RESPONSES OF YOUNG TREES TO WIND: EFFECTS ON ROOT ARCHITECTURE AND ANCHORAGE STRENGTH

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Abstract

Since the Great Storm of October 1987, public and political interest in wind damage to trees has heightened, resulting in increased research efforts to reduce windthrow.

This thesis examines the responses of young Sitka spruce (*Picea sitchensis* (Bong) Carr.) and European larch (*Larix decidua* (Mill.)) to wind stress. Two laboratory experiments were performed in which Sitka spruce and European larch were grown in wind tunnels. Trees responded to wind stress by increasing the number and altering the morphogenesis of windward woody lateral roots which provide the most resistance to overturning. Responses of shoot growth to wind stress were small, however, uneven irradiance levels appeared to cause asymmetric growth. The distribution of root biomass around the tree was related spatially to the distribution of shoot growth. A third experiment investigated the translocation pathway in Sitka spruce by feeding one root per plant with dye. The dye ascended spirally, reaching branches at many points around the stem. It was concluded that a different mechanism, such as an increase in stem cambial activity, must be occurring to stimulate asymmetric root growth.

Trees with characteristics likely to promote stability, such as increased root growth, could be selected for in breeding programmes. Clones of Sitka spruce were examined for their response to mechanical stimulation by flexing. Flexed trees increased biomass allocation and branching in woody roots under the most stress. Anchorage tests showed that some flexed clones of Sitka spruce had an increased resistance to overturning. In order to identify whether changes in architecture can affect pull-out resistance of roots, a model which simulates the uprooting of a root system with different branching patterns was designed, allowing predictions of anchorage abilities with regard to architecture.

If features which enhance tree stability are identified, foresters may utilize that knowledge when selecting trees to plant in the field.

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Many thanks to Keith Partridge and Colin Abbot in York and to Keith Clifford and Dave Clark in Roslin for looking after all my plants, and to the latter pair for building that wind tunnel and making all those temperature measurements. Thanks are due to James (*Jaaaaaaames*) Perrins and Tim Stickland for their invaluable guidance as I learned to operate the image analyzer. Bruce Nicoll has indulged in many post-lunch provocative arguments regarding roots, and has provided some of the data presented in Chapter 5. I would like to thank especially Jonathan Ball for his support during the months of writing up and for his and Andy Sedman's help with the modelling of root anchorage presented in Chapter 6. Many thanks are due to all members of F2, both past and present, especially Julie Watson and James Merryweather, for everything. Finally, I would like to thank my parents for their moral (and financial!) support during my years as a student.

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Declaration

The material presented in this thesis is the product of my own research efforts. The study presented in Chapter 5 was part of a larger experiment carried out at The Forestry Commission's Northern Research Station, Roslin, where I spent five months during my studentship. Mike Coutts and Bruce Nicoll provided some of the data used in Chapter 5.

The paper included in the appendix is published in a conference proceedings, listed below.

Appendix 1 - A. Stokes, A.H. Fitter and M.P. Coutts, *Responses of young trees to wind; effects on root growth*, Proceedings of the Edinburgh IUFRO conference "Wind and Wind-Related Damage to Trees," (Eds. J. Grace & M.P. Coutts). Paper accepted November 1993.

Chapter 1

General Introduction

1.1 The Problem

Damage by windthrow causes huge economic losses for British forestry and will carry on doing so especially if predictions about climatic change and increasing windspeeds prove to be correct (see Gribbin 1990). The Great Storm of October 1987, which struck south-east England caused the worst damage to trees since 1703 (Grayson 1989). Approximately 15 million trees (3.9 million m^3 of timber), mainly private woodlands and urban trees, were blown down. This amount almost equals the total volume of the three previous major storms, which occurred in January 1953, January 1968 (both in Scotland) and January 1976 (in Wales and the Midlands), which in total blew down an estimated 4.1 million m^3 of timber (Grayson 1989). As a result of the 1987 storm, public and political interest was higher than in the three previous storms, because it happened in a densely populated area around the capital. Consequently, the Forestry Commission received supplements to their planting grants for replanting blown woodlands, and research into reducing the effects of windblow has increased over the last few years (*e.g.* see Grace and Coutts 1993).

Windthrow, the uprooting of trees, is much more common than stem breakage, or "windsnap" (Holtam 1971). Extensive research has been carried out in attempts to predict and reduce wind damage (Booth 1974, Somerville 1980) but less has been done on the mechanics of how plants are uprooted (Coutts 1983a, 1986, Ennos 1989, 1991), or how root form influences uprooting (Ennos 1993b). Furthermore, only limited work has been carried out on the effects of wind action on tree root growth (Fayle 1968, 1976, Wilson 1975).

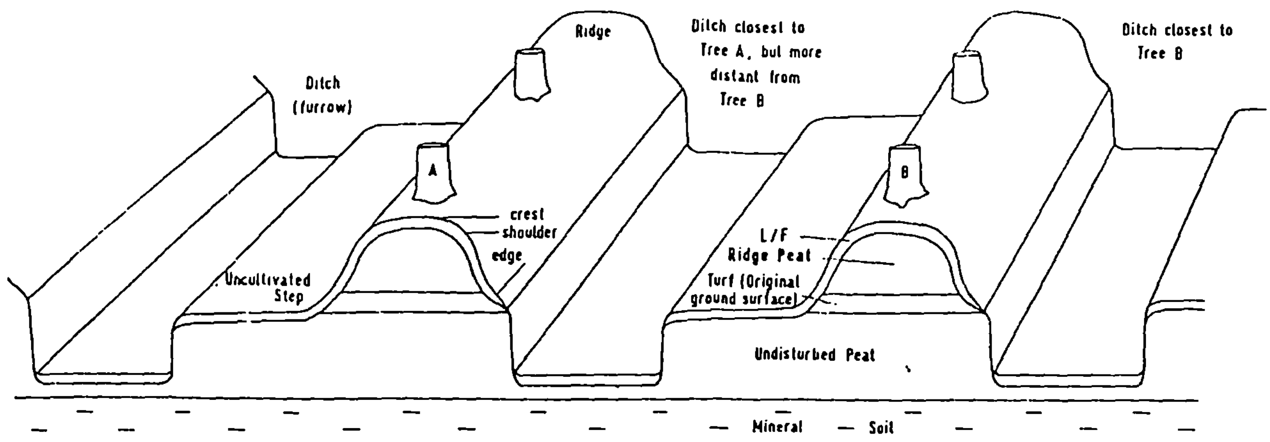
At the juvenile stage of tree growth, failure due to bending at the root or stem base leads to "toppling." As the tree continues to grow, the stem becomes permanently displaced and timber value is reduced (Burdett 1979). When trees mature, windthrow becomes much more of a serious problem, sometimes as a consequence of the initial instability caused by toppling, but more often as a result of poor soil conditions and root growth. Upland sites in much of the U.K. are seasonally waterlogged, which causes periodic dieback of root systems of trees such as Sitka spruce (*Picea sitchensis* (Bong) Carr.) and European larch (*Larix decidua* (Mill.). Sitka spruce is the main commercial forest species grown in the U.K. and European larch, a deciduous conifer, has recently become popular with foresters. Larch grows faster than Sitka spruce and allows more light to penetrate the canopy and reach the forest floor, resulting in greater ecological diversity. Both species are highly susceptible to waterlogging damage. The sinker roots grow downwards off the main horizontal lateral roots in the summer. When the water table rises in the winter, the sinker roots are killed. As a result, "shaving brush" root systems are formed, which consist of many thin, weak and decaying roots growing down off the horizontal lateral roots (Fraser and Gardiner 1968); consequently, a shallow root-soil plate forms which can easily be overturned in high winds. Attempts to reduce windthrow usually involve treatment of the site, for example by using drainage techniques to increase the depth of the root-soil plate (Saville 1976), but selection of trees with characteristics likely to promote stability has only just been investigated (Nichol *et al.* 1993). It is not known exactly what root characteristics best promote tree stability. The horizontal woody lateral roots function for anchorage and it is thought that an even distribution of these around the main axis will make the tree less vulnerable to windthrow (Coutts 1983b).

When the crowns of trees are subjected to wind, the tree stems must act as long lever arms producing high bending moments which must be counterbalanced by the root-soil moment to prevent trees from falling. In the case of mature trees such as Sitka spruce and larch growing under waterlogged conditions, the root systems are very shallow and the counterpoise root forces must be in excess of the wind loads. Therefore, trees need a rigid root system to resist turning moments transmitted by the stiff trunks aboveground. A rigid root system is achieved in two ways: by stiffening the root axis to make a tap root which will act as a place for insertion for horizontal lateral roots which act as guy ropes, and by having a plate of horizontal roots with sinkers growing down (Fitter and Ennos 1989). When these sinkers die as the water table moves upwards, the tree loses an important component of anchorage. Therefore it is important that a tree allocates enough biomass to the structural roots in order to remain upright.

For the last 40 years, most British forests have been established by transplanting young trees into ridges of soil produced by ploughing. The ridges run parallel to each other approximately 1.6 - 2 m apart (Fig. 1.1) and are separated by furrows (ditches) 15 - 30 cm deep which are created during ploughing (Deans 1983). This method of planting allows better drainage (Lees 1972), reduced competition from natural vegetation (Taylor 1970) and an increased supply of available nutrients along the ridge (Binns 1962). It has frequently been observed that horizontal lateral roots develop preferentially along the ridge rather than downwards into the furrow, probably due to the increased nutrient supply and aeration in the ridge (Zehetmayr 1954, Deans 1983, Coutts *et al.* 1990). Consequently, a highly asymmetric root system forms in most forest trees. This asymmetry might make trees prone to windthrow, as observed by Yeatman (1955). Yeatman found that Japanese larch (*Larix kaempferi*) was more susceptible to windthrow when planted on ridges aligned cross-wind than on ridges parallel with prevailing winds. Clearly, the ridge and furrow method of planting alleviates problems of plant establishment, but as the trees mature, the development of asymmetric root systems will not function so effectively for anchorage. Alternative methods of cultivation are currently being investigated, but a greater knowledge of root form and development is needed to identify the optimal characteristics to resist overturning.

Fig. 1.1

The ploughing method used to prepare a peaty gley site. The upturned peat from the ploughing is deposited next to the furrow edges rather than midway between furrows (after Deans 1983)



1.2 The root-soil system

As the trunk of a tree sways in the wind, roots must transfer the forces which the shoot experiences into the soil in order to achieve anchorage. During overturning the root-soil plate is lifted up on the windward side and tensile and shearing forces are present in the windward part of the system. On the leeward side, the roots and soil are subjected to compressive and bending forces as they bear down on the soil beneath the system. The point of bending is much nearer the stem than on the windward side (Coutts 1983a). The stronger the soil and root-soil bond, the greater the root surface area and the larger the uprooting force that can be resisted. The root surface area will be increased if either more biomass is allocated to each root, increasing radial growth, or if morphogenesis of individual roots results in increased branching. In the first case, increased radial growth of a root will increase its bending resistance. If a root is considered to be a circular cantilever beam, its stiffness is related to its second moment of area (a function of radius to the fourth power). If the beam forks into two of even size with a total cross-sectional area (CSA) of the parent, the total stiffness of the beam will be halved. Therefore, branching on the lee side of the tree will cause a substantial reduction in stiffness. The fulcrum (at which the root-soil plate is levered out of the ground) will then occur closer to the stem and stability would be reduced (Coutts 1983a). However, bending is less important on the windward side of the tree, as roots are held in tension and bending occurs further away from the stem. A higher incidence of branching would increase the sum of the root surface area because a higher concentration of roots per unit volume of soil increases the tensile strength of the soil (Wu 1976). However, if there is a very large amount of highly branched roots present in the soil, the root-soil resistance (R_{rs}) will exceed the tensile strength of the soil. The whole mass will behave as a unit of fibre-reinforced matrix (Waldron & Dakessian 1981). If R_{rs} is greater than the soil strength, horizontal strain will cause fracture of the soil because of its low elasticity. After soil fracture, if a force is applied to the proximal end of the root, the root will break distal to the soil fracture and project from the sheared soil. The amount of root material in the soil required to increase R_{rs} to equal the soil strength is termed the critical rooting density (CRD). The CRD is modified by soil factors which influence the root-soil bond and during overturning will largely determine the distance between the main axis and fracture of soil and roots in the windward side.

The tensile strength of soil is 3 - 5 orders of magnitude weaker than that of roots under tension (Coutts 1983a). The shear strength of soils decreases with increasing moisture content and increases with stress normal to the shear plane. In winter, the peaty gley on which much Sitka spruce and larch are planted, becomes so wet that shear values at or near saturation point tend to be an order of magnitude larger than the tensile strength (Coutts 1983a). Root slippage through saturated soil is an important reinforcement factor. In clay soil, roots do not break, but pull out (Waldron 1977) and R_{rs} is determined by the soil rather than root morphology or strength. On saturated peaty gleys, some roots may slip out in tension while others break.

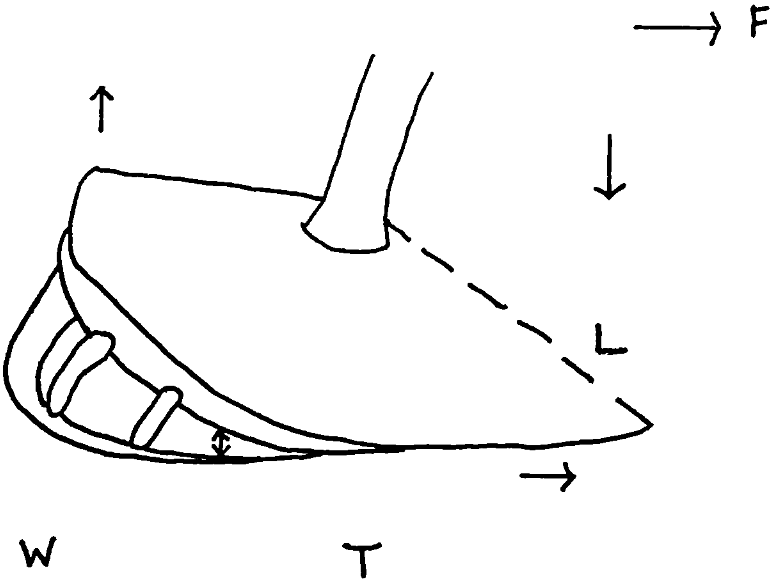
1.2.1 Components of root anchorage

Coutts (1983a, 1986) measured the forces involved in anchorage of shallowly rooted Sitka spruce, by measuring the turning moment during displacement of the root-soil plate when pulling mature trees with a winch attached to the stem. Then by sequentially cutting or breaking the roots and soil, the total resistive turning moment of the anchorage system was split into four components (Fig. 1.2): resistance to uprooting by soil underneath and at the sides of the plate, the weight of the plate, the resistance of leeward roots to bending and the resistance of windward roots in tension. The most important component in resisting uprooting when applied forces were maximal was resistance from windward roots held in tension (54 %). Other factors contributing to resistance included the weight of the root-soil plate (31 %), the bending of roots at the leeward hinge (8 %) and finally, soil resistance underneath and at the edges of the plate (7 %) (Coutts 1986). In two non-woody species (*Impatiens glandulifera* and *Helianthus annuus*), Ennos *et al.* (1993) found that the windward roots again provided the most resistance to uprooting.

Coutts (1986) recognized the need for identifying and measuring the different components of anchorage. Once understood, it is easier to assess those parts of the root system most sensitive to manipulation. Characteristics which influence tree stability might possibly be selected for.

Fig 1.2

Components of anchorage of Sitka spruce on a peaty gley soil
(after Coutts 1983b, 1986)



Where:

F = horizontal force of wind
W = Fracture of root-soil plate on windward edge
T = Centre of tree stem
L = Hinge on lee side

1.3 Tree response to wind

The growth of woody roots, which function for anchorage, is influenced by a number of internal and environmental factors (Coutts 1987). Mechanical stresses such as those induced by wind action (Hintikka 1972) must affect the activity of the root cambium since there is an increase in diameter growth when roots are stimulated (Jacobs 1954, Fayle 1968, 1976, Wilson 1975). The forest industry needs to know if comparable effects also take place underground, where the tree is anchored. Jacobs (1954) attached guy ropes to the stems of young *Pinus radiata* so that only the tops of the trees would sway. The diameter of the guyed stems was greater than the controls above the point of attachment, but smaller below. After two years, the ropes were removed and in the first high wind, all the stems broke or blew over. Jacobs also found that guyed trees had thinner roots. Fayle (1968) repeated this experiment on *Pinus sylvestris* saplings. After two years, the lateral roots of free-standing trees showed a 75 % increase in their annual ring widths when compared to the guyed trees.

Mechanical stimulation has been most thoroughly researched in the aboveground parts of plants (see Telewski 1993). The term "thigmomorphogenesis" was coined by Jaffe (1973) to describe the phenomenon in which mechanical stresses influence plant organogenesis. Wind action induces developmental changes in trees, resulting in a more compact form, with increased stem taper, shorter branches and smaller leaves (Heiligmann & Schneider 1974, Rees & Grace 1980, Telewski & Jaffe 1986a,b).

Mechanical perturbation can result in two types of responses in plants, primary and secondary effects (Telewski 1993). The direct effects include the mechanical movement of the tree resulting in displacement of the stem and failure of the stem or roots, the fluttering of leaves and branches. The influence of gravity due to wind-induced lean and changes in the atmospheric conditions around leaves are known as secondary stresses. As wind velocities increase, so do the resulting strains, resulting in many and varied physiological responses. Foliage is swept away from the direction of a prevailing wind, causing the clustering of leaves on the lee side. This clustering results in a decrease in effective photosynthetic area and so net photosynthesis may be reduced (Vogel 1989). Leaves rubbing together can result in the mechanical abrasion of young foliage, and at higher windspeeds leaves may become distorted and torn, causing water stress (Wilson 1980, 1984, Van Gardingen & Grace 1991). Wind can also increase the uptake of airborne pollutants, such as SO_2 (Hoad *et al.* 1993).

Wind is known to reduce leaf area (Heiligmann & Schneider 1974, Flückiger *et al.* 1978, Rees & Grace 1980). It was originally thought that a reduction in leaf size was due to water stress caused by an increase in transpiration, leading to dehydration, but studies have shown that there is no direct effect of wind on stomatal conductance (see Dixon & Grace 1984). Responses of plants to wind action and shaking, flexing (movement in two directions only), brushing or rubbing are similar. Reduced foliar enlargement is one of the most consistent responses of plants to mechanical perturbation, so is considered a direct thigmomorphogenetic response. The mechanism by which it occurs is discussed in section 1.4.

When a tree is blown by the wind, it sways backwards and forwards and the wind velocity determines the displacement of the stem. If wind loading forces have not exceeded the strength of the tree, the tree will return to the vertical once the wind has stopped. However, if the stem does not return to the vertical, due to prolonged exposure to the wind, failure of the system *i.e.* windthrow or windsnap, may occur. In order to induce a response in the tree, it must be allowed to return, as far as possible, to the vertical. The tree must be stressed for a certain length of time, known as the "presentation time" in order to induce a response (Telewski 1993). If trees are allowed to return to the vertical after a period of swaying, the wind-induced response in gymnosperm stems is the formation of eccentric woody growth, known as "flexure" wood, on the lee side of the tree (Larson 1965, Telewski 1989). Flexure wood results from an increase in the number of tracheids (Quirk *et al.* 1975, Telewski & Jaffe 1986a,b, Telewski 1989) which alters the internal compressional strain. Flexure wood has also been observed at branch bases and at the branch nodes of flexed trees (Telewski & Jaffe 1986a). However, if a tree is subjected to prolonged displacement, "reaction" wood also forms on the leeward side of wind-stressed gymnosperms (see Boyd 1977, 1985, Wilson & Archer, 1977, Telewski 1990). Reaction wood consists of a different type of cell to normal wood. The cells are reddish in colour and rounded with heavily lignified cell walls and intercellular spaces between the cells. Chain-saw blades have been known to jam on reaction wood because of its toughness. The formation of eccentric growth and reaction wood allows the displaced tree to return to the vertical, hence maximising effective photosynthetic leaf area as far as possible. The mechanisms of perception which can induce such changes in woody growth are unclear, however, researchers working in different fields have provided some clues as to the signals involved in the stimulation of secondary growth.

1.4 What is the mechanism?

The mechanism by which plants sense movement is not fully understood. It has been thought that the signal might consist of a series of electrical impulses. Researchers (for review see Siboaka 1969) studying the movement of the trap in Venus fly trap (*Dionaea muscipula*) found that each time a trigger hair in the lobe was touched, it produced a localised receptor potential in sensor cells which fires an action potential (a wave of electrical activity). If a second hair was touched, a second action potential was fired and then the trap shut. The action potentials were produced by currents of calcium ions (Ca^{2+}) which flux rapidly into the sensory cells. Action potentials travel through the cells *via* plasmodesmata in the cell walls at a rate of about 2 cm s^{-1}. An efflux of potassium ions K^+ and possibly chloride (Cl^{2-}) ions appears to sustain the action potential as it travels through the cells (see Siboaka 1969).

Touch sensitive movements in plants occur in over 1000 species, spread across 17 families of flowering plants. These plants too probably depend on electrical impulses (Simons 1992). If touch-sensitive plants, such as the venus fly-trap and sensitive plant (*Mimosa pudica*) use electrical impulses to relay mechanical stimulation, then "ordinary" plants may well use the same mechanisms. Studies described in the previous section show that trees can respond to mechanical stimulation. It is possible that this signal is a series of electrical impulses, as suggested by Asher (1968), but much more work would have to be carried out to confirm this; it seems more likely that a chemical signal is involved.

Braams & Davis (1990) found that *Arabidopsis* leaves and stems respond to touch by switching on at least four separate genes in shoot cells. Three of the genes encode calmodulin and calmodulin related proteins. Calmodulin is the primary intracellular receptor and functions to mediate cellular responses to fluxes in Ca^{2+} ions (see Cheung 1980). Calmodulin binds Ca^{2+} and is activated to interact with a large number of enzymes. Ca^{2+} is probably a second messenger in plant cells and has been implicated in plant processes such as cytoplasmic streaming, cell growth, nastic movements and photosynthesis (see Marmé & Dieter 1983). Calmodulin may act as a molecular switch, converting the Ca^{2+} into a more complex set of signals in the plant (Simons 1992).

Ca^{2+} has recently been thought to be involved in thigmomorphogenesis. Knight *et al.* (1991) inserted the gene for a Jellyfish molecule called Aequorin into genetically engineered tobacco seedlings. Aequorin luminesces in response to Ca^{2+} ions. They reported that each time the plants were touched, a burst of luminescence was fired off, suggesting that Ca^{2+} ions were being released inside the plant cells. It is not known why Ca^{2+} is released on touch. One theory is that inositol phospholipids are hydrolysed, a mechanism common in animal cells (Berridge & Irving 1984). An alternative and more researched theory is that mechanical stimulation directly causes a cytoplasmic Ca^{2+} influx. Stretch-activated ion channels in the protoplasts of cultured cells of tobacco stem pith facilitate the transport of Ca^{2+} across cell membranes (Edwards & Pickard 1987). It appears that these mechanotransductive channels are sensistive to mechanical stimuli. Cosgrave & Hedrich (1991) discovered that these stretch-sensitive channels are involved in the opening and closing of stomata. Three types of channels were observed, specific for Cl^{2-}, K^{+} and Ca^{2+} in the stomata of *Phaseolus vulgaris*. It has been suggested that these stretch-sensitive sensors induce the closure of stomata as leaves rub against each other on a windy day (Blatt 1991, Simons 1992).

Increased ethylene synthesis is the result of higher levels of Ca^{2+} in the cytosol (Pickard 1984) and levels of ethylene are known to increase under mechanical stimulation (Brown & Leopold 1973, Biro & Jaffe 1984, De Jaegher *et al.* 1987). An increase in cytosolic Ca^{2+} is also associated with callose formation (Kauss 1987). The most immediate physiological response to mechanical flexure in *Phaseolus vulgaris* is a reduction in the rate of translocation of photosynthate in the phloem, occurring almost simultaneously with the formation of callose plugs in the phloem (Jaffe & Telewski 1984). In mechanically perturbed *Pinus taeda*, the rate of callose deposition in the phloem almost parallels the response of *Phaseolus vulgaris* (Jaffe & Telewski 1984, Telewski & Jaffe 1986c). The formation of callose plugs can be inhibited by treatment with the compound 2-deoxy-D-glucose (DDG) (Jaffe & Telewski 1984). DDG was found to block stem radial growth of mechanically perturbed *P. vulgaris* but did not completely block ethylene formation. Therefore, callose deposition appears to be only a *part* of the causal mechanism of ethylene biosynthesis.

The release of ethylene in mechanically stressed plants has been seen to peak some hours after flexure began, suggesting a lag period exists when ethylene is synthesized. In glasshouse grown seedlings of *Pinus taeda* which had never been stressed before, levels of ethylene peaked 15 hours after flexure began (Jaffe & Telewski 1984). In preconditioned seedlings (had already been subjected to flexing), less ethylene was produced, suggesting a physiological adaptation to mechanical stress (Telewski & Jaffe 1986c).

Ethylene is a known growth regulator of cambial activity (Little & Savidge 1987, Roberts *et al.* 1988, Savidge 1988). If ethylene is applied as Ethrel (an ethylene generating solution) to *Pinus taeda*, ethylene production per unit area, of vascular cambium correlated negatively with wood density and positively with stem diameter (Telewski 1990). Ethrel application also stimulates cell enlargement radially and inhibits cell extension (Barker 1979, Wakefield & Jaffe 1983, Telewski & Jaffe 1986c). The biosynthetic precursor of ethylene is 1-Aminocyclopropanecarboxylic acid (ACC). ACC has been induced in *P. vulgaris* by mechanical perturbation and also observed in the reaction wood of *Pinus contorta* (Savidge 1983). When ACC was applied to *P. vulgaris* stems, radial growth was increased and elongation decreased.

Ethylene production can also be stimulated by indole-3-acetic acid (auxin) (see Jacobs 1979). Larson (1965) suggested that the increased taper observed in wind stressed

Larix laricina stems might be due to an increased downwards shift of assimilates under the influence of auxin concentrations. Reaction wood in compression has been induced by the application of supraoptimal concentrations of auxins (Onaka 1940, see Timell 1986). Fayle (1968) applied auxin to woody roots of *Pinus sylvestris*. Reaction wood did not form, but cambial activity was increased, as occurs in shoots when stimulated by auxin (Wareing *et al.* 1964). However, reaction wood in tension appears to be stimulated by a deficiency of auxin (see Timell 1986). Ethylene is a known blocker of auxin transport and may function to alter the local concentration of auxin in the cambial zone during stimulation (see Telewski 1993).

Ethylene appears to be the main stimulant of thigmomorphogenetic responses in plants, but may also interact with auxins to alter cambial activity. Mechanical stimulation must trigger a signal to start the cascade of reactions involved in the synthesis of ethylene and perhaps auxin. It might be assumed that this signal is transmitted down to the roots, or triggered in the roots, where there may be an increase in ethylene production at the root bases in the stressed areas. Higher levels of ethylene could stimulate radial growth of roots which would in turn have consequences for tree stability.

1.5 Biomechanical properties

The morphological changes which occur in wind-stressed trees result in a more streamlined, flag-shaped tree which has the effect of reducing speed-specific drag of the crown (Telewski & Jaffe 1986a). A shorter, sturdier tree results, which is less likely to fail under windy conditions (King 1986, Telewski & Jaffe 1986a,b, Holbrook & Putz 1989). Anatomical and morphological changes in the woody stem will influence the biomechanical properties. If a stem is considered to be a circular cantilever beam, a shorter, wider one should be able to resist overturning better than a longer, thinner one. The flexural stiffness of a beam (EI) is the product of Young's modulus of elasticity (E) and the second moment of area (I). The flexural stiffness of a stem or a root can be increased by increasing I (a function of radius to the fourth power) or by increasing E. However, E was found to decrease in stems of flexed *Abies fraseri* and *Pinus taeda* (Telewski & Jaffe 1986a,b). The increase in stem radial growth caused by mechanical stimulation was thought to override the increase in elasticity caused by decreased E. Therefore, changes in stem allometry may account for changes in biomechanical properties.

If the shape and size of the stem alters biomechanical properties, so would the shape of a root alter its strength, as discussed earlier. Wind-stressed plants might develop roots which increase in radial growth, as already suggested by Jacobs (1954), Fayle (1968, 1975) and Wilson (1975). Further changes in root development may occur which would enhance anchorage strength. Root architecture and uprooting strength of flexed plants has only been measured in one study (B.L. Gartner 1993, unpub.). No differences in root growth or anchorage strength were found between flexed and unflexed *Lycopersicum esculentum* (tomato). However, the plants were only flexed for 60 seconds a day for six weeks, so the presentation time may have been too short.

It seems likely that changes in root development of wind-stressed plants might occur. Secondary thickening in the stem is continuous with that in the top lateral roots, so an increase in stem radial growth may be reflected in root growth. This in turn would influence the resistance to bending of the roots and hence improve anchorage strength. A detailed analysis of root growth in mechanically perturbed plants is needed to identify the changes, if any, which occur. Characteristics which enhance stability might then be manipulated and selected for.

1.6 Optimization of tree growth

One of the most consistent responses of mechanically perturbed trees is the laying down of wood in areas of mechanical stress (Larson 1965, Quirk *et al.* 1975, Telewski & Jaffe 1986a,b) which has been observed as early as 1908 (Metzger). Metzger (1908) proposed that cambial activity is affected by stretching and compression of the tree trunk. Over 80 years later, his hypothesis was verified. Telewski (1989, 1990) found that in the stems of *Abies fraseri* and *Pinus taeda*, flexure stress stimulated an increase in the average growth ring density and also in the ratio of cell wall area to cell lumen area compared to control trees. Flexure stress must be inducing the production of a greater mass of xylem per cm^2 of cambial surface area.

If new wood is laid down faster in areas of high mechanical stress, the rigidity of that area increases, thus reducing the stress to which it was first subjected (Mattheck 1991). Hence, when applied to the whole of a tree, the tree will experience the same maximum stress all over its surface, resulting in a tree with a constant surface stress (Wilson & Archer 1979). This "constant stress hypothesis" has yet to be proven experimentally, but would help explain the cause of localised woody growth in trees, such as the swelling around wounds and branch joints (Mattheck 1991) and the formation of buttress roots (Ennos 1993a). Root buttresses frequently form in lowland tropical rainforest trees. They are found around the base of a tree, each one being a plate-like woody growth on the upward side of a lateral root. As most trees must resist uprooting by the wind, roots must transmit bending and compression forces into the ground. Without buttresses, the leeward roots will experience much larger bending forces and possibly fail under loading. When buttress roots are present, they are able to transmit tension to windward sinkers and compression to leeward sinkers much more smoothly. Therefore, buttresses act as mechanical props and provide a very efficient means of holding up a tree (Ennos 1993a, Mattheck 1993). The constant stress hypothesis also suggests that mechanically perturbed tree roots increase their radial growth at the root base so that forces can be transmitted more smoothly into the soil. There is strong evidence to support the constant stress hypothesis, but it needs to be experimentally verified. If a relationship between mechanical stimulation and extra woody growth can be elucidated, the mechanism by which it occurs may be further understood.

1.7 Aims of this thesis

This thesis aims to investigate some of the missing areas of knowledge regarding responses of young trees to mechanical stimulation. In particular, the changes in root systems of young Sitka spruce and European larch exposed to wind stress will be examined, with emphasis on the influence any such changes might have on tree stability and whether any responses to wind could be viewed as adaptive. Anchorage tests where young trees are deflected with a spring balance or measuring device will be carried out to determine if wind action has an effect on the resistance to overturning in young trees. Ideally, such experiments should be done on large trees, but it is difficult to work with mature trees. However, since the main lateral roots of a mature tree develop early on in life (Coutts 1983b), the roots laid down by a seedling will determine the structure of the mature system. Experimentation on young trees can therefore be a realistic experimental model.

If changes in root architecture occur due to mechanical stress, can they be modelled to illustrate optimal rooting characteristics in terms of anchorage strength? Trees with characteristics likely to promote stability may be selected for in breeding programmes, but it is necessary to identify those characteristics first. Both these possibilities will be investigated in later chapters of the thesis, and discussed in Chapter 7.

Chapter 2

The effects of wind action on young Sitka spruce and European larch

2.1 Introduction

Wind action on plants represents a physical perturbation, and yet only a few wind tunnel studies exist in which trees have been subjected to wind from an early age (*e.g.* Heiligmann & Schneider 1974, Rees & Grace 1980, Telewski & Jaffe 1986a). Most research into thigmomorphogenesis - plant growth responses to mechanical perturbation, has concentrated on flexing or shaking (Jacobs 1939, Jaffe 1973, Telewski 1990). This is an artificial and often unrealistic way to mimic changes in a plant exposed to wind. The stimulation has often been rubbing plant stems between finger and thumb, which could in itself damage plant tissue. Flexing or shaking plants is usually concentrated at the same rate in a number of directions so the stresses around a plant are very even. The movement of air around plants *e.g.* in a wind tunnel, appears to be a more natural way to perturb plants. Wind tunnels provide a stream of unidirectional air which mimics the effect of a prevailing wind. Wind tunnels are also known to create eddies and produce uneven airflow around objects in the tunnel. A relatively turbulent zone forms immediately downstream of the canopy some containing reverse flow (Ruck & Schmitt 1986). The flow of air through a wind tunnel causes trees to sway. When a tree bends over, it stores energy (elastic or potential energy) which it releases on the back swing. The tree then sways back and forth at a "natural" frequency, which for a conifer 15 metres tall is every 2 to 3 seconds (Milne 1988). For a very young tree, the natural frequency will be much reduced.

Wind or other mechanical perturbations typically increase stem radial growth and retard stem, branch and leaf elongation (Jacobs 1954, Neel & Harris 1971, Jaffe 1973, Telewski & Jaffe 1986a,b). In wind-stressed gymnosperms extra wood and reaction wood form on the lee side of the tree (Larson 1965, see Boyd 1977), which corrects the deflection of the stem. The plant is therefore more likely to stand upright. Only two wind tunnel studies refer to root growth. Satoo (1962) observed growth reductions in root length and shoot and root dry weight of *Robinia pseudoacacia* seedlings exposed to continuous wind velocities of 3.6 m s^{-1} (8.1 mph) for four weeks compared to control plants which received no wind. Heiligmann and Schneider (1974) found that shoot and root dry weight was decreased when *Juglans nigra* was grown at windspeeds of 2.8 m s^{-1} (6.3 mph). In both studies, root and shoot growth were equally affected *i.e.* there were no direct effects on root growth. The changes were interpreted as detrimental because wind reduced total plant growth, however, as discussed in Chapter 1, a smaller plant would be more stable under windy conditions. Both these wind tunnel studies used relatively fast continuous windspeeds, unlike field conditions, where windspeeds can be low or zero for extended periods. On the Beaufort Scale, where 0 = calm (< 1 mph) and 12 = storm (> 72 mph), the wind loading experienced by the plants in the two studies was of a magnitude of 3 and 2, respectively, equivalent to a light wind. Telewski (1993) has found that plants do not respond to continuous wind in the same way as when the wind is applied and stopped periodically; far greater responses occur when plants are stressed over several intervals rather than continuously.

In this investigation, young trees were grown from seed in a wind tunnel and the wind was intermittent in order to determine whether effects on plants occur under more realistic wind conditions, whether there are any specific effects of wind on root growth, and whether any responses to wind could be viewed as adaptive in a similar fashion to those occurring in stems under wind loading. Ideally, such experiments should be done on large trees, but this would be difficult to accomplish in practice. However, since the lateral roots of a mature tree develop early in its life, the roots laid down by a seedling tree largely determine the structure of the mature system (Coutts 1983b). Experimentation on young trees can therefore be a realistic model.

2.2 Materials and Methods

2.2.1 Growth Conditions

A wind tunnel, consisting of a dexion frame with polythene sides, 3 m long, 1 m wide and 1 m high was erected in a heated, lit glasshouse alongside a south facing window (Fig. 2.1). Three wind generators, consisting of fans placed at the end of plastic tubes, 10 cm in diameter x 100 cm long, were placed at one end of the tunnel. The wind generators were operated from 10.00 to 16.00 and 22.00 to 04.00. Windspeeds were measured before planting on 6 March 1991 using an anemometer at ground level in each plant pot (Fig. 2.2).

Seed of Sitka spruce (lot no. 83{1012}Q.C.I.) and European larch (lot no. 87{430}837 03 lot 3) were stratified at 4°C for 4 weeks. Seeds were sown on 6 March 1991 in the centre of 13.5 l capacity plastic polythene pots filled with Irish Shamrock peat, mixed with 2 g l^{-1} Osmocote Plus 8-9 month formulation slow release fertilizer, (N P K, 16.18.12 + 2 MgO). Twenty-four pots of each species were placed in the wind tunnel as 6 columns x 4 rows of pots. Each row was a specified distance from the wind-generators and contained two pots per species placed alternately. After 27 days, the seedlings were thinned out to one per pot.

2.2.2 Anchorage Tests

Anchorage was investigated quantitatively by measuring the deflection of the stem in two places when young Sitka spruce plants were pulled in a horizontal direction at a given fixed force, before each plant was harvested on 3 October 1991. A spring balance was hooked around the stem 45 cm above ground level (where possible) and the tree slowly pulled horizontally until a force of 20 N measured on the spring balance had been reached. The deflection of the stem at 45 cm was measured on a ruler positioned behind the stem (Fig. 2.3). The test was then repeated with the spring balance hooked halfway up the stem and the deflection measured at this point. Each tree was pulled over in four directions: to windward; to leeward, to shaded and unshaded quadrants. The order in which they were pulled was random.

Fig 2.1

Design of the wind tunnel.

Three generators are positioned at one end, and Sitka spruce and European larch are placed alternately in the wind tunnel.

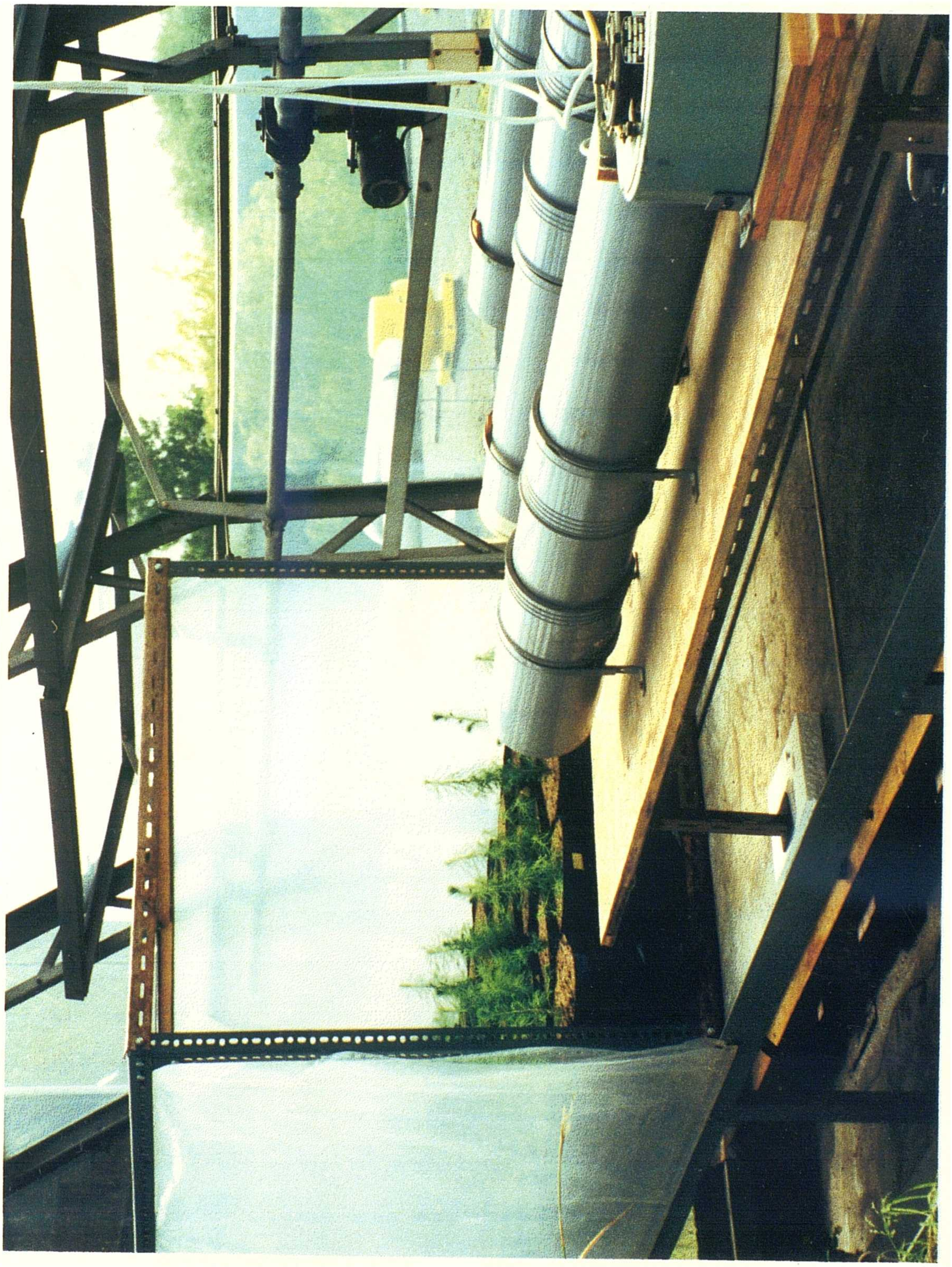
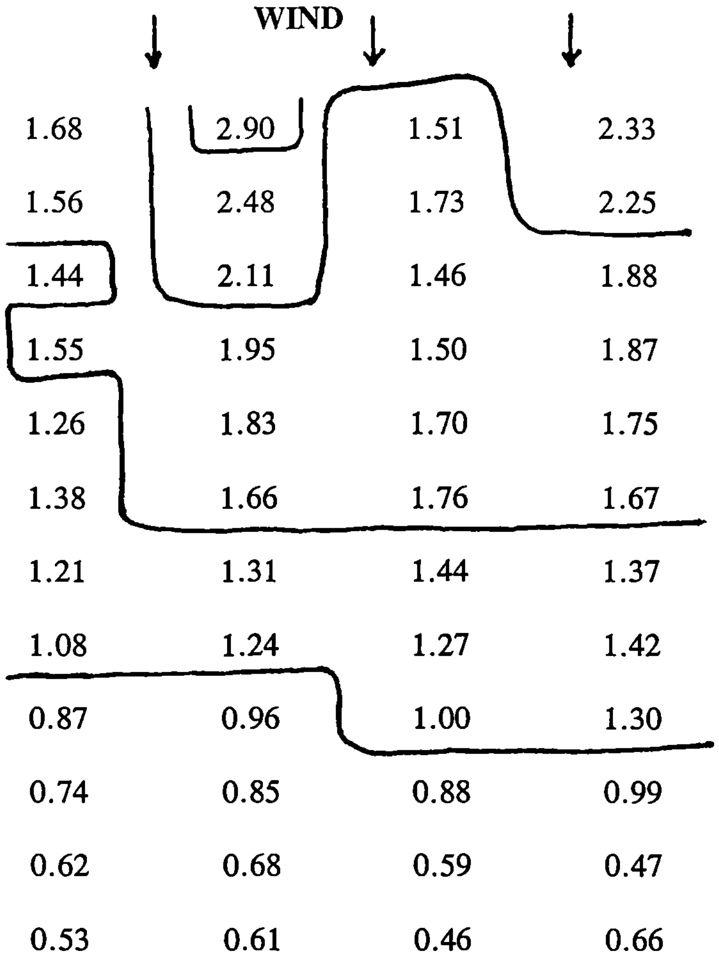


Fig. 2.2

Map of windspeeds (m s^{-1}) for each plant at ground level



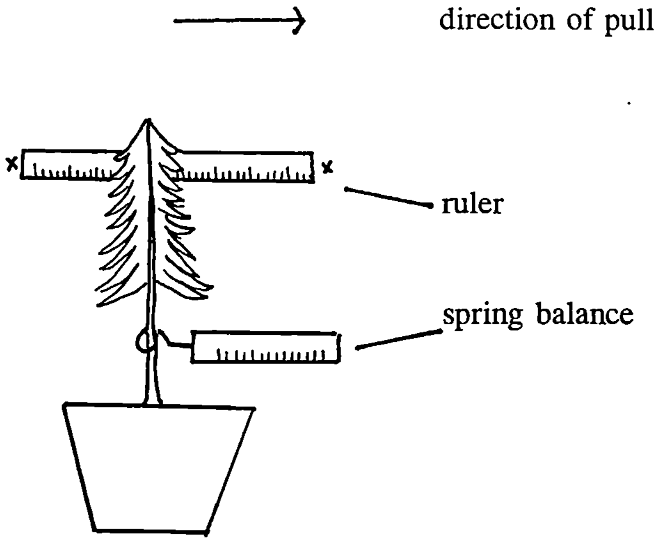
1.68	2.90	1.51	2.33
1.56	2.48	1.73	2.25
1.44	2.11	1.46	1.88
1.55	1.95	1.50	1.87
1.26	1.83	1.70	1.75
1.38	1.66	1.76	1.67
1.21	1.31	1.44	1.37
1.08	1.24	1.27	1.42
0.87	0.96	1.00	1.30
0.74	0.85	0.88	0.99
0.62	0.68	0.59	0.47
0.53	0.61	0.46	0.66

Contour lines show the unequal flow of wind through the tunnel. Windspeeds (m s^{-1}) are divided into the following ranks:

0.50 - 1.00
1.10 - 1.50
1.51 - 2.00
2.10 - 2.50
2.51 - 3.00

Fig. 2.3

Apparatus for measuring deflection of young Sitka spruce at a given force



Trees were pulled halfway up tree and at 45 cm up tree.

2.2.3 Harvest of Plants

Stem length and stem basal diameter were measured every six weeks and the experiment was harvested after 30 weeks growth. Stem length and stem basal diameter were measured for each plant. Basal diameter was measured at ground level in two directions: along the axis of the wind direction and perpendicular to it, so that any eccentric growth occurring in the stem could be investigated. Larch needles were taken from the windward and leeward sides of the the middle of the stem and their length measured. Larch stems were sectioned at ground level and the length from the biological centre to the furthermost point on the perimeter of the bark on that side of the stem was measured with a graticule under a dissecting microscope at x 6 magnification.

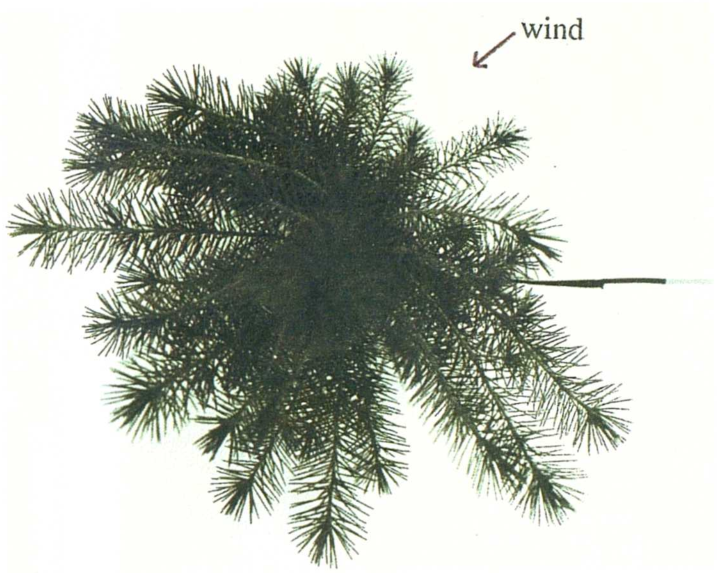
Measurements of photosynthetically active radiation (PAR) showed that the canopy received approximately 50 % less light on the side away from the south-facing window than towards it. Values of PAR lay in the ranges 1600 - 4500 μmol m^{-2} s^{-1} (towards the south-facing window) and 600 - 300 μmol m^{-2} s^{-1} (away from the window). Shoot growth of both Sitka spruce and larch had deflected away from the wind and also towards the south-facing window and it appeared root growth was following a similar pattern. To analyse this deformation, photos were taken of shoots and washed root systems against a white background (Fig. 2.4a,b). The photographs indicate which way the canopies and root systems had developed in each plant because although the point of attachment of a branch or root may be on one side of a stem, that branch or root may curl around the stem and be growing on the opposite side to its origin. In larch, each plant was divided into two halves around the central axis: shaded (away from the window) and unshaded (adjacent to the window) (Fig 2.5a). The plants were then divided into halves perpendicular to the first two: windward and leeward, so that the amount of shoot flagging (deflection of branches away from the wind) could be measured (Fig. 2.5b). A more accurate method of determining how canopy and root cover is altered by environmental gradients may be to divide each plant into quadrants around the central axis: windward (45°-134°), shaded (away from the south-facing window: 135°-224°), leeward (225°-314°)and unshaded (next to the window: 315°-44°) (Fig. 2.5c). The photographs of Sitka spruce were divided in this way. The proportion of canopy and root cover in each sector of the plant was quantified using a Joyce Loebl Magiscan II image analysis machine, as the area covered by an object's silhouette on the screen.

The following components of the root system were measured: lateral root basal diameter (using vernier callipers), number and azimuth of the tap-root (using a protractor), where 0° is south, and depth below the soil surface. This was measured for roots > 2 mm diameter at the base as these were considered the most important for anchorage. In Sitka spruce the lateral roots < 2 mm diameter at the base were also measured to find out if root initiation had been affected by wind stresses. The fine roots were stripped off the woody lateral roots and a random selection of 88 lateral roots of 24 Sitka spruce plants was taken from the top 2 cm of soil and retained for architectural analysis. The shoots of both species, the whole root systems of larch and all the individual roots of Sitka spruce separated into fine and woody components were dried at 80°C for three days and dry mass recorded.

Fig. 2.4 (a & b)

Silhouettes of a shoot and washed root system of Sitka spruce

a) Shoot system



b) Root system

2.2.4 Architectural Analysis

The 88 lateral roots of Sitka spruce retained for architectural analysis were compared with thirty Sitka spruce root systems of the same age grown in the same glasshouse, but not in the wind tunnel. Three architectural variables were measured: topology, link (branch) length and the diameter of the middle of each link (Fitter 1991). The latter two variables were measured using vernier callipers.

The following parameters were then calculated:

- magnitude (μ): number of exterior links;
- altitude (a): number of links in the longest unique path from the base link to an exterior link;

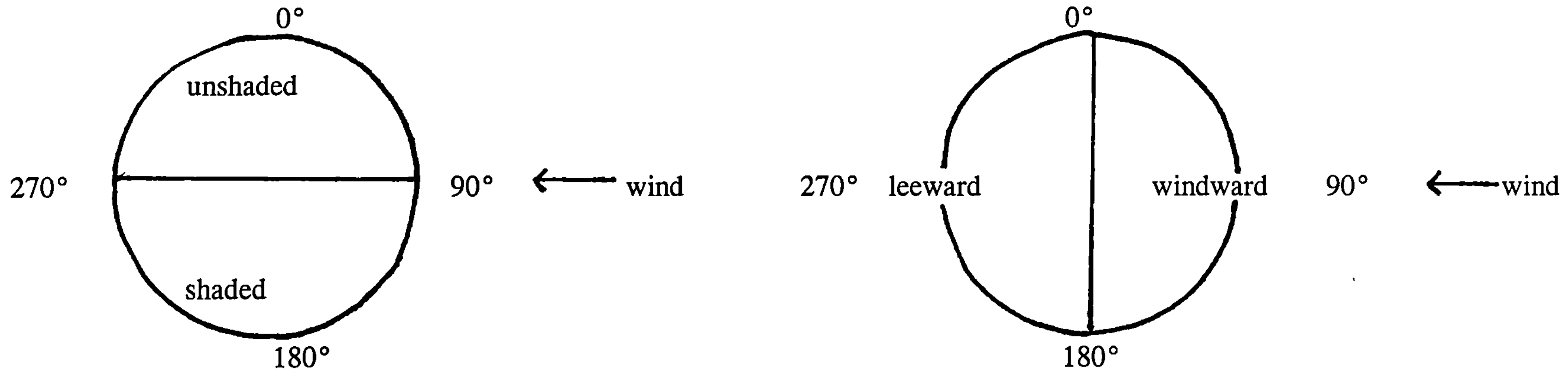
A topological index was then calculated from this parameter:

- altitude-slope: the slope of the regression of $\log_{10}a$ on $\log_{10}\mu$ for a set of roots.

High values of this index represent a root with a "herringbone" structure, where branching is mainly confined to a single axis (Fig. 2.6a). Low values of this index represent a dichotomous pattern, where there are always two exterior links at the end of an interior link (Fig. 2.6b). Both types of root system are extreme and most root systems have more or less random branching patterns with a value between the two.

Fig. 2.5 (a & b)

Division of silhouettes into regions so that canopy and root cover could be quantified



a) European larch

b)

Fig. 2.5 (continued)

Division of silhouettes into regions so that canopy and root cover could be quantified

c) Sitka spruce

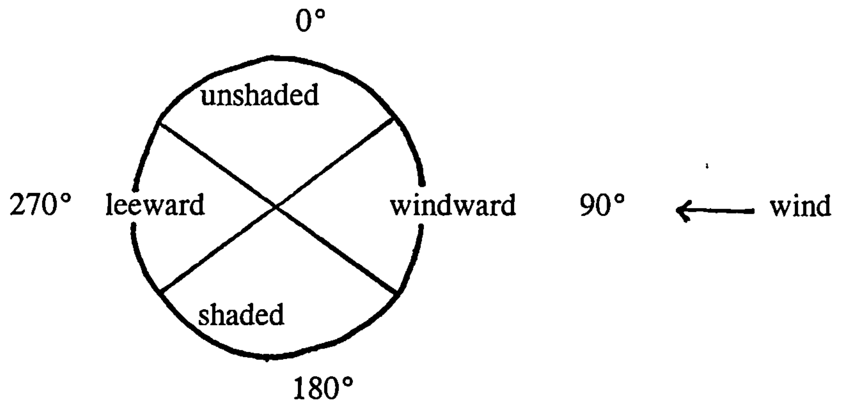
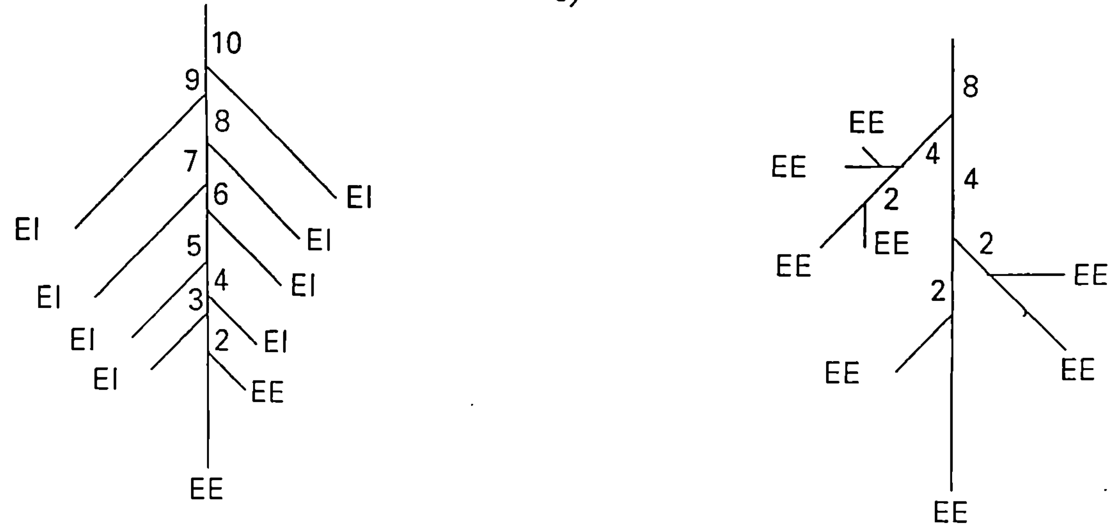


Fig. 2.6 (a & b)

Herringbone and dichotomous root branching patterns (after Fitter & Stickland 1991)

a)

b)



Where:

magnitude is the number next to the links

EI = exterior - interior link

EE = exterior - exterior link

unlabelled links are interior

2.3 Results

2.3.1 Anchorage Tests

Analysis of variance of the deflection of wind-stressed Sitka spruce stems (at 45 cm above ground and halfway up the stem) between quadrants, using stem height and basal diameter as covariates, showed no differences in the amount of resistance to overturning in any direction. The mean stem deflection of Sitka spruce in any one direction 45 cm up the stem was 7.5 ± 5.11 cm and halfway up the stem was 4.9 ± 2.64 cm for a fixed overturning force of 20 N. The mean height of Sitka spruce was 40.1 ± 8.6 cm.

2.3.2 Plant Performance

Windspeeds in the tunnel were measured the day before harvesting (2 October 1991). Plants at the far end of the tunnel were experiencing windspeeds of only 0.01 - 0.05 m s^{-1}, whereas the two rows of trees in front of the generators were subjected to the same windspeeds as those at the beginning of the experiment. Therefore, as the plants grew, canopy started to shelter the trees immediately behind the first two rows, thereby causing a much steeper gradient of windspeeds in the tunnel.

Windspeed did not affect stem length, stem basal diameter and shoot or root biomass of either Sitka spruce or larch as determined by regressions of these variables on wind velocity. However, there was a significant overall increase in wood formation on the leeward side of the biological centre (Fig. 2.7, Table 2.1). Under high wind velocities the increase was greater, but not quite significant when the difference between windward and leeward stem radii was plotted against windspeed ($R^2 = 0.15$, $P = 0.083$). Reaction wood was present on the leeward side in 7 of the 24 stems (Fig. 2.7). Needle length was significantly decreased by 7% ($P = 0.033$) on the windward side of larch stems (Table 2.1). The difference between the leeward and windward needles increased with windspeed (Fig. 2.8, $R^2 = 0.26$, $P = 0.038$).

Analysis of variance was used to determine the difference between the quadrants in proportions of canopy and root cover, using an arc-sine square root transformation. The canopy cover for larch was greatest in the unshaded half of the plant, where it was

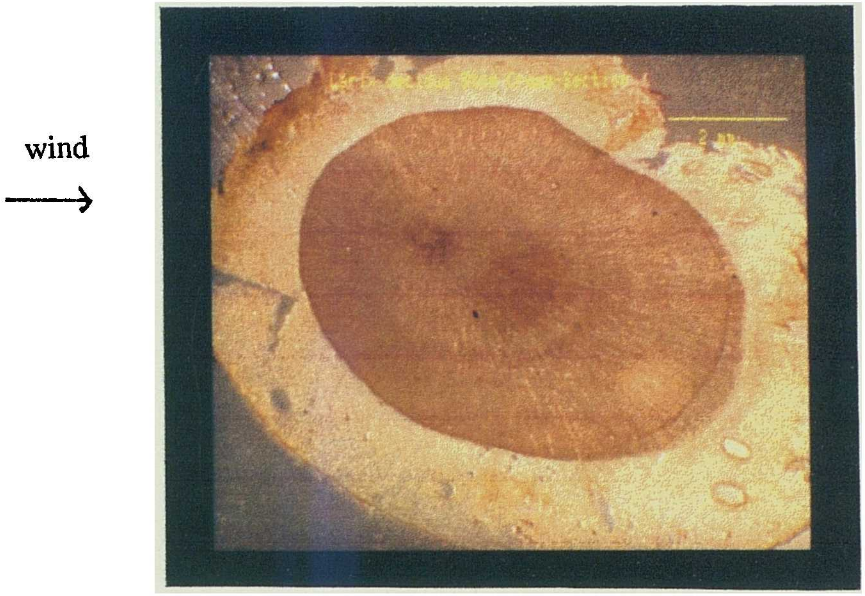
Table 2.1

Two sample T-Test - means of needle length and cross-sectional stem radius (mm) on windward and leeward sides of European larch

	Plant Region				
	Windward (0°-180°)	**Leeward (180°-360°)**	**df**	**P**	**T value**
Mean radius (from biological centre)	30.7	41.5	32	< 0.001	3.76
Mean needle length	4.9	5.3	26	0.033	2.26

Fig. 2.7

Extra wood formation and presence of reaction wood on the leeward side of wind stressed European larch stems



Reaction wood is reddish in colour (x 200).

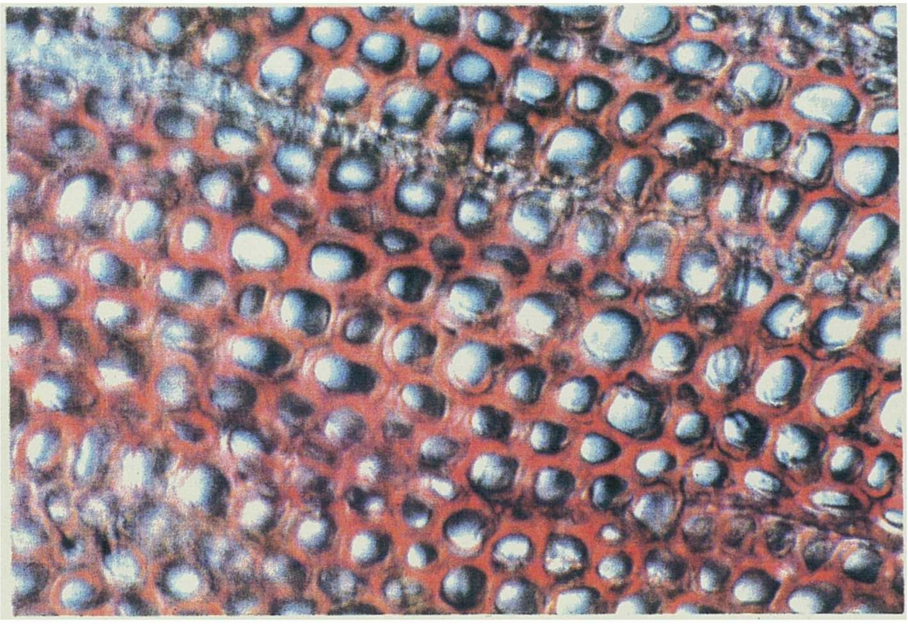
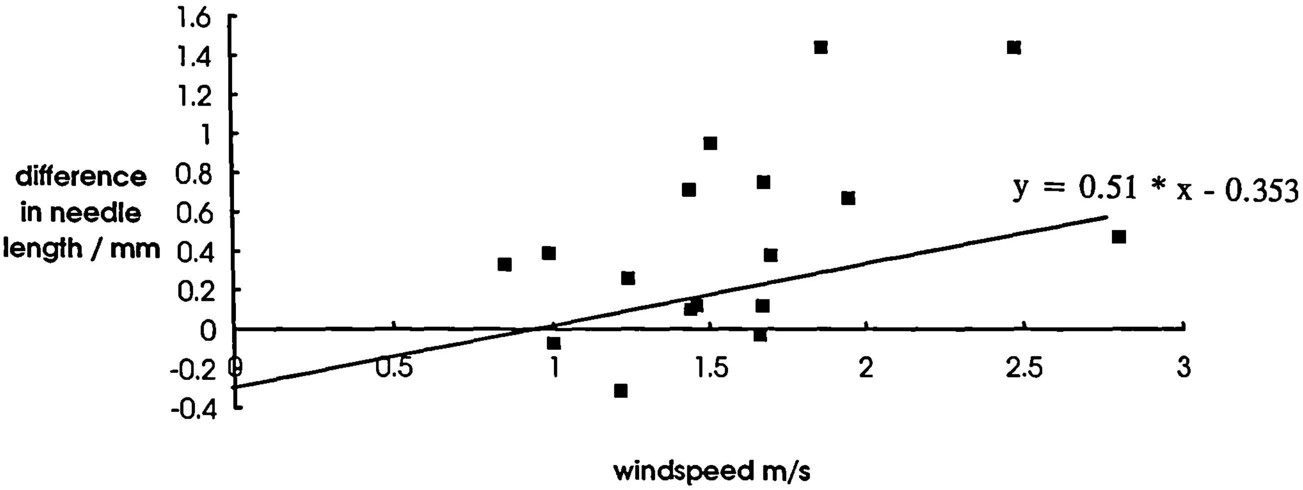


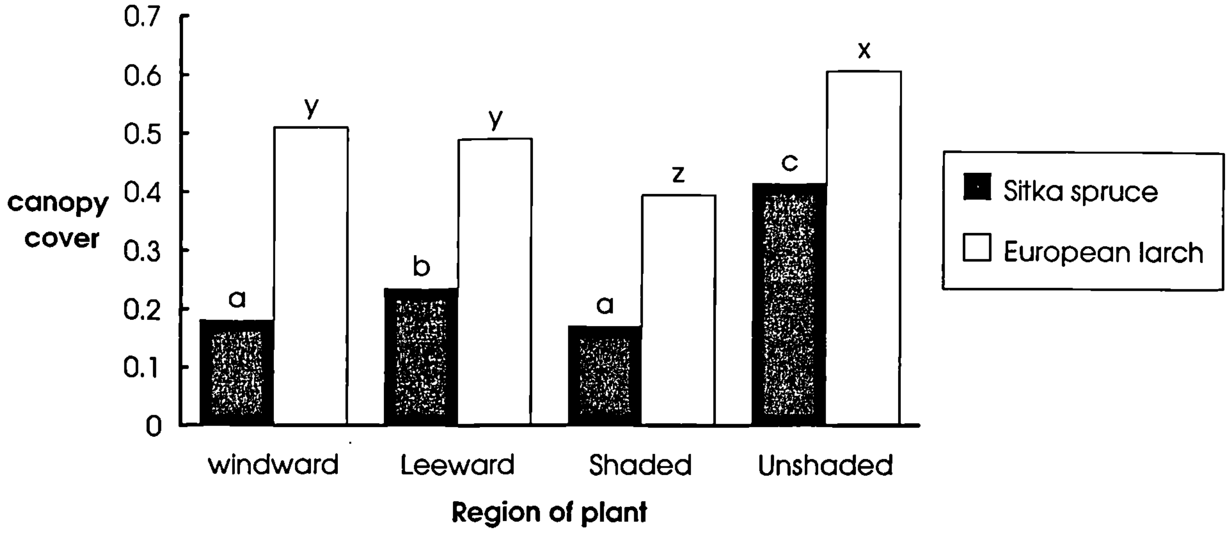
Fig. 2.8 Relationship between windspeed and the difference in needle length of windward and leeward needles of European larch



significantly larger than in any other region around the plant. The least amount of canopy was on the shaded side (Fig. 2.9, $F_{3,72} = 37.91$, $P < 0.001$). There were no differences in canopy cover between windward and leeward sides. There were no significant differences in the proportion of root cover on any region although in the unshaded quadrant of larch, root cover was correlated with shoot cover (Fig. 2.10, $R^2 = 0.22$, $P = 0.049$). However, the R^2 value of 0.22 is small, therefore the proportion of the variation accounted for by the fitted line is also small so the relationship should be treated with caution.

In Sitka spruce, canopy cover was lower in both windward and shaded quadrants. The unshaded quadrant again had the largest canopy cover (Fig. 2.9, $F_{3,72} = 72.27$, $P < 0.001$). The proportion of root cover was significantly greater in the windward quadrant than in the other quadrants (Fig. 2.11, $F_{3,72} = 3.58$, $P = 0.018$) and there was no difference between the other quadrants.

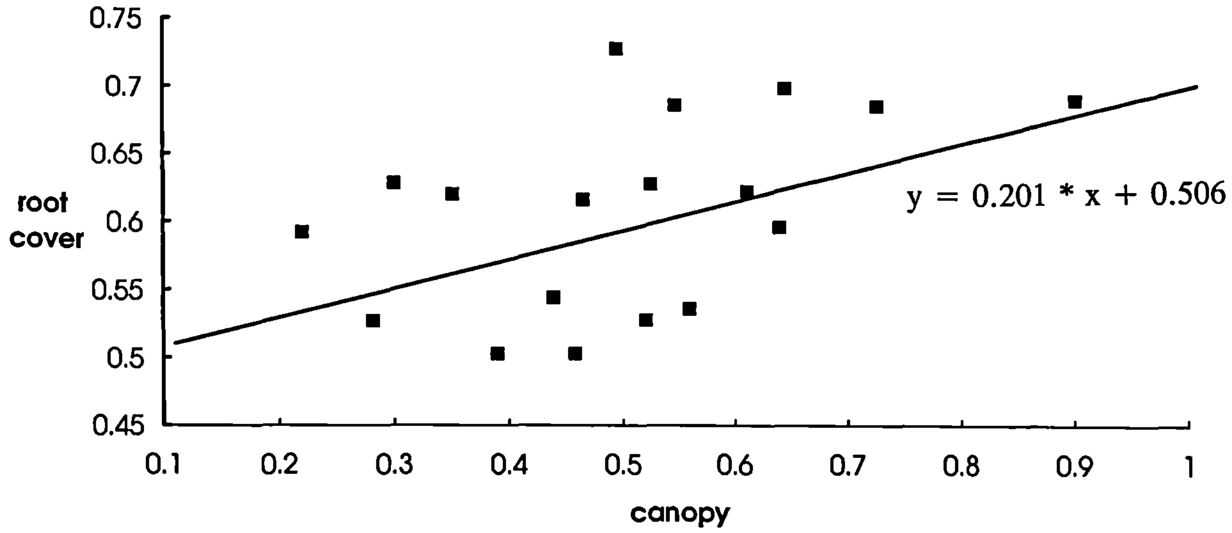
Fig. 2.9 Proportion of canopy of Sitka spruce and European larch in each quadrant* around the plant's central axis



* In larch, each plant was divided into two halves around the central axis: shaded and unshaded. The plants were then divided into halves perpendicular to the first two: windward and leeward. Therefore, each pair of matching columns will add up to 1.

Columns differently superscripted differ at $P = 0.05$

Fig. 2.10 Relationship between the proportion of canopy and root cover in the unshaded half of European larch



2.3.3 Root Measurements.

To test whether the method used for determining the silhouette gave an accurate measure of plant growth, the mean and the sum of the cross-sectional area (Σ CSA) of lateral root bases > 2 mm was determined for each quadrant in each plant. Lateral roots were ordered by their orientation into the following quadrants: windward (45° - 134°), leeward (225° - 314°), shaded (135° - 224°) and unshaded (315° - 44°). Analysis of variance was used to determine the differences between the sectors, for mean CSA per root and Σ CSA of lateral root bases per plant, using logarithm transformations where appropriate. In larch, as with the proportions of root cover, there were no differences in either the mean or the Σ CSA of root bases. In Sitka spruce, the pattern of Σ CSA of the root bases differed from that of proportion of root cover, in that the shaded quadrants had a lower Σ CSA than all other quadrants (Fig 2.12, $F_{3,88} = 5.6$, $P < 0.001$). Mean CSA per root in each quadrant showed a similar pattern to Σ CSA except that the only significant difference was between shaded and unshaded quadrants ($F_{3,151} = 1.46$, $P = 0.028$).

Since there appeared to be differences in root growth in the four quadrants, a more detailed study of root initiation and development was made, using smaller sectors in an attempt to discover whether wind was altering root formation. On harvesting, it was noted that plate systems were forming as the tap root was very short in most of the root systems. The number of large lateral roots (> 2mm diameter at the root base), for both species, was calculated for each 15° sector around the stem, where 0° = south (wind direction was west to east). A large peak of roots showed at 90°, towards the wind direction, for both Sitka spruce and larch (Fig. 2.13). The data for larch also suggested two lesser peaks of enhanced growth on the leeward side (270°), in the unshaded region (0°) and perpendicular to the wind direction. Chi-square analysis of the numbers of roots and their orientation for both species show that both distributions of roots are significantly different from a uniform distribution (Sitka spruce: $\chi^2_{23} = 92.65$, $P < 0.001$; European larch: $\chi^2_{23} = 88.6$, $P < 0.001$). When the numbers of all the lateral roots of Sitka spruce, including those < 2 mm diameter, were classified by orientation (Fig. 2.14), there was a prominent peak at 180° - 195°, and a smaller peak at 345° - 15°, both perpendicular to the direction of wind. This

Fig. 2.11 Proportion of root cover of Sitka spruce in each quadrant around the plant's central axis

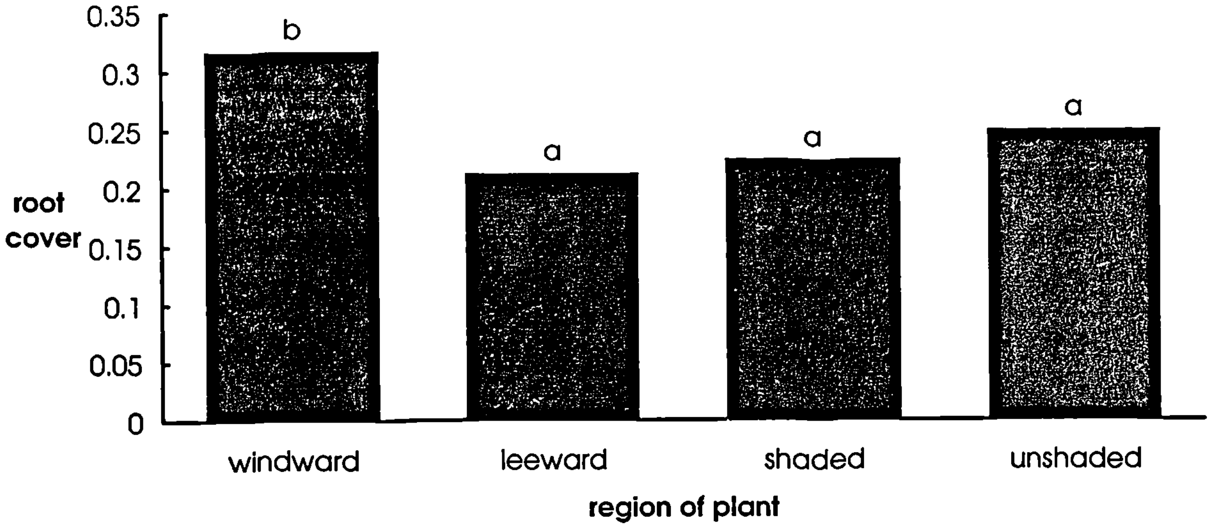


Fig. 2.12 Sum of CSA of Sitka spruce lateral root bases > 2 mm diameter in each quadrant around the plant's central axis

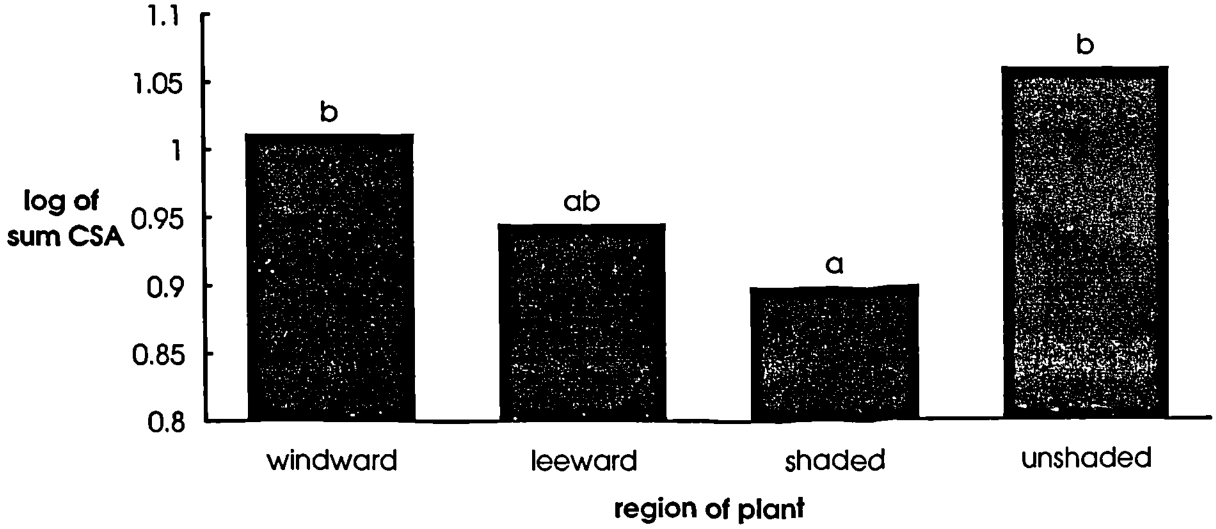


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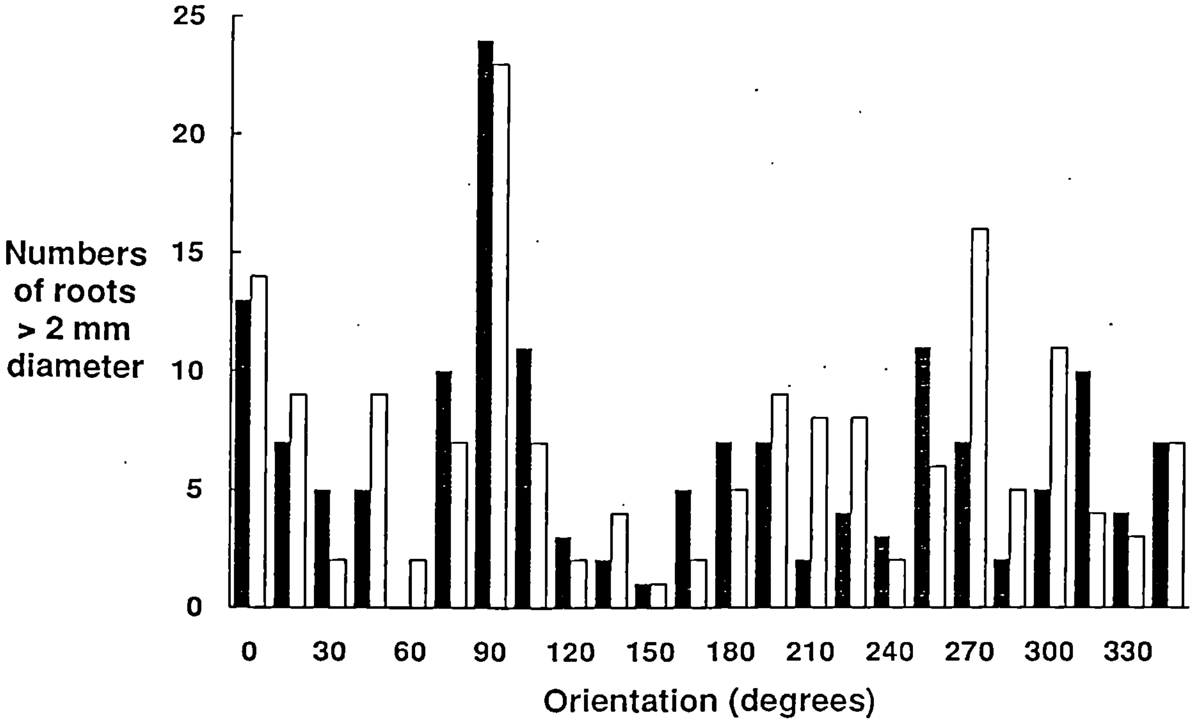
Fig. 2.13 Numbers of European larch and Sitka spruce lateral roots > 2 mm diameter, for wind-stressed plants only. Both distributions differ significantly from uniform (Sitka spruce: $\chi^2_{23} = 92.65$, P = 0.001; European larch: $\chi^2_{23} = 88.6$, P = 0.001). Black bar = Sitka spruce, white bar = European larch.



distribution also differed significantly from uniform (χ^2_{23} = 108.7, P < 0.001) and from that of the larger lateral roots (χ^2_{23} = 76.6, P < 0.001).

The increase in numbers of roots > 2 mm diameter on the windward and to a lesser extent on the leeward sides of the plants could imply greater total root growth in those regions. The Σ CSA of the bases of the roots growing on windward and leeward sides and perpendicular to these directions was calculated using 30° sectors. The two perpendicular sectors were combined to counteract the effect of shading. Analysis of variance was used to determine the differences between the sectors of mean CSA per root and Σ CSA of lateral root bases per plant, using logarithm transformations where appropriate. Root bases of both Sitka spruce and larch (Fig. 2.15) had greater Σ CSA's in the windward sector than in the leeward sector (Sitka spruce: $F_{2,92}$ = 3.53, P = 0.033; Larch: $F_{2,89}$ = 4.25, P = 0.017). However, there were no differences in mean CSA per root between any sector for either species. In the windward sector, therefore, there were more large roots than in other sectors, but there was no increase in the size of the individual roots.

Analysis of variance of large, woody and fine root biomass between quadrants in Sitka spruce showed no significant differences.

Fig. 2.14 Numbers of all Sitka spruce lateral roots, both < 2 mm and > 2 mm in diameter

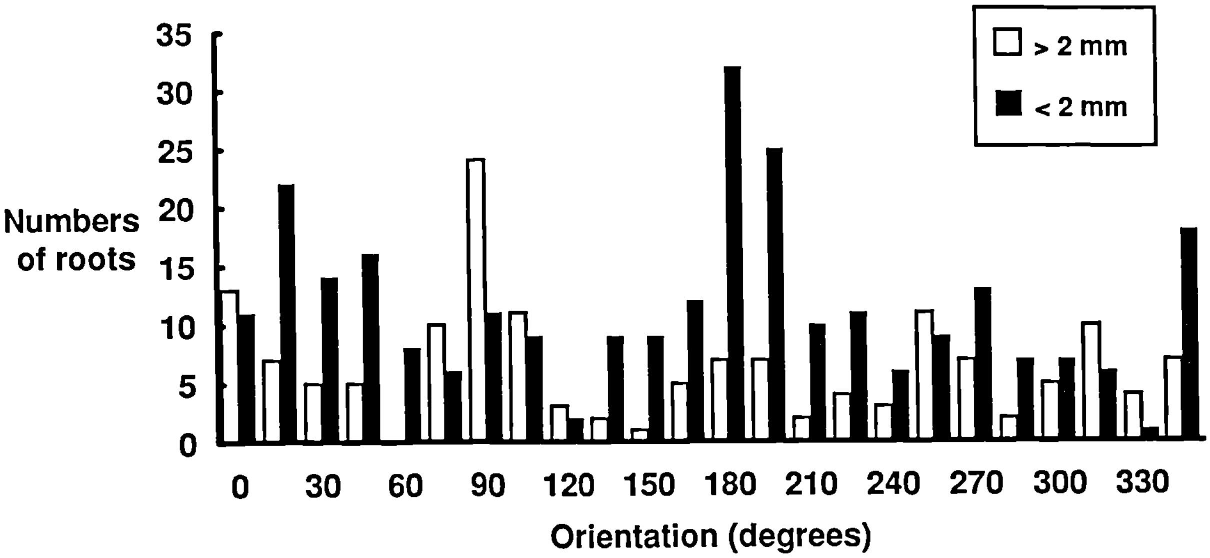
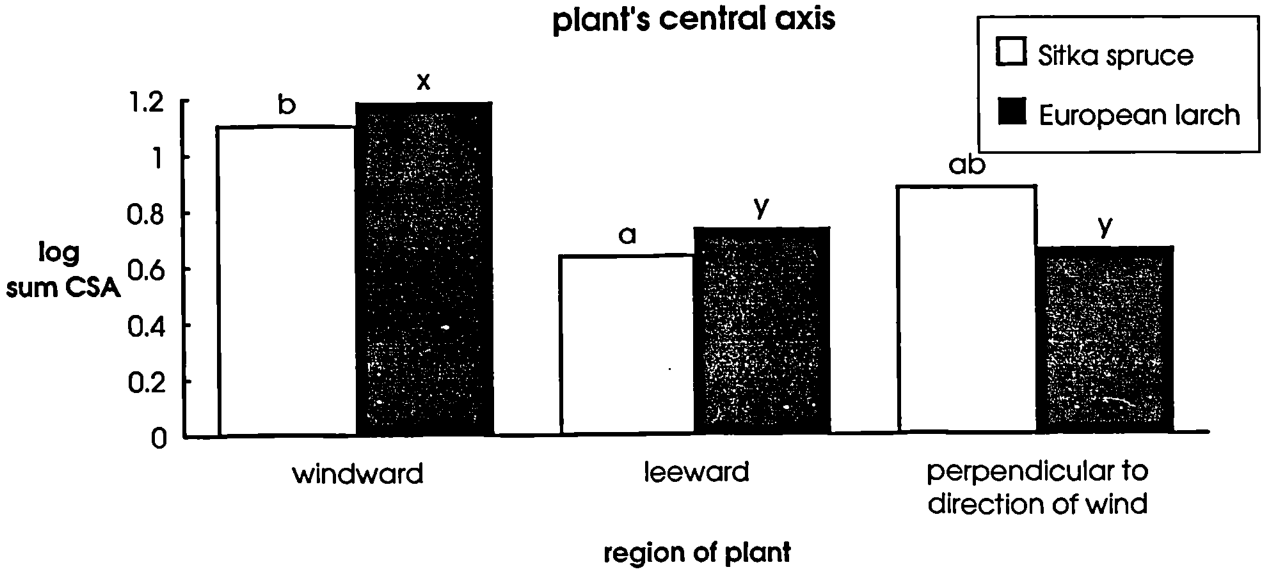


Fig. 2.15 Sum of CSA of Sitka spruce and European larch lateral root bases > 2 mm diameter in 3 sectors around the plant's central axis



Columns differently superscripted differ at P = 0.05

2.3.4 Architectural analysis.

A regression of the logarithms of altitude (a) against magnitude (μ) quantifies the root branching patterns as the regression coefficient, referred to as the topological index. Herringbone systems have the highest value of 1, dichotomous systems have a minimal value and random branching patterns have a value of 0.53 (Fitter 1985). Sitka spruce roots with log $\mu < 0.8$ (*i.e.* $\mu < 6$) were not used in the analysis because very small root systems always have herringbone patterns and their inclusion biases the calculation. The regressions of the logarithms of magnitude and altitude of windward and leeward woody roots produced significantly different coefficients (windward roots: $R^2 = 0.63$, $P = 0.002$, leeward: R^2 0.55, $P = 0.004$). Leeward roots had a value of 0.52 and windward roots had a more highly branched pattern with a value of 0.38 (Fig. 2.16). Sitka spruce of the same age grown in the same glasshouse, but not in the wind tunnel had a topological index of 0.55. The roots on the shaded and unshaded sides of Sitka spruce had coefficients of 0.73 and 0.75 respectively, so were not different from each other, but they were significantly less branched than either windward or leeward sides (Table 2.2).

In all root systems, EE links come in pairs, one typically much longer (Long EE) than the other (Short EE), since there is often a long unbranched region behind the growing tip. Analysis of variance of link lengths and diameters showed that the windward roots had Short EE links that were nearly twice as long and also wider (Table 2.3) than those on the leeward side, but there were no significant differences between exterior links on the shaded and unshaded sides. The diameter and lengths of the interior links in the roots were not significantly different between leeward and windward sides or between the shaded and unshaded sides.

Fig. 2.16 Relationship of log altitude and log magnitude for woody roots > 0.8 log magnitude on windward and leeward sides of Sitka spruce

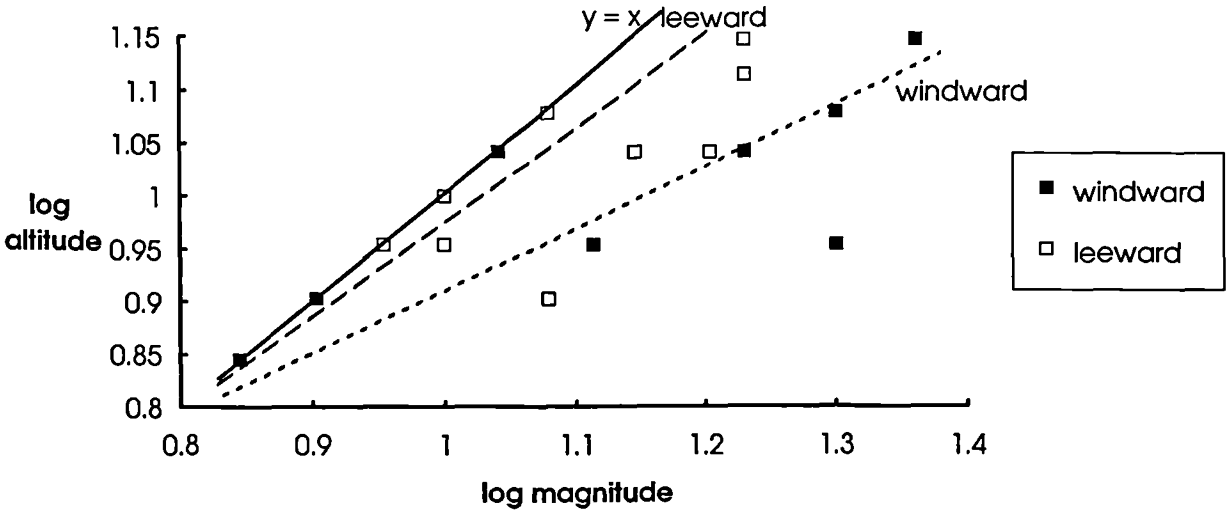


Table 2.2

Regression coefficients of log a and log μ for Sitka spruce

Type of root	**Coefficient value**
Windward	0.38
Leeward	0.52
Shaded	0.73
Unshaded	0.75
Untreated	0.55
Herringbone	1.0
Random	0.53
Dichotomous	minimal

Table 2.3

Mean link lengths and diameters (mm) of exterior roots of Sitka spruce

	Windward **45°-134°**	Leeward **225°-314°**	$F_{1,33}$	P
Long EE length	28.6	17.6	3.51	0.07
Short EE length	10.7	5.8	4.70	0.037
Long EE diameter	1.2	1.0	1.74	0.196
Short EE diameter	0.9	0.6	10.79	0.002

2.4 Discussion

Shoot height, biomass and stem basal diameter were not significantly affected by wind action, which may be due to the large variation noticed in the plant material and to the low windspeeds (ranging from 1 mph - 6.5 mph). At higher windspeeds, changes in shoot growth may become more obvious, such as the 20 % reduction in growth of stem length and lateral shoot length of *Pinus contorta* grown in windspeeds of 8.5 m s^{-1} (19 mph) compared to plants grown without wind (Rees & Grace 1980). An experiment using stronger windspeeds may clarify the role the strength of the wind plays in influencing shoot growth.

There were significant differences in canopy cover between the four quadrants in that shoot growth (both the stem and branches) in both species had deflected towards the south-facing window, and to the lee side in Sitka spruce only. The correlation between shoot and root cover in the unshaded half of larch plants suggests that there is a relationship between the amount of shoot and root growth on the same side of a plant. The increased radial growth of root bases in the unshaded quadrant for Sitka spruce and the increase in numbers of large roots in the unshaded regions for both species may be due to the roots in the unshaded regions receiving more photoassimilates which travel down the phloem sectorially, remaining on the side of the tree where they are synthesised. Using radioactive carbon fed to the shoots of sunflower seedlings, Aguirrezabal *et al* (1991) found that it was deposited as structural carbon in the root system nearest to the sites where it was assimilated. It is unclear exactly what is meant by this, but we may assume that the carbon was deposited in the roots on the same side of the plant to which it was applied. This implies that uneven irradiance levels around the plant may play a part in carbon allocation to different parts of the root system. It is unlikely that the cause of the extra root growth on the unshaded side of the tree was due to increased soil temperature on that side of the plant. The canopy covered most of the soil surface by June and the pots were packed closely together, so could not be warmed up at the sides except for the edge row. Unfortunately soil temperature was not monitored in each quadrant around the plant.

The anchorage tests carried out on young Sitka spruce showed no differences in stem deflection in any one direction at a fixed force of 20 N. Either no changes had occurred, or any changes may have been obscured by variation between trees or the measurement technique. The spring balance used was large and clumsy and hooked straight onto the stem of the plant. A less cumbersome device attached to the plant by means of a winch would probably give more accurate readings.

The wind stressed plants had all deflected away from the wind to form flag shaped plants (Fig. 2.4a); in larch the needles were shorter on the windward side of larch trees. Telewski & Jaffe (1986a) found a 28% reduction in needle area of trees of mature *Abies fraseri* growing in an exposed site compared to trees of the same species growing in sheltered sites and explained the effect as "wind clipping." A 20 % reduction in needle extension of *Pinus contorta* grown in high windspeeds compared to plants grown without wind was observed by Rees & Grace (1980). However, there are no studies where needle length was examined on the windward and leeward sides of the same tree and a significant difference found between the two regions. The difference in needle length between the two areas is surprising and it is not clear how wind stress can affect needle extension on both sides of the tree. Mechanical damage to leaves such as tearing and cuticular lesions have been observed (Wilson 1980, 1984) and windward leaves will experience this more than the sheltered leeward needles. The leaves knocking into each other might trigger off the signal which induces thigmomorphogenetic responses (see Chapter 1). As mentioned in the discussion to this chapter, canopy causes a break in the flow of wind. On the leeward side of the canopy, a "dead" zone is formed, containing some reverse flow. Therefore, leeward needles are subjected to much smaller wind velocities than windward needles. Wind breaks work in the same way; rows of planted trees break up the flow of wind, causing reverse flow behind the wind break. The reduction in needle area will reduce the effective photosynthetic area which in turn will affect plant performance. If photoassimilates are transported sectorially down one side of young larch trees, this would directly affect stem and root development on the windward side of the tree.

An increase in woody tissue coupled with the formation of reaction wood was found on the leeward side of the stem base of nearly all the larch trees. The forces transmitted down the stem to the roots are maximised at the stem base, as the wind generators were aligned with the top of the plant pots. An increase in the eccentricity of stem radial growth is a common occurrence in mechanically stressed gymnosperms (Larson 1965, see Boyd 1977, Telewski 1989). Reaction wood in compression has thick-walled cells with intercellular spaces between the tracheids, with secondary walls (S) lacking an inner S_3 layer and with microfibrils in the thick S_2 layer oriented at much larger angles to the cell axis than normal wood (see Boyd 1977). This larger angle ensures that toughness is increased and axial stiffness is reduced. If a single normal wood tracheid is held in tension, the microfibrils shear apart and buckle inwards to the lumen of the cell, where they are still capable of supporting a load. When this happens, cracks in the S_2 wall run parallel with the fibres and the S_2 wall decreases locally in diameter at the early stages of buckling and separates locally from the outer primary wall. Then the S_2 wall folds inwards (Gordon & Jeronimidis 1980). Therefore, a tree with reaction wood in compression, which has microfibrils at large angles to the cell axis will be able to bend over further before breaking.

Telewski (1989) has coined the phrase "flexure wood" to describe the extra wood formation found in tree stems as a result of bending. Flexure wood forms when the stem is displaced but then returns to the vertical, as opposed to reaction wood which forms when the stem is permanently displaced. Both types of wood formation act in order to keep the stem in an upright position. Flexure wood is more dense than normal wood, with a smaller tracheid lumen size and microfibrils in the cell wall approaching an angle to that found in reaction wood. Flexure wood tracheids do not have a thicker S_2 cell wall layer with intercellular spaces, such as those found in reaction wood (Telewski 1989). Flexure wood is more rigid with a greater inertia and flexural stiffness than normal wood (Telewski & Jaffe 1986a,b) and so is more effective at maintaining the stem in a vertical position during windy conditions.

The results show an increase in the numbers of large roots on the windward side for both Sitka spruce and larch and also on the leeward side for larch. The windward side of Sitka spruce, in the region of 75° to 105°, is the only area where roots > 2 mm diameter at the base outnumber smaller roots (Fig. 2.14). The Σ CSA of large roots in this region is greater than Σ CSA found in any other sector, which was also the case in larch. However the mean CSA per root base for both Sitka spruce and larch showed no significant changes between either sectors or the larger quadrants. This suggests that more roots turn into large roots on the windward side, not that more roots are initiated or that large roots grow larger.

The proportion of root cover of Sitka spruce was found to be largest in the windward quadrant, which probably reflects the degree of branching in that region. The topological analysis of the lateral woody roots provides an insight to the changes occurring in the root system. A higher incidence of branching was found on the windward side of the Sitka spruce trees compared to the leeward side and both were more branched than the roots growing perpendicular to the wind direction. This suggests that wind action affects morphogenesis of lateral branches. The increase in length and diameter of exterior links implies that more resources may be reaching the windward roots, although it is unclear how this occurred. The higher the concentration of roots per unit area of soil, the greater the tensile strength of the soil (Wu 1976), so when branching becomes more random on the windward side only, resistance to overturning increases. A decrease in topological index in windward roots is therefore a feature with obvious adaptive value with regards to mechanical stability.

It is very striking that these apparently adaptive changes in root morphogenesis occurred at windspeeds too low to exert large effects on the shoots. It is not clear therefore what signal was transmitted to the roots, or whether a signal was triggered locally within the root system. Larson (1965), referring to young *Larix laricina*, suggested that assimilates are diverted from height to diameter growth under the influence of wind sway. He visualized the lower, stressed bole of a tree as a metabolic sink to which assimilates flow, possibly under the influence of increased auxin conditions. If this is the case, the increase in larch leeward needle length may be one of the factors contributing to the production of extra wood formation on the leeward side of the stem base. Auxin transport is basipetal (travels from the apex to the base of a plant) and stimulates ethylene production (see Jacobs 1979). Ethylene production in stems increases under mechanical stress and is thought to be the mediator of increased radial growth and reduced elongation (for mechanism, see Chapter 1). It is possible that an increase in ethylene production at the root bases in stressed areas stimulated the radial growth of more larger roots. Each root produces many branches, only some of which form large roots with secondary thickening. The latter arise only from large root primordia, thus the signal could begin to act at the time of root initiation. The extra wood formation suggests that these roots are receiving more assimilates, but probably at the expense of another part of the plant, such as the windward needles.

It appears that those roots which provide the greatest contribution to anchorage receive more resources in both Sitka spruce and European larch, by increasing the number of larger windward lateral roots and hence the surface area. The topological index of Sitka spruce windward roots decreases, resulting in an almost dichotomous type of branching pattern. These roots may improve resistance to overturning, especially on the windward side, as they will be held in tension and are the most important component in resisting uprooting by wind (Coutts 1983a, 1986, Ennos 1993b). Roots perpendicular to the direction of wind are subject to torsion and will offer little resistance to uprooting. Unfortunately, this was not reflected in the anchorage tests, possibly due to their crudeness and also the young age of the trees. As the trees mature, responses to wind should be amplified and the effects on anchorage strength made more obvious.

Little is known about how tree root systems alter in shape and size throughout their life and if it is indeed valid to scale root anchorage allometrically. Material properties are known to differ as roots age, with tensile strength decreasing as root diameter increases, which is attributed to the increase of lignin in older tissues (Commandeur & Pyles 1987). In young seedlings, the taproot is the fastest growing member, but its growth slows down as that of the lateral roots increases (Lyford 1980). At the time of harvesting, the wind stressed Sitka spruce and larch seedlings had poorly developed tap roots compared to the woody lateral roots and a plate system was already forming. As the trees were grown from seed in the wind tunnel, with the generators switched on at the time of seedling emergence, wind-induced responses may have occurred before woody growth was initiated. However, this seems unlikely as forces imposed on the stem can only be transferred to the roots *via* a stiff element in the stem, *i.e.* woody growth. As soon as secondary growth occurs in seedlings, forces can be transmitted down the stem. The fibrous roots then hold the tap root in position like guy ropes. The tap root in turn resists rotation like a stake embedded in the soil and the soil resists the sideways motion of the tap root (Fitter & Ennos 1989). The more laterals develop, the less is the optimum length of the tap root (Ennos 1993). In order to withstand uprooting, root system strength must exceed stem strength. Therefore, the root radius will increase with the radius of the stem and so the volume of the root system will be proportional to the cube of the stem dimensions. However, in plate systems, the weight of the root-soil plate is proportional to the cube of linear dimensions and acts a distance proportional to the linear dimensions away from the hinge. Hence, the anchorage provided by the weight of the root-soil plate will rise with the fourth power of linear dimensions, rather than their cube (Ennos 1993). As trees get larger, the plate system will become more efficient. Ennos (1993) suggests that this may be one reason why trees develop plate systems as they grow. Experimentation on young trees which already have plate systems will determine whether the changes in root growth observed in the wind stressed Sitka spruce and larch seedlings are amplified during growth and whether it is valid to scale the anchorage of such young trees allometrically.

Uneven irradiance levels around a plant may result in an uneven distribution of structural carbon in the root system, which in itself could have large effects on tree stability. In forest stands, trees are rarely illuminated evenly around the trunk, so the uneven light levels around the seedlings in the experiment were not unnatural. In particular, trees growing at the edges of forest stands tend to develop very eccentric growth away from the stand, perhaps as a result of shading. Mature trees in dense forest stands will receive less light vertically than the wind stressed seedlings, which had canopy down the full length of the stems. However, the experimental technique needs to be improved to remove influences of differing light levels around each plant so that the effect of this parameter on growth can be determined.

There are few published studies (Aguirrezabal 1993) on the sectorial transport of photoassimilates to the root system. Movement of water through conifers has been examined and is known to ascend spirally (Kozlowski 1961, Waisel *et al* 1972, Coutts & Philipson 1976). Phloem is closely linked with xylem so we may presume that photoassimilates descend sectorially. An investigation to clarify this has been carried out (see Chapter 3), so that we can properly assess the uneven root growth between the shaded and unshaded regions of the young Sitka spruce and larch, and verify that it was not an artefact of the experiment.

The true nature of the wind in the tunnel could have been revealed more accurately by the release of smoke or small particles rather than with a cup anemometer (Van Gardingen & Grace 1991). Flow is turbulent and both horizontal and vertical components of velocity are inherent characteristics of wind (Baldocchi & Hutchinson 1987). The profile of intensity within the canopy can be related to the spatial distribution of plant parts and their flexibility (Finnigan 1979). Air penetrates into the canopy from gusts above it and through gaps in plants. Consequential movement of leaves and stems results in increased turbulence. Baldocchi and Hutchinson (1987) calculated a probability density distribution of three components of turbulence: horizontal streamwise; horizontal lateral and vertical. They were able to estimate the probability of recording extreme gusts which may be important in causing tree breakage (Van Gardingen & Grace 1991). Gusts of wind can be found throughout the height of the canopy, even at the forest floor (Allen 1968). Although this turbulence has been observed mainly in forests, Van Gardingen and Grace (1991) suggest that it could also be present in shorter vegetation, such as the vorticular air movement observed in cereal crops (Arkin & Perrier 1974).

Wind flow in the natural environment consists of a complex number of variables, thereby making it very difficult to imitate under artificial conditions. However, as Fraser (1964) points out "the greatest drawback of using a wind-tunnel is that turbulent airflow cannot be reproduced, but useful data can, nethertheless, be obtained." Therefore, the use of wind tunnels, despite their limitations, provide the best opportunity for studying tree response to wind in a controlled environment. Increasing the windspeed and making it more intermittent, may result in amplifying the changes already observed in plant growth. It is not known whether turbulence plays a part in the physiological response of plants to wind. Telewski (1993) states that the time period in order to induce a thigmomorphogenetic response in young trees is approximately one hour. The magnitude of this presentation time implies that the length of exposure to wind is more important than the nature of the wind. Further experimentation with young trees grown under intermittent wind or with wind blowing from different directions around the plant might provide more information about the changes occurring when plants are exposed to gusting wind. The validity of exposing plants to a steady stream of wind in tunnels in order to monitor their response could then be verified.

The changes in root growth which have occurred in the trees exposed to wind loading are of an ecological advantage, in that the increase in the number of larger windward lateral roots should result in a tree able to withstand greater stresses with less likelihood of uprooting. As mentioned earlier, forestry uses marginal land, often with poor or waterlogged soils. Such soils promote the formation of a shallow root plate. Further work where young trees are grown in wind tunnels under such conditions, will help clarify the role wind plays in the development of root systems in the field.

Chapter 3

Transport pathway in Sitka spruce

3.1 Introduction

The woody root systems of trees often show an irregular and sometimes highly asymmetric form (Coutts 1983b). Several environmental factors could account for uneven distribution of biomass allocation around a main axis. Soil heterogeneity results in nutrient patchiness. Pockets of nutrients influence primary root radial growth enormously, as shown by split root experiments (Drew *et al.* 1973, Coutts & Philipson 1976). The enhanced primary radial root growth in turn encourages woody root growth. Primary roots proliferate in nutrient-rich patches of soil. Uneven root growth can also be induced by small differences in soil water potential (Coutts 1982) and soil temperature (Bowen 1991) on either side of the plant. Exposure of woody root bases to light and mechanical stress stimulates local radial growth (Fayle 1968). It is not known if environmental factors affecting shoot growth may influence asymmetry.

In the experiment described in Chapter 2, Sitka spruce and European larch were grown alongside a south-facing window for 30 weeks. The plants were kept in the same position and orientation throughout the experiment. Shoot growth was greatly stimulated on the side of the tree next to the window and was correlated with increased root growth on that side of the tree, suggesting that uneven irradiance levels around the plant influenced development of the woody root system. There may have been a downward shift of assimilates from the shoots to roots on the same side of the plant. Aguirezzebal *et al.* (1991) found that in sunflowers, radioactive carbon fed to the shoots was deposited as structural carbon in the roots nearest to the sites it was fed to. A relationship between tree roots and shoot branches has been supported by work conducted since the end of the last century. Hartig (1891) girdled (cut a ring through the cambium around the complete circumference of the stem) one fork of a double leadered *Pinus sylvestris*. No further diameter growth was seen in the stem or roots beneath the girdled fork. Auchter (1923) concluded that assimilates produced on one side of the tree were translocated directly to the roots below. Rowe (1964) suggested that where tree crown development increases, root growth under that part of the crown is also stimulated.

Carbon supply is known to affect root system development as a whole, including features such as biomass and root length. It also can affect parameters which determine the architecture of the root system (Aguirrezabal 1993). One of the ways carbon supply might influence root development is by the sectorial transport of assimilates from the shoots to the roots. The sectorial transport of $^{14}CO_2$ has been observed in *Malus* (Apple) (Barlow 1979). The label to a single leaf was transported to the nearest leaves. The resulting distribution after 1-2 hours agreed with the vascular phyllotaxis of 3/8 for *Malus*. Therefore over short distances, the pattern of photosynthate movement was sectorial .

Photosynthates are transported in the phloem which is closely associated with the xylem. The pattern of water movement through the xylem has been observed by feeding individual roots with acid fuchsin (Kozlowski *et al.* 1965, Waisel *et al.* 1972, Coutts & Philipson 1976). Coutts & Philipson (1976) found that in Sitka spruce seedlings, dye was translocated into the shoot branches *via* a spiral pathway. Waisel *et al.* (1972) also observed the spiral ascent of dye in stems of *Pinus halepensis* and *Cupressus sempervirens*. However, a sectorial straight ascent of water movement has been found in some desert shrubs. Water is therefore directly translocated to the shoots above the root (Waisel *et al.* 1972). It is not known how much of the dye is distributed around the main axis. Coutts & Philipson (1976) suggested that nutrients from the roots move along xylem pathways to certain regions of the shoots where they stimulate assimilation. An increased supply of assimilates will then move to the same roots along the closely associated phloem pathways, reinforcing the system by stimulating localized growth of the conducting tissues. If there is a greater distribution of dye found on the side of the main axis above the root to which the dye was fed, it is possible that stimulated growth might occur in the roots since they would receive more photosynthates down the spiral pathway of phloem.

If the relationship between root and shoot branches can be understood further, it would increase our knowledge of the transport system in the plant. The development of asymmetric root systems can create instability in the tree and the factors determining localised woody radial root growth are not fully understood. This study investigates the distribution of dye uptake around the main axis of young Sitka spruce. If dye is concentrated on the side of the tree to which it was supplied, it may be assumed that xylem and phloem translocate assimilates or water and solutes mainly on one side of the tree. Stimulated asymmetric growth in the shoot or root system would therefore be reflected in the counterpart system below or above ground.

3.2 Materials and Methods

3.2.1. Growth conditions

Seeds of Sitka spruce (lot no. 83(1012) Queen Charlotte Island) were stratified at 4° C for 4 weeks. Seeds were sown on 27 April 1992 in the centre of 13.5 l capacity plastic polythene pots (4 seeds per pot) filled with Irish Shamrock peat, containing 2 g l^{-1} Osmocote Plus 8-9 month formulation slow release fertilizer (N P K, 16.18.12 + 2 MgO). 24 pots were placed on a greenhouse bench as two columns of 12 pots. After 27 days, seedlings were thinned out to one per pot. Every three days each pot was turned 90° so that irradiance levels around each plant were relatively even. The plants were overwintered from 12 December 1992 until 1 April 1993 in a coldroom at 2° C.

3.2.2. Treatment

The pathway of the transpiration stream was examined on 28 May 1993, when mean plant height was 26.3 ± 8.6 cm, by allowing one root per plant to take up 0.1 % acid fuchsin. A small hole was dug in the soil 2 cm from the plant stem and a 4 cm long glass phial was inserted into the hole (Fig. 3.1). The glass phial was carefully filled to the brim with 0.1 % acid fuchsin, taking care not to spill any into the surrounding soil. One large woody root (approximately 5 mm in diameter at the base) from each plant was excavated and the region beyond the proximal 5 cm removed. The remainder of the plant was left intact. The root was immersed in the dye solution for 48 hours (Fig. 3.1). As the dye solution was taken up by the plant, more dye was poured into the phial, so that the woody root did not dehydrate.

The dye taken up by the roots was deep pink in colour and was translocated from the roots to the shoots, turning the needles pink in the branches to which the dye flowed. The orientation of the branches from the root that was immersed in the dye, which turned pink was measured after 24 and 48 hours. The plants were harvested on 30 May 1993. The stems were sectioned at ground level, half-way up the stem, and at the top of the stem, to show the internal distribution of the dye.

Fig. 3.1

One lateral root of Sitka spruce was cut and immersed into a phial of dye 2 cm from the plant stem.

The concentration of pink colour in each shoot branch could be classified into three ranks (Table 3.1).

Table 3.1

Classification of dye concentration in the shoot branches of Sitka spruce

Classification	Degree and Distribution of Pink Colour
1	< 25 % of needles on branch are pink
2	half of needles on branch are pink
3	all needles on branch are pink

The degree of pink colour was measured for each branch with pink in it and the height of the branch up the stem.

3.3 Results

The ascent of dye was seen to follow a spiral pathway up the plant. At the base of the plant, the staining of branches was much more sectorial than further up the plant, where the pink colour was distributed more evenly in branches around the plant (Fig. 3.2). Generally, the upper side of the branch and the tips of the needles were stained pink (Fig. 3.3).

Each tree was divided into two halves around the main axis: "treated" = 271° - 90° and "untreated" = 91° - 270° where 0° is the point where the treated root was initiated at the stem base. In the treated half of all the trees, there were 47 branches which were stained pink, and in the untreated half there were 56 branches stained pink. The branches in both halves were stained to a similar degree (untreated: 1.7 ± 0.81 treated: 1.5 ± 0.58).

Observations of the dye ascent in the stem cross-sections revealed a sectorial spiral pathway in the xylem. At ground level, the dye was generally confined to a small area, but not directly above the treated root. Halfway up the plant stem, the dye was much more widespread around the central axis and at the top of the stem, the dye was present almost around the whole circumference. For each plant the mean of the orientation where the dye first appeared and ended, with respect to the treated root (Fig. 3.4), was calculated to determine the mean size of a dye sector at each cross-section examined (Table 3.2).

Table 3.2

Mean ± standard deviation of point in Sitka spruce stem where dye appears and ends

Position of stem section	Orientation where (°) dye begins	dye ends
Ground level	115 ± 114.8	146 ± 101.8
Halfway up stem	106 ± 104.0	236 ± 116.9
Top of stem	68 ± 106.0	271 ± 145.9

Fig. 3.2

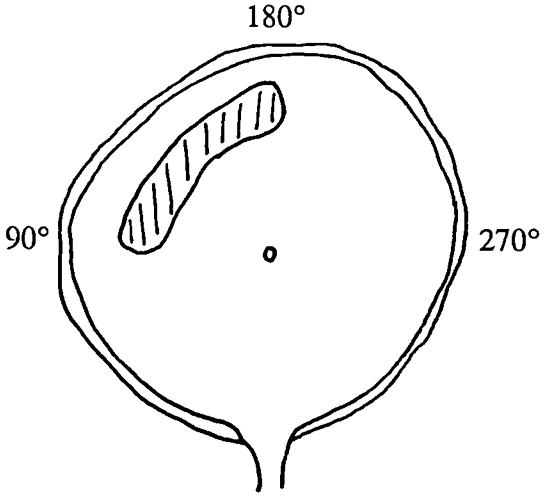
Colouration of branches with 0.1 % acid fuchsin can be seen to sectorial at the base of Sitka spruce, but more evenly distributed at the top of the plant.

Fig. 3.3

The upper sides of the branches and tips of the needles of Sitka spruce were generally stained pink

Fig. 3.4

Orientation where dye (0.1 % acid fuchsin) first appeared and ended in cross-section of Sitka spruce stem



Postion of treated root (0°)

e.g. sector of dye appeared 90° from the treated root and ended at 180°

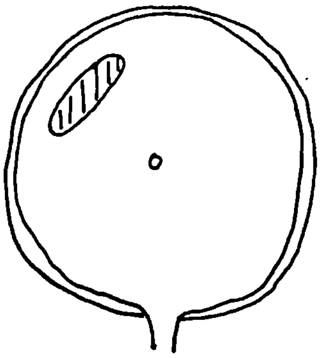
(A diagrammatic presentation of table 3.2 is shown in Fig. 3.5.)

Where the dye had a localized distribution in the stem, it was found that it only entered those branches arising from the dyed sector, but further up the stem, where the dye was more evenly distributed around the circumference, a higher proportion of branches was supplied. The mean height up the stem of branches that were supplied with dye was 10.2 ± 6.0 cm on the treated side and 8.6 ± 6.3 cm on the untreated side.

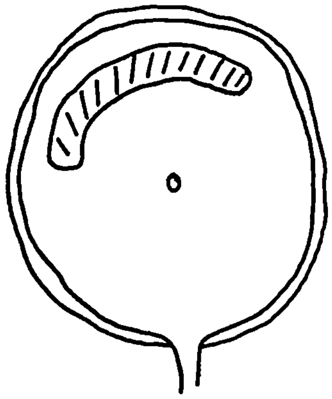
Fig. 3.5

Sectorial ascent of dye in the xylem of Sitka spruce (diagrammatic presentation of stem sections translocating 0.1 % acid fuchsin from root to shoot)

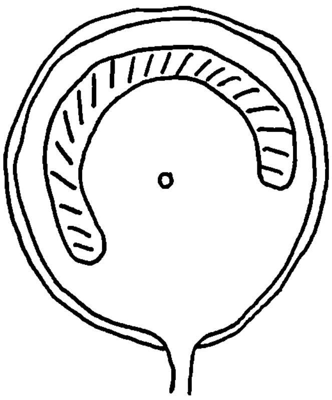
At ground level:



Halfway up stem



At apex of stem



3.4 Discussion

There was a slightly greater distribution of dye found on the side of the plant away from the root to which it was fed, both in terms of the number of branches with dye present and the concentration of the pink colour in the branches, although the increase was not significant. The spiral ascent of dye was sectorial at the base of the stem but by the time the dye reached the stem apex, it was present almost around the complete circumference, which confirms the findings of Coutts & Philipson (1976).

Waisel *et al.* (1972) found that water conduction paths were variable in many species of trees and that growth characteristics such as bud growth and cambial activity were independent of the translocation pattern. Rudinsky & Vité (1959) thought that sectorial ascent alone was less effective than a spiral system, where water is distributed more evenly around a shoot system. However, Waisel *et al.* (1972) found that sectorial ascent alone was most common in desert shrubs, suggesting that such a pattern of water movement contributes to their survival under conditions of water stress.

The pattern of sectorial and spiral ascent of water transport observed in Sitka spruce can be described by considering tree form as a series of "unit pipes" (Shinozaki *et al.* 1964). The CSA of sapwood in the stem at any point is related to that of the stem and branches above, even into the leaves, which is based on data correlating the mass of leaves in the canopy of trees and corresponding amount of conducting tissues. The sectorial and spiral ascent of water in Sitka spruce, linking a root to a few branches fits this hypothesis in that the branch and root are linked by a continuous vascular system, like a series of pipes.

The pattern of dye uptake in Sitka spruce shows that there is no direct pathway between leaves and roots confined to one side of the tree. The spiral pathway observed would not account for localised growth on the side of the plant above the treated root. Increased woody root radial growth such as that observed on the unshaded sides of Sitka spruce and European larch root systems in Chapter 2 must be the result of a different stimulating factor. Although xylem and phloem are closely associated with other, it may not be valid to extrapolate the movement of water in the xylem to the transport of photosynthates in the phloem. An experiment similar to that of Barlow's (1979) using a $^{14}CO_2$ label fed to a single *Malus* leaf, would allow observation of photosynthates through the phloem. The results obtained would confirm whether photosynthates in the phloem also follow a spiral pathway, such as that in the xylem.

Liese & Dadswell (1959) reported that tree ring width was widest on the "sunny" side of many species of trees in the Northern and Southern hemispheres. On closer examination, they found that cambial activity was stimulated in the tree stems and that tracheids were shorter but more numerous on the sunny side. They attributed this increase to a response to warmer temperatures. Liese & Dadswell did not relate their findings to wind direction data, so it may be that the increase in bole radial growth is due to mechanical stimulation. For example, Telewski (1989) reports that eccentric radial growth caused by mechanical stimulation is due to an increase in the number of tracheids, but tracheid length is also decreased. However, Richardson (1964) found that tracheid elongation was reduced at *cooler* temperatures of 20° compared to 25° in stems of young Sitka spruce, but he enclosed segments of the young tree stems, so that light could not reach the stems. Therefore, in the trees observed by Liese & Dadswell (1959) light may indeed have played a role in stimulating tracheid production but not length. The interaction between light and temperature is therefore still to be evaluated. Initiation of cambial activity is partly temperature controlled (Stewart 1957). Irradiance levels may also be an important factor in stimulating cambial activity. If cambial activity is simulated by light at the bole of the tree, woody root development may also be affected since the cambium of the root is continuous with the stem. Cambial activity was found to be stimulated in root bases of *Pinus sylvestris* and *Pinus banksiana* which were covered in clear plastic and exposed to light, compared to roots which were covered with black plastic (Fayle 1968). The increase in annual growth was up to six times greater in the exposed roots. Temperature was the same underneath both types of plastic, so the increase in woody growth was attributed to light levels. Chlorophyll was also produced in the inner bark of woody roots exposed to light (Fayle 1968), enabling photosynthesis to occur and carbohydrates to be produced locally which may increase radial growth. An increased production of chlorophyll in stems exposed to uneven irradiance levels could stimulate local radial growth. However, it seems unlikely that enough photoassimilates would be produced to cause increased wood formation of nearby roots, so extra woody growth may occur at the expense of growth elsewhere.

The influence of stem cambial activity on woody root growth could be investigated by carrying out experiments similar to those of Fayle's (1968) on tree roots. The stems of young trees could be wrapped in clear plastic, and then wrapped in aluminium foil to eliminate light and reduce temperature effects. Aluminium foil may leach toxic substances so should not be in direct contact with the plant, but is a useful medium in regulating temperature because it reflects sunlight. The treated plants could then be compared to plants whose stems were exposed or wrapped in clear plastic. After at least one growing season, both sets of plants could be examined for changes in wood formation around the biological centre of the stem and roots.

If stem cambial activity is stimulated by light and can influence root growth, it may be a factor involved in the asymmetric growth of root systems, and therefore have implications for tree stability. Edge trees of forest stands are often left standing whilst the centre of the stand has been blown down in a high wind (M.P. Coutts, pers. comm.). The stability of edge trees has been attributed to increased root growth due to decreased root competition at the edge. It appears that the stimulation of growth by light may also play a role in increasing woody growth in these regions.

Chapter 4

The effects of wind action on young European larch grown with a shallow root-soil plate

4.1 Introduction

Periodic dieback of the roots of Sitka spruce and European larch caused by winter waterlogging occurs in most British upland sites used for forestry. The dieback of the downward growing sinker roots results in the formation of a shallow soil-root plate, which is highly susceptible to windthrow (Fraser & Gardiner 1968). It is important that foresters understand the contributions of wind loading on trees with plate systems, as opposed to deeper rooting systems, so that tree stability breeding programmes can be improved utilizing the knowledge gained.

The role each component of anchorage plays in a root system resisting overturning forces has been determined by Coutts (1983a, 1986) and Ennos *et al.* (1993) and is discussed in detail in Chapter 1. Using a method of trenching, cutting and pulling, the different components of anchorage in mature Sitka spruce and two annual dicots: *Impatiens glandulifera* and *Helianthus annuus*, they found that most anchorage was provided by the "windward" roots (the terms "windward" and "leeward" are used in analogy with Coutts 1983a, 1986) which are held in tension during overturning. A breakdown of the resistive forces which develop in a tree during overturning can facilitate an understanding of them. As Coutts (1986) suggested, a knowledge of the mode and magnitudes of the components will allow for assessment of those parts of the system most sensitive to manipulation.

The results from the wind tunnel experiment described in Chapter 2 showed that both wind stressed Sitka spruce and European larch produced more larger roots (> 2 mm diameter) on the windward side of the tree than on the other sides. There was also a greater total CSA of roots growing in the 30° sector towards the wind direction and exterior links had increased in length and diameter. The topological index of the roots had decreased leading to an increased number of roots per unit volume of soil which would increase the tensile strength of the soil (Wu 1976), leading to a greater anchorage of roots on the windward side of the trees.

If indeed "windward" roots do provide the most resistance to pull-out during overturning, the production of more, larger windward roots in trees growing in a prevailing wind would be a feature with immense adaptive value. Although tests carried out by Coutts (1983a, 1986) and Ennos *et al.* (1993) show that windward roots are the most important component of anchorage, the effect of wind stress on anchorage is not known.

In this study, European larch was grown from seed in wind tunnels. The tap roots were removed from the seedlings at a young age, to simulate the formation of a shallow root plate. Mechanical tests were performed to measure the main components of anchorage, and investigate whether the contribution of each component differs in plants grown in treatments of wind and no wind.

4.2 Materials and Methods

4.2.1 Growth Conditions

Two open topped wind tunnels, each consisting of a dexion frame with polythene sides, 3 m long, 30 cm wide and 1 m high were erected in a heated, lit glasshouse. One wind generator was placed at one end of the tunnel. Running alongside each wind tunnel was a control tunnel exactly the same as the wind tunnel but without wind. To counteract any effects of a light gradient on the plants, one wind tunnel and one control tunnel were placed on the east facing side of the glasshouse with the wind generator at the south end of the tunnel and the other tunnels were placed on the west facing side of the glasshouse with the wind generator at the north. The two control tunnels were placed on the east and west sides of the greenhouse next to the glass, to reduce the possibility of plants in the wind tunnels being subjected to uneven irradiance levels (Fig. 4.1). As in the first experiment, the wind generators were operated from 10.00 to 16.00 and 22.00 to 04.00. Windspeeds were measured with an anemometer on 18 June 1992 at each plant pot site at ground level (Fig. 4.2)

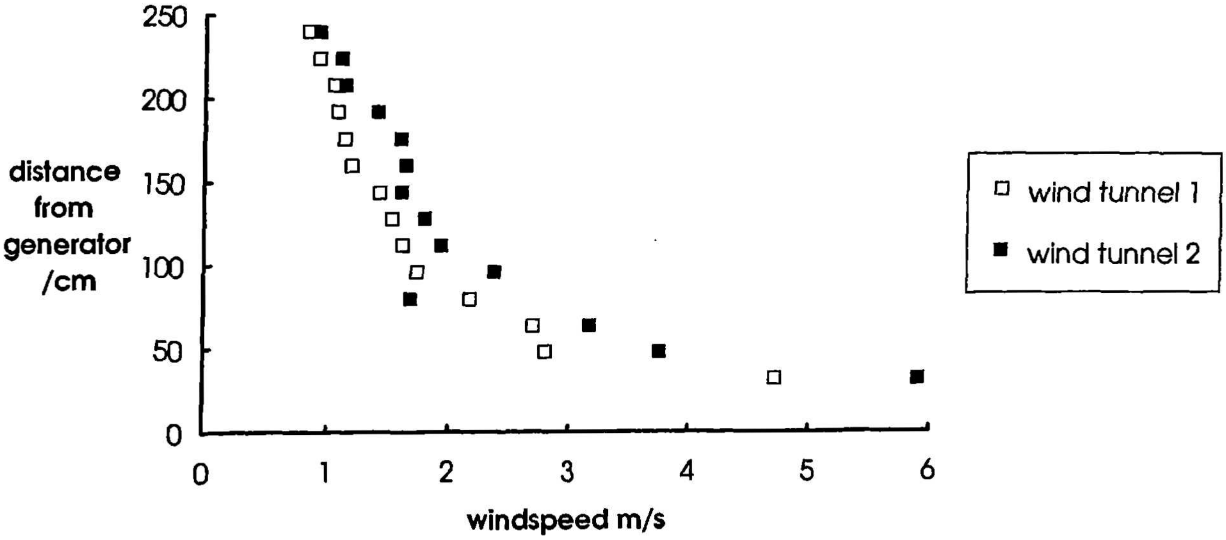
Only European larch (*Larix decidua*) was used in this experiment because it seemed slightly more sensitive to wind loading than Sitka spruce. Seeds of larch (lot no. 87{430} 837 03 lot 3) were stratified at 4° for 4 weeks. Seeds were sown on 20 May 1992 in the centre of 5.5 l capacity plastic pots filled with Irish Shamrock peat, mixed with 2 g l^{-1} Osmocote Plus, 8-9 month formulation, slow release fertilizer (N, P, K, 16.18.12 + 2 MgO). A row of 14 pots was placed in each tunnel. Four soil temperature probes were permanently buried in one pot in each tunnel along with an air temperature probe placed on the bench next to the same pot. The probes were positioned in four directions: north, south, east and west, and the maximum and minimum temperature every 24 hours was recorded along with the air temperature in each tunnel.

After 27 days, the seedlings were thinned out to one per pot and the tap roots were cut. A pair of nail scissors was carefully inserted at an angle of 45° into the soil 2 cm from the stem and the tap roots were cut 2 cm below ground level. The scissors were always inserted into the soil perpendicular to the direction of wind so that lateral roots

Fig. 4.1

Lay-out of wind and control tunnels

Fig. 4.2 Distance of each European larch plant from the wind generator and windspeed experienced by the plant



in leeward and windward directions would not be damaged. When the plants were harvested on 2 February 1993, damage to the roots caused by the cutting process was not detected.

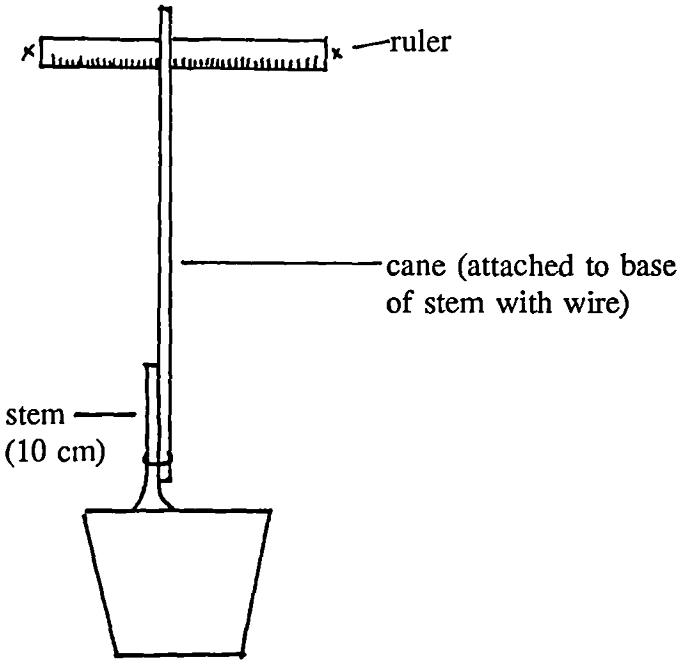
4.2.2 Anchorage tests

A random selection of 12 treated and 12 control plants was used for one series of tests to measure the moment required to cause the base of the stem to deflect laterally. The stem of each plant was cut off 10 cm above ground level and all the lateral branches were removed, so that they were not in the way as measurements were taken. A thin stick 17 cm long was attached to the base of the plant with thin wire. The stick was used to measure the lateral deflection of the plant against a ruler, placed horizontally behind the plant during the pulling tests. Even if the plant stem had curved away from the wind above the stem base, the stick was fixed in a vertical position (Fig. 4.3). The plants were pulled over with a force meter with a scale of 0 - 1 newton (N). The force meter had a hook which was attached around the stem 9 cm above ground level. The plants were pulled to an angular displacement of 15° from the vertical, with the forces measured to pull the plants over at 5°, 10° and 15°. These angles corresponded with distances of 1.5 cm, 3.0 cm and 4.5 cm as measured on the ruler. The plants were pulled over in four directions (north, south, east and west), the order of these being randomized. The plants returned to the rest position after being pulled therefore little plastic deformation had occurred in the root or shoot system.

The second series of tests determined the position of roots in the soil and their movements during overturning. The trenching method devised by Coutts (1983a) was used. A trench 10 cm deep and 16 cm wide was cut vertically downwards alongside the base of the stem in two plants of each treatment. The surface of the trench was sprayed with silver spray paint to show the development of cracks as the soil moved when a lodging moment was applied to the plant. The plant was displaced laterally from the vertical until failure occurred. Lateral roots could not be seen to break anywhere along their length so failure must have occurred in the soil and the roots displaced. When the lateral force was applied, all the plants rotated about a point on the leeward side 1-2 cm below the soil surface. Cracks in the soil formed 2 cm from

Fig. 4.3

Apparatus for measuring resistance to overturning



the stem on the windward side and 1 cm from the stem on the leeward side. Soil failure occurred around the edges of the soil ball and the soil was permanently sheared at these cracks. The soil ball was slightly displaced upwards on the windward side, horizontally underneath the plant and downwards on the leeward side. Similar observations were recorded by Coutts (1983, 1986) and Ennos (1993) who suggested that uprooting was resisted by the following components: windward roots held in tension; bending resistance of the leeward roots; the weight of the soil-root ball and the shear strength of the soil around the roots.

To find out the relative importance of the components in young larch trees and to see if they differed between the treated and the control plants, the same methods were employed as those of Coutts (1983, 1986) and Ennos (1993). The plants were pulled horizontally and resistance to overturning was measured. Each component which resisted uprooting was removed between pulls so that the components could be evaluated (Fig. 4.4):

1) The windward roots and soil were cut downwards 3 cm with scissors at a radius of 2 cm from the stem, the point of failure on the windward side.

2) The leeward hinge of roots and soil were similarly cut downwards 1 cm from the leeward side of the stem. The soil ball was prevented from sliding horizontally during pulling by holding a pair of closed scissors against it 2 cm below the soil surface on the leeward side. The closed point of the scissors were inserted into the soil at 45° where the cut had been made and held against the soil-ball. This also kept the centre of rotation in the same place.

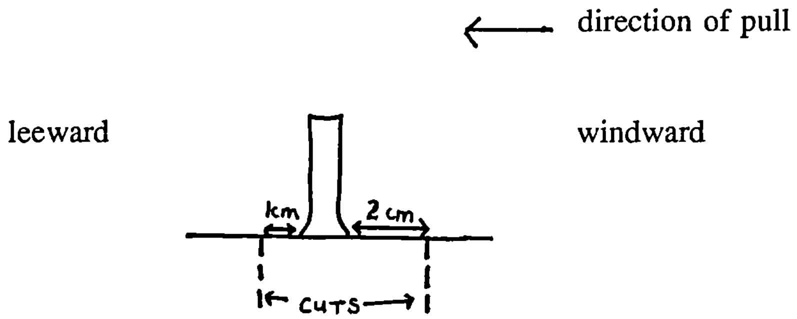
3) The soil underneath the ball was cut 2 cm below ground level so that the weight of the soil ball could be measured.

Twelve intact treated and control plants were used in the first series of tests. To measure total resistance, each plant was pulled to an angle of 10° from the vertical and allowed to return to its rest position using the method described above. This caused soil failure, and the forces measured were the sum of all components of anchorage. The windward component was then removed (1 above) and the plant pulled to an angle of 10° to the leeward side and allowed to return to the vertical. The leeward hinge

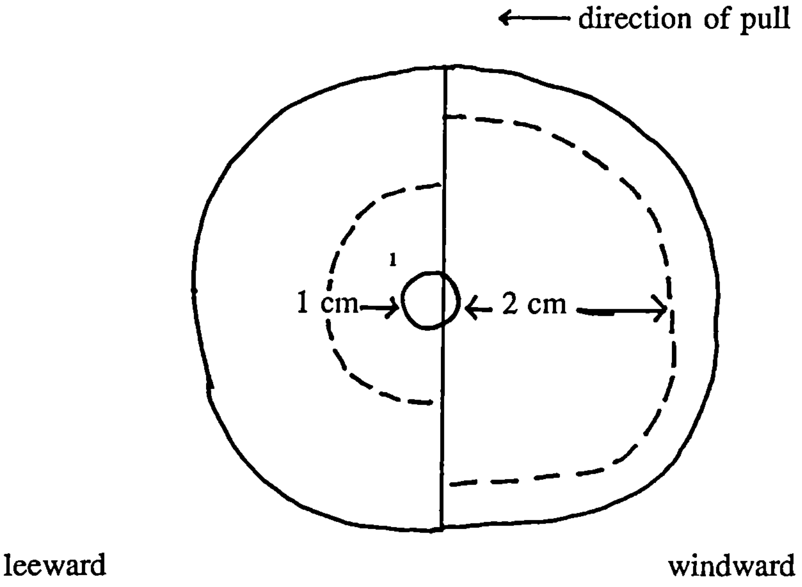
Fig. 4.4

Trenching and cutting methods used to identify and measure the components of anchorage in young European larch

a) Profile view



b) Plan view



[1] The point of rotation of the plant

was cut and the plant pulled again and finally the weight of the soil ball was measured. The sequence of manipulations were then reversed on twelve new larches, so that the leeward hinge of roots were cut before the windward roots.

4.2.3 Harvest of plants

Stem length for each plant was measured every four weeks throughout the growing season. The last measurement taken was on 2 February 1993 when the plants were harvested. The basal stem diameter of each plant was measured with vernier callipers, on 2 February 1993 in two directions: along the axis of the wind direction and perpendicular to it, so that any eccentric growth of the stem could be examined. The shoots were dried at 80° C for three days and the dry mass recorded. The following components of the root system were measured: lateral root basal diameter (using vernier callipers), number and azimuth of each lateral root off the main axis (using a protractor) and depth of each lateral root below the soil surface. The lateral roots were not woody enough to permit an architectural analysis.

Windspeeds were measured on 1 February 1993 and were found to have slightly decreased through the wind tunnels. Plants at the front of the tunnel still experienced windspeeds in the range 2.0 - 6.0 m s^{-1}, whereas plants at the far end of the tunnels were subjected to windspeeds of 0.5 - 2.0 m s^{-1}.

4.3 **Results**

4.3.1 Plant performance

There was less variation in the plant material than in the first wind tunnel experiment. There were no significant differences in any of the parameters of shoot growth measured between wind stressed and control plants (Table 4.1). Control plants appeared to have a greater biomass (8.8 ± 6.0 g) than wind stressed plants (6.7 ± 2.5 g), although the difference was not significant. However, growth increments in the wind-treated plants were affected by windspeed. The regressions of total height growth and stem diameter on windspeed were significant: plants became shorter (Fig. 4.5, $R^2 = 0.3$, $P = 0.025$); basal diameter was reduced in both directions (along axis of wind direction: Fig. 4.6, $R^2 = 0.16$, $P = 0.027$, perpendicular to wind direction: Fig. 4.6, $R^2 = 0.15$, $P = 0.039$) and shoot biomass was reduced (Fig. 4.7, $R^2 = 0.16$, $P = 0.035$) with increasing windspeed. Although the regressions of stem length and diameter on windspeed were significant, the R^2 shows that the proportion of the variation accounted for by the fitted line was small, therefore the relationship should be treated with caution. There were no differences in stem diameter towards the direction of the wind and perpendicular to it in wind-treated plants, so stems had not become eccentric in response to wind stress.

Table 4.1

Means of shoot growth variables (± standard deviation) measured in each treatment for European larch

	wind-stressed	**control**
Diameter (along axis of wind)	6.2 ± 1.1 mm	5.9 ± 1.3 mm
Diameter (perpendicular to wind direction)	6.0 ± 0.9 mm	5.9 ± 1.5 mm
Stem length	40.5 ± 11.2 cm	38.8 ± 15.6 cm
Shoot mass	6.7 ± 2.5 g	8.8 ± 6.0 g

Fig. 4.5 Relationship between total growth increment of stem length and windspeed for wind stressed European larch

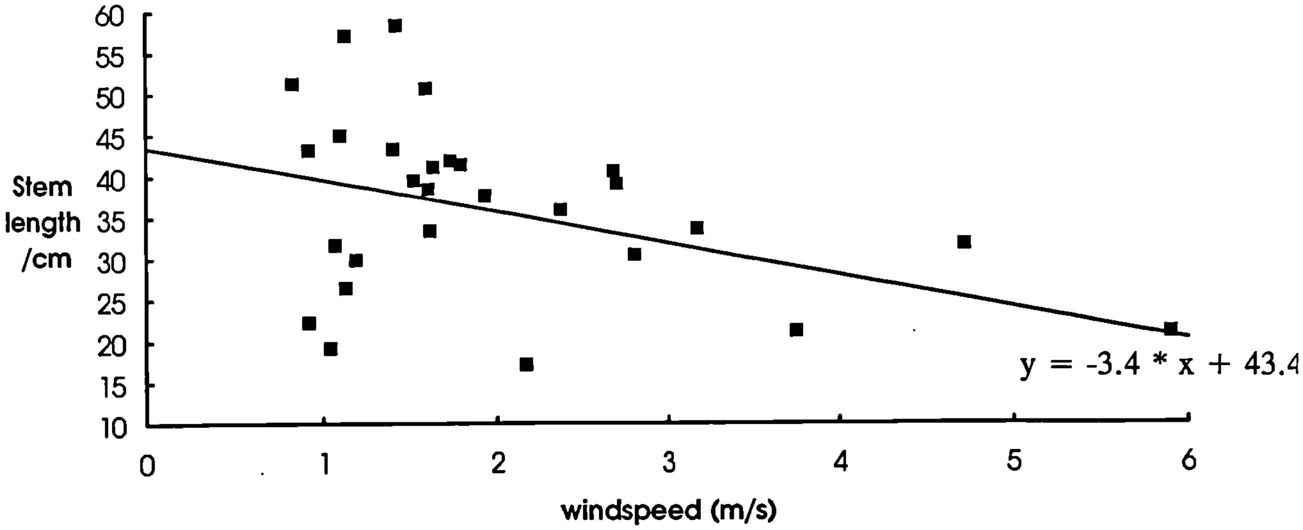


Fig. 4.6 Relationship between stem basal diameter of wind stressed larch and windspeed

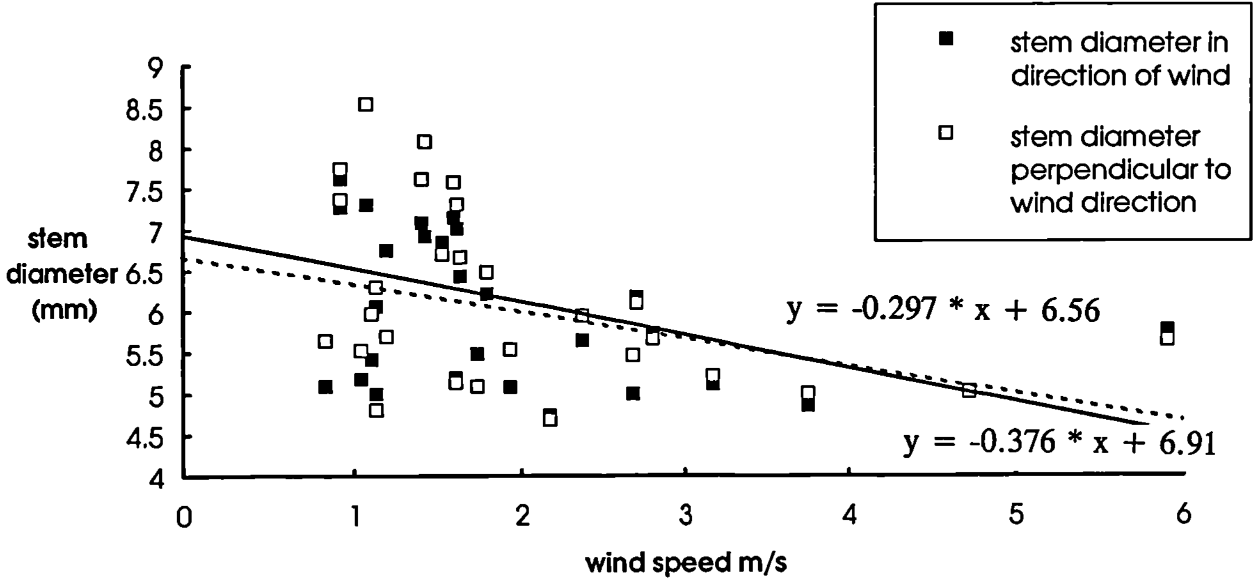
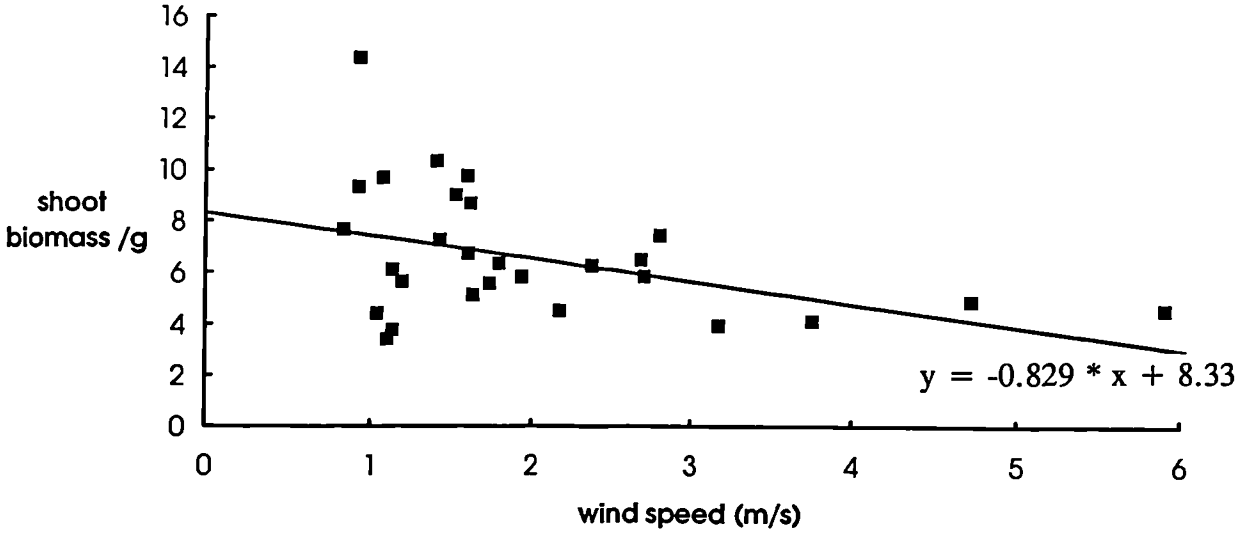


Fig. 4.7 Relationship between shoot biomass of wind stressed larches and windspeed



There were no significant differences in mean maximum or minimum soil temperature between the four directions within each pot throughout the growing season (April - October) (Table 4.2). In warmer weather, the maximum air and soil temperatures in the control tunnels were usually 2-3°C above that in the wind tunnels when the wind generators were on. However, in cooler weather, there were no differences in mean maximum air or soil temperature between the two types of tunnel (Table 4.2). There were no differences in mean minimum soil or air temperature between the wind and control tunnels in warm or cold weather.

Table 4.2

Mean temperatures (°C) (± standard deviations) between treatments for warmest and coldest weeks of growing season (April - October)

Position of probe & week starting	**Wind tunnel**		**Control tunnel**	
	maximum	**minimum**	**maximum**	**minimum**
Soil:8/8/92	31.4 ± 1.7	18.7 ± 0.1	36.5 ± 3.8	18.4 ± 0.4
26/10/92	20.3 ± 0.5	16.9 ± 0.4	19.8 ± 0.5	14.8 ± 0.8
Air: 8/8/92	31.0 ± 0.6	20.1 ± 1.2	35.3 ± 2.1	17.9 ± 0.8
26/10/92	25.2 ± 5.4	19.5 ± 2.7	21.4 ± 0.3	16.3 ± 1.0

4.3.2 Anchorage tests

First series of tests:

The force required to pull the plants over (Table 4.3) was not significant for either the direction of pull or treatment as determined by two-way analysis of variance. Generally, more force was required to pull the control plants over compared to the stressed ones. The overturning resistance was dependent on stem CSA and stem biomass at 15°, but surprisingly, not stem length as determined by analysis of variance using shoot variables as covariates (Table 4.4).

Table 4.3

Mean force (N) (± standard deviation) required to pull larch over at different deflections

Deflection	**wind stressed plants**	**control plants**
5°	0.29 ± 0.2	0.42 ± 0.6
10°	0.47 ± 0.3	0.73 ± 0.9
15°	0.65 ± 0.4	0.97 ± 1.1

Second series of tests:

The amount of resistance that each component provided against uprooting was converted into a percentage of the total turning moment for each tree (Tables 4.5, 4.6). These data were subjected to analysis of variance to determine differences between treatments and also the order of cutting of each component.

There were no significant differences between windblown and control plants in the anchorage moment or relative importance of the anchorage components. However, when windward roots were cut first, regardless of treatment, they provided less resistance to overturning than the leeward roots, a result that was marginally significant ($F_{1,23}$ = 3.98, P = 0.058). When the leeward roots were cut first, the windward roots supplied 57% more resistance than the leeward roots (Fig. 4.8, $F_{1,23}$ = 21.51, P = <0.001). The resistance provided by the weight of the soil ball was 51% greater when the leeward roots were cut first (Fig. 4.8, $F_{1,23}$ = 7.74, P = 0.011).

4.3.3 **Root measurements**

Root development was measured in 15° sectors around the central axis in an attempt to discover whether wind was altering root formation. Unlike the first wind tunnel experiment, all the lateral roots were important for anchorage irrespective of size, because the plants were younger and few roots were larger than 2 mm diameter. The numbers of lateral roots were again calculated for each 15° sector around the stem, where wind direction = 90°. Two large peaks emerged on the histogram of treated plants (Fig. 4.9). One peak was towards the direction of wind (90°) and the other exactly opposite, to the lee side (270°). There was an increase of 57 % of windward

Table 4.4

Regressions of force required to pull European larch over at a deflection of 15°, on shoot diameter and biomass

Variable	Wind stressed plants			Control plants		
	R^2	P	Equation	R^2	P	Equation
Basal stem diameter in wind direction	74.9	<0.001	0.184 * x + 0.47	86.5	<0.001	0.313 * x + 0.77
Basal stem diameter perpendicular to wind direction	77.7	<0.001	0.130 * x + 0.36	75.7	<0.001	0.334 * x + 0.81
Shoot biomass	30.0	0.028	0.128 * x + 0.15	90.2	<0.001	0.573 * x + 0.20

Table: 4.5

The components of anchorage (%) and moments (Nm) produced by the root systems of wind stressed larch

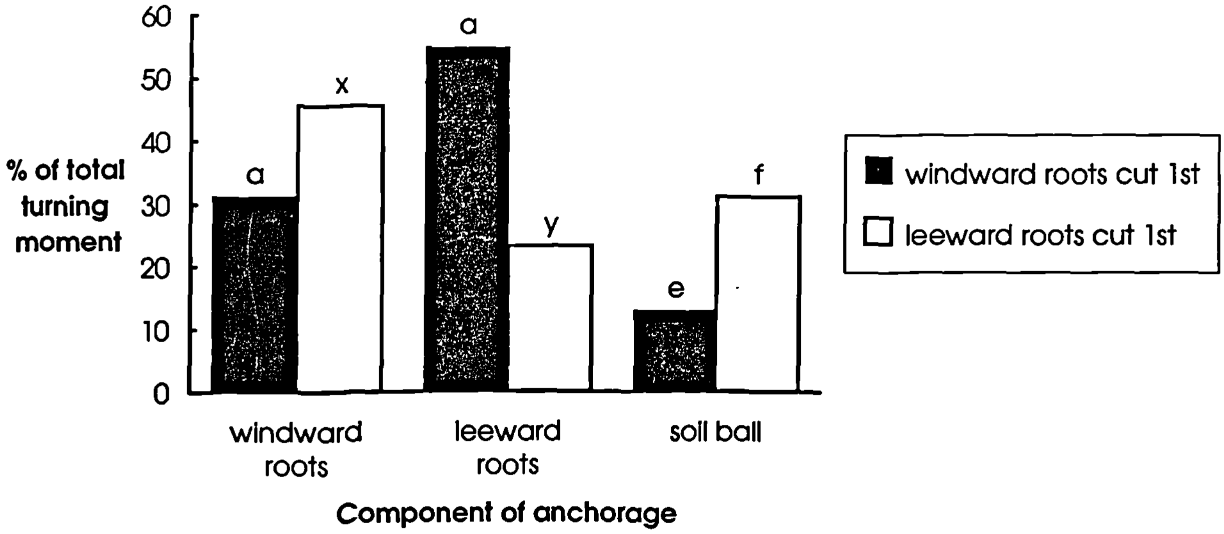
Plant	**Anchorage moment at 10° (Nm)**	**Percentage of total**		
		Windward roots	**Leeward roots**	**Weight of ball**
<u>Windward roots cut first</u>				
1	0.52	61	36	4
2	0.35	29	69	2
3	0.77	22	45	22
4	0.46	13	85	2
5	1.80	44	39	17
Mean ± st.dev.	0.78 ± 0.59	34 ± 19	55 ± 21	9 ± 9
<u>Leeward roots cut first</u>				
6	0.54	33	37	30
7	0.27	37	43	20
8	0.72	39	31	30
9	0.62	41	10	49
10	0.32	28	25	47
11	0.38	100	0	0
Mean ± st.dev.	0.48 ± 0.18	46 ± 27	24 ± 16	29 ±18

Table: 4.6

The components of anchorage (%) and moments (Nm) produced by the root systems of control larch

Plant	**Anchorage moment at 10° (Nm)**	**Percentage of total**		
		Windward roots	**Leeward roots**	**Weight of ball**
Windward roots cut first				
1	0.52	29	69	2
2	0.36	39	58	3
3	0.42	14	85	1
4	1.20	23	62	15
5	0.86	24	48	28
6	0.40	48	33	19
7	0.63	30	29	41
Mean ± st.dev.	0.63 ± 0.31	30 ± 11	55 ± 20	16 ± 15
Leeward roots cut first				
6	0.41	71	15	14
7	0.96	61	18	21
8	0.77	26	22	52
9	0.72	39	22	39
10	1.10	40	44	16
11	1.80	47	34	19
12	0.53	31	2	67
Mean ± st.dev.	0.90 ± 0.46	44 ± 15	22 ± 14	33 ± 21

Fig. 4.8 Resistance to overturning provided by each component of anchorage with regards to the order of cutting



Columns differently superscripted differ at $P = 0.05$

roots and 49 % of leeward roots compared to roots growing at right angles to the direction of the wind. In the control plants, three peaks appeared, all smaller than the two large peaks in the treated plants. One peak was in the direction of wind (90°), one opposite on the lee side (270°) and the third peak perpendicular to the flow of wind (180°). Chi-square analysis of the numbers of lateral roots and their orientation in wind stressed plants against those from the control tunnel showed that the two treatments were significantly different from each other ($P = 0.02$).

The increase in numbers of roots on the windward and leeward sides could imply a greater total root growth in these regions. The sum of the cross-sectional area (Σ CSA) of the bases of the roots growing on windward and leeward sides and perpendicular to these directions was calculated using 30° sectors. The two perpendicular sectors were combined as there should be no difference between them. Data were subjected to analysis of variance to determine the differences between sectors, using appropriate transformations (logarithm for Σ CSA where not normally distributed).

The wind stressed larches had a significantly larger Σ CSA in the leeward sector than both the other sectors (Table 4.7, Fig. 4.10, $F_{2,106} = 6.78$, $P = 0.002$). The mean CSA per root was almost significantly larger in the leeward sector (Table 4.7, $F_{2,132} = 2.48$, $P = 0.087$). The control plants had a significantly larger log Σ CSA in the sectors perpendicular to the wind direction than the other sectors (Table 4.7, Fig. 4.10, $F_{2,102} = 8.51$, $P = < 0.001$). There were no differences in mean CSA between the sectors of the control plants (Table 4.7).

Fig. 4.9 Numbers of European larch lateral roots in the top 20 mm of soil for both control and wind stressed plants

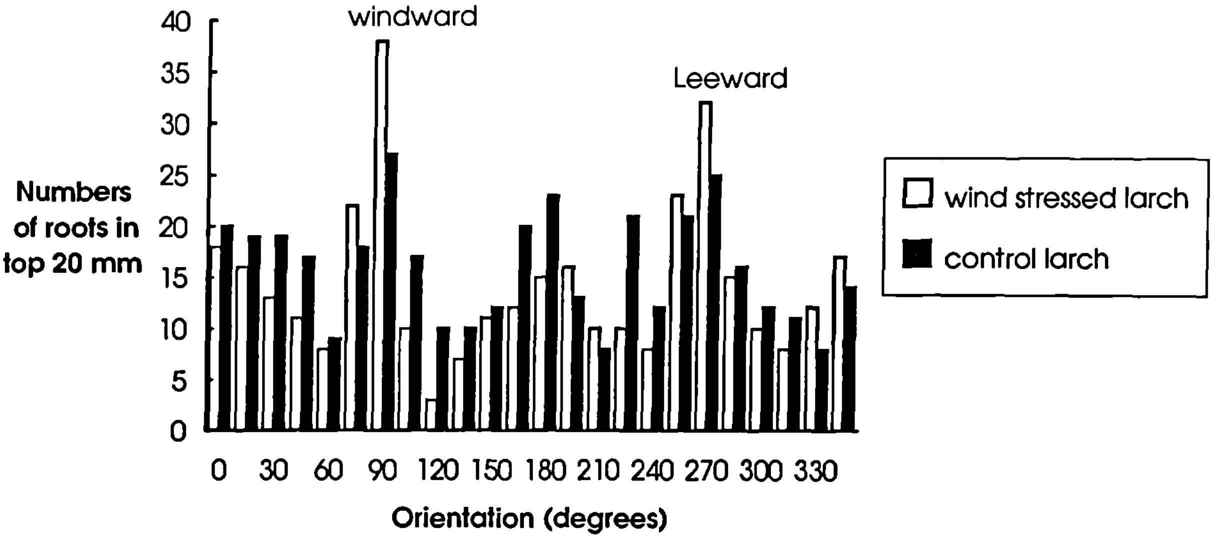
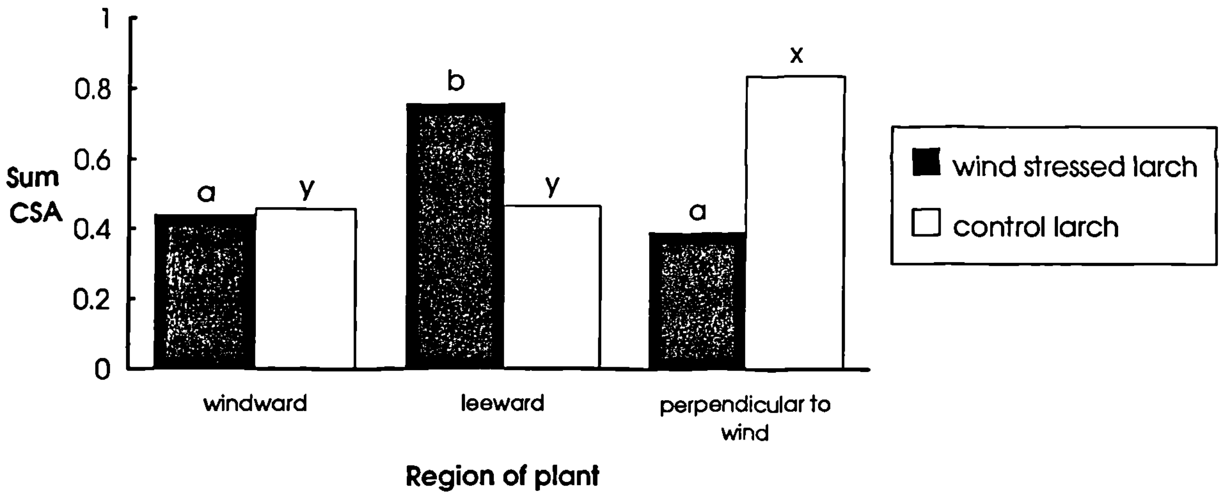


Table 4.7

Log Σ and mean CSA (mm^2) (± standard deviation) of lateral roots in each sector around the plant

	wind stressed plants			**control plants**		
	windward	**leeward**	**perpendicular to wind**	**windward**	**leeward**	**perpendicular to wind**
Σ CSA	0.44	0.76	0.39	0.46	0.47	0.83
Mean CSA	2.27 ± 2.3	4.3 ± 5.3	3.44 ± 4.3	2.80 ± 3.1	4.66 ± 4.8	3.27 ± 3.4

Fig. 4.10 Sum CSA of wind stressed and control European larch root bases in top 20 mm of soil in sectors around the plant's central axis



Columns differently superscripted differ at $P = 0.05$

4.4 Discussion

Variation in the plant material was greatly reduced in this experiment compared to European larch in the first wind tunnel experiment (Chapter 2). The air and soil temperatures were not consistently different between tunnels and there were no significant differences in soil temperature within each plant pot, so temperature as a factor affecting root growth within a root system was negligible.

Stem length and stem basal diameter of wind stressed plants were reduced with increasing windspeed. The maximum windspeed was nearly twice as strong in this experiment as in that described in Chapter 2 and the range of windspeeds experienced by the plants was larger (1.9 - 11.2 mph) which may explain the greater changes in shoot growth in the second experiment. Changes in plant physiology are known to occur with different windspeeds: wind induces a reduction in leaf area and so the effective photosynthetic area is decreased (Heiligmann & Schneider 1974, Rees & Grace 1980a). This is known to occur in mechanically shaken trees (Ashby *et al.* 1979) as well as wind stressed plants, so is considered a direct effect of mechanical stress (see Telewski 1993). However, movement by mechanical shaking would also alter the local environment around the leaf, which may affect the vapour pressure deficit (VPD) and disturb the boundary layer, so that the mechanism might be the same in both cases. Sitka spruce stomata respond to changes in the water vapour pressure of the air at the leaf surface (Grace *et al.* 1975). As windspeed increases, there is an increase in vapour pressure gradient between the evaporation site and that calculated for the leaf surface (Bunce 1985), resulting in stomatal closure. Closure reduces transpiration and increases leaf water potential (Pappas & Mitchell 1985). Ultimately, a reduction in photosynthetic rate will occur with increasing windspeed, which will have a direct effect on the amount of photosynthates available to the meristematic regions.

The negative correlation of stem basal diameter with increasing windspeed may be due to the decrease in photosynthetic rate, and has not been previously observed. These results are in contrast with most studies (*eg.* Quirk *et al.* 1975, Telewski 1989) where stem radial growth increases with mechanical stimulation, such as flexing or shaking.

However, only one study of the effect of wind action on young trees in the laboratory found that stem radial growth increased under multidirectional wind loading (Larson 1965). Rees & Grace's study on *Pinus contorta* (1980) and Heiligmann & Schneider's study on *Juglans nigra* (1975) both found no changes in stem radial growth when plants were grown under high windspeeds compared to low ones. In Chapter 2, eccentric growth of the base of the stem was observed in wind stressed larch when the shoots were removed from the root system. Extra woody material was found on the leeward side of the biological centre. It seems likely that although total CSA decreases as a result of reduced photosynthesis, there appears to be a shift in the distribution of resources which causes an increase in woody growth at stressed areas. Eccentric growth would only be obvious on sectioning the stem and external measurements would not take it into account, which may explain why Heiligmann & Schneider (1975) and Rees & Grace (1980) found no differences in stem radial growth at high windspeeds. The increase in woody growth is due to an increase in the number of tracheids on the lee side which may allow the displaced stem to return to a vertical position (see Telewski 1993).

The first series of anchorage tests which measured the overturning moment in different directions for both wind stressed and control trees showed no significant differences in the force required to pull plants over to windward, leeward or perpendicular to these two directions. As was thought in the first wind tunnel experiment, where the overturning moment of Sitka spruce was measured in four directions around the plant, this failure was probably not due to experimental technique. The force meter used had a small range (0 - 1 N) and was small and light, unlike that used in the first experiment. There was an almost significant difference in overturning moment between wind stressed and control trees. The control trees needed about 35 % more force to deflect them 10° and 15° compared to the wind stressed trees. For all trees the overturning moment was dependent on stem basal CSA and it is known that stem bending rigidity is proportional to the fourth power of its radius. There were no significant differences in basal stem radius between wind stressed and control trees. One possible explanation for the reduction in overturning resistance in wind-treated plants is that they had a larger stem CSA at the point of deflection *i.e.* 10 cm above ground level. Although the parameters of shoot growth that were measured were not significant between treatments, mean shoot biomass was 24 % greater in the control treatment (Table 4.1). The extra shoot biomass in the control plants must be distributed throughout the shoot system, possibly as radial growth further up the stem, which would increase bending resistance. An increase in the growth of the lower stem at the expense of the upper stem has been documented (Jacobs 1954, Quirk *et al.* 1975) and Larson (1965) suggests that a downward distribution of assimilates occurs in wind stressed plants thus resulting in increased stem taper. Measurements of the stem radial growth at intervals up the stem, are needed to clarify this, leading to a better understanding of the relationship between bending resistance and stem form. Trees with increased stem taper may resist wind loading more efficiently than trees with a more uniform stem CSA because the flexural stiffness will be reduced further up the stem, enabling the tree to bend more in the wind, before breaking. Mean horizontal windspeed in the field declines towards the ground (see Grace 1977), so increased stem flexibility up the stem is a feature with adaptive value. An alternative explanation for the increase in force needed to pull the control larch over, is that stem material properties may have differed between the wind stressed and the control plants. Telewski and Jaffe (1986a,b) observed that in the stems of mechanically perturbed *Abies fraseri* and *Pinus taeda*, the second moment of area (I) increased and Young's Modulus of Elasticity (E) decreased *i.e.* stems became wider with increased flexibility. A lower value of E means that a tree will absorb more energy when the same amount of bending force is applied to the stem. EI is the determinant of displacement therefore, as there was no significant difference in stem basal diameter (and therefore I) between wind stressed and control larch, a decrease in stem E might explain why it was possible to deflect the wind stressed plants further using the same amount of force as that to pull over the control plants.

The anchorage tests where the components of anchorage were removed in order to investigate each one's contribution to anchorage provided no clear answers to the mechanisms of failure during windthrow. Ennos *et al.* (1993) criticized the experimental technique used because of its "crudeness." They realised that the destruction of the different parts of the root system may have altered how other parts behaved and each pull would damage the remaining components of the anchorage system. Coutts (1986) found that with mature Sitka spruce, an important problem with the cutting technique was failure of the root-soil plate to return to its original position when lowered back into place. The possibility that the first pull may damage the hinge by an unknown amount was considered, but as low values for resistance of the hinge to bending were expected, it was presumed that the errors due to technique were small. Ennos altered the sequence of destruction in an attempt to eliminate experimental error, and although he obtained variable results, the mean results were very similar. However, the results from the series of tests described in this experiment implied that the order of cutting is an important factor to be considered. It is unclear why, when the windward roots are cut first that they should provide less resistance to overturning than if the leeward roots are cut first, and why the mass of the soil ball should alter depending on the order of cutting. If the roots were cut in the wrong positions, *i.e.* too far proximally or distally along the roots, this could make a substantial difference to the contribution of each component to anchorage. The roots were cut where soil failure was seen to occur when a trench was cut in the soil alongside the root system, and the trees were pulled over. Although the plants showed less variability than those in the first wind tunnel experiment (Chapter 2), there was still a considerable range of size class (stem length: 16.5 - 70.5 cm) within and between treatments. Such a large range would be amplified in plants with a mean stem length of only 39.7 cm stem length and may be reflected in the root growth. Consequently root growth would also be highly variable between plants. Even though four plants of different stem lengths were used to examine soil failure, they may not have been representative of all the plant material. This might mean that for each plant, cuts should have been made at different radii from the stem, depending on the size of the plant. The plants used in Coutts' and Ennos *et al.*'s experiments were much less variable in size which may explain the success of their tests. The technique of assessing anchorage components by destroying individual ones to quantify others has proved useful where fairly uniform plant material has been used, but is inadequate for variable material. In this respect, it is probably not a good technique to use to understand which components of root anchorage have been strengthened by the treating with and without wind stress, as there may be a great deal of variation in growth both within and between plants in the two treatments.

The pattern of lateral root number and orientation off the main axis that developed in the larch is more pronounced but strikingly similar, to that of both Sitka spruce and European larch in the first wind tunnel experiment (Chapter 2). In this study, the number of roots in each 15° sector was increased by 57 % in the windward sector and 49 % in the leeward sector, compared to the numbers of lateral roots growing perpendicular to the direction of wind. In the first wind tunnel experiment (Chapter 2), in both species there was an increase of almost 60 % in the number of roots in the windward 15° sector and 41 % in the leeward sector of larch trees. This suggests that a non-uniform distribution has readily developed in European larch and wind can alter that distribution with very similar patterns of root growth forming under different windspeeds.

Larch leeward roots had a slightly larger mean CSA of root base per root than roots from the other sectors, and Σ CSA was also increased in the leeward sector. The control plants had more roots and a larger Σ CSA of root bases in the sectors perpendicular to the wind direction, where the smallest roots were found in the wind stressed plants. Instead of resources being sent to the tap root which was present in plants in the first experiment, resources were diverted to windward and leeward lateral roots, which increased in number and cross-sectional area in the top 20 mm of soil. Again it appears that the distribution of resources within the root system has altered so that those roots most important for anchorage receive the most resources. The greater number of larger windward and leeward lateral roots, means that the total root surface area in these two regions has increased which may improve pull-out resistance. The higher the concentration of roots per unit area of soil, the greater the tensile strength of the soil (Wu 1976), so a larger number of roots on the stressed sides, especially on the windward side, where the roots are held in tension and are the most important in resisting uprooting, as mentioned earlier (Coutts 1983a,1986, Ennos *et al.* 1993), may increase tree stability with regards to wind from one direction. The possible increase in radial growth of root bases on the leeward side indicates that these roots have a higher resistance to bending (bending rigidity is proportional to the fourth power of radius) and implies that these roots may be receiving more assimilates. Roots perpendicular to the direction of wind are subject to torsion and will offer little resistance to uprooting. European larch therefore responds to wind-induced stresses by enhanced growth of roots in the most effective positions for promoting anchorage, namely on the leeward and windward sides of the tree.

The mechanism by which extra growth occurs in mechanically stressed regions has been mentioned in Chapter 2 and discussed in detail in Chapter 1. Again, resources appear to be diverted to regions which are subjected to a large amount of wind loading, and at the expense of other parts of the plant. European larch is obviously sensitive to wind, shown by the negative correlations of the shoot growth variables measured with increasing windspeed. These results suggest that unidirectional wind may result in adaptive responses in trees from a very early age. The increase in woody growth in areas of high mechanical stress in plants subjected to wind loading are of an ecological advantage especially as the increase in number and size of windward and leeward lateral roots should result in a tree able to withstand greater stresses with less likelihood of uprooting.

Chapter 5

Responses of young Sitka spruce clones to mechanical perturbation: effects on root growth and pull-out resistance

5.1 Introduction

Damage by windthrow causes huge economic losses to British forestry. Damage is particularly severe in upland sites which are subject to winter waterlogging causing periodic dieback of Sitka spruce and larch roots. This leads to the formation of a shallow soil-root plate which is unstable when exposed to strong winds (Fraser & Gardiner 1965, Armstrong *et al.* 1976). Drainage techniques have been used in an attempt to reduce the height of the water table (Saville 1976) but attempts to select and breed trees with characteristics likely to promote better anchorage have only just begun (Nicoll *et al.* 1993).

Clones of Sitka spruce which have been selected for improved shoot characteristics, such as fast growth rate and stem straightness, are being used more frequently in forestry plantations. Nicoll *et al.* (1993) asked whether improved shoot growth in these trees was due to a particularly efficient growth rate or was it at the expense of the root system? If the latter was true, a reduction in the root:shoot ratio might be expected to make trees more prone to windthrow. Their results indicated that improved clones of 11 year-old Sitka spruce grown in the field allocated the same biomass to fewer woody lateral roots than control trees. The root:shoot ratio was found to be a poor indicator of tree stability when the stump was included as part of the root biomass. The amount of branching in the proximal 45 cm of the root system also differed between clones. These results imply that detailed analyses of structural root systems are required to determine which clones are likely to have greater stability.

Mechanical perturbation by exposure to wind, shaking, flexing (movement in two directions only) or torque stress have been shown to reduce height and increase stem taper (Larson 1965, Quirk *et al.* 1975, Telewski & Jaffe 1986b). It has been assumed that these effects increase the plant's ability to resist mechanical stresses (Jaffe 1973, Lawton 1982). Such stresses can also influence the physical properties of plant cell walls. Studies on *Phaseolus vulgaris* have shown that mechanically perturbed plants are able to bend more than 90° without breaking whereas the control plants could only bend a few degrees before stem failure (Jaffe *et al.* 1984). An increase in Young's Modulus of elasticity, and plasticity in the stems of mechanically perturbed *Pinus taeda* and *Abies fraseri* was attributed to a wind-induced decreased flexibility caused by increased stem radial growth (Telewski & Jaffe 1986a,b). Telewski & Jaffe (1986a,b) suggested that the changes in biomechanical properties caused by wind-induced stresses are adaptive. If mechanical perturbation changes stem allometry, the resistive bending moment in trees may also alter between perturbed and non-perturbed trees. Tateno (1991) found that in *Morus bombycis* (mulberry tree) the lodging safety factor (ratio of critical lodging load to leaf fresh weight) was increased in trees which were rubbed, brushed and shaken every day compared to control (unperturbed) trees. The only significant difference in the shoot variables between the two treatments was stem length, which was reduced in the perturbed plants and was thought to be the cause of the increased lodging safety factor. It is not known whether wind-induced changes in the growth of Sitka spruce alters resistance to windthrow and whether clones differ in their response to lodging. Anchorage tests carried out in the first wind tunnel experiment (Chapter 2) showed no changes in the amount of deflection when Sitka spruce was pulled over in different directions (windward, leeward and perpendicular to the direction of wind) with a given force. However, the windspeeds experienced by the plants were very low, and there were no significant changes in stem allometry. An understanding of the effects of wind loading on pull-out resistance of Sitka spruce clones will facilitate selection and breeding of trees with characteristics likely to promote tree stability.

Results from the wind-tunnel studies carried out in Chapters 2 and 4 show that there is an uneven distribution of lateral roots around the plant's central axis, and that wind can alter that distribution. As resource allocation has changed *between* roots in wind-stressed plants, it seems possible that a change in allocation may also occur *within* a root. Wilson (1975) staked 10 m tall *Pinus strobus* and compared them with free-standing trees after four years. He reported that in the free-standing trees, secondary growth was stimulated on the bottom of the root rather than the top, for the 100 cm nearest the stem, although he could find no explanation for it. Roots that are bent on one axis can become oval or even shaped like an I-beam in cross-section. This eccentricity increases the roots' resistance to bending in the direction of stress (M.P. Coutts pers. comm.). It should be possible to identify whether wind affects the distribution of resources resulting in eccentricity within a root. If there is a change in the radial growth of the structural roots as a result of mechanical perturbation, it may be possible to use this characteristic as an indicator of tree stability.

As the distribution of biomass between the structural roots differs between clones of Sitka spruce, resulting in asymmetry (Nicoll *et al.* 1993), the responses of clones to shaking may affect such asymmetry within the root system. If there are changes in biomass allocation within root systems, the topological index of woody roots from the mechanically stressed areas may also be affected. Wind stressed Sitka spruce from the first wind tunnel experiment (Chapter 2) showed increased branching of woody roots on the windward side of the plants compared to the leeward side. The decrease in topological index on the windward side means that there was an increased concentration of roots per unit volume of soil, which would have increased the tensile strength of the soil (Wu 1976), a feature with obvious adaptive value. It is striking that a change in the morphogenesis of woody roots occurred at such low windspeeds (0.46 - 2.9 m s^{-1}). If deflection of the plant were increased, as would happen under stronger wind velocities, an increase in the branching of woody roots might occur in the region of mechanical stress. As mentioned earlier, Nicoll *et al.* (1993) found differences between Sitka spruce clones in the amount of branching in the proximal 45 cm of the root system. Clones with increased branching on the windward side of the structural root system will be more likely to withstand uprooting.

Although root development can be greatly affected by nutrient supply, responses of plants to wind loading under different levels of mineral nutrition are unknown. Under low nutrient levels, the topological index of dicots (angiosperms) is lower, resulting in increased root branching per unit volume of soil (Fitter & Stickland 1991). As seen in the first wind tunnel experiment (Chapter 2) increased lateral root branching of Sitka spruce occurs in areas of mechanical stress, namely the windward side of the tree. The combined effects of low nutrient availability and effects of mechanical stress might lead to increased stability. If trees are deficient in minerals, that response may result in them utilizing their resources in the most effective way to minimise the effects of wind loading.

In this study, three year-old clones of Sitka spruce were mechanically perturbed by flexing in two directions only. Flexing was used as the mechanical stress imposed on the plants because it allowed many replicates to be subjected to exactly the same mechanical stress. Wind-tunnel studies do not allow the same uniformity of conditions, because the wind experienced by each plant differs in velocity and direction. Trees were grown under two nutrient regimes so that the combined effects of mechanical stress and mineral nutrition could be evaluated. Resource allocation was examined with regard to pull-out resistance, asymmetry within a root system, and eccentricity and root architecture within individual structural roots.

5.2 Materials and Methods

5.2.1 Growth conditions

A tree flexing machine was set up in a glasshouse at the Forestry Commission's Northern Research Station, Edinburgh (Fig. 5.1). The machine consisted of an electric motor attached to a dexion frame with an internal dimension 3.2 x 8 m and height 27 cm. There were 16 cross-bars of dexion, oriented parallel to each other and perpendicular to the motor. Eight were connected to the main frame, and eight stationary, alternate cross-bars were not attached to the mainframe. The machine pulled the cross-bars 5.5 mm in two directions only, due north and south, from a central position. Ten plants were grown adjacent to each cross-bar; unshaken control plants were fixed to the stationary bars and shaken plants to the moving bars. Plants were fitted with protective foam rubber collars where they were attached to the cross pieces (11 cm above ground level) (Fig. 5.2). The flexing machine was operated from 0900 to 1500 and 2100 to 0300. The force applied by the machine to each plant was 4 N in each direction, assessed by deflecting each cross-piece 5.5 mm and measuring the force required with a spring balance.

Nine clones of 3 year-old Sitka spruce (*i.e.* three years from cloning) were used and one plant from each clone was attached to each cross-bar. The clones were from 4 different families (coded 68, 69, 71, 76). A Queen Charlotte Island (Q.C.I) seed lot (coded 70) was also used (Table 5.1). All plant material was supplied by Newton nursery, Silviculture North Branch, The Forestry Authority.

Fig. 5.1

Design of the tree flexing machine

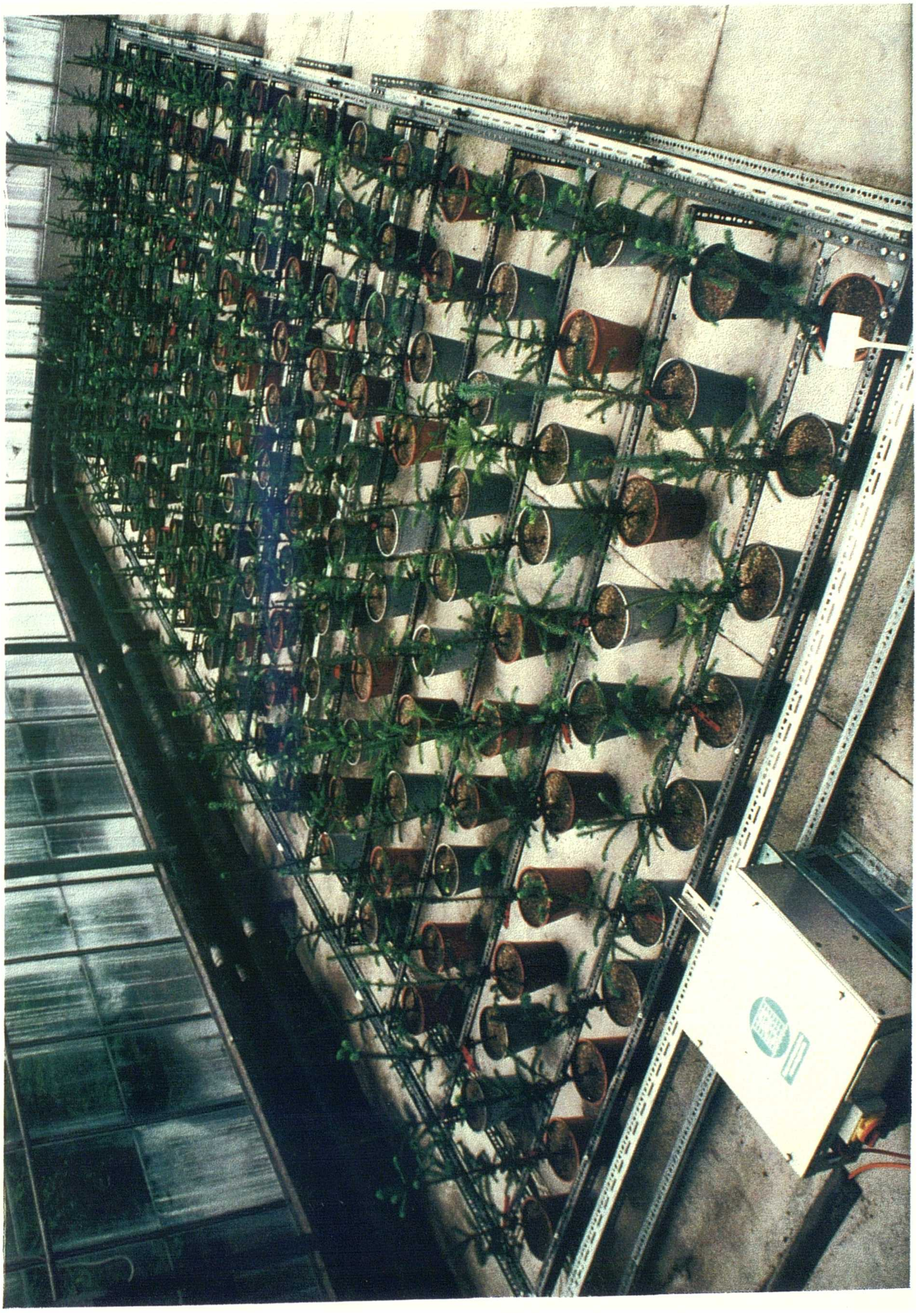


Fig. 5.2

Sitka spruce fitted with protective foam rubber collars and attached to cross-pieces

Table 5.1

Identities of Sitka spruce clones

Identity Number	**Forestry Authority Clone number**	**Letter used for labelling in the experiment**
71(4920P) 2R	C156	A
71(4920P) 2R	C157	B
71(4920P) 2R	C158	C
71(4920P) 2R	C159	D
69(4210P) 2R	C188	E
69(4210P) 2R	C191	F
76(13700P) 2R	C192	G
76(13770P) 2R	C199	H
70(7111) 1 LOT 12 R	C327	I
68(9800P) 3R	C323	K

The plants were potted up on 27 March 1992, in 5 l (19 cm diameter) pots of peat/sand (50/50 volume) containing 2 g l^{-1} or 0.4 g l^{-1} Osmocote Plus 8-9 month formulation slow release fertilizer, (N P K, 16.18.12 + 2 MgO). The pots were filled to within 3 cm of the final soil level. The roots of each plant were spread out on the soil, with one large root always placed along the axis of flexing and one perpendicular to this axis. The pots were marked to show the orientation of these roots before the soil was added to the final level, 1 cm below the rim of the pot.

The 16 plants of each clone were arranged into 8 pairs, with the plants in each pair as alike as possible with regards to stem length and diameter. Ten pairs, one from each clone, were arranged in random order along the length of two adjacent cross-bars. One plant from each pair was chosen at random to be attached to the moving cross-bar, and the other to the stationary cross-bar. Each set of 10 pairs of plants formed one block of the experiment and there were four blocks in all. Low nutrition (0.4 g Osmocote 1 l^{-1}) was applied to two blocks and high nutrition to the rest. The blocks were arranged alternately.

5.2.2 Anchorage tests

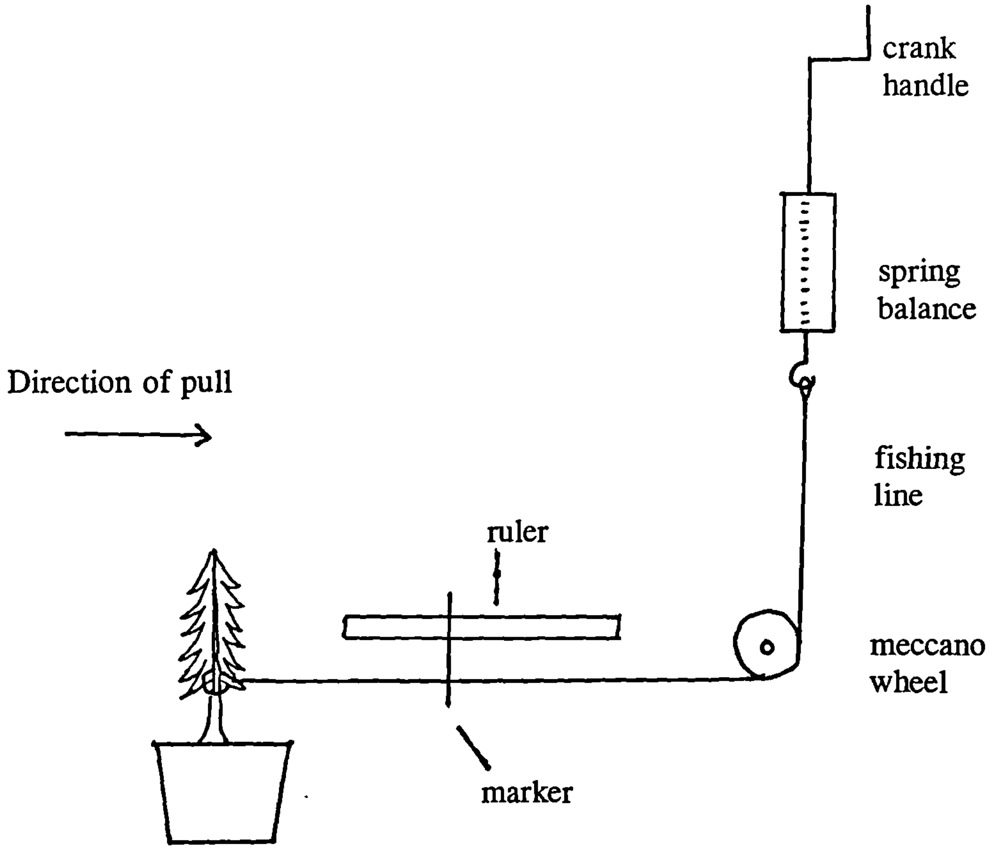
Three pairs of plants from each clone were subjected to anchorage tests on 30 July 1992 and 27 October 1992. The force required to pull each plant over laterally in 4 directions (due north, south, east and west) was calculated. Plants from the high nutrient treatment were tested initially, because plant growth in the low nutrient treatment was poor and differences were not expected between clones. A winching device was set up in which a spring balance was connected to the plant with fishing wire *via* a pulley (Fig. 5.3). The wire at the plant end was wrapped in plastic tubing and looped around the plant stem at a height of 11 cm (where the plant had been attached to the cross piece). A ruler was placed horizontally behind the plant to measure stem deflection as the plant was pulled. The plants were successively pulled to deflections of 24°, 45° and 58° (5, 11 and 17 mm as measured on the ruler), 45° being the maximum angle that the stems were deflected from the vertical when the flexing machine was in motion. The plants were pulled over at deflections of 24° and 58° so that the uprooting curve derived from the results would enable the detection of any plastic deformation of the stem or root system occurring during overturning. The force required to pull each plant was measured on the spring balance. The order of the directions in which the plant was pulled was chosen randomly and recorded. From the results of the anchorage tests performed on plants in the the high nutrient treatment, 4 clones were chosen which seemed to have contrasting mechanical properties (F, G, H and K). In addition, the same anchorage tests were carried out on three pairs of plants from each of these clones in the low nutrient treatment.

5.2.3 Harvest of plants

Stem length was measured every 14 days, and stem diameter at a height of 3 cm on 8 July 1992 and at the final harvest on 27 October 1992 by M.P. Coutts and B.C. Nicoll. From the results of the anchorage tests, four clones were chosen to analyse further (F, G, H and K) in the high nutrient treatment only, because they appeared to show contrasting mechanical properties. The stems were removed at ground level and dried at 80° for 3 days. Root systems were carefully excavated and washed. The number, orientation from due north, depth below soil surface, basal diameter and biomass of woody and fine root per lateral root, were measured for all the main lateral

Fig. 5.3

Winching device to pull young Sitka spruce horizontally



lateral roots of each plant.

The two roots on each shaken and control plant that were positioned along and perpendicular to the axis of flexing were analysed further. The fine roots were manually stripped off the main woody root and the skeleton retained for architectural analysis as described in Chapter 2.3.4. Eccentric growth at the stem base of these roots was also examined. Discs (2 mm thick) were cut with a bandsaw of the root bases and also the root stumps at ground level. The uppermost surface of each stump was marked with indelible ink on the north-facing side. The top of each root was marked in a similar way on the face of the disc nearest to the plant stem. The diameter of each disc was measured across the biological centre in two directions (due north to due south and due east to due west) with a Magiscan image analysis system, so that eccentricity between the top and bottom and sides of the roots could be examined.

5.3 Results

5.3.1 Anchorage tests

The uprooting curves (*i.e.* force required to deflect plant against angular displacement) of both flexed and control Sitka spruce appeared to be linear up to a deflection of 58° of the stem from the vertical axis (Fig. 5.4). Failure of the roots or soil matrix had therefore not occurred up to the maximum deflection of 58°, so repeating the anchorage tests on each plant in different directions was valid, but this meant that it was not possible to detect when failure occurred. Analysis of variance was used to determine the differences between the treatments, clones and direction of deflection, using log transformations where appropriate. Although the plants were pulled in four directions, only two axes were considered important, along the axis of flexing and perpendicular to it. There should be no differences between two directions along the same axis. Therefore, means were taken of the resistance to overturning required to pull the plants to due north and south (along the axis of flexing) and east and west (perpendicular to the axis of flexing).

Two way analysis of variance of the mean amount of force required for overturning showed that neither treatment (flexed or control) nor clone were significant for plants in the high nutrient treatment in the first or second series of tests at any deflection, either along the axis of flexing or perpendicular to it. When the mean of the force needed to pull each plant over in all directions was taken, the interaction term between clones and treatment was significant at a deflection of 24° in the flexed plants, in the first series of tests only (July 1992). A one way analysis of variance was then carried out for resistance of each clone to overturning at a deflection of 24° (Fig.5.5, $F_{9,20} = 2.41$, $P = 0.049$). Clone B (flexed) provided the most resistance to overturning (2.7 ± 1.37 N), and clone F (flexed) the least (1.2 ± 0.4 N).

In the low nutrient treatment (October 1992) two way analysis of variance showed that there were significant differences between flexed and control plants at all deflections along the axis of flexing only. One way analysis of variance of resistance to overturning along the axis of flexing at all deflections, showed that flexed plants always provided a larger resistance than the control plants (Table 5.2, Fig. 5.6).

Fig. 5.4 Uprooting curve for Sitka spruce

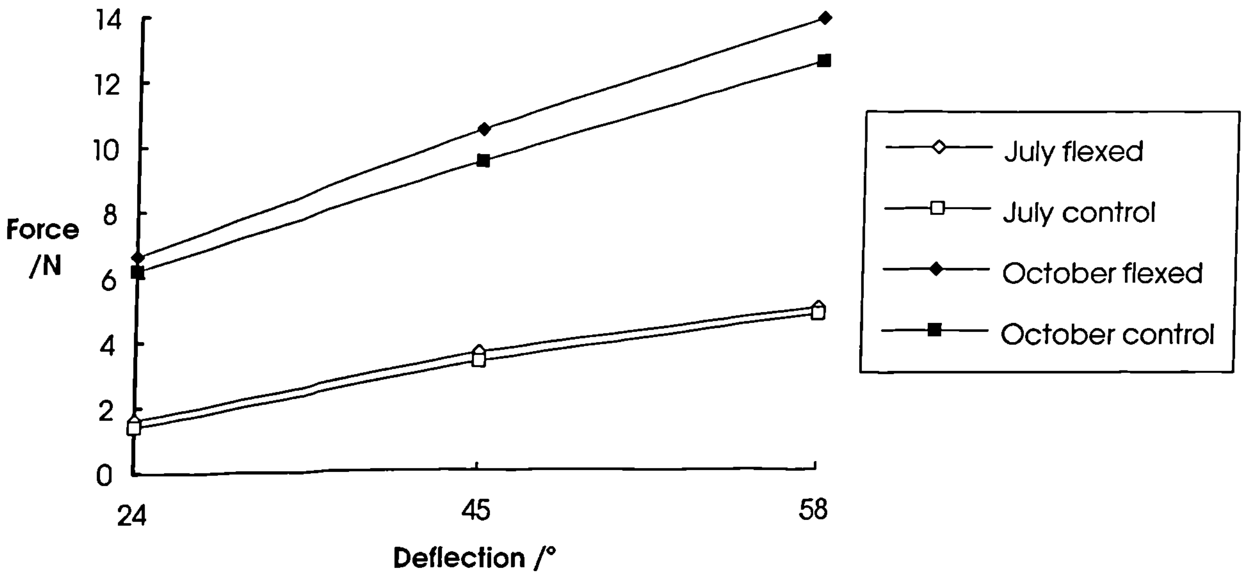


Fig. 5.5 Mean force required to pull Sitka spruce clones over 24° (High nutrient treatment, July 1992)

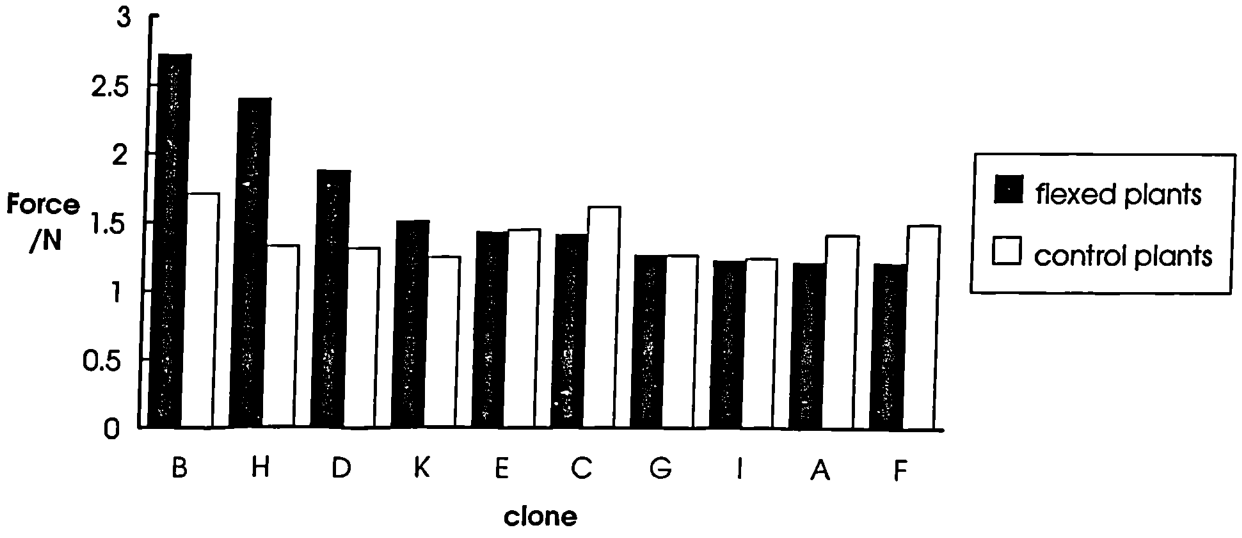
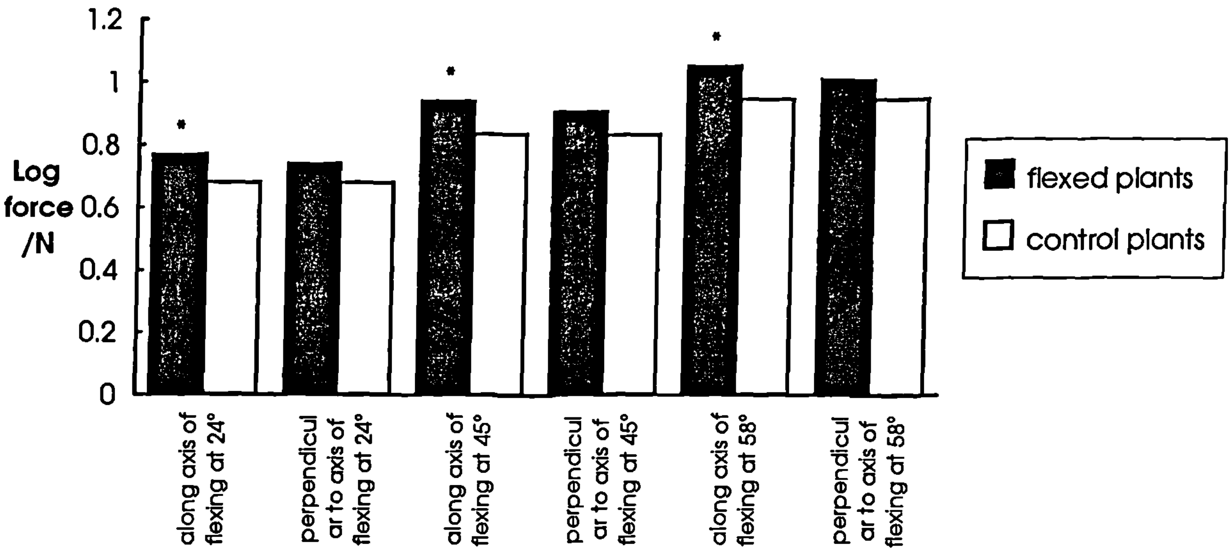


Table 5.2:

Probability of flexed Sitka spruce to resist overturning more than control plants along the axis of flexing (low nutrient treatment, clones F, G, H and K only)

Deflection	DF	F value	Probability
24°	1,22	7.22	0.013
45°	1,22	4.87	0.038
58°	1,22	4.20	0.053

Fig. 5.6 Force required to pull Sitka spruce horizontally through different deflections (low nutrient treatment, clones F, G, H & K)



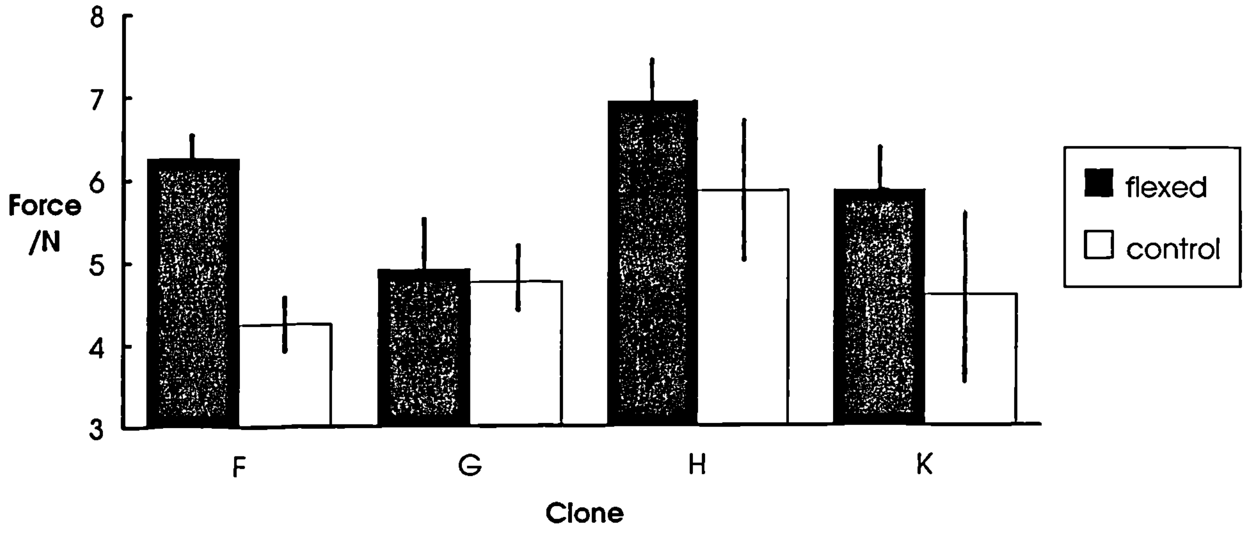
There was also a significant difference between clones F, G, H and K from the low nutrient treatment, in resistance to overturning through a deflection of 24° along the axis of flexing in the flexed plants only (Fig. 5.7, $F_{3,8} = 3.96$, $P = 0.053$). Clone H provided the most resistance to overturning (6.9 N ± 0.63 N) and clone G the least (4.9 N (± 0.8)). The mean of the amount of force required to pull each plant over in each direction was regressed on shoot biomass for each deflection (Table 5.3). There was a significant regression between the force required and the mass of the shoot in each case (Table 5.3). The regression coefficients increased with increasing angle of deflection as expected, but were also always higher for control than flexed plants. The higher regression coefficients implies that more force per unit area of shoot is required to deflect the plants, which suggests that there may be a different allocation of biomass in the shoot systems of flexed and control plants.

Table 5.3

Regressions of force required to pull Sitka spruce over at different deflections on shoot biomass

Deflection	**Flexed plants**			**Control plants**		
	R²	P	Equation	R²	P	Equation
24°	0.67	< 0.001	297 +14.1	0.78	< 0.001	141 + 20.3
45°	0.77	< 0.001	267 + 29.7	0.84	< 0.001	8 + 41.1
58°	0.78	< 0.001	223 + 44.6	0.84	< 0.001	-119 + 61.4

Fig. 5.7 Clonal differences in the force reqired to pull Sitka spruce over 24° along the axis of shaking



Bars are ± standard error

5.3.2 Plant performance

In the high nutrient treatment stem length increased exponentially with time for the first eight weeks (Fig. 5.8). There were no significant differences in the total growth increment of stem length between flexed (20.8 cm) and control trees (23.5 cm) although after six weeks growth, control trees appeared to increase in height compared to the flexed trees. In the low nutrient treatment stem length increased with time until the fourteenth week (98 days) , when the growth curve reached a plateau in both the flexed and control treatments (Fig. 5.8). Again there were no significant differences in the total growth increment of stem length between the flexed (15.4 cm) and control plants (14.8 cm). However, there were significant differences in stem length between clones and nutrient treatments and between flexed and control plants when the nutrient treatment was taken into account, as determined by three-way analysis of variance (Table 5.4, Figs. 5.9, 5.10, analysis by B.C. Nicoll, Forestry Commission).

The measurement of stem diameters taken on 8 August 1992, 3 cm above ground level showed no significant differences in the high nutrient treatment between flexed and control trees, along either the axis of flexing or perpendicular to it (Table 5.5). However, in the low nutrient treatment, flexed trees had a significantly larger stem diameter in the direction of flexing than the control trees (Table 5.5, $F_{1,78} = 4.44$, $P = 0.038$). There was no variation between clones. In the direction perpendicular to that of flexing, there was no difference between treatment or clones.

The second set of stem diameter measurements were taken 8 months after the plants were harvested on 27 October 1992 and had been stored in a cold room at 2°. Unfortunately, the stems must have shrunk from dehydration as the mean diameters are smaller than those taken on 8 July 1992 so the data are not valid.

Fig. 5.8 Stem length increments of all Sitka spruce clones measured every 14 days

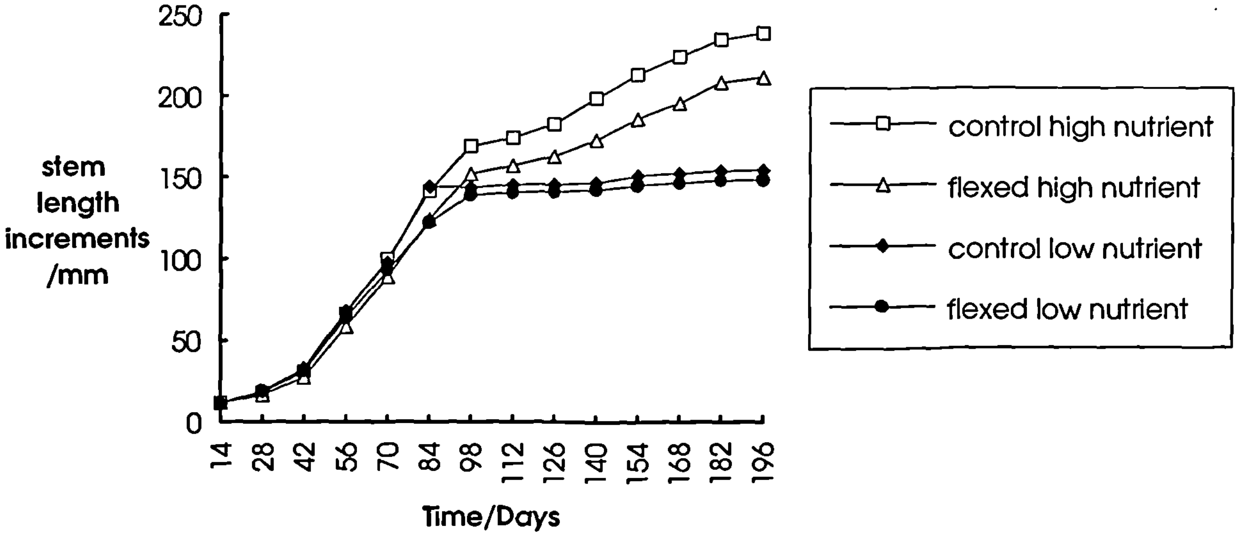


Table 5.4

Factors affecting stem length of Sitka spruce

Factor	DF	F value	Probability
clone	9	6.39	< 0.001
flexed/control	1	2.19	0.141
nutrient level	1	104.3	< 0.001
clone x flexed/control	9	0.95	0.486
clone x nutrient level	9	3.39	< 0.001
flexed/control x nutrient level	1	5.31	0.023
clone x flexed/control x nutrient level	9	1.21	0.276
Error	120		

Fig. 5.9 Response of Sitka spruce clones to different nutrient levels

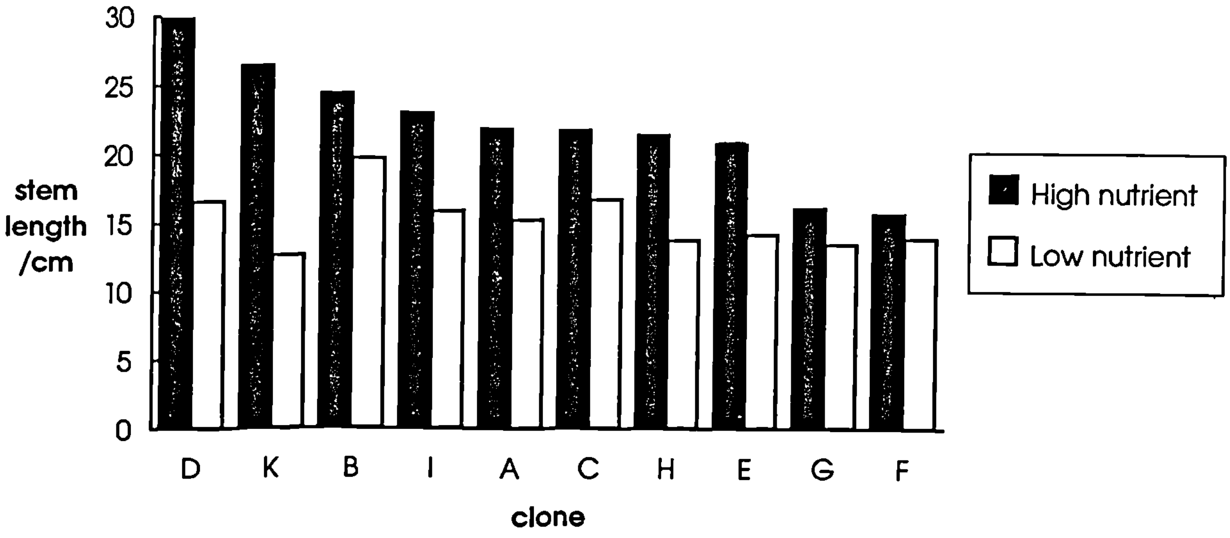


Fig. 5.10 Responses of Sitka spruce shoot extension to mechanical stimulation and nutrient levels

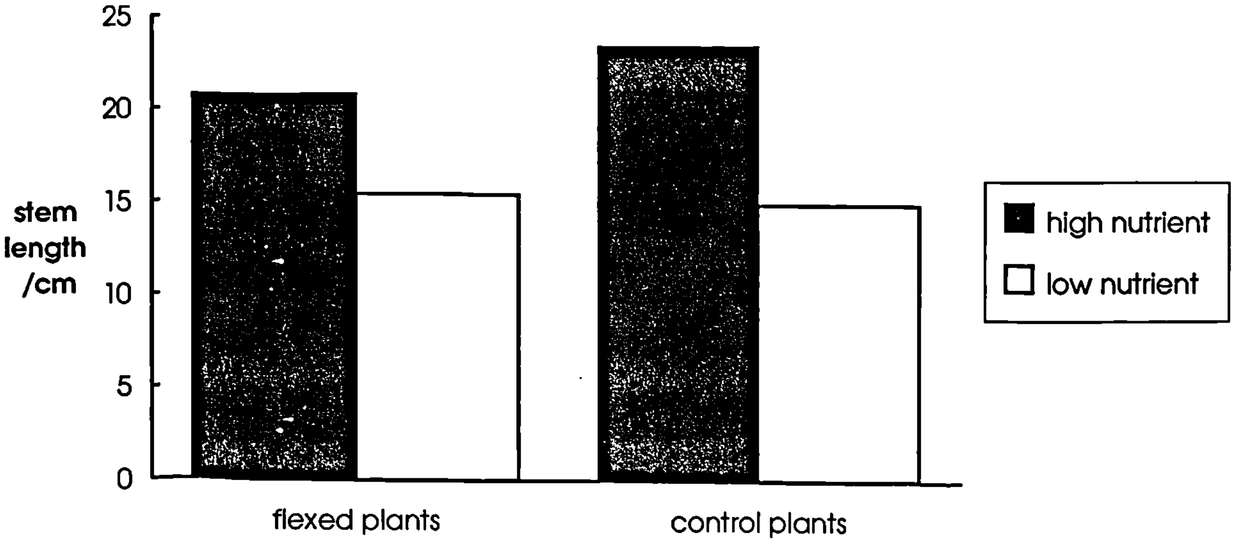


Table 5.5

Mean stem diameter (mm) (± standard deviation) for Sitka spruce

Date and axis	High nutrient		Low nutrient	
	flexed	control	flexed	control
8/7/92				
Along axis of flexing	10.3 ± 1.4	10.2 ± 1.1	9.3 ± 0.1	8.9 ± 0.1
Perpendicular to flexing axis	10.2 ± 1.3	10.5 ± 1.3	9.2 ± 0.9	9.1 ± 0.9

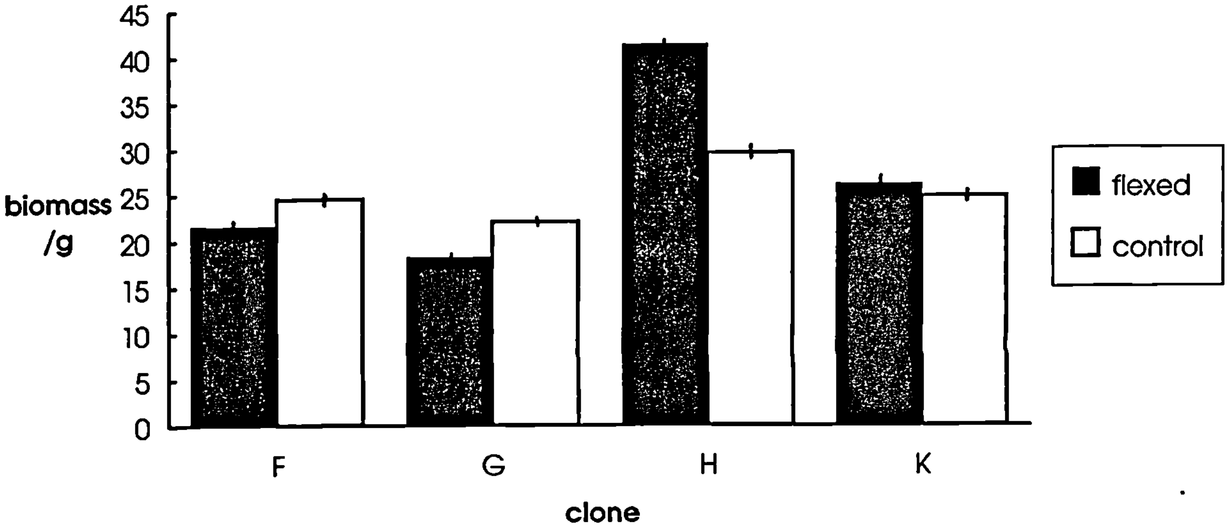
The ratio of basal stem CSA (*i.e.* the stem CSA 3 cm above ground level, using the measurements taken on 8 July 1992) and the root stump CSA (*i.e.* stem CSA at ground level) to stem length was calculated for each plant in clones F,G,H and K, in both high and low nutrient treatments, so that a measurement of stem taper could be evaluated. There were no differences in either the stem or root stump CSA:stem length ratio between control and flexed plants in either nutrient regime, or between clones, as determined by two-way analysis of variance of the data within each nutrient treatment.

There were no significant differences in shoot biomass between flexed and control plants in the high nutrient treatment, although there were significant differences between clones F, G, H and K, in the flexed treatment, as determined by two-way analysis of variance (Fig. 5.11, $F_{3,12} = 28.5$, $P < 0.001$). Clone H had the largest shoot biomass (413.6 ± 49.5 g) and clone G the smallest (183.6 ± 24.2 g).

5.3.3 Root growth

The means of the basal CSA, woody and fine mass per lateral root were calculated using 90° sectors (along the axis of flexing: 315° - 44° and 135° - 224° and perpendicular to the axis of flexing: 45° - 134° and 224° - 314°). The data from the two sectors along each axis were added together so that roots growing in the direction of flexing could be compared with roots perpendicular to that axis for both treatments. Analysis of variance, using log transformations where appropriate, was used to determine the differences between the two directions, treatments and clones, of mean CSA, woody and fine root mass per root.

Fig. 5.11 Shoot biomass in Sitka spruce clones (High nutrient treatment)



Bars are ± standard error

Two way analysis of variance of treatment, clone and axis of flexing showed that there were no significant differences in mean CSA, mean woody and fine root mass per root between the three combined factors. Differences between treatments were only found with mean CSA and mean woody root mass in the direction of flexing. Along the axis of flexing, mean CSA was 38% larger in all the flexed trees (22.9 mm^2) over all the control trees (14.3 mm^2) (Fig. 5.12, $F_{1,140} = 6.82$, $P = 0.01$). Mean woody root mass per root was 39% larger in the flexed (1.04 g) over the control trees (0.63 g) along the axis of flexing (Fig. 5.13, $F_{1,140} = 4.03$, $P = 0.047$). Clone G showed the largest differences in mean CSA of lateral root bases between flexed and control plants. The mean CSA of lateral root bases was 50 % larger in the flexed trees (22.3 ± 16.72 mm^2) compared to the control trees (11.2 ± 12.1 mm^2) and mean woody root mass per root of clone G was 60 % larger in the flexed trees (1.18 ± 1.1 g) compared to the control trees (0.46 ± 0.6 g). Although there were no differences in fine root mass between treatments or clones, fine root mass correlated with woody root mass in both the flexed and control plants (flexed: $R^2 = 0.66$, $P < 0.001$, control: $R^2 = 0.68$, $P < 0.001$).

There were no significant differences in mean total root biomass between clones F, G, H and K, when the stump was not included in the analysis. However, when the mass of the stump was incorporated into the total root biomass data, significant differences were found between clones in the flexed treatment only. Clone G had the largest root biomass (22.6 ± 6.6 g) and clone K the smallest (13.2 ± 1.0 g) (Fig. 5.14, $F_{3,11} = 3.84$, $P = 0.042$).

Fig. 5.12 Mean CSA of Sitka spruce woody roots in clones F,G,H,K

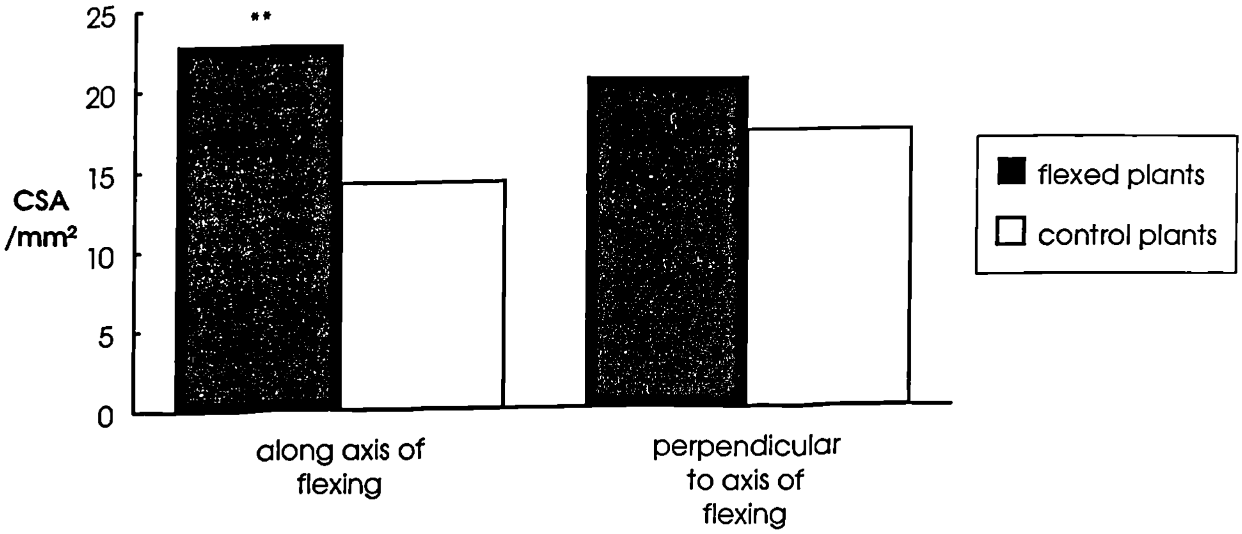


Fig. 5.13 Mean woody root mass per root of Sitka spruce in clones F, G, H, K

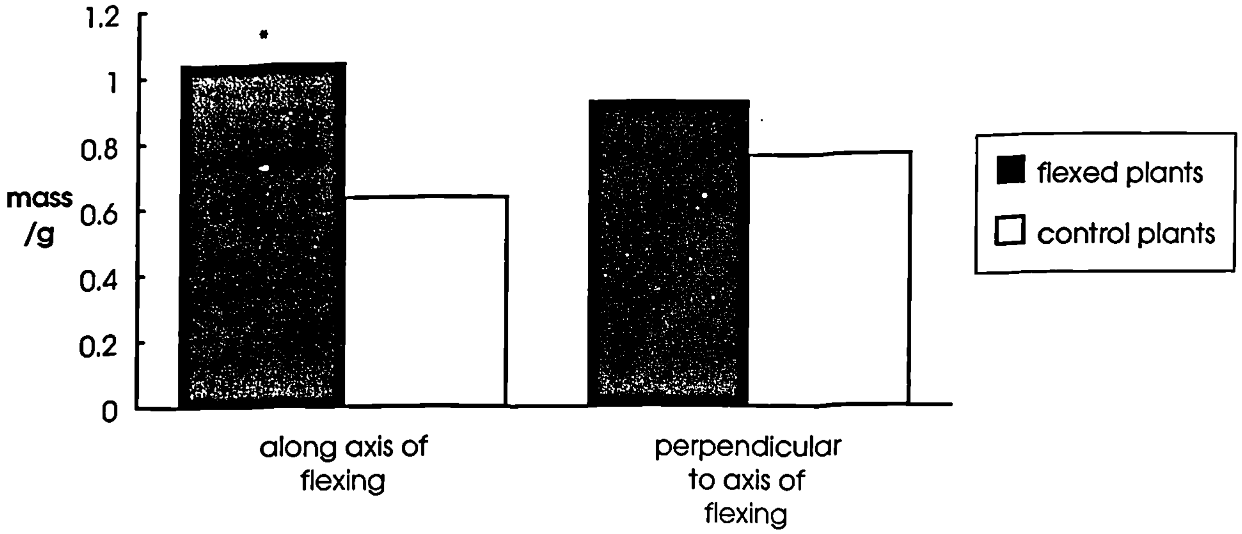
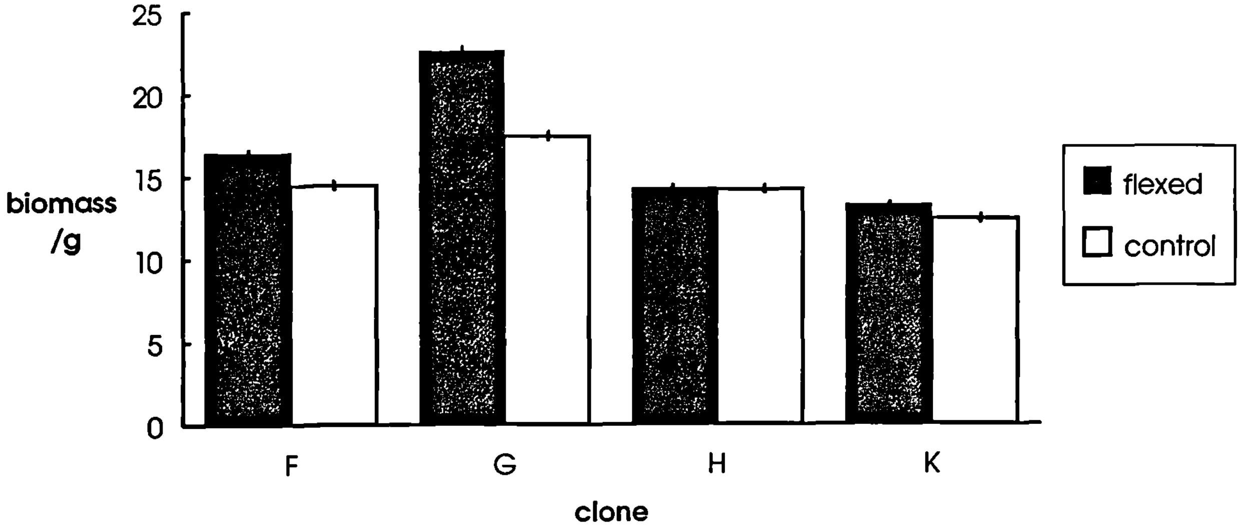


Fig. 5.14 Total root biomass (including the stump) for each clone of Sitka spruce



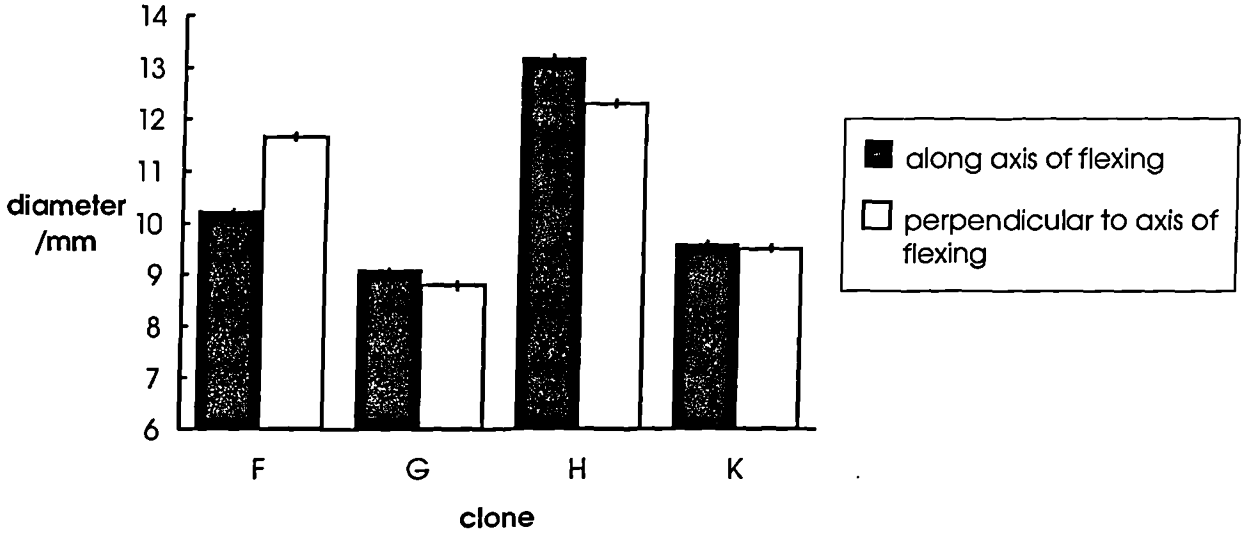
Bars are ± standard error

5.3.4 Cross-sections

The increments of diameter of each year's growth measured from the sections taken from the root stump at ground level (clones F, G, H, K, only) showed that there were no differences between flexed and control trees either along the direction of flexing or perpendicular to it. There were differences between clones from the flexing treatment only. Clone H had the largest diameter both in the direction of flexing (13.2 ± 2.5 mm, $F_{3,12} = 6.79$, $P = 0.006$) and perpendicular to it (12.3 ± 2.1 mm, $F_{3,12} = 4.02$, $P = 0.034$). Clone G had the smallest diameter in both directions (Fig. 5.15) but surprisingly the largest total root biomass (Fig. 5.14). The stump diameter at ground level did not significantly regress with stump biomass. There were no differences in the stump diameter between clones in the control treatments.

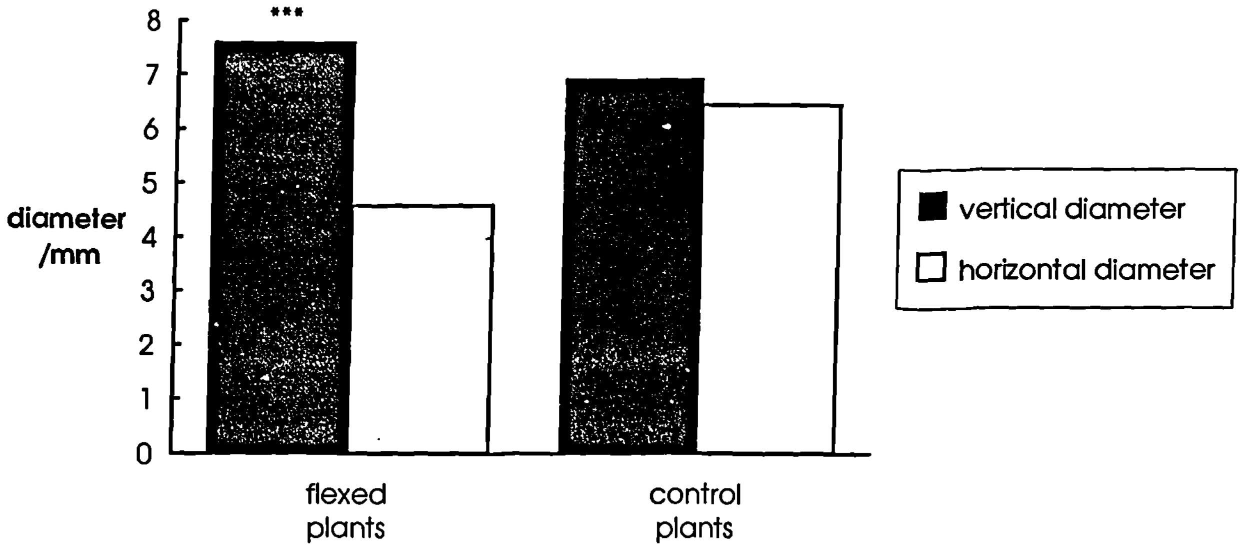
In the lateral root bases of the flexed plants, there was 40 % more growth vertically (7.6 ± 2.3 mm) than horizontally (4.6 ± 2.8 mm) (Fig. 5.16, $F_{1,60} = 21.57$, $P < 0.001$). There was no difference in the ratio of vertical to horizontal diameter between lateral roots from the direction of flexing and perpendicular to it. In the control plants there were no differences between the horizontal and vertical diameters (vertical: 6.9 ± 3.0 mm, horizontal: 6.4 ± 2.7 mm). There were no differences in either the vertical or horizontal diameter between clones in the flexing or control treatment.

Fig. 5.15 Sitka spruce root stump diameter at ground level, in two directions (Flexed plants only)



Bars are ± standard error

Fig. 5.16 Vertical and horizontal diameter of lateral root bases in Sitka spruce



5.3.5 Architectural analysis

A regression of the logarithms of altitude (a) against magnitude (μ) quantifies the root branching patterns as the regression coefficient, or topological index (see Chapter 2.3.4) Again, Sitka spruce root systems with log $\mu < 0.8$ (*i.e.* $\mu < 6$) were excluded from the analysis because very small root systems have herringbone patterns, so their inclusion biases the calculation. The regressions of the logarithms of μ and a of woody roots along the axis of flexing and perpendicular to it in the mechanically perturbed plants produced different coefficients. Roots along the axis of flexing had a value of 0.52 and roots perpendicular to this direction had a higher topological index of 0.73 (Fig. 5.17). The woody roots of the control plants had a value of 0.62 (Table 5.6). There were no significant differences in topological index between clones in either the flexed or control treatments, or in the length or diameter of internal or external links of control or flexed plants along the axis of flexing or perpendicular to it.

Fig. 5.17 Relationship between log altitude and log magnitude for Sitka spruce roots

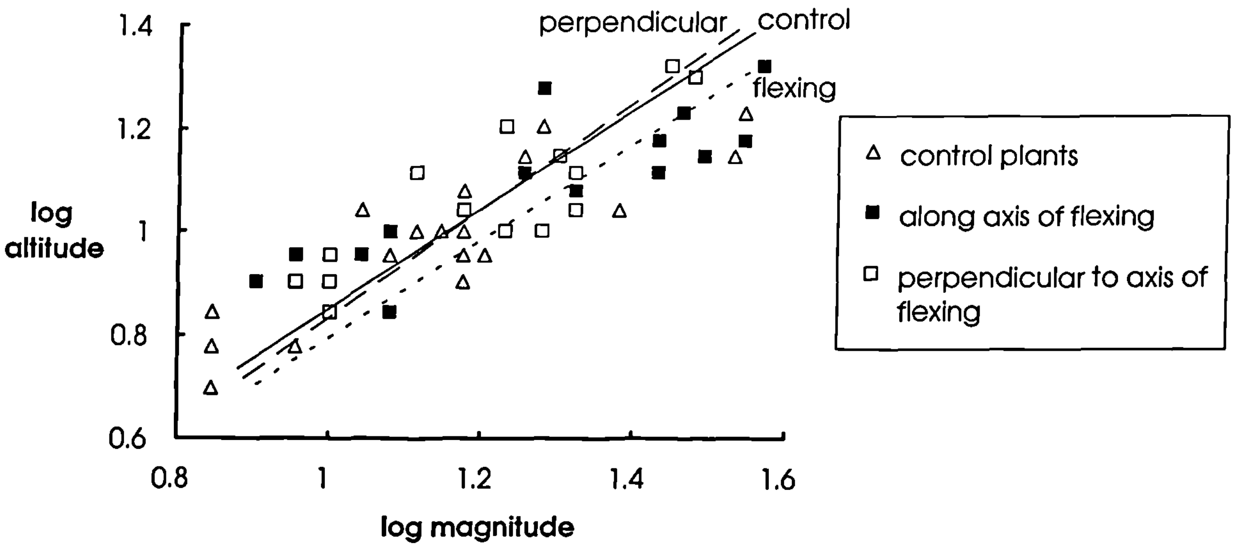


Table 5.6

Topological indices for different woody roots of Sitka spruce

Type of Root	**Values of Regression Coefficients for Log Altitude v Log Magnitude.**
Herringbone	1.0
Roots perpendicular to the direction of shaking	0.73
Control roots	0.62
Roots in the direction of shaking	0.52
Dichotomous	minimal

5.4 Discussion

The trees subjected to mechanical perturbation developed stems (in the low nutrient treatment only) and roots (in the high nutrient treatment) that should be able to resist overturning better than the control trees. In neither nutrient treatment did flexing affect stem height. There did appear to be a pattern developing in the high nutrient treatment in that flexed plants had reduced stem extension towards the end of the growing season. If the experiment had lasted longer, this growth pattern may have been amplified and significant changes in stem length might have been observed, comparable to the reduction in stem extension in mechanically perturbed *Pinus contorta* (Rees & Grace 1980) and *Pinus taeda* (Telewski & Jaffe 1986). The similar stem extension growth between flexed and control plants implies that resources were not diverted from stem height to bole or root growth as suggested by Larson (1965), assuming that height is equivalent to shoot biomass.

Radial growth of the base of the stem (in clones F, G, H and K) or 3 cm above ground level (in all clones) was not affected by mechanical stimulation in the high nutrient treatment. There was clonal variation found in root stump diameter at ground level in the flexed plants only. Clone H had the largest diameter in both directions which would increase its overturning resistance. The increase in shoot biomass in the flexed plants of clone H was probably due to the larger stem bole and would result in a higher lodging moment. As there were no differences between clones in stem diameter measurements taken at 3 cm above ground level, the root stump diameter may be a better indicator of clonal differences in terms of radial growth. The amount of stem taper did not differ between clones or treatments so this is a less reliable characteristic for assessing tree stability. Increased stem taper was the possible reason for decreased overturning resistance in wind stressed larch in the second wind tunnel experiment (Chapter 4). The results from this experiment do not confirm that idea, although the responses of Sitka spruce to flexing may differ from those of larch to wind loading from one direction.

In the low nutrient treatment, stem diameter was slightly larger along the axis of flexing compared to the control plants in clones F, G, H and K. An increase in stem diameter would increase overturning resistance along that axis. There were no differences in overturning resistance between flexed and control plants in the high nutrient treatment, but there was a significant increase along the axis of flexing in flexed plants in the low nutrient treatment. The increase in stem diameter along the axis of flexing would explain the increase in the resistive lodging moment. Clone F showed the largest difference in overturning resistance at 24°, between flexed and control plants in the low nutrient treatment. There were no significant differences in stem diameter between the clones, so the response of Clone F to overturning cannot be attributed to changes in stem allometry. Shoot biomass regressed with the mean force required to pull the trees over in all directions but this would not account for the increase in resistance along the axis of flexing only. It is possible that changes in root growth have occurred in clone F under a low nutrient regime, such as increased lateral root CSA or woody root mass. Flexing may also have induced changes in stem material properties which might affect overturning resistance. As discussed in Chapter 4, an increase in elasticity caused by mechanical perturbation, allows stems to be bent further without breaking. Less force may be required to bend such stems compared to stems which have not been mechanically perturbed. Flexed Sitka spruce grown under high nutrient levels may have more flexible stems than when grown under a low nutrient regime, thus explaining why there were no differences in overturning resistance between control and flexed plants in the high nutrient treatment. Differences in stem elasticity may also occur between clones. Further investigation of such characteristics would be needed to clarify the factors contributing to tree stability in this case.

In the high nutrient treatment at the first measurement (July 1992), there were differences in clonal response of flexed plants to overturning at 24° only. Clonal variation was only noticeable at this deflection which may be due to differences in the initial overturning resistance before soil failure occurs. Clones B, H and D required the most force to pull them over in all directions compared to the other clones. Clones H and D were the tallest plants in the flexed treatment, and probably had more biomass allocated in their stems which might explain why they needed more force to pull them over. Surprisingly, clone B required the most force to pull it over and yet the plants were of average height in the flexed treatment. The control plants of clone B were taller than the flexed ones but much less force was needed to pull them over. It seems possible that there is another explanation for clone B's high resistance to overturning which is not accounted for by stem characteristics, such as a change in stem material properties or an increase in root growth. Again, a more detailed analysis would need to be carried out to confirm the factors involved in tree stability. The same clonal differences were not present when anchorage tests were carried out in October 1992. It is striking that changes in overturning resistance were only found at the beginning of the experiment or in the low nutrient treatment. It is possible that towards the end of the experiment, the plants in the high nutrient treatment became pot bound and that clonal variation was not obvious because there was too much root mass present.

From the results of the anchorage tests alone, it appears that overturning resistance is affected by the level of mineral nutrition available to the plant. The overturning moment was increased along the axis of flexing because of the increase in stem diameter in that direction. The flexed plants should also resist the same overturning moment better along the axis of flexing because of the wider stem base. The limited resources may have been allocated to the most mechanically stressed areas (along the axis of flexing) at the expense of the stem and perhaps also the roots perpendicular to the axis of flexing. It is unfortunate that root growth was not examined in the clones from the low nutrient treatment but as there were no significant differences in stem length between flexed and control plants, it was initially assumed that root growth would also show no significant changes between treatments. A high nutrient supply is known to stimulate root growth of Sitka spruce in terms of dry weight and diameter of woody and primary tissues (Coutts & Philipson 1976). The allocation of assimilates to individual roots undergoing secondary thickening determines the development of the structural root system (Wilson 1975). If assimilates are diverted to those woody regions most important for good anchorage during secondary thickening, there will be little left to allocate to roots which have a small role to play in tree stability. Hence, the effects of a high concentration of nutrients may override responses of the trees to mechanical stimulation.

The increase in mean root CSA and woody root mass per root along the axis of flexing in clones F, G, H and K in the high nutrient treatment suggests that cambial activity must have been affected by mechanical stimulation. Clone G showed the largest increase in mean CSA, and woody root mass per root along the axis of flexing, in the flexed compared to the control plants. In terms of biomass allocation to mechanically stressed areas, clone G is best adapted to resist overturning out of the four examined. Stimulation of root thickening by mechanical perturbation has only been observed at the very base of the lateral root in 10 m tall *Pinus strobus*, causing roots to rapidly taper away from the stem. At 50 cm from the base of the trees, the root CSA was the same in free-standing trees compared to guyed trees (Wilson 1975). Although an increase in root radial growth at the base is a feature with adaptive value in mechanically perturbed trees, roots which have greater radial growth in the zone of rapid taper (ZRT) will be able to resist bending more (bending rigidity is proportional to the fourth power of radius). It is not known how far along the root the increase in radial growth extends in clone G. If clone G has a greater allocation of biomass in the ZRT, it will be better able to resist bending. The increase in biomass to roots along the axis of flexing should, however, result in an increased resistance to overturning.

The total root biomass (including the stump) was not a good indicator of tree stability, which agrees with the results of Nicholl *et al.* (1993) discussed previously. Clone H had an increased biomass allocation of 39 % in the structural roots along the axis of flexing compared with the control plants yet the total root biomass data indicated that there were no differences between flexed and control plants in clone H. Clone G had an increase of 50 % in the mass of woody roots along the direction of flexing compared to the control plants yet the total root biomass showed an increase of only 23 % in the flexed plants. The root stump biomass did not regress with stump diameter and clone H had the largest CSA yet clone G had the greatest biomass, which suggests that even the diameter is not a good indicator of stump size, and hence tree stability. The depth and width of the stump must be an important characteristic to consider.

Mechanical stresses caused by flexing resulted in an increase in vertical root diameter compared to the horizontal diameter at the base of the roots (in clones F, G, H and K in the high nutrient treatment). Roots that are bent on one axis can become oval or even I-beam in cross-section (M.P. Coutts, pers. comm.). This eccentricity increases the roots' resistance to bending in the direction of stress. In Sitka spruce, roots showing only moderate eccentricity were found to be three times more resistant to bending than comparable roots with a circular cross-section (G.J. Lewis, pers. comm.). It appears that mechanically stressed Sitka spruce can reallocate resources to alter root shape and improve resistance to uprooting, but it is not known how far along the root this eccentricity develops, and whether the extra vertical growth is laid down at the top or bottom of the root. Wilson (1975) staked 10 m tall *Pinus strobus* for four years. He reported that in free-standing trees compared to the staked trees, secondary growth was stimulated on the bottom of the root rather than the top in the ZRT, for the 100 cm nearest the stem. However, when Fayle (1976) looked for this response in 4 m tall *Pinus sylvestris*, he could find no differentiation of secondary growth distribution between the top or bottom of roots after two years of swaying, although root radial growth was markedly increased in the free-standing trees compared to staked trees.

Mechanical stimulation resulted in a decrease in the topological index of structural roots along the axis of flexing, resulting in roots with more branches per unit volume of soil, as mentioned earlier, increase the tensile strength of the soil (Wu 1976). However, if a root is considered to be a circular beam, its stiffness is proportional to the fourth power of its diameter so thicker, unbranched roots along the axis of flexing will increase resistance to bending, especially if extra woody growth is continuous down the root through the ZRT. As Sitka spruce was flexed in two directions, roots along the axis of flexing were loaded under tension and compression. In the first wind tunnel experiment (chapter 2) the topological index of Sitka spruce was decreased on the windward side only, where roots were held in tension, which may explain why a very low index was found. Also, the plants in the wind yunnel experiments were stressed when they were germinated, therefore growth of roots at the initial stage may have been affected. In this flexing experiment, stress was applied to older roots which already had branches near their base. If roots are loaded in both tension and compression, there may be a compromise in root development between the two types of loading to produce roots which are thick at the base and can resist bending and ones which can resist pull-out when held in tension. Ideally, a root would be unbranched in the proximal region (*i.e.* between the stem and hinge of the soil-root plate), with a highly branched region beyond the hinge. It is not known exactly where branching developed in Sitka spruce structural roots from the direction of flexing, but a more detailed analysis of root architecture may provide an insight into induced responses of root systems to mechanical perturbation. Lateral roots growing perpendicular to the direction of flexing had an even higher topological index (0.73) than the control plants (0.62), which means that they have developed a more herringbone-like topology. Roots growing in this region are subject to torsion and will offer little resistance to overturning so a highly branched root system in this region is less of an adaptive feature. The mechanism by which morphogenesis is altered in mechanically stressed root systems is unclear (see Chapter 1).

The results presented support the hypothesis of Telewski & Jaffe (1981, 1986b) that plants of the same species but of different genetic background respond in different ways to mechanical perturbation. There was no one consistent morphological response to flexing in the clones so any one growth characteristic cannot be relied upon to predict tree stability. As a random selection of clones was used in the experiment, there is certainly the potential for improvement by clonal selection. An examination of more clones might reveal which are the best at withstanding external loading. In the high nutrient treatment, clone G is the most promising clone in terms of biomass allocation to areas important for increased anchorage strength, whereas in the low nutrient treatment, clone F provided the most resistance to overturning. It is surprising that at two nutrient levels, clones appeared to respond differently to mechanical perturbation, with two different clones minimising loading effects. However, a detailed analysis of root growth in trees from the low nutrient treatment is required before a comparison of trees between treatments can be made.

Further investigation of selection and breeding of trees for characteristics likely to withstand overturning by windthrow is worthwhile. Selection for other traits such as stem length and straightness may consequently alter stability, so foresters need to understand which tree characteristics do affect stability. An ultimate goal of studies such as this and the one by Nicoll *et al.* (1993) is to assess the ability of clones to withstand wind stress and these studies give important pointers in that direction. Nicoll *et al.* (1993) realised that the relationship between growth characteristics and tree stability must be examined in practice, but the loss of trees to windthrow might be reduced by using clones with an increased biomass allocation to the lateral roots, as opposed to clones with a large biomass allocation in the root stump. Furthermore, the responses of trees to long term mechanical perturbation both in the laboratory and in the field must be considered when selecting for growth characteristics to withstand windthrow.

Chapter 6

The development of a model to describe the uprooting of a root system with different branching patterns and angles

6.1 Introduction

The type of branching pattern found in the root systems of plants determines their efficiency to exploit the soil for water and nutrients (Fitter 1987). Herringbone root systems (where laterals arise off one main axis) are the most effective at resource capture. The depletion zones around the lateral branches do not overlap to the same extent as would occur in a root system with a more random branching pattern (*i.e.* with second and third order lateral roots). The architecture of the base of a root system also influences its ability to withstand uprooting. A vertical force is best resisted by a large number of thin fibrous roots which have a large surface area over which the load can be distributed (Ennos 1990). Rotational forces transmitted by a tree stem to the roots *e.g.* when the stem is loaded under wind, would need to be resisted by a rigid element in the root system such as a tap root with horizontal laterals (Fitter & Ennos 1989).

The studies in chapters two and five show that when young Sitka spruce was grown with unlimited nutrients, in a wind tunnel under intermittent wind or flexed in two directions by means of a mechanical shaking device, branching was more random on windward and flexed sides. Tests of anchorage strength on flexed Sitka spruce grown under limited nutrients, showed that resistance to overturning along the axis of flexing was increased. The increased resistance to overturning may have been a function of increased surface area of the mechanically stressed root bases or a change in the morphogenesis of stressed roots. It is important to identify whether a change in branching pattern can affect pull-out resistance of roots. If this is the case, those clones which can best adapt to wind loading and hence increase their mechanical stability will be of greater economic value on exposed sites with poor soils.

The pull-out resistance of individual roots of mature Sitka spruce has been investigated on two types of soil, a peat and a brown earth (Anderson *et al* 1989). The extraction force needed to pull single roots out of soil was related to the root cross-sectional area at the pulled end. Roots needed significantly more force to pull them out on stronger, wet peat than brown earth, when roots of a similar CSA at the pulled end were used. The difference in extraction force was small between the two soil types, yet the roots on the brown earth site broke slightly further up the root, nearer the root base. Anderson *et al* (1989) attempted to explain this by assuming that if all the force applied to the pulled end was transmitted to the point of breakage, the mean force at the broken end was twice as much for roots on the brown earth than for those on the peat. This result implies that the similar extraction forces for the roots on the two sites resulted from different causes *e.g.* differences in branching characteristics and in the strength of the root-soil bond. There was a difference in root morphology between the two sites, shown by a difference in taper of the extracted roots. Therefore, any differences in tree stability between the two sites would have to be explained by other features of anchorage, such as branching.

Another component which may affect anchorage strength of root systems is the angle of branching between the tap root and primary laterals and between lateral roots. There are no published studies which quantitatively relate the parameters of tree root branching angles to the anchorage capability. Angles between the stem and branches of the tropical tree *Terminalia catappa* have been examined above ground (Honda & Fisher 1978). Theoretical branch angles which result in exposure of maximum effective leaf area to sunlight, were close to the values observed in nature. Information regarding root branching angles is scant (Fitter 1987, 1991), primarily because of the difficulty in extracting non-woody root systems from soil without deforming them. Techniques are currently being developed to study root systems using non-invasive methods *e.g.* nuclear magnetic resonance (NMR) imaging (appendix 2; Southon & Jones 1992, Southon *et al* 1992). When a sample of roots in soil is placed inside a strong magnetic field, an antenna detects the signal generated by the excited sample, which in this case is water from the roots. A skeleton outline of the root system can then be obtained. A less sophisticated and very laborious, destructive method of measuring root geometry is to impregnate resin into soil. When the resin solidifies, the soil and roots can be sectioned. The three-dimensional architecture of the root system can be determined by reconstructing the coordinates of the roots (Commins *et al* 1991).

The shape of a tree root system has been related to its anchorage strength (Fitter & Ennos 1989). As mentioned earlier, a tree with a tap root and horizontal laterals will best resist overturning by the wind, although no quantitative studies have yet been carried out on the infuence of branching angle between the tap root and first order laterals and anchorage strength of the tree. It is known that the branch joints between the tap root and first order laterals increase in cross-sectional area when subjected to tension or compression forces, such as those transmitted down the stem during the swaying of a tree (Fayle 1968, 1976, Wilson 1975). *Mattheck (1990) suggests that the* branch joints at in this region are shaped in an optimum manner. He believes that the areas of a tree which are subjected to stress lay down new wood to increase rigidity. Therefore, a tree will have an even distribution of stress over its surface, a feature with adaptive value.

The angle of branching between all orders of roots will be one of the parameters determining the ability of the tree to withstand uprooting and also to acquire nutrients. Fitter (1990) discusses the need to identify optimum branching angles with respect to nutrient acquisition. The angle at which a branch emerges from the parent root will determine its efficiency in escaping the depletion zone and hence its ability to explore the soil.

This chapter describes a model which simulates the uprooting of a root system with different branching patterns and angles. The relationship between architectural characteristics and anchorage efficiency will be investigated. Predictions of anchorage abilities can be made with regard to architecture.

6.2 Materials and Methods

6.2.1 Development of the physical model

A series of mechanical tests were carried out on artificial root systems made out of copper coated steel wire, embedded in sand. Steel wire was used because of its strength and the difficulty of deforming it. The lateral roots could also easily be soldered into holes drilled in the tap root. Anchorage was quantified by measuring the maximum pull-out resistance before failure in the sand, thus simulating the behaviour of roots in soil. The tap root was represented by 3 mm thick wire and the laterals by 1.5 mm thick wire, which are representative of roots found in young trees. Three basic types of root systems were developed to determine the pull-out resistance of the following components:

Type of root system:

"1" Main axis alone (30 cm long) (Fig. 6.1a).

"2" First order lateral (1° L) roots; one main axis (30 cm long) with two 1° L roots (each 10 cm long), at 90° angles off the base of the main axis (Fig. 6.1b).

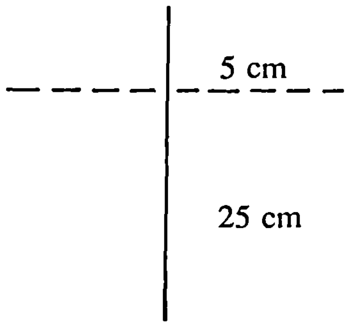
"3" Second order lateral (2° L) roots; one main axis (30 cm long) with two 2° L roots as above, and one 2° L root (5 cm long) positioned 5 cm along a 1° L root, at 1 of 3 angles (30°, 60° and 90°) in the horizontal plane (Fig. 6.1c).

There were 3 replicates of root system type "1", 9 replicates of root system type "2" and 2 replicates of type "3". There were more replicates of types "1" and "2" because variation in the tests of these two types was large compared to the tests with type "3". Each model root system was put into a cylindrical container 30 cm high and 20 cm wide and damp sand was manually packed around it, leaving the top 5 cm of the axis exposed. The sand in the container was replaced with fresh sand after each series of tests. The fresh sand was kept in a sealed bag until use, to prevent it drying out and to ensure uniformity. An Instron tensile testing machine was used to pull each type of model root system vertically out of the sand and measure the force required. The jaws of the Instron were clamped onto the top 2 cm of exposed axis. The root systems were pulled out of the sand at a speed of 10 mm/minute.

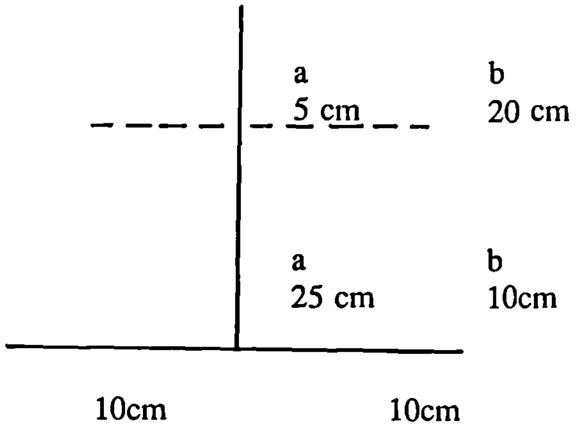
Fig. 6.1

Types of artificial root systems

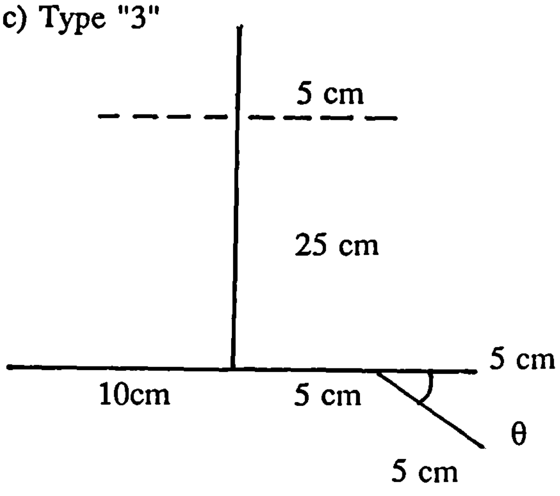
a) Type "1" Main axis alone



b) Types "2" a & b



c) Type "3"



θ = 30°, 60° or 90°

Root system type "1"

The main axis was buried to a depth of 25 cm and the maximum pull-out resistance measured. Wire cutters were then used to prune the root by 1 cm, and the test was repeated with only 24 cm of the main axis buried. This procedure was carried out until all the main axis had been removed.

Root systems type "2"

a) In an initial series of tests, type "2" was buried at a depth of 25 cm and the pull-out resistance measured. The depth of the root system was decreased by 5 cm intervals until 10 cm below the surface was reached, when 2 cm intervals were used. This was to obtain greater accuracy near the surface of the sand where failure was more likely to occur at lower forces. The lateral roots were left intact so that the combined lateral and main axis effect on pull-out resistance could be investigated.

b) The same root systems were used in a second series of tests and were buried at a fixed depth of 10 cm in the sand. After each test, 1 cm was cut off each lateral root and the test repeated.

Root systems type "3"

These were buried at a depth of 25 cm and after each test, the depth was decreased by 5 cm intervals until 10 cm below the surface when the intervals were 2 cm.

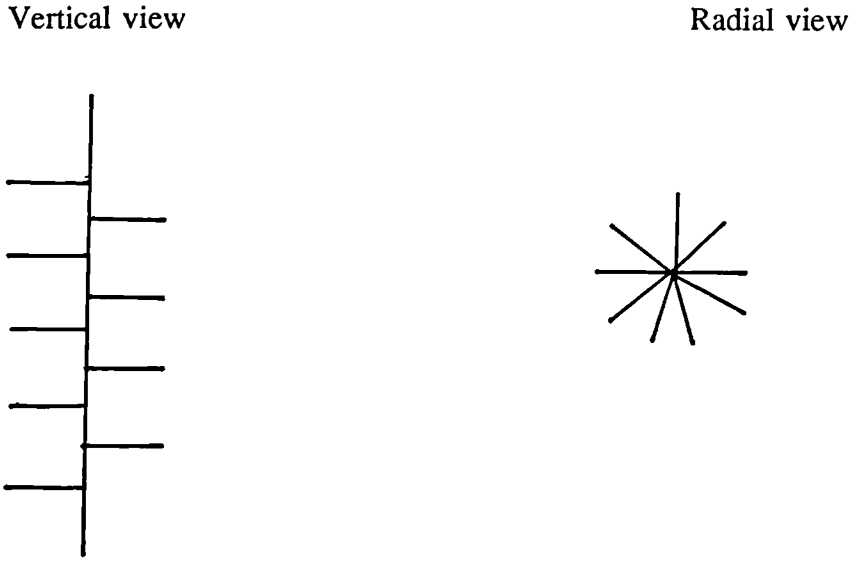
Herringbone and random branching root systems (Types "4" and "5")

Two more elaborate artificial root systems were developed in order to test whether the amount of force required to pull up a basic root system was linearly related to the depth of that root system in the sand and the number of lateral branches present. The two new model root systems were designed so that they had different branching patterns but a similar amount of surface area. To prevent the sand above a lateral root being broken up by a lateral root higher up the main axis, both models had lateral roots positioned so that there was no root above any other. One model had a typical herringbone pattern (Type "4") (Fig. 6.2a) and the other an approximately random branching pattern (Type "5") (Fig. 6.3). Two replicates of each model were made and the root systems were pulled out of sand in a container 60 cm high and 20 cm wide.

Fig. 6.2a

Types of artificial root systems

a) Type "4" Herringbone pattern



Vertical view

Radial view

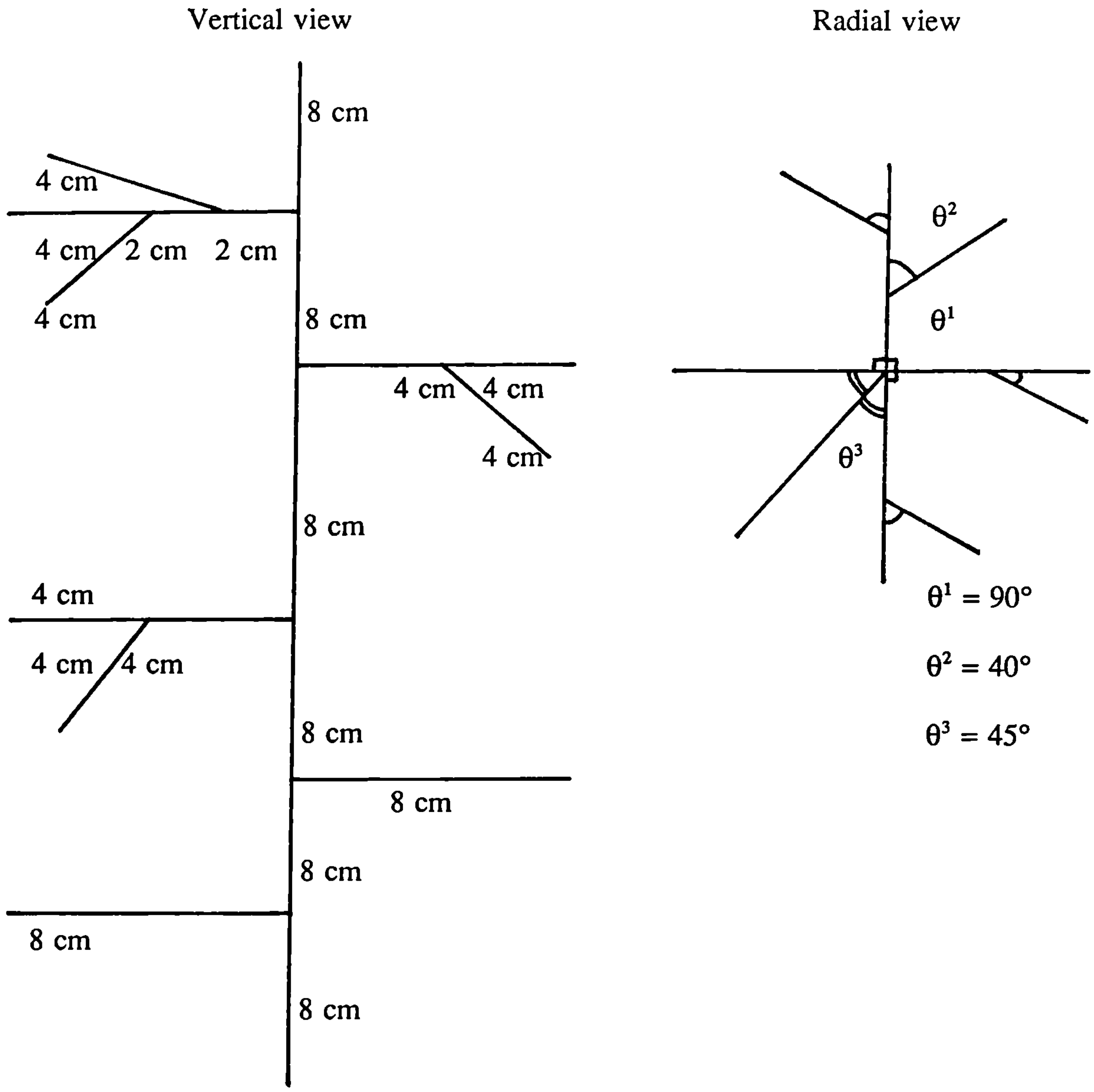
All exterior links are 8 cm long and interior links are 3 cm long.

$\theta = 40^\circ$ between each 1° L in the same plane.

Fig. 6.2b

Types of artificial root systems

b) Type "5" Random branching pattern



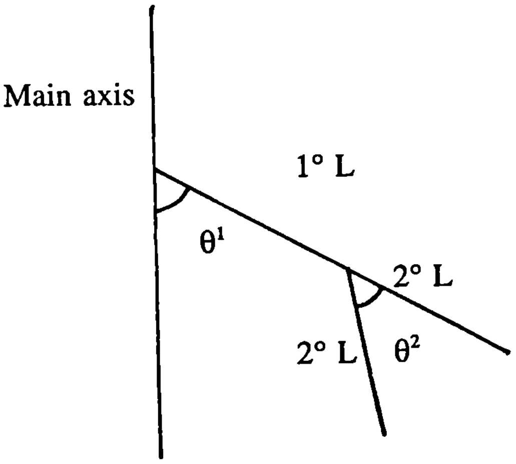
When the complete herringbone root system had been tested, 4 branches were removed and the model re-tested with 5 branches at the top and then with the 5 branches at the bottom. The randomly branching model was tested with the 2° L's at the top of the system and then again with them at the bottom.

6.2.2 Measurement of real branching angles

Branching angles of woody root systems were examined so that the mean angle could be compared to the optimum branching angle predicted by the model. Non-woody roots were ignored as they may have altered their shape on uprooting. The young larch trees grown in the first wind tunnel experiment were used to measure the angle between the tap root and primary lateral root (Fig. 6.4). The remainder of the root system was not woody enough to measure branching angles between lateral roots, so four, 20 year old, washed Sitka spruce root systems were examined. Sixty branching angles, between the 1° and 2° L roots within 50 cm distance of the stump were measured. Roots which had branched as a result of damage to the apex were ignored, as these form "forks," *i.e.* when a third lateral root grows between the first and second order laterals (Wilson 1970) and the branching angles are therefore very small.

Fig. 6.4

The location of the angles measured on real root systems of Sitka spruce



θ^1 = branching angle measured in European larch

θ^2 = branching angle measured in mature Sitka spruce

6.3 **Results**

6.3.1 The physical model

Root system type "1"

The main axis slid out of the sand when pulled vertically, and the surface of the sand did not crack as the root was pulled up. The maximum force required to extract the main axis from the sand was 3.65 N at a depth of 23 cm. The longer the main axis, the greater was its pull-out resistance, but the uprooting curve of force (N) against length of the main axis appeared to be non-linear (Fig. 6.5). There were two distinct linear sections; the first covering 0 - 7 cm of the root axis and the second 7 - 25 cm. The regressions of mean force (N) against length of the main axis for each section were highly significant (0 - 7 cm: $R^2 = 0.87$, $P = 0.002$, 7.5 - 25 cm: $R^2 = 0.88$, $P < 0.001$), with a much greater coefficient for the second section (Table 6.1).

Root system type "2"

As the main axis and two lateral roots emerged from the sand, the sand cracked around the lateral roots and some sand was also lifted up with them but dropped off after the lateral roots were clear of the surface.

a) The maximum force required to uproot the root system in the first series of tests, at different depths in the sand, was 30 N at 25 cm below the surface. The regression of mean of force against the depth of the lateral roots below the sand surface was highly significant for a linear slope (Fig. 6.6, $R^2 = 0.94$, $P < 0.001$).

b) In the second series of tests, where the lateral roots were cut before each uprooting, the maximum force needed to pull the system vertically out of the sand was 16.5 N. The regression of mean of force against length of lateral roots was highly significant for a linear slope (Fig. 6.6, $R^2 = 0.99$, $P < 0.001$). The slopes of the lines were calculated for each set of data (Table 6.1).

Root system type "3"

When the roots with 2° L's were pulled vertically out of the sand, a plate of sand was also lifted up, between the 1° and 2° L's. This plate was approximately 1 - 2 cm^3 when lifted up by roots with branching angles of 30° or 60°. When the lateral roots had a branching angle of 90°, the plate was only 0.5 - 1 cm^3. Due to the formation

Table: 6.1

Slopes of lines from each regression equation

Type of root system	**Equation of slope where force is the dependent variable in each case**
Root system type 1)	
Main axis: 0 - 7 cm	-0.023 + 0.025 * length of main axis
Main axis: 7.5 - 25 cm	-0.079 + 0.139 * length of main axis
Root system type 2)	
Main axis & uncut laterals at different depths	3.42 + 0.835 * depth below surface
Main axis & laterals of different lengths at a fixed depth	0.606 + 0.666 * length of lateral
Root system type 3)	
Main axis & laterals at different depths with 2° L's at:	
0°	3.99 + 0.974 * depth below surface
30°	4.24 + 1.09 * depth below surface
60°	3.97 + 1.15 * depth below surface
90°	3.64 + 1.11 * depth below surface
Variation in branching angle (θ) between laterals	$0.972 + 0.005 * \theta - 0.000043 * \theta^2$

Fig. 6.5 Relationship between pull-out resistance and length of main axis

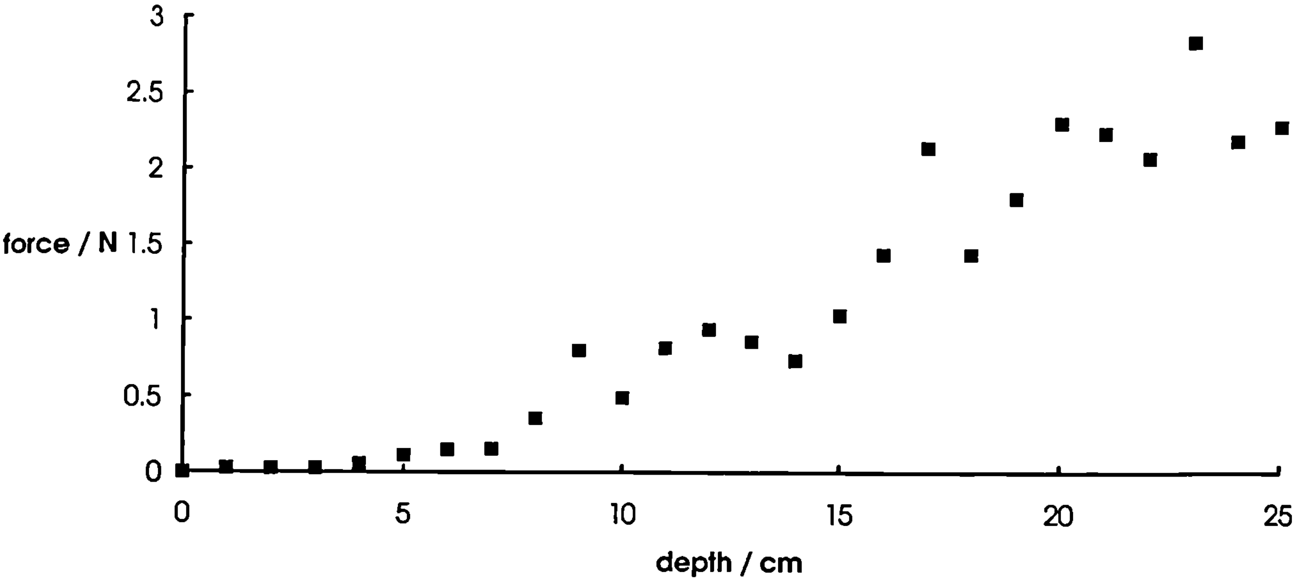
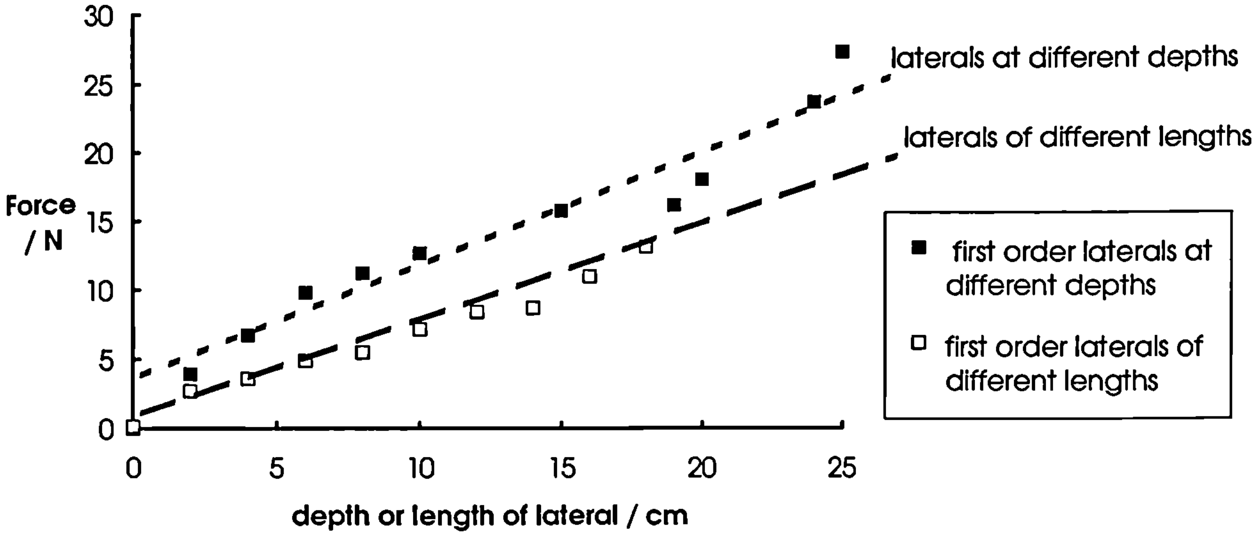


Fig. 6.6 Relationship between pull-out resistance and depth or length of first order laterals



of this plate and the extra weight of sand the root system had to carry through the soil, it was very difficult to pull the root systems out of the sand below a depth of 20 cm. Below this point, the wire roots bent downwards and slid out of the sand diagonally, as they were not rigid enough to counteract the weight of the sand. Consequently, the results below 20 cm deep for roots with 30° and 60° angles, showed a decrease in the force needed to pull the system up and were ignored. The maximum force required to pull each system up was: 30° = 26 N, 60° = 26 N, both at 19 cm and 90° = 25 N at 24 cm below the surface. The regression of mean of force against depth below the surface was significant for linear slopes of each type of root system (Fig. 6.7, Table 6.2).

Table 6.2:

Probability of mean force regressing with depth of root system beneath the sand surface

Angle between lateral roots	P value	R^2 value	Degrees of freedom (df)
30°	< 0.001	0.95	1, 5
60°	< 0.001	0.95	1, 5
90°	0.011	0.91	1, 3

The slope of the line of 0° was inferred from the slopes of lines of root system type "2" above. A root system without a 2° L must have 25 % more lateral root surface area than type "2", to account for the 2° L which is not present. Therefore, the slope of the line type "2a" was increased by 25 % of the slope of the line of type "2b" (Table 6.1).

The slope of the line was calculated for each set of data (Table 6.1) and plotted to give an uprooting curve for 2° L's with different branching angles (Fig. 6.8). The polynomial regression of force against branching angle was not quite significant (R^2 = 0.99, P = 0.07), probably because of the very small number of points. Differentiation of the equation of the slope of the line (Table 6.1) gives an optimal branching angle of 58°, where the pull-out resistance is greatest.

Fig. 6.7 Relationship between depth and pull-out resistance with additional second order laterals at different branching angles

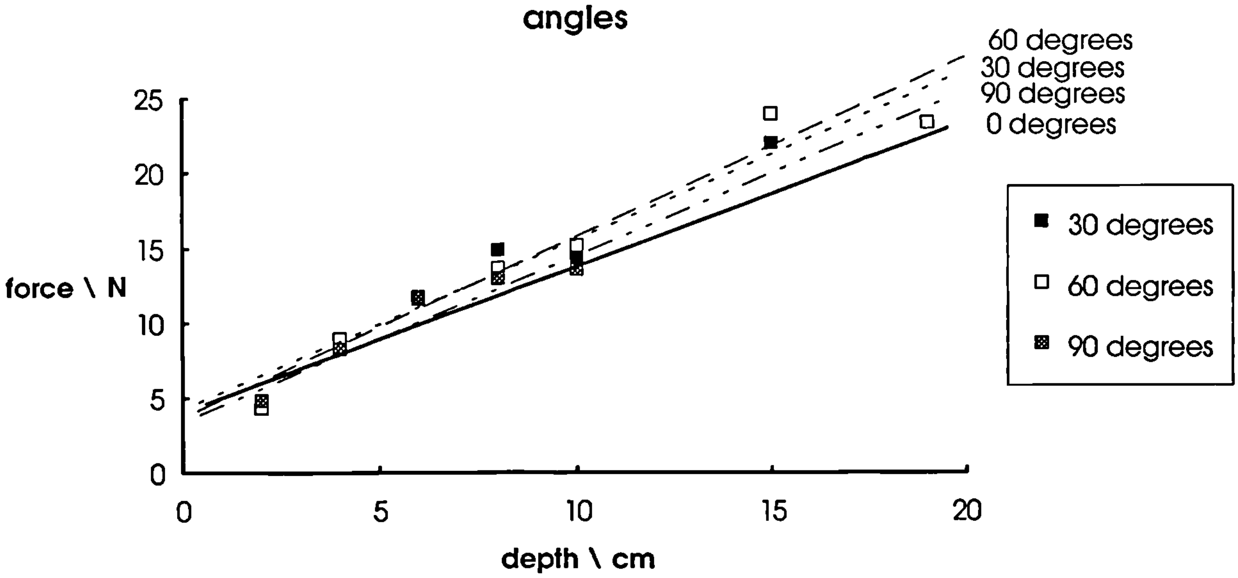
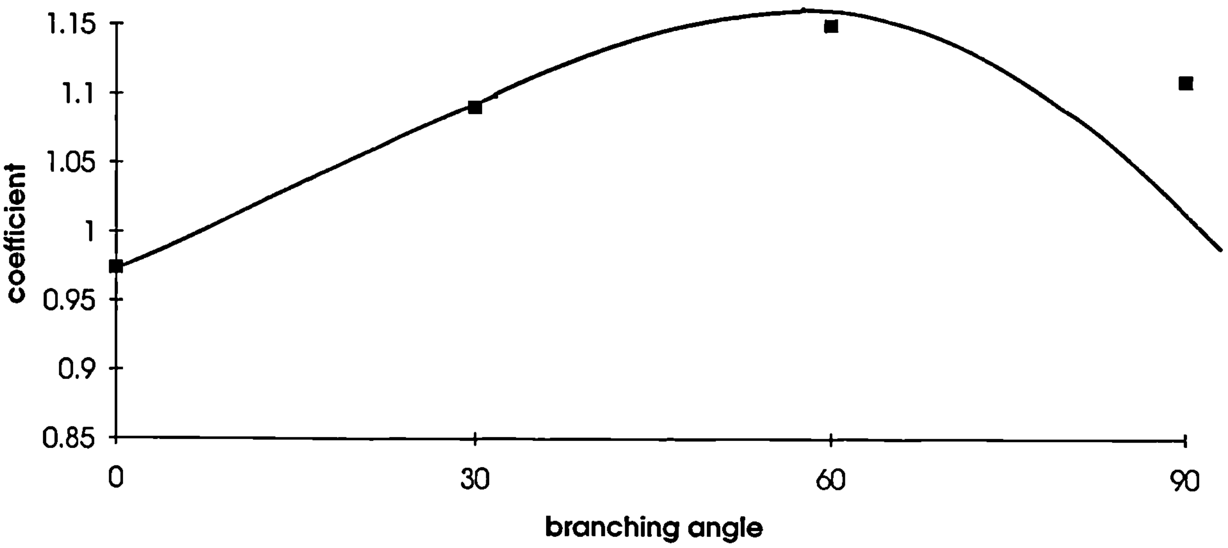


Fig. 6.8 Relationship between the coefficient of pull-out resistance and branching angle



6.3.2 Development of program ROOTFORCE

A computer program was written in QBASIC (Appendix A). The program accepts data on an artificial root system and calculates the force required to pull that root system out of the sand. During uprooting, each section of a root system is additive in its contribution to the total pull-out resistance of the whole root system. Each component may be taken and the forces on it calculated in isolation. The sum of these forces gives the total pull-out force for the complete system. To make the program accurately predict the pull-out forces, some modifications had to be made to the data and equations of slopes of the lines:

i) To determine the resisting force of the lateral components in isolation, it was necessary to remove the contribution of the main axis from the total observed values of the tests on root system types "2a,b" and "3". The regression equation of force against length for the main axis (0 - 7 cm = -0.023 + 0.025 * length, 7.5 - 25 cm = -0.079 + 0.139 * length) was subtracted from the observed values for pull-out resistance.

ii) The equation of the slope of the line for root system type "2a" describes a main axis with two 1° L's, each 10 cm long. Therefore, the actual force on a lateral of a given length will be proportional to that on one of 10 cm. The equation used in the program is:

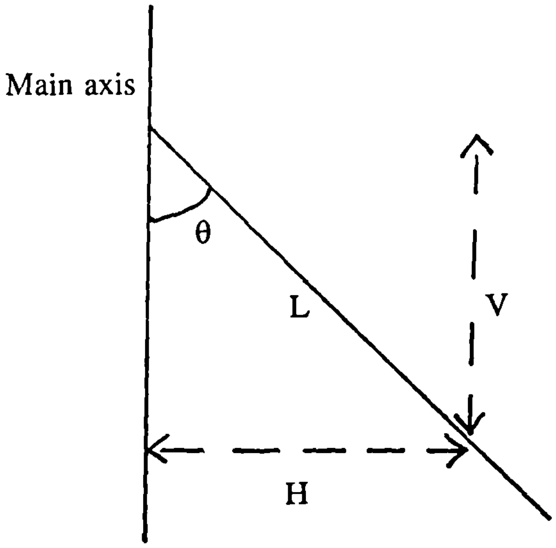
force = 0.835 * depth / 10

iii) The regression equation of force against length of lateral root in root system type "2b" (force = 0.606 +0.666 * length of 1° L) contains a constant (0.606) which relates to the main axis component. The constant was removed from the equation in the program because the slope of the line should pass through zero *i.e.* when both the main axis and lateral roots are absent.

iv) The force on a lateral root which is angled other than at 90° to the main axis may be considered as having two components (Fig 6.9). The first is the force to pull out the horizontal component of the lateral. The second is the force needed to pull out the

Fig. 6.9

The two components of force on a 1° L which is not at 90° to the main axis



Where: H = horizontal component

V = vertical component

L = length of lateral branch

vertical component of the lateral. The pull-out resistance from this system is derivedfrom the equations used in root systems types "1" and "2b", using the equations:

$$Fh \propto \sin\theta * Length * 0.666$$

$$Fv = \cos\theta * (-0.0133 + 0.023 * Length)$$

where the vertical component of length < 7.0 cm

$$Fv = \cos\theta * (-0.0789 + 0.139 * Length)$$

where the vertical component of length > 7.1 cm

where Fh is the force on the horizontal component and Fv is the force on the vertical component.

6.3.3 Testing of ROOTFORCE

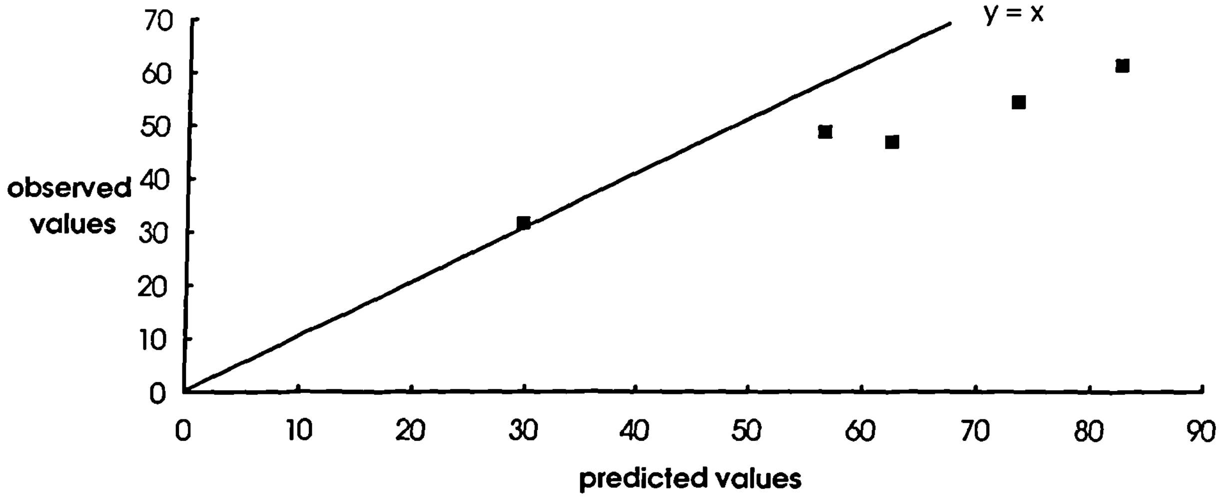
The complete root systems developed to test the accuracy of the predictions made by ROOTFORCE did not have an uprooting force similar to that predicted by ROOTFORCE (Table 6.3; Fig. 6.10). The complete herringbone root system took 19 N less force to extract it than predicted by the program. The randomly branched root system, with the 2° L's at the top, took 16 N less force to uproot it than predicted by the program. In both cases, the lateral roots were not bent downwards when removed from the sand, so there may be another reason why it took less force than predicted to pull them upwards. When the randomly branched root system with the 2° L's at the bottom was pulled out of the sand, the branched laterals were bent downwards and one of the 2° L's had broken off. However, the force required to uproot the system was 21 N less than that predicted by the program. The herringbone root systems with some branches removed had uprooting forces similar to that predicted by the program (Table 6.3). The program appeared to reach a level where the forces predicted above a certain point were incompatible with the observed values (Fig. 6.10), possibly due to the sand shearing at the top of the container before all the branches were extracted and also the deformation of the artificial root systems themselves.

Table 6.3

A comparison of predicted and observed values of pull-out resistance for different types of branching pattern.

Type of branching pattern	**Predicted value (N)**	**Observed value (N)**	**± Standard deviation**
complete herringbone	73.2	54.0	2.0
herringbone with lower 4 branches removed	29.6	31.5	2.5
herringbone with upper 4 branches removed	56.3	48.5	6.5
complete random, with 2° L's at the top	62.2	46.5	2.5
complete random, with 2° L's at the bottom	82.0	61.0	-

Fig. 6.10 Relationship between observed and predicted values of pull-out resistance for different types of branching pattern

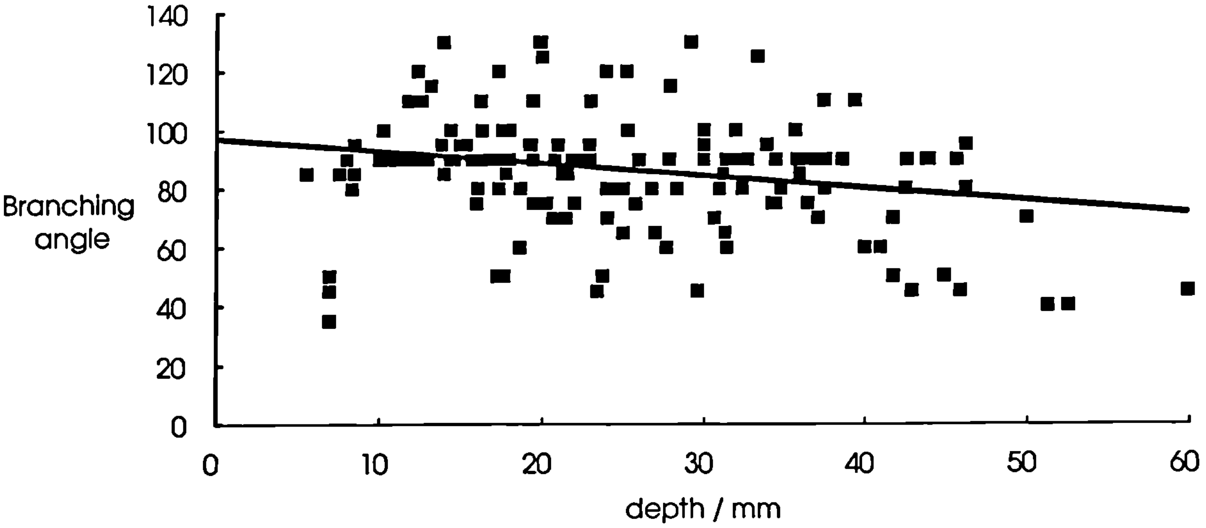


6.3.4 Real branching angle measurements

There was a significant relationship between the branching angles of young European larch 1° L's and the depth below the soil surface; the greater the depth, the smaller the branching angle (Fig. 6.11, $R^2 = 0.81$, $P < 0.001$). The mean branching angle in the top 4 cm of soil was 88.6° (± 18.0), and below this, the mean angle was only 66° (± 20.0).

The mean root branching angle calculated from the 60 1° and 2° L's of mature Sitka spruce measured, was 58° (± 13.6) which is the same as the optimum angle *predicted* by the model.

Fig. 6.11 Relationship between the branching angles of European larch first order lateral roots and the main axis, and depth below the soil surface



6.4 Discussion

6.4.1 The physical model

In all the tests with the artificial root systems, resistance to uprooting increased with depth in the sand. Apart from the main axis, the graphs of uprooting curves were all linear for the first 20 cm below the sand surface. The largest resisting force acting on the main axis alone was friction between the wire and the sand. It is not clear why this force should act less in the top 7 cm of sand. It may have been due to differences in the strength of the sand-root bond, as the sand was more difficult to pack around the small amount of buried axis. The soil-root bond is an important factor in the failure of rooted soil (Waldron & Dakessian 1981). The branched structures were more difficult to pull out because sand was carried upwards on the forks of the branches. If the branching angle was too large (around 90°), the sand fell through the fork leaving a much smaller amount on the crux of the fork. The unbranched structures were able to move through the medium, carrying little sand up with them. The length of a lateral branch is a key component of anchorage, because the weight of the soil above a branch determines the force required to uproot it. The branching angle between the main axis and the 1° L will alter the projected length of that branch. Consequently, a lateral at 90° to the tap root which is the same length as a lateral at 45° will be better anchored because the weight of soil above the latter will be reduced by half. Mechanically, therefore, the optimum branching angle for primary lateral roots would be 90° to the tap root.

A bending moment was set up at the junction of a 1° L and the main axis, causing the artificial roots to begin to bend and the joints to break, when the weight of the sand above the 1° L exceeded the strength of the root. Steel is four times stronger in tension than Sitka spruce wood and fifteen times stiffer (Gordon 1968). Real roots of the same diameter would therefore bend a lot sooner than steel wire resulting in a quicker reduction of the branching angle to the main axis. The required pull-out force diminishes with the decrease in branching angle. The soil would not be carried up in plates, as it would fall away around the edges of the soil-root plate.

A fundamental aspect of root anchorage is the transfer of tension from the root to the soil, especially on the windward side of the tree during overturning. We can consider the roots in the soil as elastic fibres of a relatively high tensile strength embedded in a matrix of plastic soil. When the fibre is pulled, tractive forces between the fibre and the surrounding matrix develop. These forces in turn mobilize the tensile resistance in the fibres (Waldron 1977, Gray 1978, Waldron & Dakessian 1981). The tractive forces are produced by friction or by bonding between the fibre and surrounding soil matrix. The tractive forces around the fibre will fail if the adhesion between the fibre and the matrix is less than the strength of the matrix material, so the fibre will pull out, linked by only weak frictional forces, as in the case with the artificial root systems and the weak sand. However, if the fibre-matrix bond is greater than the strength of the matrix, the fibre will be pulled out still linked to the matrix via the remaining shear resistance of the matrix. If the matrix tensile strength is less than its shear strength, failure of the matrix in tension may occur, with the fibre being pulled out attached to a mass of matrix around it, as would probably occur with real roots in soil (Russell 1961). This would in turn increase the roots' resistance to uprooting. If the modulus of elasticity (*E*) for the fibre equals or is less than *E* for the matrix, tension applied at the top will cause the fibre to stretch at its upper part, concentrating shear stress at the matrix surface and causing failure of the fibre at the top. If the *E* of the matrix is less than that of the fibre, shear stress is concentrated at the tip of the fibre (Kelly & Macmillan 1986, Ennos 1989).

The tensile strength of a root varies with its diameter (Wu 1976, Ennos 1990). Therefore, it is possible to determine the tensile strength per unit area of soil by calculating the distribution of root sizes in a specific soil cross-section (Wu 1976). This assumes that the tensile strength of the roots is fully mobilized during failure *i.e.* the roots are long enough and / or frictional enough so that the frictional bond between the roots and the soil matrix exceeds the tensile strength of the roots. If a root is too short, it will slip or pull out before mobilizing maximum tensile resistance and breaking in tension. Therefore, a fibrous root system, or one with many branches, will be better adapted for anchorage than one, wide tap root, which would have to be proportionally longer to withstand uprooting (Ennos 1990). Therefore, in order to maximise pull-out resistance, a herringbone root system would need to be proportionally longer than a root system with 2° and 3° L's which would have a higher concentration of roots per unit volume of soil.

6.4.2 Branching angles

The mean branching angle for larch primary laterals in the top 4 cm of tap root was 89°, which is close to the optimum predicted by the model *i.e.* 90° for vertical pull-out resistance. Although trees are seldom, if ever pulled upwards, a tree with horizontal laterals at 90°, to the tap root will probably also resist rotational movement best. The horizontal laterals resist tension and keep the tap root vertical (Fitter & Ennos 1989). 1° L roots are known to grow horizontally from the tap root and may then change direction due to environmental stimuli (Coutts 1989). They are initiated in vertical lines related to the position of the vascular strands in the tap root. Conifer primary lateral roots are plagiotropic (aligned at an angle to the direction of gravity), roots of higher orders are ageotropic (not responsive to gravity) and have poorly developed caps. The 1° L roots are maintained in a growth direction away from the tap root by corrective curvatures. The root probably senses gravity by sedimentation of the amyloplasts in the root cap (Moore & Pasieniuk 1984). The root cap becomes larger as the root grows and becomes more sensitive to gravity. The root then begins to grow downwards which also allows the root to fully exploit the soil away from the mother root in the fastest time (Fitter 1987).

The lateral roots further down the tap root grew at a more acute angle to the main axis (66° ± 20). Fitter (1987, 1991) has predicted that the optimum branching angle, in terms of nutrient capture, after emergence of a daughter root from the epidermis is the one which allows it to reach the outer shell of the parent root's depletion zone the fastest. In the case of an actively growing root system, this would mean roots with branching angles $>75°$. The actual optimum angle depends on the age and growth rate of the parent root and the diffusivity of a local limiting resource. So when laterals emerge further down the tap root, the depletion zone, growth rate and resource diffusivity may have altered so a more acute angle is required to escape the depletion zone.

Applying Fitter's model to the branching angles between lateral roots suggests that the mean angle of 58° found in mature root systems of Sitka spruce may be a little low. The mean angle of 58° is the same as that predicted by the model for optimum pull-out resistance. This suggests that the observed branch angles result in the maximum effective pull-out resistance possible for a root system with this kind of branching. There may be a compromise between the shortest path out of the depletion zone and the mechanical stability of the tree.

6.4.3 Critique of the uprooting model

The model can be criticised for its artificiality. Steel wire is very unlike woody material, and the type of sand used would only be found naturally in the littoral zone of the sea shore. A compaction machine should have been used to compact the sand to the same compression for each series of tests. Using different types of soil would provide a greater insight into the mechanics of the real system, although variability in the media would be increased greatly. A shear meter could be used to measure the shear strength of the different soils. The moisture content of the sand was an important factor. Even though fresh sand was used from a sealed bag before each series of tests, a moisture meter should have been used to check consistency.

Unfortunately, what happens to the root system as it is being pulled out of the sand cannot be observed. When studying the processes of soil failure and uprooting of Sitka spruce in the field, Coutts (1986) used microphones buried in the soil near the stem centre to record the sounds of breakage in the soil and roots. This type of system would be complicated to set up in the small types of container used in this experiment but would be feasible on a larger scale. To examine exactly how failure occurs, such as when bending moments arise in the root system and when soil shearing begins, the development of a clear medium out of which to pull the root systems could provide a solution. A mixture of a clear gel and glass ballotini (to provide heterogeneity such as that found in soil) in a clear container, may be one possibility.

The model could be extended by using artificial root systems with different wire thicknesses or by using materials with an elasticity similar to that of real woody roots.

Rubber tubing with flexible wire inside the tubing, to maintain the pattern of the desired architecture, might be a possibility. The model root branches would then not break as they were lifted out of the sand, but would deform as they were pulled upwards, similar to real woody roots.

To investigate the processes of failure in real roots, which have a different strength and stiffness to steel wire, real root systems could be used in conjunction with the soil, in order to develop a more realistic model. They could be treated in a similar way to the wire roots, using the pruning technique to test different branching patterns. More replicates would be needed because of the variability found in root systems.

Sitka spruce lateral roots tend to grow in the horizontal plane and they twist their apex when growing (M.P. Coutts unpub.). They are able to twist so far and then correct themselves in the opposite direction so that their daughters can emerge at any point around the root axis (Wilson 1971). A model investigating the effect of different branching angles in different planes might be important in defining a further parameter of mechanical stability and increase our overall knowledge of the mechanics of anchorage in trees.

The model does not take into account the effect of branches positioned directly above each other. A root a short distance above another one may greatly reduce the effect of the weight of the soil on the root below. If there is a large distance between the two roots, the weight of the soil on the lower one may still be effective. This could be tested using artificial root systems.

Although the model can be criticised for its artificiality, it has nonetheless provided sensible predictions for the pull-out resistance of root systems with different architectures. The optimum predicted branching angles for anchorage, between both the main axis and 1° L's and between 1° and 2° L's, were the same as found in real root systems, thereby alluding to the reliability of the model. The model can therefore stand on its own with regards to predicting pull-out resistances of simple root systems. With further development, the anchorage strengths of much more complex root systems (*e.g.* fibrous, plate and tap root systems) could be evaluated.

6.4.4 Conclusion

The most efficient type of branching pattern predicted by the model is one with an increased number of roots per unit volume of soil. The studies in chapters two and five show that when young Sitka spruce was grown in a wind tunnel under intermittent wind or flexed in two directions with a shaking device, branching was increased per unit volume of soil. This increases the tensile strength of the soil (Wu 1976). A herringbone root system would have to be proportionally longer than a root system with 2° and 3° L's, which would have a higher concentration of roots per unit volume of soil. Herringbone root systems are favoured in nutrient poor conditions but for a given number of meristems, they require a greater tissue volume and are expensive to construct and maintain (Fitter 1987). However, herringbone roots are usually found in seedlings where anchorage is not the most important function, or in distal areas which would be unlikely to be stressed mechanically since failure would probably occur in the basal region.

The type of random branching pattern observed in the stressed areas of mechanically perturbed Sitka spruce in chapters two and five indicates that there is an increased amount of root per unit area of soil. This suggests that branching pattern in Sitka spruce is correlated with the efficient anchorage of the tree under wind stresses. We can presume that the maximum effective use of the soil matrix is an important adaptive feature.

In Sitka spruce, the branching angles are the same as theoretical values which maximise resistance to pull-out, a feature with adaptive value. Branching angle can be interpreted to be an intrinsic characteristic of a species (Honda & Fisher 1978). It is shown here to be adapted to provide the most resistance to pull-out. However, it is important not to assign any parameter to one aspect of root function such as mechanical stability. There are numerous biological functions which determine root form, such as resource capture and storage capability. The correlation of two aspects of root system architecture with function is nonetheless an important contribution to our understanding of the adaptive geometry of trees.

## Appendix A		Program to calculate resistance to uprooting.

```
REM ******************************************
REM               ROOTFORCE
REM    Resistance To Uprooting (Oct 1993).
REM The force is calculated for each branch root
REM    and then summed for the whole plant.
REM ******************************************
REM Repeat runs of calculations controlled by progrun$
PI = 3.141592654#
progrun$ = CHR$(89)

DO WHILE progrun$ = CHR$(89)
    REM Routine to accept data on tap root/branch length, number & angle.
    CLS
    fplant = 0
    PRINT "Calculation of uprooting forces for a branched root system:"
    INPUT "How many 1st order lateral root branches are there"; roots

    FOR turns = 1 TO roots + 1
        PRINT

        REM Accepts basic tap root data:
        REM fd is the coefficient for depth.
        REM fh is the force on the horizontal component of an angled root.
        REM fv is the force on the vertical component of an angled root.
        REM lats is the number of 2nd order laterals of a 1st order lateral.
        IF turns = 1 THEN
            INPUT "Length of tap root (cm)"; length
            angle = 0
            lats = 0
            fh = 0
        REM Accepts 1st order lateral root data:
        ELSE
            PRINT "1st order lateral number:"; turns - 1
            INPUT "Length of lateral (cm)"; length
            INPUT "Angle lateral to tap root (degrees)"; angle
            INPUT "Depth of lateral (cm)"; depth
            fd = .835 * depth / 10
            fh = SIN(angle * (PI / 180)) * length * .666 * fd
        END IF

        REM Slope of line of vertical component increases deeper than 7cm.
        IF COS(angle * (PI / 180)) * length < 7.1 THEN
            slope = .025 * length
        ELSE
            slope = .139 * length
        END IF
```

```
        fv = COS(angle * (PI / 180)) * slope

        IF turns > 1 THEN
            INPUT "How many 2nd order laterals are there"; lats
        END IF

        REM pullit is the force for the current lateral.
        IF lats = 0 THEN
            pullit = fh + fv
        ELSE
            REM Force on 2nd order lateral depending on angle with 1st order:
            REM factor is the coefficient of force dependant on angle.
            REM ftwo is the force on one 2nd order lateral.
            REM ftwotot is the sum of the ftwo’s for a given 1st order lateral.
            ftwotot = 0
            FOR cycle = 1 TO lats
                INPUT "Length of 2nd order lateral (cm)"; length
                INPUT "Angle between 1st and 2nd order laterals"; angle
            IF angle > 90 THEN
                angle = 180 - angle
            END IF
                factor = .972 + (.00546 * angle) - (.000043 * angle ^ 2)
                ftwo = length * .666 * factor * fd
                ftwotot = ftwotot + ftwo
            NEXT cycle
                pullit = fh + fv + ftwotot
        END IF

        PRINT "Force for root number"; turns - 1; "="; pullit
        fplant = fplant + pullit
    NEXT turns

    REM Gives force for whole root system and offers another run.
    PRINT "Total force required to uproot plant ="; fplant; "Newtons"
    PRINT "Do you want to repeat for another root system (Y/N)?"

    DO
        progrun$ = UCASE$(INKEY$)
    LOOP WHILE progrun$ <> CHR$(89) AND progrun$ <> CHR$(78)

LOOP
PRINT : PRINT
PRINT "End of root modelling session."
END
```

Chapter 7

General discussion

7.1 Can trees adapt to wind stress?

Trees exposed to wind loading in the experiments described, have been shown to alter their form in a manner which is intuitively adaptive. Wind-stressed young trees have a reduced stem extension, which reduces the length of their lever arm and hence turning moment (Chapter 4). Extra wood was laid down on the leeward side of stressed stems of European larch trees, which increases the trees' resistance to bending in that direction (Chapter 2). Such changes in allometry and biomechanics of stems are well-documented in the literature (see Telewski 1993). Much less well-known are the responses of root systems to external forces, despite the fact that anchorage is a major function of root systems (Coutts 1983a, Ennos 1993b). The main question addressed in this thesis is whether mechanical stress influenced woody root development in conifers, as suggested by Jacobs (1939, 1954), Fayle (1968, 1975) and Wilson (1975), who all found that lateral woody root radial growth increased when the trees were subjected to mechanical stimulation.

Root architecture of wind-stressed or flexed trees was seen to develop in such a way that intuitively could be assumed to increase the anchorage strength of the tree. In all the studies, woody lateral roots lying in the direction of stress increased in Σ CSA, and hence resistance to overturning (Coutts 1983a). Roots growing at right angles to the direction of stress are less well-developed in mechanically perturbed trees. These structural roots were subject to torsion and will offer little resistance to overturning along the axis of stress.

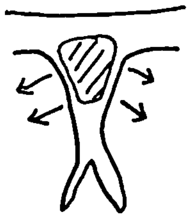
One of the most striking and unexpected responses of Sitka spruce root systems to wind stress was a decrease in topological index of windward roots compared to leeward roots (Chapter 2). Morphogenesis of the root systems had altered to increase branching on the windward side, resulting in a greater number of roots per unit volume of soil, hence increasing the tensile strength of the soil (Wu 1976). The exterior links of the windward woody roots were also longer than those on the leeward side. Wind-induced movement causes roots to rub against the soil and stones or each other, thereby stunting growth (Hintikka 1972). The exterior links of wind stressed Sitka spruce leeward roots might have been subjected to such abrasion as they would be pressed down on the hard bearing surface of the soil. Such pressure may damage the roots, perhaps resulting in smaller woody exterior links.

Forces experienced by the shoot must be transmitted to the soil *via* the roots in order to resist uprooting. These forces, acting as tensile or compressive forces, are transferred to the soil at some point along the root. According to Mattheck (pers. comm.), roots in tension transmit forces further away from the main axis of the tree than roots in compression. Therefore, windward lateral roots should have more, wider and longer second and third order woody roots than leeward roots, in order to transfer forces smoothly into the soil (Fig. 7.1). As leeward lateral roots are held in compression during overturning, higher order roots are pushed downwards onto the bearing surface of the soil (Coutts 1983a). Therefore, the compressive forces are transmitted into the soil much nearer to the main axis, at the junction of first and second order lateral roots. Second and third order leeward lateral roots are therefore not as important for anchorage as on the windward side of the tree (Fig. 7.1). If there is increased woody growth at the junction, forces will be transmitted more smoothly into the soil. There were no differences in interior link length or diameter between windward and leeward roots. As all orders of lateral roots were included in the analysis, any increase in radial growth at the junction between first and second order roots would not be obvious. A detailed examination of woody growth in the region between first and second order lateral roots around the main axis would help to verify Mattheck's theory.

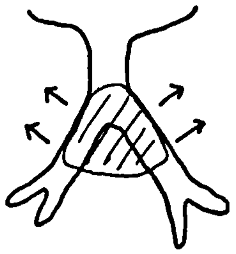
The root systems of flexed Sitka spruce clones (Chapter 5) also showed changes in architecture. Again, an increased topological index was found in roots subjected to the least stress *i.e.* perpendicular to the direction of flexing. The index (0.73) was the same as for woody roots perpendicular to the wind direction in wind stressed Sitka spruce (0.73). Roots perpendicular to the direction of stress appear to receive less resources than stressed roots and have a more herringbone topology. The forces on the stressed roots of the flexed plants were both tensile and compressive forces. In

Fig. 7.1
The point of transmission of forces from the roots to the soil in a shallow root system (after Mattheck, pers. comm.)

Forces will best be transmitted into the soil by a tapering root:



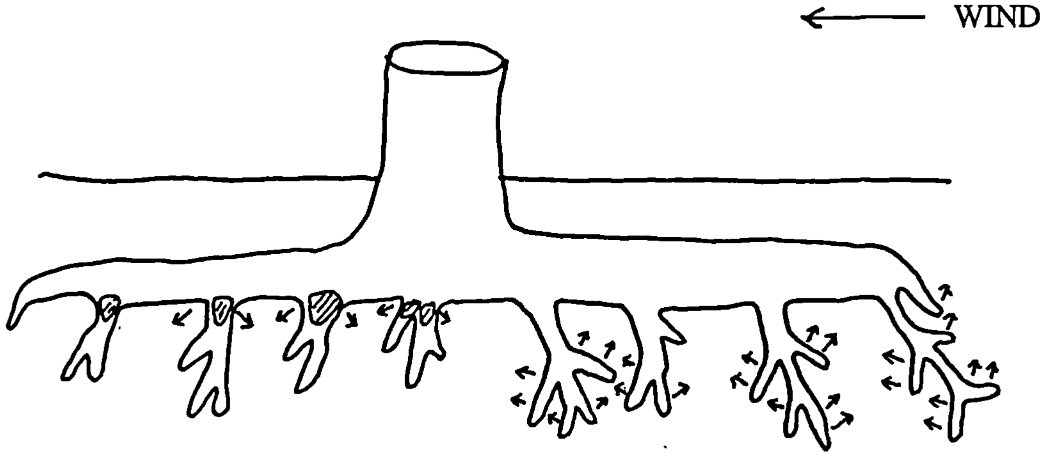
Compressive forces will best be transferred best by a downwards taper



Tensile forces will best be transferred by an upwards taper

Arrows refer to transmission of forces from root to soil

Applied to a tree root system, this means that there should be thicker roots on the leeward side and highly branched laterals on the windward side.



order to transmit these forces into the soil in the most effective way, structural roots might have increased branching to transfer the tensile element and thickened junctions between the first and second order lateral roots to transfer the compressive element. However, woody lateral roots held in compression act like a cantilever beam, so branching would greatly reduce the stiffness of the beam (Coutts 1983a, see Chapter 1). A compromise between the two extremes of branching pattern which best transmit forces into the soil may be reached. This compromise may have been achieved by producing a random branching pattern (index = 0.52), the same as that found in leeward roots of wind-stressed plants. It is surprising that leeward roots of wind-stressed Sitka spruce are so branched, because their stiffness will be reduced. It is possible that the leeward roots are unbranched near the root base and then begin branching distally down the root, but such speculation could only be satisfied with a more detailed examination of the root architecture.

Results from this thesis show that woody trees respond to mechanical stimulation. Even though the responses of the shoots were minimal, significant changes occurred in the development of the woody root systems, which suggests that signals, such as those described in Chapter 1.4 were relayed from the shoot to the roots. Ethylene appears to be the main stimulant of thigmomorphogenetic responses in plants, but may also interact with auxins to alter cambial activity. Mechanical stimulation must trigger a signal to start the cascade of reactions involved in the synthesis of ethylene and perhaps auxin. This signal may be transmitted down to the roots where there might be an increase in ethylene production at the root bases in the stressed areas. An alternative explanation is that forces transferred down the stem result in an area of localised stress in the roots, to which the plant responds directly. Thigmomorphogenetic responses would then be induced *within* the root system. The higher levels of ethylene which could then result would stimulate the radial growth of more roots as observed in Chapters 2, 4 and 5.

7.2 The safety factors of trees

The mechanical stability achieved by a tree must be gained at a metabolic cost. Resources must be utilized to lay down extra wood at the most mechanically stressed areas. However, structural reinforcement beyond a certain limit will be too expensive, unless the possibility of mechanical failure is high enough to warrant the extra cost (see Niklas 1992). The safety factor (*i.e.* the ratio of maximum loadings likely to be experienced, to the operational loadings on a structure (Niklas 1992)) should depend on the magnitude and frequency of loadings experienced by the tree. For example, Tateno & Bae (1990) simulated thigmomorphogenesis by treating mulberry trees (*Morus bombycis*) with succinic acid 2,2-dimethylhydrazide (SADH), which dwarfs growth by stimulating the production of ethylene levels in the plant. The treated plants had an increase in dry leaf mass at the expense of stem elongation, compared to untreated plants. The critical lodging moment (the minimum leaf fresh weight required for lodging) had increased but so had fresh leaf weight. Consequently, the lodging safety factor of plants from both treatments was similar. Therefore they concluded that shoot morphogenesis of non-stressed plants was controlled to maintain the lodging safety factor at a constant level. The lack of change in overturning resistance observed between wind-stressed and control European larch (Chapter 4) and flexed and non-flexed Sitka spruce (Chapter 5), both grown under levels of high nutrients, indicate that a similar mechanism might be occurring. As stem length was reduced in stressed trees, stem biomass must be partitioned elsewhere *e.g.* in the roots or shoot branches and needles. Therefore the critical lodging load and hence safety factor may be similar between perturbed and non-perturbed plants. A more detailed examination of biomass partitioning in mechanically stimulated trees might verify Tateno and Bae's (1990) theory.

The responses of trees to wind loading and flexing presented in this thesis illustrate a possible adaptation to the magnitude and frequency of loading. The overturning resistance of mechanically stimulated trees did not differ from that of control trees when the trees had a plentiful supply of nutrients, although other morphological characteristics were altered. An increase in overturning resistance between flexed and non-flexed trees was only observed when nutrients were limited. As nutrients were scarce, perhaps an increase in biomass could only be allocated to those parts of the tree under the most stress, such as the woody roots. Consequently, an increase in the lodging safety factor may have occurred. However, it is the comparison between trees grown under high and low nutrient treatments which are of practical significance to foresters. High nutrient levels resulted in larger plants which resisted overturning better than trees grown under a low nutrient regime, therefore the application of fertilizers to young trees would ensure a faster growth rate and a greater stability.

7.3 Implications for survival

Modelling of optimal shapes of tree growth, such as described in Chapter 6, will allow us to predict to a certain extent what might happen when environmental parameters are altered. It is important to acknowledge however, that there is no "optimal" pattern of growth for any one species and that "optimal" forms will change with a changing environment. Niklas and Kerchner (1984) used a computer program to generate branching patterns of plant shoot systems. The structures generated had to have the ability of sustaining their own weight and maximising effective leaf area to sunlight. They found that there were many branching patterns capable of such a maximum performance level. Therefore, there was no single "optimal" branching pattern. The optimal branching pattern for a shoot system must depend on the amount and quality of light available, and the loading to which the shoots will be subjected. For example, desert trees should have an optimal pattern of shoot branching which would not be beneficial to a tree subjected to wind and snow loading in Northern Europe. In the same way, root branching patterns will also differ enormously in their ability to obtain water and nutrients and act as plant anchors. The local environment of the soil will determine branching patterns to a certain extent (Fitter & Stickland 1992) but the growth of the above ground parts must also affect root development. There will presumably be many different optimal branching patterns for tree roots, depending on the local conditions of the tree and the loads it is subjected to. A tree in a protected environment may not need to allocate many resources to woody roots, so the root branching pattern might be optimal for scavenging nutrients. In a windy environment, resources must be allocated to structural roots in order to enhance stability.

Responses to thigmomorphogenesis (*i.e.* a shorter stem and increased radial growth in stressed areas such as the woody root bases) will reduce the effects of wind loading, but at a cost to the tree. A shorter tree might have a reduced photosynthetic area due to shading by other trees, so the assimilation of photosynthates will be reduced. A reduction of assimilation would in turn result in a total reduction of plant growth, leading to the characteristic stunted trees of windy places, *e.g.* the Highlands of Scotland. Decreased growth will in turn mean that flowering and fruiting periods are delayed which might be an advantage in itself *e.g.* flowers are produced after the worst conditions of a severe winter are over. In extreme conditions, flowers may not be produced at all, which would have consequences for the survival of species growing in very windy regions. Exposure to prolonged periods of strong winds may cause long-term effects in a species. As Niklas (1992) points out, "subtle differences in the environment may have driven natural selection to produce extremely small, albeit important, morphological and structural differences among species." The large genotypic variation found in the development of characteristics of Sitka spruce clones when mechanically stimulated (Chapter 5), suggest that features reducing the effects of wind loading might be selected for in a species. One place to look for such natural selection would be at the tree line, where trees are often exposed to high winds. In less exposed regions, the responses of trees to wind loading can be subtle compared to other environmental stresses imposed on plants such as temperature, light levels and water stress, but are important for survival nonetheless.

7.4 Implications for forestry

Windthrow is one of the most important factors a forester must consider when deciding where to plant trees, how to prepare the ground and when to fell trees. Losses by windthrow are often greatest in a stand which has recently been thinned. Not only do the trees provide little timber, but the forester will be forced to sell when the trees have blown down, instead of waiting for the optimal market value. However, trees must be thinned to a certain extent to allow increased stem radial growth. Thinned trees will also have larger root-soil plates, therefore anchorage will be increased. Foresters currently base their choice of thinning regime largely on local experience and the windthrow-hazard class for that area. The windthrow-hazard class is a calculation of the critical height to which trees can grow before they start to blow over in normal winter gales (see Cannell & Coutts 1988). As a tree grows, the likelihood of windthrow becomes more of a risk until the risk becomes so great that the trees must be felled. The amount of thinning during the crop rotation also takes the risk of windthrow into consideration. If a stand is thinned too much, gaps between the tops of the trees will be greater and the wind loads on each tree will be larger. In a heavily thinned stand, the forest also yields less timber per hectare and trees produce larger branches with more knots in the trunk, thus reducing the quality of the timber (Cannell & Coutts 1988). Line thinning (removing a complete row of trees from a stand) is a common practice in British forestry. Instead of removing a line of trees parallel to the prevailing wind direction, it may be advantageous to remove a line aligned cross-wind. Root growth would then be encouraged in the windward and leeward directions and stability may be increased, as shown in Chapter 5.

Without thinning, the top of the canopy stays continuous so that wind can move over the top of the forest. More trees can be grown per hectare and the wood is of a better quality. Ideally, a stand should be thinned to allow better shoot and root growth, and the trees should adapt to the newly imposed wind forces in the fastest possible time so that they can be better able to withstand gales. The time needed for a tree to adapt to wind stresses after thinning is unknown, but some phenotypes may be able to adapt faster than others. Clones of Sitka spruce differed greatly in their response to flexure stress as shown in Chapter 5, but as this experiment lasted only one growing season, it is unknown whether trees all develop in the same way to wind stress, but at different rates. The response time of tree adaptation to wind stress might be an important characteristic to consider in breeding programmes; clones with high adaptation rates will be of value in regions where wind damage is a major threat.

A forester can address the risk of wind damage to his crop by dealing with it in various ways. When planting trees, the choice of ground preparation techniques should be a factor to be considered with regards to wind. Trees planted on ridges (see Chapter 1.1) aligned with cross-winds are more prone to windthrow (Yeatman 1955) because woody root growth increases along the ridges. As increased woody root growth in the direction of a prevailing wind is likely to enhance stability, ploughing parallel to the direction of the wind might reduce the risk of windthrow.

If waterlogging is not a problem with the site, other planting techniques are employed such as direct planting; a nursery tree is planted directly into uncultivated soil. It is possible that anchorage might be increased by increasing the depth of the pivot point (the point at which the plant rotates about its axis, see Chapter 4). Casada *et al.* (1980) examined the wind resistance of tobacco (*Nicotiana tabacum*) plants as influenced by the depth of burial of the pivot point beneath the soil. They found that the roots of tobacco plants provided only a small percentage of the total resisting moment, while soil pressure against the buried stems provided most of the resistance to wind loading. At extreme depths of burial however, the root system will not pivot and mechanical failure of the stem may occur instead of the roots *e.g.* toppling in young trees (failure of the stem due to bending). The risk of toppling also increases with stem length (Holbrook & Putz 1989), so very tall trees will be less stable.

As short trees have smaller lever arms, the turning moment is reduced and they are less susceptible to windthrow, but also provide less timber. Trees < 18 cm in diameter are only suitable for pulp or products of low value. Wider trees are much more valuable because they provide sawlogs which are used as structural timbers. Foresters must balance the economic losses caused by windthrow with those of timber quality. Ultimately, plantations need to be managed so that trees grow taller and wider faster, without increasing the risk of windthrow. Foresters must consider wind stability factors in tree selection if they are to reduce losses due to windthrow. If characteristics leading to better tree stability are identified, breeding with regards to wind damage will be improved. It has been shown by Nicoll *et al.* (1993) and in Chapter 5 that the root:shoot ratio is a poor indicator of tree stability because of the proportion of biomass allocated to the stump, which plays a small role in anchorage. An increased allocation of biomass to structural roots would however, be advantageous. Studies such as these may have implications for the wind stability of trees and could provide opportunities for improving stability by clonal selection. Clones of forest trees which develop strong anchorage may be able to have longer rotations in exposed conditions, and clearance costs of wind blown timber will be reduced. Felling timber is much cheaper than clearing wind blown trees, therefore the value of the crop is comparatively greater. More flexibility is also possible in selecting the year of felling, which in turn will take advantage of market fluctuations.

Screening of young trees with features which best promote tree stability might be possible if these features were identified. Seedlings with characteristics capable of improving anchorage could then be selected out. Silvicultural intervention at this point might help in producing trees less likely to blow over by altering the phenotype. If characteristics in the structural root system were selected for, they would be retained, as the structural root system of a tree develops early on in life (Coutts 1983b). Trees with a high resistance to windthrow would be extremely valuable to the forest industry; such trees could be planted in areas of high risk *e.g.* at the edges of plantations, or in particularly exposed sites. A summary of the most important shoot and root characteristics contributing to tree stability, as identified in this thesis, are presented in Table 7.1.

Table 7.1

Summary of the most significant characteristics contributing to tree stability

Shoot characteristics	**Root characteristics**
Flag-shaped canopy	More lateral roots
Shorter stems	Larger lateral root bases
Wider stem bases	Increased biomass allocation to woody lateral roots
Flexure/reaction wood in stem	Increased biomass allocation to vertical growth of lateral root bases
Increased stem flexibility	Increased woody lateral root branching on windward side
	Exterior links of woody laterals longer and wider on windward side

It would be of interest to foresters to know how a tree which had reacted to wind from one direction, would respond to wind stresses if the wind direction were changed. It is believed that most damage to a forest is caused when wind comes from an unusual direction thereby suggesting that forest trees may also adapt to unidirectional winds. Further work where young trees are exposed to different wind directions and durations will help clarify the role wind plays in the development of root systems and hence anchorage strength.

7.5 Further work

As there has been so little work carried out on tree response to wind with regard to root growth (see Chapter 1), this area of research requires a lot of development. A young tree will develop differently if exposed to multi-directional winds compared to a unidirectional wind, as shown by the changes in root development of Sitka spruce subjected to wind from one direction and flexing in two directions (Chapters 2 and 5). The presentation time (length of time a plant is mechanically stressed) is an important factor to consider when carrying out such experiments and there may be a critical presentation time required to induce a response (Telewski 1993). The length and magnitude of exposure may also determine the extent to which the physiological responses occur, which would be reflected in the plant form. Experiments incorporating the effects of different wind directions, windspeeds and presentation times on young trees would be relatively straightforward and provide a great deal of information about the responses of trees to mechanical stimulation.

The results presented in this thesis were all carried out on young trees grown in glasshouses under controlled conditions. Conditions in the field vary enormously and trees are subjected to many different wind velocities, the most extreme of which are in the winter, when the trees are dormant. Experimental work where trees of different ages are grown in the field and staked to prevent movement (*e.g.* Holbrook & Putz 1989) could be compared with control (free swaying) trees to allow a more realistic assessment of tree response to wind in natural conditions. Such experiments could be carried out over a number of years and measurements made during such a time period would allow a calculation of how quickly a tree can adapt to wind stresses. Anchorage tests carried out on trees treated in such a way, may show larger differences between staked and free swaying trees which, in short term laboratory experiments, are not large enough to observe.

The mechanism by which thigmomorphogenesis occurs is not fully understood. It is not known whether the same processes occurring in the shoots also exist in the roots.

If ethylene is the mediator of increased radial growth in stressed areas, the pathway of its synthesis should be clarified so that it might be manipulated. Treatment of nursery stock with an ethylene generating solution such as Ethrel (Telewski 1990) might induce thigmomorphogenetic responses, such as reduced stem extension, increased stem radial growth and and changes in root development.

If the responses of trees to mechanical stimulation were understood in greater depth, it might be possible to model those responses. Laboratory work usually involves totally unstressed trees, and trees under a single dose of stress. In the field, totally unstressed trees do not exist. It is important to establish the shape of the stress-response curve (where stress is the force, frequency and duration of loading). From such a curve, it could be possible to predict species response to growth in a windy region. Knowledge of tree stability characters and the response of trees to wind will in the future help foresters and arboriculturalists decide which species to plant in a particular site, depending on the weather conditions in that region. However, our current understanding is still a long way from being able to predict accurately how improved trees will perform in the field.

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Appendix 1

Responses of Young Trees to Wind: Effects on Root Growth

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Abstract

Two experiments were carried out with Sitka spruce and European larch grown under intermittent wind in tunnels. In the first, both species were grown to determine whether there are any specific effects of wind on root growth, as opposed to effects on growth in general. In the second experiment, larch seedlings had their tap-root removed 20 mm below the soil surface to mimic the formation of a shallow root plate, such as develops when larch is planted on seasonally waterlogged peat in much of the U.K.. In both experiments, lateral roots were counted and their orientation relative to the tap root recorded. In the wind stressed trees in both experiments, there was an increase of almost 60 % in the number of large roots on the windward side of the trees and of 45 % on the leeward side of larch trees compared to the number of roots growing at right angles to the direction of wind. In the first experiment, the sum of the cross-sectional area (Σ CSA) of lateral root bases was greater on the windward side of the tree compared to the other sides in both species. In the second experiment, Σ CSA of lateral root bases of wind stressed larches was greatest on the leeward side whereas the control plants had a larger Σ CSA in the regions perpendicular to the wind direction. It appears that wind action stimulates the diameter growth of those roots most important for anchorage, but has a smaller effect on root development than other factors such as uneven nutrient supply. Once the tree is established and has reached a point where it is more vulnerable to wind, even these small changes may however be important in determining resistance to windthrow. A prediction of the role wind plays in the development of young trees is important to the forest industry.

Keywords: *Picea sitchensis*, *Larix decidua*, root anchorage, wind tunnel, windthrow, root architecture.

Introduction

Damage by wind is an important problem for forestry in the British uplands. Windthrow, the uprooting of trees, is much more common than stem breakage (Holtam 1971). Extensive research has been carried out in attempts to predict and reduce wind damage (Booth 1974, Somerville 1980) but less has been done on the mechanics of how plants are uprooted (Coutts 1983, 1986, Ennos 1989, 1991). Furthermore, only limited work has been carried out on the effects of wind action on root growth (Satoo 1962, Heiligmann & Schneider 1974) even though root form is the dominant influence on uprooting resistance (Ennos 1993).

Coutts (1983, 1986) quantified the forces involved in anchorage of shallow rooted *Picea sitchensis* Bong. (Carr.) (Sitka spruce) by measuring the turning moment during the displacement of the soil-root plate when pulling mature trees with a winch attached to the stem. By sequentially cutting or breaking the roots and soil, he then divided the total resistive turning moment of the anchorage system into four components (Fig. 1): resistance to uprooting by soil underneath and at the sides of the plate, the weight of the plate, the resistance of leeward roots to bending and the resistance of windward roots in tension. When applied forces were maximal, the most important component in resisting uprooting was resistance from windward roots held in tension (54%). Other factors contributing to resistance included the weight of the root-soil plate (31%), the bending of roots at the leeward hinge (8%) and finally soil resistance underneath and at the edges of the plate (7%). In two non-woody species (*Impatiens glandulifera* and *Helianthus annuus*) Ennos *et al.* (1993) found that the windward roots again provided the most resistance to uprooting.

In order to achieve anchorage, roots must transfer into the soil forces which the shoot experiences. The stronger the soil and root-soil bond and the greater the root surface area, the larger the uprooting force that can be resisted, although the cost of constructing such a root system must be balanced against the benefits gained in anchorage (Fitter & Ennos 1989, Ennos 1993). For trees, the relevant uprooting force is when the wind or weight of the tree causes the plant to topple over from the base. This horizontal force will set up a moment about the base of the stem. The roots will be held in tension or compression and both forces will be transferred to the soil. In order to resist the turning moments transmitted by the stiff stem, trees need a rigid root system. This is achieved either by having a tap root from which horizontal lateral roots are attached, or by having a plate of lateral roots with sinkers growing downwards. If these sinkers quickly reach the water table and die off, as happens for example when Sitka spruce is planted on peat in much of the U.K., then anchorage strength is reduced.

The growth of woody roots, which form the essential structure for anchorage, is influenced by a number of internal and environmental factors (Coutts 1987). Mechanical stresses from wind action must affect the activity of the root cambium, since there is an increase in diameter growth when roots are stimulated (Jacobs 1954, Fayle 1968, Wilson 1975), Mechanical stimulation has been most thoroughly researched in stems (Jaffe 1973, Telewski 1993, this volume) where thigmomorphogenesis, in which stem elongation is reduced and radial growth increased, occurs and is intuitively adaptive. The forest industry needs to know if comparable effects also take place underground, where the tree is anchored. Jacobs (1954) attached guy ropes to the stems of young *Pinus radiata* so that only the tops of the plants would sway. The diameter of the guyed stems was greater than the controls above the point of attachment, but smaller below. After two years the ropes were removed and, in the first high wind, all the stems broke or blew over. Jacobs also found that guyed trees had thinner woody roots. Fayle (1968) repeated this experiment on *Pinus sylvestris* saplings. After two years, the lateral roots of free-standing trees showed a 75% increase in their annual ring widths when compared to the guyed trees.

Most research into thigmomorphogenesis has concentrated on flexing or shaking (Jacobs 1939, Jaffe 1973, Telewski 1990) which is an artificial and often unrealistic way to mimic changes in a plant exposed to wind stresses. There are few studies in which young trees have been subjected to wind from an early age (Satoo 1962, Heiligmann & Schneider 1974, Rees & Grace 1980, Telewski & Jaffe 1986) and only two of these refer to root growth. Satoo (1962) exposed *Robinia pseudoacacia* seedlings to constant wind velocities of 3.6 m s^{-1} for four weeks and recorded reductions in root length and root and shoot dry weight compared to controls in still conditions. Heiligmann and Schneider (1974) found that shoot and root dry weight were decreased when *Juglans nigra* was grown at windspeeds of 2.8 m s^{-1} compared to plants grown at windspeeds of 0.1 m s^{-1}. In both experiments, exposure to wind resulted in a general reduction in growth, with no specific effects on roots recorded. However, both these wind tunnel studies used relatively fast continuous windspeeds, unlike field conditions, where windspeeds can be low or zero for extended periods. Telewski (1993, this volume) states that plants do not respond in the same way to continuous and intermittent wind action: far greater responses occur when plants are stressed periodically rather than continuously.

The present study, carried out in two wind tunnels, examines the changes in shoot and root growth of Sitka spruce and European larch seedlings under intermittent wind, in order to determine whether effects on plants occur under more realistic wind conditions; whether there are any specific effects of wind on root growth and whether any responses to wind could be viewed as adaptive. Ideally such experiments should be done on large trees, but it is difficult to work with mature trees. However since the lateral roots of a mature tree develop early in its life (Coutts 1983), the roots laid down by a seedling tree will determine the structure of the mature system. Experimentation on young trees can therefore be a realistic experimental model.

Experimental Tests.

Wind tunnels were set up in glasshouses; each was constructed of dexion frames with polythene sides. In the first experiment, the tunnel was 3 m long, 1 m high and 1 m wide with 3 wind generators (electrically driven fans, 20 cm diameter) positioned at one end. In the second experiment, 2 wind tunnels and 2 control tunnels (no wind) 0.25 m wide, were set up, with 1 generator per wind tunnel. 24 European larch (*Larix decidua* Mill.) and 24 Sitka spruce (*Picea sitchensis* Bong. (Carr.) were grown from seed in the first, but only European larch (14 plants in each tunnel) in the second experiment. In the second experiment the tap-roots were cut 20 mm below the soil surface, using carefully inserted scissors, to mimic the formation of a shallow soil-root plate. The wind generators were operated for six hours during the day and a further six hours at night. The generators were positioned at soil level. Windspeeds experienced by plants ranged from 0.5 - 2.9 m s^{-1} in the first wind tunnel, 0.8 - 5.9 m s^{-1} in the second, and was approximately 0 m s^{-1} in the control tunnels. The plants were harvested from the first and second experiments after 30 and 20 weeks respectively. In the first experiment, after 30 weeks Sitka spruce reached a height of 40.2 ± 8.6 cm with a basal diameter of 9.9 ± 2.0 mm and larch were 58.3 ± 16.7 cm tall with a basal diameter of 12.2 ± 1.9 mm. In the second experiment, larch were 39.6 ± 13.5 cm tall with a basal diameter of 6.0 ± 1.0 mm after 20 weeks. The number, orientation, depth and diameter of lateral roots were recorded for all plants in both wind tunnels.

There was much variation in shoot growth between plants of both species in the first experiment although regressions of stem length, biomass and stem basal diameter on wind velocity were not significant, therefore variation was not due to wind action. In the second experiment, the regressions of larch shoot height and stem diameter on windspeed were significant: plants became shorter, and biomass and basal diameter were reduced with increasing windspeed ($R^2 = 0.30$, $P = 0.025$, $R^2 = 0.16$, $P = 0.035$, $R^2 = 0.16$, $P = 0.002$, respectively).

Root systems were examined in order to discover whether wind was affecting root growth and development. In the first experiment, roots > 2 mm basal diameter in the top 50 mm of soil were studied as they were considered to be the most important for anchorage (lateral root basal diameter ranged from 0.2 - 10.5 mm in Sitka spruce and 0.2 - 13.5 mm in larch). The numbers of these lateral roots were calculated for each 15° sector around the stem for all the plants (Fig. 2). There was a large peak of roots in the direction of the wind (90°), for both species, where the number of roots had increased by 58 % in Sitka spruce and 59 % in larch, compared to the number of roots growing at right angles to the direction of the wind. The data for larch also suggest two lesser peaks of enhanced growth perpendicular to the wind direction (0°) and also on the leeward side (270°), where there was an increase of 41 % in the number of roots compared to the number growing at right angles to the wind direction. Chi-square analysis of the numbers of roots and their orientation for either Sitka spruce or larch show that both distributions of roots are significantly different from uniform (Fig.

2, $P < 0.001$ in all cases).

For plants in the second wind tunnel, where the tap-root had been cut, all lateral roots were included in the analysis, irrespective of size, because the plants were younger and few roots were larger than 2 mm diameter. The numbers of roots were again calculated for each 15° sector around the stem. Two large peaks emerged on the histogram of treated plants (Fig. 3). One peak was towards the direction of wind (90°) and the other exactly opposite, *i.e.* on the lee side (270°). The numbers of windward and leeward roots had increased by 57 % and 49 % respectively, compared to the numbers of roots perpendicular to the wind direction. In the control plants, three peaks appeared, all smaller than the two large peaks in the treated plants. One peak was in the direction of wind (90°), one opposite on the lee side (270°) and the third peak perpendicular to the flow of wind (180°). The distribution of lateral roots in wind stressed plants was different from those in the control tunnel (Fig. 3, $P = 0.02$).

The increase in numbers of roots on the windward and to a lesser extent on the leeward side could imply a greater total root growth in these regions. The sum of the cross-sectional area (Σ CSA) of the bases of the roots growing on windward and leeward sides and perpendicular to these directions was calculated using 30° sectors. The two perpendicular sectors were combined as there should be no difference between them. In the first experiment, root bases of both Sitka spruce and larch had greater Σ CSA's in the windward sector than in the leeward sector (Fig. 4). However, there were no differences in mean CSA per root between any sector for either species suggesting that the effect was not due to increased growth of a few roots. In the second experiment, wind stressed larches had a significantly larger Σ CSA in the leeward sector than all other sectors (Fig. 5). The mean CSA per root was almost significantly larger in the leeward sector ($F_{2,132} = 2.48$, $P = 0.087$). The control plants had a significantly larger Σ CSA in the sectors perpendicular to the wind direction (Fig. 5). There were no differences in mean CSA between the sectors of the control plants.

Discussion

Shoot growth in the first experiment was not altered by wind action, which may be due to the large variation noticed in the plant material or the low windspeeds experienced by the plants. In the second experiment where windspeeds were greater, shoot growth was significantly reduced, although stem basal diameter did not increase with windspeed, as reported earlier (Larson 1965, Grace 1977). However, in both experiments significant differences were found in root growth between wind stressed and control plants, and between roots with different azimuths in wind stressed trees, even at windspeeds which were too low to cause any large responses in shoot growth.

In the first experiment, both species had an increase of almost 60 % in the number of larger roots growing towards the direction of the wind compared to roots growing perpendicular to the wind direction. As only roots > 2 mm diameter at the root base were recorded, this implies that the numbers of larger roots had increased. Although the windward roots did not have a larger mean CSA of lateral root base per root, Σ CSA of root bases was significantly larger in this sector. In the second experiment, root number in wind stressed larch was increased by 57 % on windward and by 49 % on leeward sides. The leeward roots had a larger mean CSA of root base per root than roots from the other sectors, and Σ CSA was also increased in the leeward sector. The control plants had more roots and a larger Σ CSA of root bases in the sectors perpendicular to the wind direction, where the smallest roots were found in the wind stressed plants. It is striking that in both species, there was a consistent increase in the numbers of roots important for anchorage on the windward side and in larch on the leeward side also. This suggests that non-uniform distributions readily develop in Sitka spruce and larch and that wind can alter the distribution with very similar patterns of root growth forming under different windspeeds.

It appears that the distribution of resources within the root system has altered so that those roots which provide the greatest contribution to anchorage receive more resources in both Sitka spruce and European larch. This was more pronounced in the second experiment where the tap root was removed. Instead of resources being sent to the tap root, which is an important component in resisting uprooting in young plants (Ennos 1993), resources were diverted to windward and leeward lateral roots, which increased in number and cross-sectional area in the top 20 mm of soil. The increase in number of leeward and windward roots will mean a higher concentration of roots per unit area of soil, which in turn increases the tensile strength of the soil (Wu 1976). Resistance to pullout will therefore be increased, especially on the windward side as these roots will be held in tension and are the most important component in resisting uprooting by wind (Coutts 1983,1986). The possible increase in radial growth of root bases on the leeward side in the second experiment indicates that these roots have a higher resistance to bending (bending rigidity is proportional to the fourth power of radius). Roots perpendicular to the direction of wind are subject to torsion and will offer little resistance to uprooting. These species therefore respond to wind-induced stresses by enhanced growth of roots in positions most efficient in promoting anchorage, namely on the leeward and windward sides of the tree.

Wind action has a smaller effect on root architecture than uneven nutrient (Drew *et al* 1974) or water supply (Lesham 1970, Coutts 1982) and may be less important during this stage of plant growth. The results show an increase in allocation of resources to roots on the windward and leeward sides of the treated trees, however the magnitude of the increase is small compared to the increases in root base radial growth seen in experiments where trees were staked in the field for 2-4 years (Fayle 1968, 1976) and Wilson (1975). This could be due to the brevity of the laboratory experiments, lasting only 20 and 30 weeks. There may also be a change in the importance of factors affecting root allocation once the tree is established and has reached a point where it is more vulnerable to wind. The responses to wind stress may be amplified as the tree matures.

It is very striking that these apparently adaptive changes in root growth occurred at windspeeds too low to exert large effects on the shoots. It is not clear therefore what signal was transmitted to the roots. Larson (1965), referring to young *Larix laricina*, suggested that resources are diverted from height to diameter growth under the influence of wind sway. He visualized the lower, stressed bole of a tree as a metabolic sink to which assimilates flow. Ethylene production in stems increases under mechanical stress and is thought to be the mediator of increased radial growth and reduced elongation (Telewski 1993, this volume). It can be assumed that an increase in ethylene production at the root bases in the stressed areas, stimulated the radial growth of more roots. The extra wood formation, especially in the leeward roots of wind stressed larches in the second experiment, implies that these roots are receiving more assimilates, but probably at the expense of another part of the plant.

These results suggest that unidirectional wind may result in adaptive responses in tree root systems from a very early age. The changes which occur in trees exposed to wind loading are of an ecological advantage, in that the increase in number and size of windward and leeward lateral roots should result in a tree able to withstand greater stresses with less likelihood of uprooting.

It would be of interest to foresters to know how a tree which had reacted to wind from one direction, would respond to wind stresses if the wind direction were changed. It is believed that most wind damage to a forest is caused when wind comes from an unusual direction thereby suggesting that forest trees may also adapt to unidirectional winds. Further work where young trees in wind tunnels are exposed to different wind directions and durations, will help clarify the role wind plays in the development of root systems and hence anchorage strength.

Acknowledgements

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Figures

Fig. 1. Diagrammatic view of a shallow rooted tree, showing four components of the anchorage which resist overturning.

Fig. 2. Numbers of European larch and Sitka spruce lateral roots > 2 mm diameter, for wind-stressed plants only. Both distributions differ significantly from uniform (Sitka spruce: $\chi^2_{23} = 92.65$, $P = 0.001$; European larch: $\chi^2_{23} = 88.6$, $P = 0.001$). Black bar = Sitka spruce, white bar = European larch.

Fig. 3. Numbers of European larch lateral roots in the top 20 mm of soil for both control and wind-stressed plants. Both distributions differs significantly from each other ($\chi^2_{23} = 39.21$, $P = 0.02$). Black bar = treated plants, white bar = control plants.

Fig. 4. Σ CSA of Sitka spruce and European larch root bases > 2 mm diameter in 3 sectors around the plant's central axis. Windward roots have a significantly greater Σ CSA than leeward roots (Sitka spruce: $F_{2,92} = 3.53$, $P = 0.033$; Larch: $F_{2,89} = 4.25$, $P = 0.017$, log transformation in both cases). Columns differently superscripted differ at $P = 0.05$. Black bar = Sitka spruce, white bar = larch.

Fig. 5. Σ CSA of wind-stressed and control European larch root bases > 2 mm diameter in sectors around the plant's central axis. Leeward roots of wind-stressed plants have a significantly greater Σ CSA than other roots ($F_{2,106} = 6.78$, $P = 0.002$, log transformation). Roots perpendicular to the direction of wind in control plants have a greater Σ CSA than other roots ($F_{2,102} = 8.51$, $P = < 0.001$, log transformation). Columns differently superscripted differ at $P = 0.05$. Black bar = wind-stressed plants, white bar = control plants.

Fig. 1

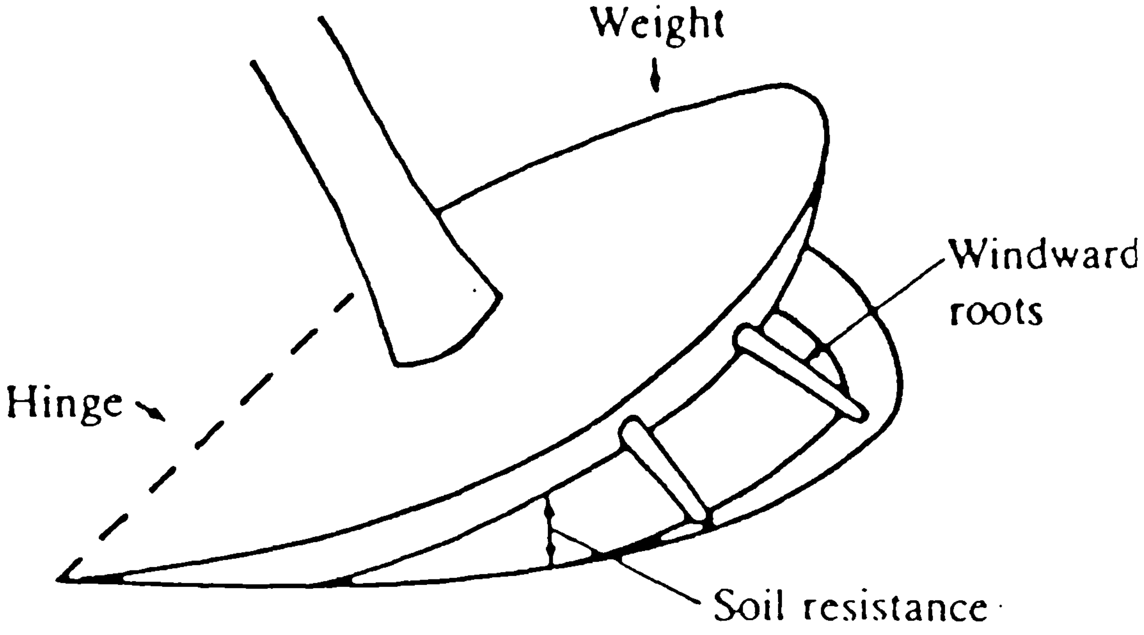
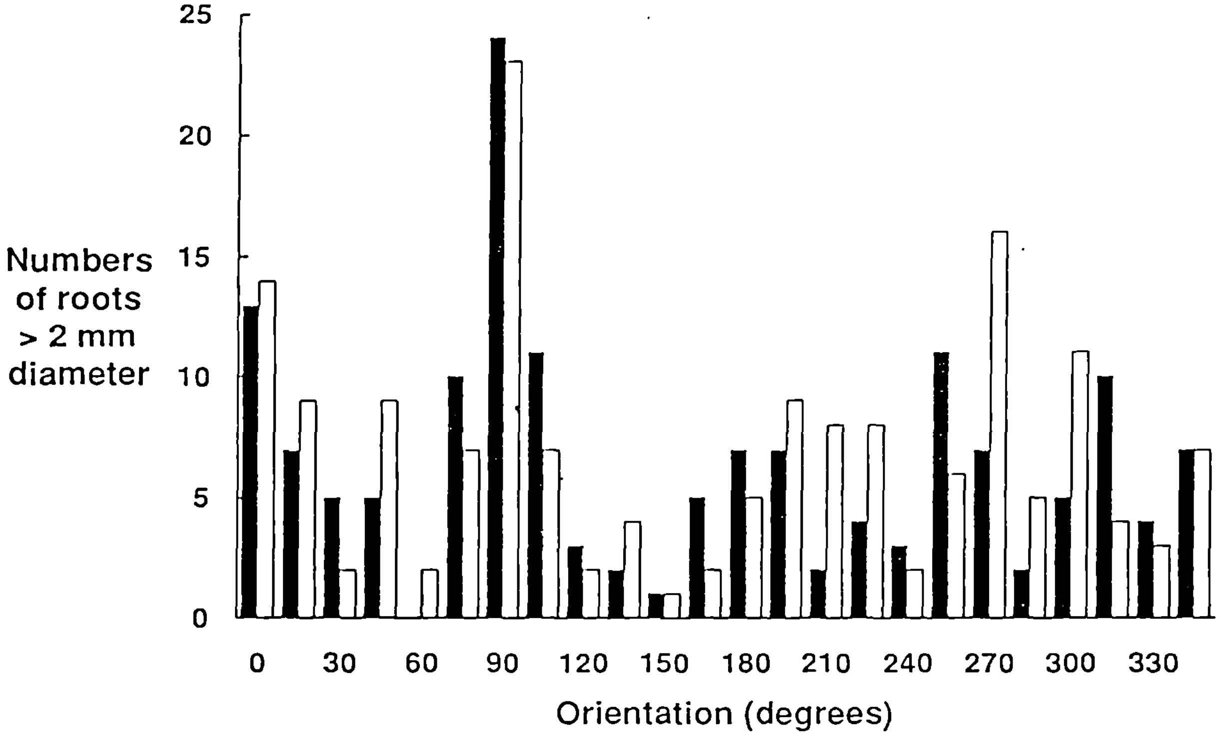


Fig. 2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20
15
10
5
0
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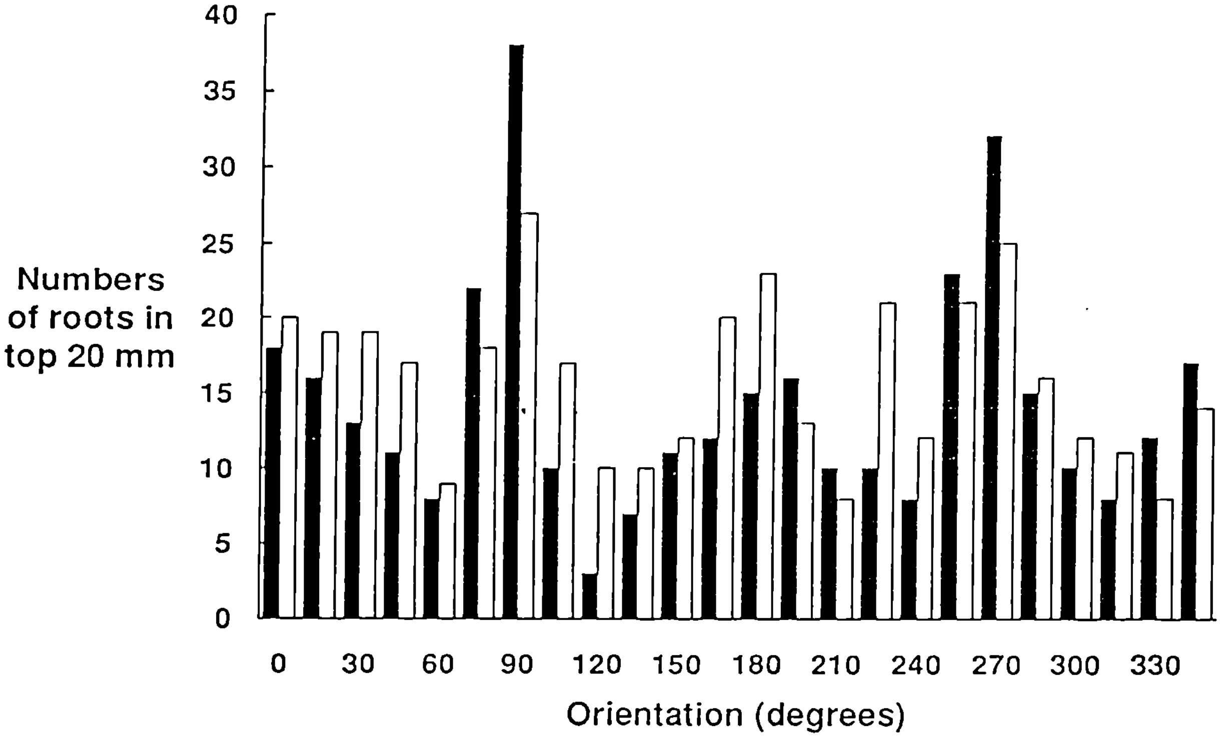
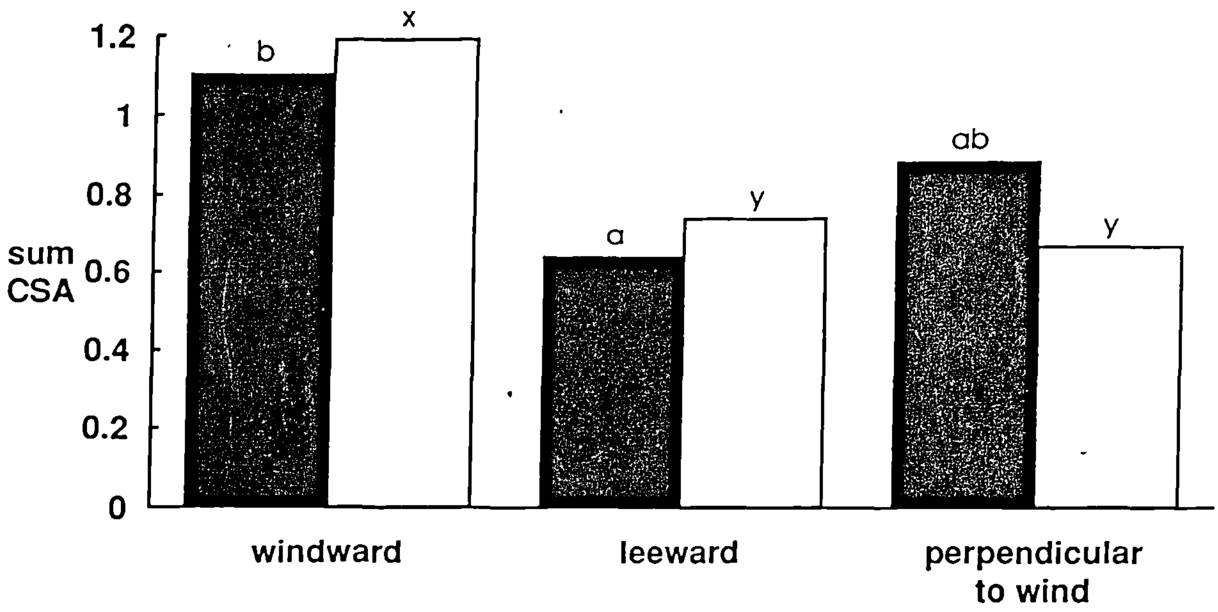
30
60
90
120
150
180
210
240
270
300
330
Orientation (degrees)

Fig. 3



Numbers of roots in top 20 mm
40
35
30
25
20
15
10
5
0
0
30
60
90
120
150
180
210
240
270
300
330
Orientation (degrees)

Fig. 4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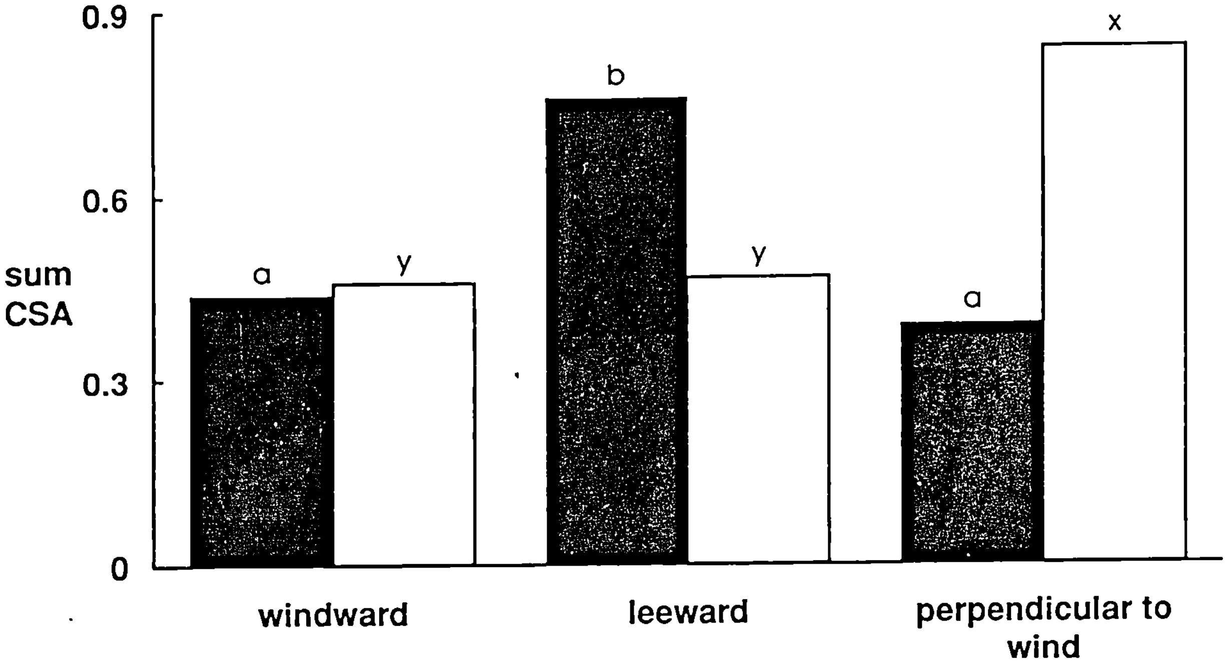
0.8
0.6
0.4
0.2
0
sum CSA
b
x
a
y
ab
y
windward
leeward
perpendicular to wind

Fig. 5


0.9
0.6
0.3
0
sum CSA
a
y
b
y
a
x
windward
leeward
perpendicular to wind

Appendix 2

The Use of Image Analysis and NMR for a Detailed Quantification of Root Systems *in situ*,

A. Stokes, A.H. Fitter and M.P. Coutts

International Society of Root Research 3rd Symposium, Book of Abstracts, "Root Ecology and its Practical Application," Vienna 1991.

TEXT: Automatic image analysis is used as a powerful tool for fast, quantitative measurements at all scales in many and varied scientific disciplines. The application of this to roots enables large amounts of data from images to be processed rapidly with minimal operator guidance, thereby replacing previous and laborious methods of estimating root dimensions. This allows an accurate and detailed investigation into the architecture and life history of a root system. In many applications however, image capture is a major problem, because of the opaque nature of soil. We are therefore currently exploring non-invasive techniques for studying root architecture. Nuclear magnetic resonance (NMR) imaging provides two-dimensional images of root systems *in situ* which are enhanced by image analysis. NMR imaging allows the study of branching and radial angles *in vivo*, through the analysis of several images taken at different coordinates around the root/soil container.

The monochrome video image is captured and digitized to 512 x 512 pixels and converted to a binary image by thresholding the selection of pixels according to grey value, on the scale zero to 63. Automatic analysis quantifies a binary image to give a range of object and arc measurements which are sent directly to the statistics package provided for the system.

The program TRACKROOT has been written to trace along a skeletonized binary tree image such as a root system. Output data consists of two vectors describing the topology and geometry of the system, each vector comprising one value per link in the system. The program SMARTER reads the vector data and calculates the topological indices and internal/external link length data that describe the root system branching patterns.

Appendix 3

Responses of young trees to wind

A. Stokes, A.H. Fitter and M.P. Coutts

Society of Experimental Biology, Book of Abstracts, J. Exp. Bot. Vol. 43, No. 250, May 1992 Supplement.

Sitka spruce was grown from seed in a wind-tunnel at very low wind speeds for one year. Although shoot growth was unaffected, root growth was altered considerably. Large lateral roots (>2 mm diameter) were counted and their orientation relative to the tap root recorded. There were more large roots on the windward and leeward sides of the tree than on the other sides. However, when the numbers of small lateral roots (<2 mm diameter), were added, there was no difference in total root numbers in any one direction. Wind action evidently has no effect on root initiation, but it stimulates the diameter growth of certain roots. As a tree sways in the wind, windward and leeward lateral roots are placed under the most stress. Larger roots in these directions will counteract wind stresses on the tree whereas lateral roots growing at right angles to the direction of the wind are subject to torsion and will offer little resistance to windthrow.

An analysis was made of woody root architecture; fine roots were stripped off large, lateral roots taken from the top 2 cm of soil. For each root, topology, link length and diameter were measured. Roots on the windward side of the tree had a much higher incidence of branching than those on the leeward side. Exterior links (those ending in a meristem) on windward roots were significantly longer with a larger diameter than on leeward roots. These data also support the conclusion that preferential allocation of assimilates has occurred in favour of windward roots although the mechanism for these changes is unknown.

Appendix 4

Responses of young trees to wind: effects on root growth

A. Stokes, A.H. Fitter and M.P. Coutts

In: 1) Society of Experimental Biology, Book of Abstracts, J. Exp. Bot. Vol. 44, May 1993 Supplement.

2) 4th International Symposium "Structure and Function of Roots" Book of Abstracts, Slovakia 1993.

Two wind tunnels were set up, with Sitka spruce (*Picea sitchensis*) and larch (*Larix decidua*) grown in the first and larch with their tap root removed in the second. To mimic the formation of a a shallow soil-root plate, as found in most commercially grown forest trees, the tap roots were cut 20mm below the soil surface using carefully inserted scissors.

The number, orientation, depth and diameter of lateral roots were recorded for all plants in both wind tunnels. Of the plants growing in the first wind tunnel, roots >2mm diameter were considered to be the most important for anchorage. There was found to be a tight aggregation of such roots growing towards the direction of the wind. For plants growing in the second wind tunnel, where the tap root had been cut, all lateral roots were considered important, irrespective of size. There was a similar clustering of roots to that seen on plants in the first wind tunnel. There was also preferential growth of lateral roots on the leeward side. As a tree sways in the wind, windward and leeward lateral roots are placed under the most stress. Larger roots in these directions will counteract wind stresses on the tree whereas lateral roots growing at right angles to the direction of the wind are subject to torsion and will offer little resistance to windthrow.

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