters at the 1.25 m radius were smaller on deep rooted trees than on shallow rooted trees, and at this distance, the cross-sectional shapes of deep rooted trees were more ovoid ($P < 0.05$), i.e., smaller I-angles.

Thickening of individual roots in the vertical plane was usually greater above the biological center than below it, especially close to the stem. The mean V_a/V_b ratios for all trees at 0.5, 0.75, 1.0, and 1.25 m, were 4.24, 3.58, 2.60, and 1.20, respectively. This change in allocation pattern with increasing distance from the tree center varied between windward and leeward sector roots (Figure 5c). The largest mean V_a/V_b ratio at 0.5 m was for shallow roots on the leeward side of the tree. The differences at 0.5 m approached significance ($P = 0.07$). Leeward roots had significantly greater V_a/V_b ratios than windward roots at both 0.75 m ($P < 0.05$) and 1.0 m ($P < 0.01$). The V_a/V_b ratios were similar for all groups at the 1.25 m radius.

Examination of growth rings on the sections revealed that asymmetric growth frequently occurred before the tree was

3 years old (Figure 4). Roots initially became elliptical, but then often developed an I-beam shape (Figure 4c). As roots thickened further, the narrow central section often filled in, producing a slab shape (Figure 4d), or if the root was close to the stem, a buttress T-beam shape (Figures 4a and 4b). Compression wood was not observed in any of the root sections. Growth rings were usually widest on the upper side of the root, whereas it was frequently impossible to differentiate the growth rings on the lower side.

Discussion

Because shallowly rooted trees have little anchorage from downward roots, stability depends largely on the rigidity of the soil-root plate. Soil under a flexible soil-root plate will shear when subjected to a smaller force than soil under a rigid plate of the same area: i.e., a fracture can propagate outward from one point under a flexible plate, whereas a larger area must shear to start overturning of a rigid plate. In addition, the hinge point will develop further from the tree center on a rigid root plate than on a flexible root plate, and this will increase the force required to overturn the tree (Coutts 1983a, Deans and Ford 1983). Trees in this study showed a large range of soil-root plate thicknesses, with roots surviving on average 14 cm below the winter water table depth. The variation in rooting depth allowed comparison of structural root development among trees that experienced different amounts of wind-induced root movement. The development of surface roots can be limited by plough furrows (Savill 1976, Deans 1981, Hendrick 1989), but despite this restriction, trees growing above shallow water tables in this study adapted to inhibited downward root growth in several ways. Root spread was increased, a larger proportion of total biomass was allocated to the roots, and allocation was altered within the structural root system to provide optimum bending resistance. The increased spread of surface roots also increased the occurrence of root contact between trees, and the resulting fusion between root systems further improves stability (Coutts 1983a).

Roots respond to flexing by optimizing the allocation of available assimilates for maximum strength. We demonstrated a progression of the root shapes described by Rigg and Harrar (1931) from a buttressed T-beam shape close to the stem, through an I-beam shape within structural roots, to oval roots close to the edge of the plate. This differential thickening started within the first 3 years of radial growth in these roots.

Close to the stem, roots thickened more on the upper side to form rigid buttresses that support the stem and crown. This uneven development increased as thickening of the stem enveloped roots and brought other parts of the root system closer. Large differences in buttress dimensions (of tropical trees) have been observed among species and also among individuals within species (Henwood 1973). Several factors may influence the development of buttresses; for example, soil pressure, aeration, moisture, temperature and light are reported to stimulate radial growth in structural roots (Fayle 1968). However, buttress formation is necessary for mechanical strength between stem and root (Mattheck and Bethge 1990) and has been

Figure 4. Root cross sections showing (a) buttressed T-beam shape of a single root, (b) buttressed T-beam shape formed by four fused roots, (c) I-beam shape root, and (d) tabular shape root.

demonstrated to coincide with areas of high surface stress (Ennos 1995). In contrast to previous studies in angiosperm species (e.g., Senn 1923; reanalyzed by Barlow 1994) where buttresses were larger on the windward side of the tree and appeared to function for strength in tension, we found greater buttress development on the leeward side, implying that, in gymnosperms, these structures develop to function in compression. The differing roles of buttresses are reflected in the shape of the root. Angiosperm species produce tabular, "plank" buttresses (Smith 1972) suitable for support in tension, whereas Sitka spruce produces T-beam shape buttresses more suited for support in compression.

Distal to the buttressed part of the system, surface roots must resist both upward and downward flexing. The I-beam shape reflects the optimum use of resources for this role to supplement the inherent weakness of a thin soil matrix. The I-beam shaped roots were less common on deeper rooted trees where strong anchorage was provided by roots held by a thick matrix of soil. At distances greater than 0.75 m from the tree center, the I-beam structural root shape was found particularly on the windward side of shallowly rooted trees.

Wilson (1975) reported that the distribution of secondary thickening in *Pinus strobus* L. roots changes from being greatest on the top to being greatest on the bottom with increasing distance from the stem. Similarly, Deans (1981) described an individual Sitka spruce lateral root as having greatest thickening alternating between the upper and lower surfaces in the 1.2 m proximal to the root base. Although there were some root sections in the current study that had the most thickening on the lower side, the majority of root sections had the greatest thickening on the upper side, and means based on measurements taken from 10 roots on 39 trees show this epinastic
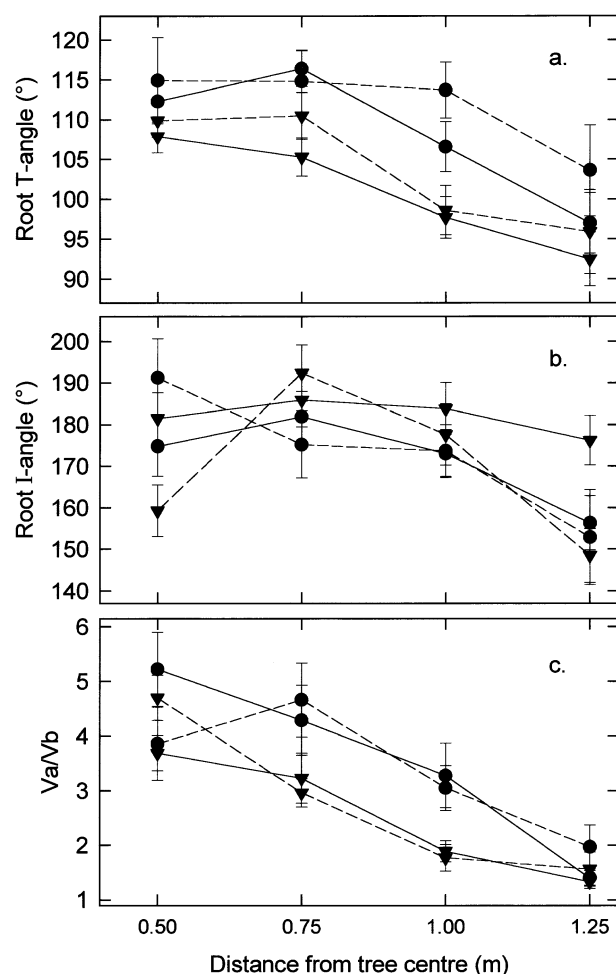
Figure 5. Descriptors of root cross-sectional shape (as shown in Figure 1) against sample distance from the tree stem center. (a) T-angle, (b) I-angle, and (c) V_a/V_b ratio. Solid lines, trees with soil-root plates less than 0.6 m deep; broken lines, trees with soil-root plates greater than 0.6 m deep. Circles, leeward sector roots; triangles, windward sector roots. Means ± SE are shown.

growth to be a strong, but decreasing, feature up to 1.25 m from the stem center. This growth pattern was most pronounced on roots on the leeward side of the trees. At the edge of the plate, smaller roots contribute toward stability in a manner analogous to guy ropes, and their circular or elliptical shape will satisfactorily dissipate the tensile forces.

The large differences in shape and size of roots over the 1.25 m distance from the tree center are unlikely to reflect differences in root age, because main lateral roots of Sitka spruce can grow over 1 m in the first year after planting (Coutts and Nicoll 1990*b*). The changes in rate of secondary thickening and the pattern of allocation were related more to the proximity of the root to the tree stem, and hence the loading the root was subjected to in the soil.

The allocation of biomass among roots would be expected to have a large effect on tree stability (Coutts 1983*b*). Where root biomass is clustered asymmetrically in the root plate, trees

may be overturned relatively easily if they are loaded in a direction other than that of the center of mass. The evenness of biomass distribution within the structural root system is related to genotype (Nicoll et al. 1995) and competition between roots for nutrients early in their development (Coutts 1987); however, the study trees were all unrelated individuals grown from seed, and there was no evidence of uneven nutrition around trees on this site. The allocation of assimilate within root systems is also influenced by wind action, and Stokes et al. (1995) found increased growth of roots on both the leeward and windward sides of young trees. In larger trees, Nicoll et al. (1995) showed that the center of mass of the root system was clustered down-slope, and away from the prevailing wind direction. In the present study, root mass was clustered up-slope and away from the prevailing wind direction, implying that the response to wind loading is the important factor, and that trees allocate greater resources to develop roots on the leeward side of the tree. The results of this study are comparable to those of Robertson (1991) who reported an increase in thickening on the leeward side of stems of coniferous trees. We conclude, therefore, that gymnosperm species react to wind loading by increasing growth on parts of the roots and stems in compression.

The various mechanical adaptations of the root system increase rigidity and move the hinge point away from the tree, thereby increasing the length of the lever arm and the tree's resistance to overturning (see Blackwell et al. 1990). Using the same trees as described here, Ray and Nicoll (unpublished data) demonstrated a significant correlation between soil-root plate rigidity and resistance to overturning. Therefore, the adaptive growth of structural roots counteracts the greater wind movement of shallowly rooted trees and reduces their vulnerability to windthrow.

Acknowledgments

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