REVIEW OF TREE ROOT STUDIES

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EXECUTIVE SUMMARY

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This review focuses on principles of root growth and development, practical aspects of root behaviour, i.e. root initiation and root elongation in relation to soil moisture and temperature, and practical and theoretical aspects of toppling in young stands.

REVIEW OF TREE ROOT STUDIES

1.0 BACKGROUND OF STUDY

The current review paper is part of the material collected for a PhD study in the Department of Plant Science, Lincoln University, New Zealand. The long term agroforestry experiment, of which this research forms part, was established to study the biophysical relation between five genotypes of radiata pine with six understorey types. The experiment was established in 1990 (Mead *et al.*, 1993).

Results to date show a difference in growth between the radiata pine genotypes, and an influence on tree growth by the different types of understorey pasture. The pasture has not competed with the trees for above-ground space and light, but there has been strong below ground competition. Further, periodic soil water measurements have shown that soil moisture levels are different between treatments with and without understorey pastures. Also there has been an effect on soil moisture levels due to the rain shadow of the tree (K. Pollock, pers. comm.)

My study focuses on the causes of this below-ground competition. In particular, whether radiata pine grown under the silvopastoral system can meet the requirement of below-ground complimantism sometimes observed (Ziehm *et al.*, 1992; Mead *et al* 1993).

Roots are the below-ground interface between the trees and understorey pasture crops. Knowledge of the root growth and development, root spatial and temporal dynamics in relation to soil conditions and above ground growth patterns, should assist understorey selection in farm and plantation forestry. In addition, tree toppling is studied in relation to root architecture.

2.0 ROOT GROWTH AND DEVELOPMENT

2.1 Initial Development

In a conifer tree the first developed root is called the primary root or tap root and it is strongly geotropic. Some species, such as radiata pine develop large woody tap roots that, under suitable site conditions, may penetrate to depths of several meters, providing support as well as a place for lateral feeder roots to grow (Dickman and Pregitzer, 1992; Sutton, 1980). Other species, such as bald cypress (*Taxodium distichum* Rich.) and balsam fir (*Abies balsamea*(L). Mill) develop short, weak tap roots which function primarily as a source of laterals.

Sutton (1969) mentioned in his review that the initial tap root form is frequently transitory, more so in some species than in others. For example, Norway and White spruce tend to quickly lose their tap root form, whereas jack pine tends to retain it. In radiata pine tap root development is also altered by nursery treatments and whether the planting stock is derived from seed or vegetative propagation (Nambiar 1980).

2.2 Development of Lateral Roots

The lateral development of a root system begins soon after the initial phase of primary root elongation (Sutton, 1969). These roots emerge with some predictability in relation to the vascular pattern of the parent roots (Sutton, 1980). In favourable sites, they emerge and develop in two, three, four or more longitudinal rows (Sutton, 1980; Henderson *et al.*, 1983).

The lateral roots which arise in a normal sequence from the primary root are termed first order lateral roots. Lateral roots arising from a first order lateral are called second order laterals and so on. As a root system grows, multiples of lateral root orders arise from the primary axes (Sutton, 1980; Stone *et al.*, 1962; Gregory, 1994; Pages *et al.*, 1993) with up to seven orders of lateral roots having been described (Dickman and Preziter, 1992).

Many factors influence the branching of laterals. The most important factors are an appropriate system of soil pores into which roots can grow, the shear strength and compressibility of the soil (often lumped together as mechanical impedance), the soil water content, the soil temperature, the O_2 supply, the presence of toxins or pathogens and the nutrient supply (Gregory, 1994).

2.3 Suberisation or Browning of root

As pine roots develop and age they undergo changes, due to metacutisation (Wilcox, 1954) which leads to a brown external appearance. The rate of browning differs with species and temperature. Sutton (1980) indicated that in most conifers browning occurs within 8 to 20 days following cessation of root growth.

Browning occurs more quickly in spring than summer in noble-fir (Sutton, 1980) whereas in mugho pine, there is a high rate in summer and low rate in autumn (Mason *et al.*, 1969). Suberisation apparently has not been studied in radiata pine.

2.4 Secondary Thickening

Secondary growth, i.e. diameter increment, of roots occurs in gymnosperm and most dicotyledons but rarely in monocotyledons. As root diameter increases the root assumes a brown, woody appearance, and the cortical and endodermal tissue sloughs off (Richards and Considine, 1980; Coutts, 1983).

Diameter increment of the root is much less stable and it is much more irregular than in the stem and growth rings of the root are frequently eccentric (Coutts, 1983).

The relationship between diameter increment of the stem (at breast height) and diameter increment of major lateral roots is still not clearly understood. For example, diameter increment of the lateral roots in *Pinus resinosa* Ait. ceased when stem diameter was increasing (Fayle, 1975). In contrast Coutts (1983) found that diameter of lateral roots did not cease when stem diameter was increasing. Furthermore the rate of diameter growth of the major roots did not fluctuate as much as stem diameter.

3.0 ROOT GROWTH BEHAVIOUR AND SOIL ENVIRONMENTAL FACTORS

3.1 Introduction

Root growth is strongly influenced by species and its soil environment. The great variability in root growth within a species is strongly dominated by environmental factors (Sutton, 1983). Therefore, to understand the growth and development of plant roots, it is important to study environmental factors and in particular soil temperature and soil moisture.

3.2 Soil Temperature

A knowledge of soil temperature and root growth (initiation and development) is particularly important for the establishment and growth of a tree planted under forestry or agroforestry conditions. Etter and Carlson (1973) argue that the root tip initiation is a hormonal process and subsequent elongation is due to carbohydrate supply from the leaves; both these are affected by the soil temperature. The soil temperature requirement for root initiation (regeneration), their growth and maturation varies between species and different genotype of the same species (Nambiar *et al.*, 1982; Nambiar *et al.*, 1979; Abod *et al.*, 1979).

3.2.1 Root Initiation: With regard to root regeneration, Bowen (1970) and Nambiar *et al.* (1979) demonstrated that low soil temperature was a major limiting factor for root regeneration in *Pinus radiata.* They both observed that root initiation was severely restricted at 5^0C but increased significantly between 10^0C and 15^0C. Nambiar *et al.* (1982) found that root regeneration was highly correlated with family type. The eight families of radiata pine studied showed marked difference in their ability to initiate new roots under given soil temperatures. Soil temperature requirements for optimum root initiation also differ by species. Abod *et al.* (1979) found that the critical soil temperature for radiata pine root regeneration was between 11^0 to 15^0C, whereas in tropical pines (*Pinus caribea* and *P. kesiya*) negligible root regeneration occurred at 15^0C and below. Kuhns *et al.* (1985) observed that the critical root initiation soil temperature, for a mature black walnut root system, was from 4^0 to 13^0C.

3.2.2 Root Growth and Development: The root elongation and maturation of radiata pine seedlings has been tested in the nursery under different soil temperature levels. Increasing the soil temperature from 15^0 to 25^0C approximately doubled total root length (Bowen 1970). Root growth was severely suppressed at or below 11^0C.

In another study with radiata pine by Nambiar *et al.* (1979), root elongation was low below 5^0C but increased significantly from 10^0 to 15^0C. The rise in temperature increased rate of elongation of the first order lateral (1^0L) roots but did not affect their total number. Warmer temperatures increased both the number and length of second order lateral roots (2^0L) on these two year old seedlings. Nambiar (1980) argued that warmer soil temperature resulted in rapid elongation of 1^0L to form a framework for the production of 2^0L and 3^0L on them. This was a major root regenerating strategy. At low temperatures production of 2^0L and 3^0L from existing lateral root was the major strategy.

Later Nambiar *et al.*, (1982) conducted radiata pine experiment on root elongation within a narrow temperature range, and described the optimum temperature for root elongation and total root weight were between 11^0 to 14^0C.

The rate of elongation of a root varies by species. Kuhns *et al.* (1985) observed that the black walnut root elongation rate was nil below 4^0C, with a steadily increase from 4^0 to 17^0C. However, Stone and Schubert (1959) found the root elongation with ponderosa pine was very similar to that of radiata pine (Nambiar *et al.* 1979).

The rate of root elongation not only varies with the species but, by genotypes within radiata pine (Cotterill and Nambiar 1981; Nambiar *et al.*, 1982). Under a given soil temperature, root elongation rate and total root weight varied with different families. For example, one family produced six times longer root than the another even under a sub-optimum soil temperature of 8^0C.

Anderson *et al.*, (1986) suggested that there is an interplaying relationship between root elongation and root initiation with different soil temperature regimes. The root initiation in red pine seedlings increased with temperature from 8^0 to 16^0C and decreased at 20^0C, the temperature at which the root elongation was greatest. Furthermore, the temperature required for root initiation and elongation can be different. For example, the rate of root initiation in black walnut peaked at 17^0C, whereas the rate of elongation peaked at 19^0C when the initiation had dropped sharply (Kuhns *et al.*, 1985).

3.3 Soil Moisture

Root development is inhibited under low soil moisture or dry conditions due to inhibition of root initiation (Khuns *et al.*, 1985; Squire *et al.*, 1987) and elongation (Becker *et al.*, 1987; Hallgren *et al.*, 1991). Root elongation, which contributes most to root weight, is more sensitive to soil moisture levels than root initiation (Holobrada and Ciampovora, 1992)

Both root elongation and root initiation processes vary with soil moisture status (Squire *et al.*, 1987). Heiligman and Schneider (1974) observed that low soil moisture (4% by weight) levels in black walnut seedling reduces the total root elongation. Kuhns *et al.* (1985) found that with a mature black walnut the root length decreased sharply as soil water potential decreased from 0 to -0.5MPa, and approached zero as soil water potential went from -0.5 to -1.0MPa. With the seedlings of ponderosa pine the rate of root elongation was higher at 100% than 30% soil moisture levels (Stone and Jenkinson, 1970). Heth (1980) demonstrated that the mean total root growth of radiata pine seedlings was highest with moist-cool treatment compared to dry-cool, moist warm or dry-warm conditions.

The effect of moisture stress on root elongation varies with species. Jarvis and Jarvis (1963) found that *Pinus sylvestris* was very sensitive to changes in soil moisture. It had the highest root growth at the level of -11 bar soil water potential (about 20% soil water by volume) and the lowest root growth at -25 bar soil water potential (about 16% soil moisture by volume). With *Betula verrucosa* and *Picea abies*, the root growth was relatively less affected with change of the above moisture soil levels. Bartsch (1987) found that the rate of root elongation for *Pinus sylvestris* and *Picea abies* was 4.8 mm/day and 12.3mm/day respectively, but that the root elongation of both of these species ceased as soil moisture dropped to 50% of field capacity.

The rate of root elongation not only varies by the species but, it is also characterised by the genotypes/family of a species (Nambiar *et al.*, 1982). They found that elongation of 1^0L 2^0L 3^0L roots were markedly higher with one family then other families of radiata pine. Becker *et al.* (1987) found that with different water cycle regimes, three stock types of red pine were markedly different in their rate of root elongation and the total average root weight. Further, for all the stock types the rate of elongation was reduced with longer intervals between watering compared to a frequent watering regime. Working with the seedlings of loblolly pine, Hallgren *et al.* (1991) found that the root growth was sharply affected by their family as well with the induced water regimes. The root growth was higher in the wet regime than in the dry regime.

The wet and dry regimes were maintained by watering twice a week to saturation, and watering once in two weeks to saturation respectively. In addition the coarse roots developed very early in the wet regime compared to the dry regime.

Holobrada and Ciampovora (1992) argued that where excessive soil water fills the pores in the soil, air is expelled from the pore and gas diffusion is markedly impaired. Accessibility of oxygen in water is much lower than the soil, and the plant may suffer from insufficient supply (hypoxia) or complete lack (anoxia) of oxygen. McColl (1973) examined the effect of three soil moisture treatments on *Pinus radiata* and *P. rigida* seedlings. Both species had lower root dry weights at high soil moisture than the low water regime. The high soil moisture level was maintained at the saturation point. Once the soil was saturated watering was not done until it dried up to 15 bars, this was to maintain low soil moisture level. The effect of high and low soil moisture on root dry weight was more pronounced in sandy soil than sandy loam soil. Becker *et al.* (1987) argued that the relatively low rate of root growth found in red pine seedlings under a frequent watering cycle was due to excessive water.

4.0 TREE STABILITY

4.1 Introduction

Tree stability is often a problem in forest plantations (Potter and Lamb, 1974; Coutts, 1986). Tree stability has been widely studied in the British Columbia, British Isles (Burdett *et al.*, 1986; Coutts, 1986, 1987; Boot, 1974) and in New Zealand (Chavasse, 1969; Mason, 1985). Based on the age of the tree and its instability, tree instability has been classified as either juvenile instability or windthrow. In the current study the main focus has been given to juvenile instability and its relation to tree root system.

4.2 Juvenile Instability

Compared to naturally seeded and established seedlings, planted pine trees often require a number of years to achieve a firm anchorage. This appears to be partly due to root pruning. During this time they may easily be blown over by the wind or weighed down by snow. Trees thus affected are not uprooted and so continue to grow. Such a tree is said to topple when it leans by pivoting about a point below the ground (Mason 1985; Moss, 1971).

Toppling occurs frequently in radiata pine plantations in New Zealand (Mason, 1985; Potters and Lamb 1974) and in British and Swedish lodgepole pine stands (Burdett, 1979). However, it is not common in naturally established stands except where it is caused by soil movement (Harington *et al.*, 1989). Toppling also occurs in some eucalyptus stands in New Zealand (Chavasse, 1969) and in *Cupressus macrocarpa.*

Toppling can occur for at least 12 years after planting. In New Zealand it generally occurs from the second to the sixth season after planting with a very high rates on fertile farmland sites (Chavasse, 1969). Research from south and central US with loblolly pine (*Pinus taeda* L) and shortleaf pine (*P. echinate* Mill) has indicated that planted seedlings and saplings, aged 3 to 12 years undergo changes in root system morphology that may lead to instability or toppling. However it is uncommon in plantations where trees are greater than two to three metres high in British Columbia (Burdett *et al.*, 1986).

In New Zealand, toppling is mostly induced by wind (Mason, 1985). Wind induced toppling is quite different from snow toppling. In snow induced toppling the pressure applied is a relatively constant destabilising load whereas wind places trees under fluctuating periodic stresses.

Whatever induces the toppling, it has an economic significance. When a tree topples it acquires a geotropic stem curvature or sweep or bow which under present day or foreseeable market conditions greatly reduces its value (Moss, 1971; Burdett *et al.*, 1986). Toppling leads to compressed wood formation and lumber from a swept stem will be prone to greater checking and longitudinal shrinkage, and will have a lower strength than normal wood. This will be the case even if the curvature of the stem has been obscured by asymmetrical radial growth (Lines and Booth, 1971; Mason and Cullen, 1986; Burdett *et al.,* 1986).

4.3 Toppling related to tree characters

4.3.1: There are many causes for this such as species, site factors, nursery practice, and cultivation methods (Mason, 1988; Lines and Booth, 1972). These causes can classified into two groups.

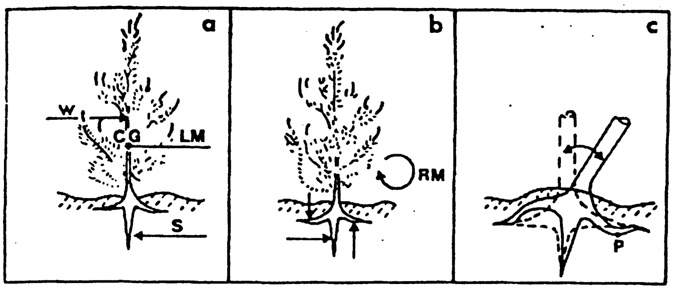
Genotype/stock types:- Differences in seedling stability of different genotypes of lodgepole pine have been reported (Lines and Booth, 1972; Lines, 1960). Burdett *et al.* (1986) suggested that selection of provenances or genotypes through breeding was necessary to improve lodgepole pine juvenile stability. In New Zealand different degrees of toppling were reported for two stock types of seedlings of *Pinus radiata* D. Don (Mason *et al.*, 1988). Mead *et al.* 1995; and Mason *et al.* (in preparation) compared the incidence of toppling between 3 genotypes of radiata pine in an agroforestry experiment at Lincoln University. They noticed that open pollinated seedlings had a relatively higher incidence of toppling than the other genotypes derived from tissue culture, and even within the tissue cultured clones some were more stable than others.

4.3.2: **Root form and Toppling**:- Root system can be characterised by the quality (arrangement) and quantity (biomass) parameters being important for tree stability (Mason, 1985; Coutts, 1986). Clarke (1956) found a large proportion of planted trees had been toppled while naturally established trees of a similar size were unaffected. A similar result was noticed in a young tree pulling experiment in British Columbia with lodgepole pine (Burdett, 1979). Both studies concluded that eventually, the relative instability of planted trees was strongly related to root structure which provides tree stability.

4.4 Mechanism of toppling and role of vertical roots

In Figure 1a (from Burdett 1979) shows how the wind or any other force acting on the aerial portion of a tree imparts a tendency to rotate about a point near the base of the stem. The tension in the windward-side lateral roots opposes this moment. However some rotation in the root system occurs because of stretching in the windward-side laterals. This rotation is resisted by forces in the soil acting on the upper surface of the windward-side laterals, the windward-side of the tap root and the lower surface of the lee-side laterals (figure 1b). Finally, increasing these forces will cause bending in the roots and deformation of the soil (figure 1c).

Figure 1. The acquisition of, and resistance to, a turning moment by pine seedling (Burdett 1979).



Burdett (1979) demonstrated that the vertical roots play a significant role in tree stability against toppling. Mason (1985) found that vertical roots (tap roots and sinker roots) of radiata pine were of a significantly higher in untoppled trees than that of toppled trees, whereas the lateral root measurement between toppled and untoppled trees did not differ. Later studies by Mason and Cullen (1986) and Mason *et al.* (1988) conformed these findings. The higher rate of stability against toppling was also associated with well developed vertical roots of lodgepole pine (Halter *et al.* 1993).

5.0 CONCLUSIONS

Soil temperature and moisture both play a major role in root initiation and development. In the current review, most of the research information is the result of either nursery, glass-house or growth cabinet studies. These studies have been done with seedlings of eight months to 18 months old under controlled levels of constant temperature and moisture.

In practice, soil temperature and soil moisture fluctuates on short term and seasonal cycles. The soil temperature and moisture act together, so the magnitude of these combined effects may well be amplified.

In an agroforestry situation the understorey may act as a live-mulch which could alter the dynamics of soil temperature and moisture. Furthermore the tree canopy creates shade and rain-shadow to the surrounding micro-sites. Therefore, the dynamics of soil moisture and temperature may be different in pure forestry or agricultural systems, and could influence the growth and development of roots of both the tree and understorey.

Changes in root growth and development effect root quality (root types, distribution, configuration, and suberisation) and quantity (biomass, length and diameter) which eventually effects the growth of the tree and crop. Tree juvenile stability may also be altered. Therefore understanding root dynamics, growth and development by space and time in a field situation is important to both silviculturist and agroforesters.

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