Factors affecting the direction of growth of tree roots

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Introduction

The direction of growth of the main roots of a tree is an important determinant of the form of the root system. It affects the way the system exploits the soil (Karizumi, 1957) and has practical significance for the design of containers and for cultivation systems which can influence tree growth and anchorage. This review discusses the way in which root orientation is established and how it is modified by the environment.

The form of tree root systems can be classified in many ways but the commonest type in boreal forests is dominated by horizontally spreading lateral roots within about 20 cm of the ground surface (Fayle, 1975; Strong and La Roi, 1983). A vertical taproot may persist or may disappear during development. Sinker roots are more or less vertical roots which grow down from the horizontal laterals. They are believed to be important for anchorage and for supplying water during dry periods. Roots which descend obliquely from the tap or lateral roots are also present and the distinction between these and sinkers is a matter of definition. Differences in root form could arise from differences in root direction or from differential growth and survival of roots which

were originally growing in many directions. In practice, both the direction of growth and differential development contribute to the final form.

There is scant information about the principal controls over the orientation of tree roots. Most studies deal with herbaceous species, and even for them experimental work and reviews have generally been confined to geotropism of the seedling radicle. The direction sensing apparatus lies in the root cap (Wilkins, 1975). The structure of the root cap is variable, but there is no essential difference between those of herbaceous species and trees. Work on herbaceous species therefore has a strong relevance for trees, but certain differences must be noted. For example, any correlative effects between the taproot and laterals may be modified in trees by the size, age and complexity of their root systems. Furthermore, the roots of herbs, and especially of annuals, may have evolved optimal responses to seasonal conditions, whereas the young tree must build a root system to support it physically and physiologically for many years. An example of response to temporary influences is given by soybean, in which the lateral roots grow out 45 cm horizontally from the taproot, then turn down vertically during the summer (Raper and Barber, 1970), possibly in response to

drought or high temperature (Mitchell and Russell, 1971). A forest tree could not survive on a root system so restricted laterally.

Orthogeotropic roots

In both herbs and trees the seedling taproot (or radicle) is usually positively geotropic. If the root is displaced from its vertical (orthogeotropic) position, the tip bends downwards. The signal for the direction of the vector of gravity is given by the sedimentation of starch grains onto the floor of statocytes in the central tissues of the root cap. This signal results, in an unexplained way, in the production and redistribution of growth regulators, including indole-3-acetic acid and abscisic acid (ABA), which become unevenly distributed in the upper and lower parts of the root. Unequal growth rates then occur in the upper and lower sides of the zone of extension, resulting in corrective curvature. There are many reviews of geotropism (Juniper, 1976; Firn and Digby, 1980; Jackson and Barlow, 1981; Pickard, 1985) and the mechanism will not be discussed further here.

The detection of and response to gravity are rapid. The presentation time for the seedling radicle of *Picea abies* L. is only 8–10 min (Hestnes and Iversen, 1978) and curvature is often completed in a matter of hours. Orthogeotropic taproots retain their response to gravity indefinitely, although 2 m long roots of *Quercus robur* (L.) responded more slowly to displacement and had a longer radius of curvature than shorter, younger roots (Riedacker *et al.,* 1982).

Plagiogeotropic and diageotropic roots

First order lateral roots (1° L) grow from the taproot horizontally (diageotropic) or are inclined at an angle (plagiogeotropic). The angle between the lateral root and the plumb line is called the liminal angle, and is known to vary with species (Sachs, 1874). Billan *et al.* (1978) even found differences in the liminal angles between two provenances of *Pinus taeda* L.: the provenance from the driest site had the smallest angle (*i.e.,* the most downwardly directed lateral roots). They also found that the liminal angle of the upper laterals was about twice that of those lower on the taproot, a finding in general agreement with Sachs' (1874) observations on herbs.

The responses of plagiotropic roots to gravity have been demonstrated by reorienting either entire plants growing in containers (Sachs, 1874; Rufelt, 1965), or individual roots (Wilson, 1971). When Wilson (1971) displaced horizontal *Acer rubrum* L. roots to angles above the horizontal, the roots bent downwards. When displaced below the horizontal, the roots did not curve, they continued to grow in the direction in which they had been placed. Such roots are described as being weakly plagiotropic (Riedacker *et al.,* 1982). However, some species show an upward curvature of downwardly displaced roots (strong plagiotropism). In his review, Rufelt (1965) concluded that the liminal angle is determined by a balance between positive geotropism and a tendency to grow upwards, *e.g.,* a negative geotropism.

Certain correlative effects between the tip of the taproot and the growth and orientation of 1° L have been described. In *Theobroma cacao* L., if the taproot is excised below very young laterals, some of them will bend downwards, increase in size and vigour, and become positively geotropic replacement roots, *i.e.,* roots which replace the radicle. However, if the taproot is cut below laterals more than 7 d old, they do not change in growth rate or

orientation; their behaviour has become fixed (Dynat-Nejad, 1970; Dynat-Nejad and Neville, 1972). Experiments by these workers, which included decapitation of the taproot tip and blocking its growth by coating it with plaster, showed that the progressive development of a rather stable plagiotropism by the lateral roots was related to the growth rate of the taproot, but not to that of the lateral roots themselves. Experiments on *Q. robur* indicated that the behaviour of the lateral roots in that species is determined even earlier than in *T. cacao,* at the primordial stage (Champagnat *et al.,* 1974). Riedacker *et al.* (1982) largely confirmed this work. They found that if the tip of the taproot was blocked rather than cut, the growth of new laterals above the blockage was enhanced and they became weakly orthogeotropic. However, it took time for the roots to acquire this response and, in *Q. suber* L., the lateral roots grew 20–30 cm and developed thicker tips before turning downwards. It is not entirely clear whether such a response was also induced in lateral roots already present at the time the taproot tip was blocked.

When the tip of a main vertical or horizontal root is injured, replacement roots are free from apical dominance effects and curve forwards, to become parallel to the main root, instead of growing at the usual liminal angle, or angle with respect to the mother root (Horsley, 1971). In this way, the direction of growth of the main root axes is maintained, both outwards, away from the tree, and in the vertical plane.

The way in which the direction of root growth with respect to gravity becomes fixed, or programmed, has not been studied. Although gravity is sensed by the cap, the programme must lie elsewhere, because the cap dies when the root becomes dormant (Wilcox, 1954; John-son-Flanagan and Owens, 1985), yet the direction of growth can remain unaltered over repeated cycles of growth and dormancy. Furthermore, loss of the entire root tip generally gives rise to replacement roots which have the same gravitropic responses as the mother root, indicating that the programme lies in the subapical portion. Work on the acquisition of the plagiogeotropic growth habit by lateral roots requires further development and extension to other species. Plagiogeotropism is even less well understood than geotropism of the radicle, on which much more work has been done, but the experiments on correlative control indicate that in the developed tree root system, it is unlikely that the vertical roots influence the orientation of existing plagiogeotropic laterals.

Lateral roots of second and higher orders of branching and diminishing diameter become successively less responsive to gravity. Since gravity is sensed by the sedimentation of the amyloplasts in the root cap, higher order roots may have caps too small to enable a geotropic response. Support for this idea comes from work on *Ricinus.* The first order lateral roots grow 15–20 mm horizontally from the taproot, then turn vertically downwards. Moore and Pasieniuk (1984) found that the development of this positive response to gravity was associated with increased size of the root cap. The gradual development of a gravitropic response in laterals of *Q. suber* might also be associated with growth of the root cap. The ectomycorrhizal roots of conifers, which are ageotropic, have poorly developed caps and the cap cells appear to be digested by the fungal partner (Clowes, 1954). Whether there are important anatomical differences between the root caps of the larger, first order plagiotropic lateral roots of trees, and the caps of taproots and sinkers, has not been determined.

The orientation of root initials

Root orientation is determined first by the direction in which the root initial is facing before it emerges from the parent root and, subsequently, by curvature. The 1° L maintain a direction of growth away from the plant, an obvious advantage for soil exploration and for providing a framework for anchorage. Noll (1894) termed this growth habit of roots exotropy. The laterals are initiated in vertical files related to the position of the vascular strands in the taproot. The taproot of *Q. robur*, for example, has 4–5 strands (Champagnat *et al.*, 1974), and the existence of 4–5 files of laterals ensures that the tree will have roots well distributed around it. In conifers, the taproot is usually triarch or tetrarch, whereas the laterals are mostly diarch, *e.g., Pseudotsuga menzesii* (Mirb.) Franco (Bogar and Smith, 1965), *Pinus contorta* (Douglas ex Louden) (Preston, 1943). In some species, the files of laterals are augmented by adventitious roots from the stem base and trees produce additional main roots by branching near the base of the 1° L (see Coutts, 1987).

The diarch condition of most of the lateral roots of conifers restricts branches of the next order to positions opposite the two primary xylem strands. Thus, if a line drawn through these strands in transverse section, the 'primary xylem line', is vertical, roots will emerge pointing only upwards and downwards (Fig. 1a). This vertical orientation is present in the 1° L at its junction with the taproot (Fig. 1b). In practice, many branches on 1° L at a distance from the tree are produced in the horizontal plane, as observed by Wilson (1964) in *A. rubrum,* therefore twisting of the root apex must occur. Wilson noted a clockwise twisting (looking away from the tree) in *A. rubrum.* Twisting is also common in *Picea sitchensis* (Bong.) Carr. Many roots which were sectioned showed partial rotation of the axis, followed by corrections in the opposite direction (Coutts, unpublished). Examination of 24 roots, 2–5 m long, showed that the primary xylem line was more commonly oriented horizontally than vertically, favouring the initiation of horizontal roots. As the root twists, the next order laterals can arise in any direction.

The angle of initiation may account for the production of sinker roots from laterals. In an unpublished study on *P. sitchensis,* sinkers were defined as roots
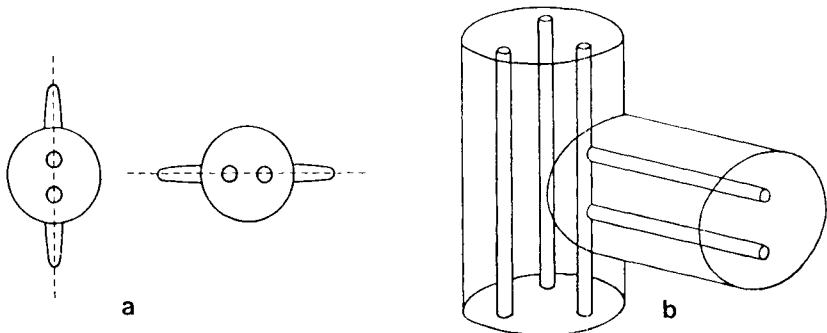
Fig. 1. a. Positions of lateral roots in relation to the primary xylem orientation and the 'primary xylem line', in a diarch conifer root. b. Origin of a lateral root on a triarch taproot, showing the original, vertical orientation of the primary xylem line on the branch.
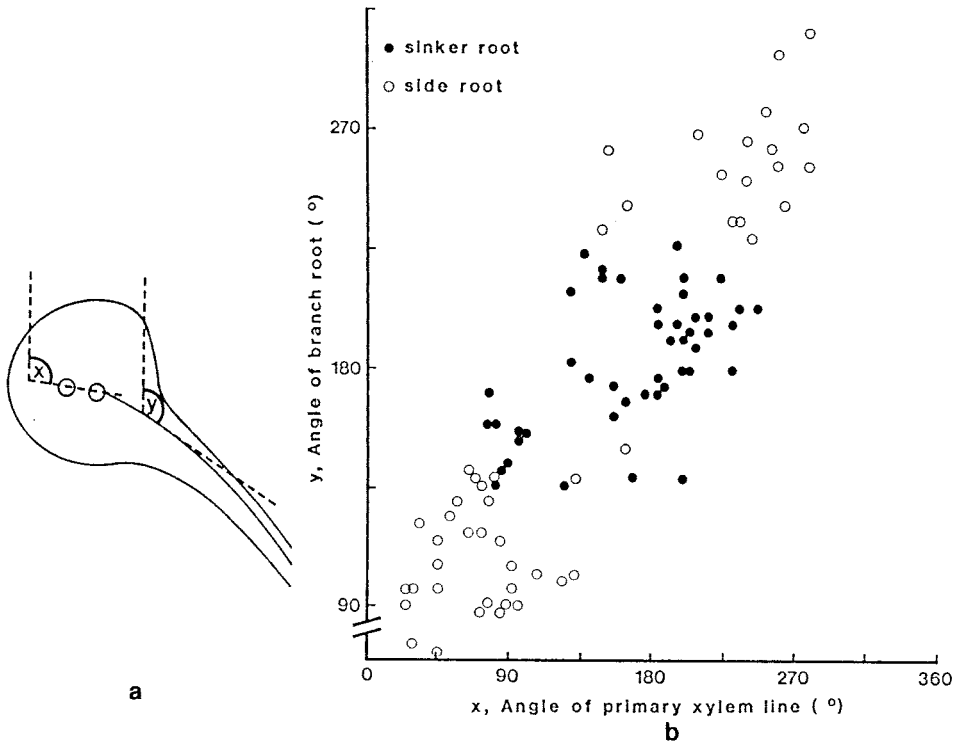
Fig. 2. Origins of sinker and side roots in *P. sitchensis*. **a.** The angle of the primary xylem line *(x)* in the mother root, and the angle of the branch root *(y)* measured 3.2–4.2 cm from the centre of the mother root. **b.** Angle of primary xylem line, plotted against angle of branch root measured as shown in **a.** The roots were classified as sinkers or side roots depending upon their angle at a distance of 12–15 cm from their point of origin (see text).

growing downwards at angles of less than 45° to the vertical 12–15 cm from their point of origin, while roots at angles within 45° of the horizontal were called side roots. An examination of 50 roots of each type on 10 yr old trees showed that the angle of growth was strongly related to the angle of initiation, and thus to the angle of the primary xylem line (Fig. 2).

Sinkers and side roots were predominantly initiated in a downward and in a horizontal direction, respectively. Roots of both types tended to curve slightly downwards after they emerged from the 1° L. Some species, *e.g., Abies*, ha-

ve sinker roots with a stricter vertical orientation than those of *Picea*, and they may therefore originate in a different way.

It is not known whether sinker roots are weakly plagiotropic, their direction being mainly a matter of the direction of initiation, or whether the tip becomes positively geotropic, perhaps by some process of habituation. Observations on *Pinus resinosa* Ait. indicate that the sinkers may have special geotropic properties: lateral roots from them emerge almost horizontally, but then turn sharply downwards (Fayle, 1975).

Surface roots

Many 1° L curve gently downwards with distance from the tree (Stein, 1978; Eis, 1978), but some, which may originate from the upper part of the taproot and therefore have the largest liminal angles, grow at the soil surface, in or beneath the litter. Many surface roots are 2° L and 3° L (Lyford, 1975; Eis, 1978). Surface roots grow up steep slopes as well as downhill (McMinn, 1963). Presumably they are programmed to grow diageotropically, but their orientation is modified by the environment. The remainder of this review deals with environmental effects.

Mechanical barriers

Barriers which affect root orientation include soil layers with greater mechanical impedance than that in which the root has been growing, and impenetrable objects in the soil. Downwardly directed roots can deflect upwards to a horizontal position on encountering compacted subsoil, but turn down if they enter a crack of hole (Dexter, 1986). Horizontal roots or *A. rubrum* deflected upwards when they encountered

a zone of compacted vermiculite (Wilson, 1971), but roots growing downwards at 45° into compacted but penetrable layers did not deflect. Wilson (1967) found that when horizontal roots of *A. rubrum* encountered vertical barriers, they deflected along them, sometimes with the root tip distorted laterally towards the barrier (Fig. 3a). On passing the barrier, the roots deflected back towards the original angle. The correction angle varied with the initial angle of incidence between root and barrier, and with barrier length. Barrier length in the range 1–7 cm had only a small effect on correction angle. Riedacker (1978) obtained similar results with the roots of *Populus* cuttings and barriers up to 7 cm long. With barriers 10–12 cm long, nearly half of the roots continued growth in the direction of the barrier. Roots made to deflect downwards at barriers inclined to the vertical, made upward corrective curvature; they were slightly less influenced by barrier length than horizontal roots. Orthogeotropic taproots of *Q. robur* seedlings deflected past a series of 2 cm long barriers, maintaining a remarkably vertical orientation overall (Fig. 3b). Replacement taproots formed after injury appeared to be insensitive to barrier length.

The mechanism by which roots make corrective curvatures after passing barriers is not known. Large variation in correction angles has been reported, and it is possible that barrier length is less important than the time for which the root has been forced to deflect. The mechanism is an important one for maintaining exotropic growth.
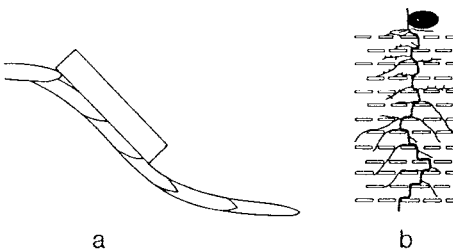
Fig. 3. a. Deflection of a horizontal *A. rubrum* root at a barrier, showing temporary distortion of the root tip against the barrier (Wilson, 1967). b. Path taken by the positively geotropic taproot of *Q. robur* past 2 cm wide barriers in the soil (Riedacker *et al.*, 1982).

Light and temperature

Light from any direction can increase the graviresponsiveness of the radicle and lateral roots of some herbaceous species (Lake and Slack, 1961). Light is sensed by

the root cap (Tepfer and Bonnet, 1972). Wavelengths which elicit a response vary with plant species, *e.g., Zea* (Feldman and Briggs, 1987) and *Convolvulus* (Tepfer and Bonnett, 1972) respond to red light and show some reversal in far red, whereas the plagiotropic roots of *Vanilla* turn downwards only in blue light (Irvine and Freyre, 1961).

There is little information on trees. Iversen and Siegel (1976) found that when *P. abies* seedlings were lain horizontally in the light, subsequent growth of the radicle in darkness was reduced, but curvature was unaffected. Lateral roots of *P. sitchensis* showed reduced growth and downward curvature in low levels of white light (Coutts and Nicholl, unpublished). Such responses indicate that care must be exercised when using root boxes with transparent windows for studies on the direction of growth. In the field, light may help regulate the orientation of surface roots, just as it does for *Aegeopodium* rhizomes, which respond to a 30 s exposure by turning downwards into the soil (Bennet-Clark and Ball, 1951).

The growth of corn roots is influenced by temperature. At soil temperatures above and below 17°C, plagiotropic primary roots become angled more steeply downwards (Onderdonk and Ketcheson, 1973). No information is available for trees.

Waterlogging and the soil atmosphere

Waterlogging has a drastic effect on soil aeration and consequently on tree root development (Kozlowski, 1982). Waterlogged soils are characterised by a lack of oxygen, increased levels of carbon dioxide and ethylene, together with many other chemical changes (Armstrong, 1982). The tips of growing taproots and sinkers are killed when the water table rises, and regeneration takes place when it falls during drier periods. Such periodic death and regrowth produce the well-known 'shaving brush' roots on many tree species. In spite of poor soil aeration, the tips of taproots and sinkers maintain a generally downward orientation. This could be because periods of growth coincide with periods when the soil is aerated. However, in an experiment on *P. sitchensis* grown out of doors in large containers of peat, main roots which grew down at 0–45° from the vertical did not deflect when approaching a water table maintained 26 cm below the surface (Coutts and Nicholl, unpublished). The roots penetrated 1–5 cm into the waterlogged soil and then stopped growing. This behaviour contrasts with certain herbaceous species. Guhman (1924) found that the taproots and laterals of sunflower grew diageotropically in waterlogged soil, and Wiersum (1967) observed that *Brassica* and potato roots grew upwards towards better aerated zones. The finest roots of trees may also grow upwards from waterlogged soils, as found for *Melaleuca quinquenerva* (Cav.) Blake by Sena Gomes and Kozlowski (1980), and for flooded *Salix* (see Gill, 1970). However, the emergence of roots above flooded soil does not necessarily mean that the roots have changed direction, they may have been growing upwards prior to flooding.

Little is known about the response of plagiotropic roots to waterlogging. Armstrong and Boatman (1967) considered that the shallow horizontal root growth of *Molinia* in bogs was a response to waterlogged conditions, but did not present observations on growth in well-drained soil. The proliferation of the surface roots of trees on wet sites may be a result of compensatory growth rather than a change in orientation.

The direction of growth of plant organs is influenced by CO_2. For example, the diageotropic rhizomes of *Aegeopodium* deflect upwards in the presence of 5% CO_2 (Bennet-Clark and Ball, 1951), and this response has been supposed to help maintain their position near the soil surface. Ycas and Zobel (1983) measured the deflection of the plagiotropic radicle of corn exposed to various concentrations of O_2, CO_2 and ethylene. Substantial effects on the direction of growth were obtained only with CO_2. Roots in normal air grew at an angle of 49° to the vertical, whereas in 11% CO_2 they deflected upwards to an angle of 72°. The minimum concentration of CO_2 required to cause measurable deflection was 2%. Concentrations of 2–11% CO_2 are above those found in well-drained soils but, in poorly draining, forested soils, Pyatt and Smith (1983) frequently found 5–10% CO_2 at depths of 35–50 cm. However, concentrations were usually less than 5% at a depth of 20 cm and would presumably have been lower still nearer the surface, where most of the roots were present. In Ycas and Zobel's (1983) experiments, ethylene at non-toxic concentrations had little effect on the direction of corn root growth, and only small effects on corn had been found by Bucher and Pilet (1982). In another study, orthogeotropic pea roots responded to ethylene by becoming diageotropic but the roots of three other species did not respond in this way (Goeschl and Kays, 1975).

It appears as though the downwardly growing roots of trees do not deflect on encountering waterlogged soil. This failure to deflect is consistent with the conclusion of Riedacker *et al.* (1982) that the positive geotropism of tree roots is difficult to alter. There is not enough information on plagiogeotropic roots to say whether soil aeration affects their orientation.

Dessication

The curvature of roots towards moisture is called hydrotropism. Little work has been done on it and Rufelt (1969) questioned whether the phenomenon exists. Sachs (1872) grew various species in a sieve of moist peat, hanging inclined at an angle in a dark cupboard. When the seedling roots emerged into water-saturated air, they grew downwards at normal angles, but in drier air they curved up through the smallest angle towards the moist surface of the peat. Sachs concluded that they were responding to a humidity gradient. Loomis and Ewan (1935) tested 29 genera, including *Pinus,* by germinating seeds between layers of wet and dry soil held in various orientations. In most plants tested, including *Pinus,* no consistent curvature towards the wet soil occurred. In species which gave a positive result, the 1° L were unaffected, only the radicle responded. Some of the non-responsive species had responded in Sachs' system, an anomaly which may be explained by problems of methodology. The containers of wet and dry soils in Loomis and Ewan's experiments were placed in a moist chamber and the vapour pressure of the soil atmosphere may well have equilibrated during the course of the experiment.

Jaffe *et al.* (1985) studied hydrotropism in the pea mutant, 'Ageotropum', which has roots not normally responsive to gravity. Upwardly growing roots which emerged from the soil surface continued to grow upwards in a saturated atmosphere but, at relative humidities of 75–82%, they bent downwards to the soil. No response took place if the root cap was removed and it was concluded that the cap sensed a humidity gradient.

These results have implications for the behaviour of tree roots at the soil surface and where horizontally growing roots

encounter the sides of drains. For example, when *P. sitchensis* roots grow from the side of a furrow made by spaced-furrow ploughing, they turn downwards on emerging into litter or overarching vegetation. Experiments to investigate this behaviour showed that horizontal roots which emerged from moist peat into air at a relative humidity of 99% grew without deflecting, but at 95% they deflected downwards to the peat (Coutts and Nicholl, unpublished). This behaviour could have been a hydrotropic response, but roots which grew out from the peat at angles above the horizontal into air at 95% humidity, also turned downwards, rather than upwards towards the nearest moist surface. This suggests that localised water stress at the root tip had induced a positive geotropic response. It is relevant to note that water stress induces the formation of ABA in root tips (Lachno and Baker, 1986; Zhang and Davies, 1987), and ABA has been implicated in geotropism. An explanation of geotropism induced by water stress could also apply to the downward curvature of otherwise ageotropic roots already mentioned, but not to upward curvatures in Sachs' experiments. It is in any case unlikely that roots growing in soil exhibit hydrotropism because the vapour pressure difference, even between moist soil and soil too dry to support root growth, is so small (Marshall and Holmes, 1979) that roots would be unlikely to detect it. A positive geotropic response by roots in dry soil would be likely to direct them to moister layers lower down.

Conclusions

The seedling radicle, and roots which replace it after injury, are usually positively geotropic. Sinker roots, at least in one species, appear to originate from root primordia which happen to be angled downwards. Their georesponsiveness is unknown. The gravitropism of taproots is a stable feature and the vertical roots of trees do not seem to deflect from waterlogged soil layers, unlike the roots of certain herbs. They have been made to deflect only on encountering impenetrable barriers.

The direction of growth of first order laterals around the tree in the horizontal plane is set by the position of the initials on the taproot. The direction of growth is maintained away from the tree by corrective curvatures, when the root is made to deflect by obstacles in the soil. If the tip is killed, replacement roots also curve and continue growth in the direction of the main axis. In the vertical plane, geotropic responses of the laterals are subject for a short period to correlative control by the tip of the taproot. Work on broadleaved species indicates that during that period, the lateral root apex becomes programmed to grow at a particular angle to the vertical. This angle can be modified by the environment: temperature, light and humidity can alter the graviresponsiveness of lateral roots. It is not certain whether hydrotropic responses occur nor whether the lateral roots of trees respond to soil aeration or deflect from waterlogged soil. The way in which the growth of main lateral roots is maintained near the soil surface, even in roots growing uphill, is not properly understood. Thin roots of more than first order, including mycorrhizas, have small roots caps and do not appear to respond to gravity.

Acknowledgment

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