ROOT DISTURBANCE AND WASHING EFFECTS ON SHOOT AND ROOT GROWTH IN FOUR PLANT SPECIES

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Abstract

Bare-rooting techniques have been widely use in New Zealand nursery production for the preparation of live plants for export to overseas or domestic markets. Bare-root transplants can fail quality requirements due to death or deterioration of regrowth following repotting. The potential for improving bare-root nursery stock quality has prompted study of the morphological effects of removed medium treatment on plant. Two experiments were conducted to explore the effects of physical root disturbance by shaking and washing on the growth and development of camellia (*Camellia × saluenensis* cv. 'Donation'), pittosporum (*Pittosporum tenuifolium* cv. 'Kohuhu'), pumpkin (*Cucurbita pepo* cv. 'Crown Hybrid'), and coleus (*Coleus blumei*). The shaken plants in both dry and wet conditions suffered a reduction in the growth rate of their leaves compared to the unshaken controls. Root washing influenced the vegetative growth of four species and reproductive growth of pumpkin. The two woody species were more sensitive to treatment stress. Very short time of washing (three seconds) affected camellia bud break and new shoot growth, and inhibit pittosporum root and shoot growth. Similar effects were not sosevered in coleus and pumpkin.

DEDICATION

THIS THESIS IS DEDICATED TO MY DEAREST FATHER, POSTHUMOUSLY,

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Chapter one: Introduction

Root washing of transplants has its principal application in the export across trade barriers of plants free of growing medium (bare-root) and associated pathogens. In the nursery industry, many field-grown herbaceous perennials are harvested bare-root in the autumn and stored so that plant material will be available for processing and shipping during winter and spring months (Cameron and Maqbool, 1986; Heiden and Cameron, 1986). Woody plants such as fruit and forest trees (Ritchie et al., 1985; Lefevre et al., 1991) and ornamental trees and shrubs (Vanstone and Ronald, 1981; Murakami et al., 1990; Welch and Cameron, 1990; Englert et al., 1993; Bates et al., 1994) are commonly bare-rooted to many destinations. Forestry seedling are increasingly being produced as bare-root stock because of the improved growth control and flexibility in production scheduling (Coutts, 1981; van Dorsser, 1982; Sucoff et al., 1985). California produces 30 to 40 million bare-root rose plants each year at a value of more than 35 million dollars (Sucoff et al., 1985; Schuch et al., 1995). Almost 70% of woody stock leaving in some nurseries in New Zealand are sent out bare-rooted to overseas or domestic market (Anon., 1996).

However, up to 20% of the harvested stock leaving nurseries never reaches the ultimate consumer due to deterioration of regrowth in the following repotting (Cameron and Maqbool, 1986). The problems involved root damage during to bared-rooting procedures, such as shaking plants or washing the roots (van Noordwijk and Floris, 1979), and desiccation during storage and handling. Damage to the root system is believed to be an important feature of planting shock and would be expected to reduce shoot growth in various ways (Gallardo et al., 1994). If the root is unable to supply the shoot with sufficient water, water stress will develop and other types of stress due to reduce nutrient uptake and reduced or altered root activity may also occur.

Previous studies had been established of injurious and non-injurious controlling of shoot and root growth and development. For instance, mechanical conditioning was used to control growth and quality of vegetable transplants (Heuchert and Mitchell, 1983; Akers and Mitchell, 1984; Biddington and Dearman, 1985a) and fruit or ornamental tree seedlings (Neel and Harris, 1971; Parkhurst and Pearman, 1971; Grace et al., 1982). Shoot (Fordham, 1972; Beyl and Mitchell, 1977b; Young and Werner, 1982) and root (Insley and Buckley, 1985; Watson and Sydnor, 1987; Costa et al., 1992; Gilman, 1992; Beeson, 1993) restriction has been used as a horticultural tool to produce a sturdier nursery stock, force development of a more compact, fibrous root system, retard top growth, and increase transplant survival. However, very little research has been conducted on root damage during washing. Thus root washing practice was completed with two woody ornamentals *Camellia saluenensis* cultivar 'Donation' and *Pittosporum tenuifolium* cultivar 'Wendell Channon' (Anon., 1992; Clemens and Christie, pers. comm.). Their study demonstrated the different root system became progressively cleaner as washing duration increased up to 15 minutes. However, shoot regrowth after transplanting was most severely affected during the initial minute of washing time. The above study did not cover short-term (< 1 minute) effects of root washing. A major factor has been lack of understanding of shoot-root regrowth and relationship between the degree of root damage and regrowth capacity in a range of short-term physical disturbance and root washing. A greater understanding on effects of root disturbance and washing is required.

The objective of this study was to determine the immediate effects of disturbance and washing in terms of medium and root loss, and to examine how woody and herbaceous species plants may differ in their response to physical disturbance of root. In this respect, it would be desirable to prepare and allow a contrast to be drawn with the woody plants studied earlier. The effectiveness of root cleaning by washing would be comparable between different species and different shaking or washing methods which was as little disturbance as possible, but as more clean and more easy as possible. Root damaged degree in a range of root disturbance was determined by corresponding root loss from removed medium and shoot-root growth parameters. Regrowth and withstand capacity also would be comparably between various species and different shaking and root washing treatments.

Chapter two: Literature review

2.1 Shoot-root growth relationships

The different physiological activities characterising the root and shoot developed with respect to the life history of these structures of terrestrial plants. The root developed in the soil and thus has become fully dependent upon assimilates produced by the shoot in the course of photosynthesis (Eshel and Waisel, 1996). By contrast, the shoot growing in air and light is dependent on water and mineral nutrients largely taken up by the root from the soil. These activities decisively link the weight and volume increments of both the root and the shoot. Between the root and shoot there exists a functional balance which remains unchanged for long intervals of a plant's life. The balance is a dynamic and not a static one, being renewed following any disturbance. As a whole plant, the root functions are regulated in close relationship to functions of the shoot, and vice versa. Within certain limits, an equilibrium must then exist between the functions of the root and those of the shoot. The basic requirement for the establishment of such a functional equilibrium is that the root and the shoot supply each other with a minimal necessary amount of substances which they take up from the external environment or which they themselves produce (Jesko, 1991). Otherwise, at least a part of the plant, overground or underground, would die or become modified. Therefore, the growth equilibrium has been compared on the basis of an activity shared by the root and shoot (Johnson, 1985).

Functional equilibrium (Johnson and Thornlley, 1987) has been described by the equation:

$$\text{shoot mass} \times \text{shoot specific activity} \propto \text{root mass} \times \text{root specific activity},$$

for plants in 'balanced' growth. The shoot and root specific activities are the rates of photosynthesis and nutrient uptake per unit of shoot or root mass respectively, and depend directly on environmental conditions. This expression is commonly referred to as depend directly on environmental conditions. This expression is commonly referred to as the rate of photosynthesis being proportional to the rate of nutrient uptake (Carmi and Koller, 1978). A plant achieves this balance by adjusting the relative size of the shoot and root mass (Davidson, 1969).

The relationship of root and shoot growth can most simply be expressed by the dry weight root:shoot or shoot:root ratio (Jesko, 1991). This ratio varies with changing conditions of internal and external plant environment, the changes being of an adaptive character. For example, an increase in the shoot:root ratio as a result of lower light intensity is reflected in an improvement in the conditions of light uptake due to an increase in the assimilating surface area. An decrease in the shoot:root ratio under conditions of water and mineral nutrient deficit causes a relative increase in root surface absorption area capable of utilising a greater volume of soil (Schildwacht, 1989). An increase in the shoot:root ratio after the onset of the generative phase of plant development reflects a lower ability of the root to compete for assimilates in comparison with developing fruit, especially when the production of assimilates or their supply in the plant is small.

In physiological and ecological studies, the ratio of root dry weight to shoot dry weight has been used as an index of growth pattern, often to draw attention to differences between species or cultivars. Some of the factors that could influence root:shoot ratio include genetic differences and the age of planting materials. Othman et al. (1991) found that different monoclonal seedlings and propagation techniques appeared to maintain a consistent root:shoot ratio, which become more apparent with age of the planting materials. They confirmed the existence of an allometric relationship between shoot and root development in *Hevea* as shown by many other tree species. The following sections provide result of some studies to explain the growth responses of shoot and root under conditions of external physical restriction.

2.2 Plant growth under physical disturbance

Physical disturbance has been shown to retard the growth rate of herbaceous (Jaffe, 1973; Heuchert and Mitchell, 1983; Latimer et al., 1991) as well as woody plants (Larson, 1965; Neel and Harris, 1971; Akers and Mitchell, 1984). Physical disturbance of plants or plant parts results in a mechanical stress response from the plant. Injurious and non-injurious mechanical stress inhibited various shoot and root physiological activities, and these effects were the result rather than the cause of the growth reduction. Physical disturbance had been used to refer to the commercial application of mechanical stress under controlled conditions in many horticulture and forestry practices, such as shaking seedlings to remove medium, shaking potted plants, rubbing stems or brushing shoots to control height, washing root to clean roots stock, training branches, pruning roots, and modifying roots by container design.

2.2.1 Noninjurious mechanically stress

Noninjurious mechanically stress in plants, caused by such actions as rubbing or bending the stem (Jaffe et al., 1984), brushing (Biddington and Dearman, 1985a), and flexing or shaking the shoot (Mitchell et al., 1977), induces a retardation of plant growth, particularly a reduction in stem or petiole elongation. Mechanical stress has also been shown to strengthen the petioles in stems of tomatoes (Heuchert et al., 1983) and to induce resistance to drought (Suge, 1978). Such treatments could prove valuable to condition glasshouse-raised vegetable transplants and tree seedling to withstand both the physical and physiological damage which may occur at or following transplanting into the field.

Jaffe (1973) has demonstrated that rubbing the internodes of a number of herbaceous species for 10 seconds once or twice daily, stops elongation growth within three minutes. Hammer et al. (1974) reported that flexing reduced the elongation of greenhouse chrysanthemums. Their results indicated that brief stress applied daily resulted in plant height 20-30% shorter than the controls. Increasing the stress from one to 30 seconds intervals per day increased the effect slightly.

Mechanical manipulation may have effects equivalent to wind, especially in reducing elongation in woody and herbaceous species. Noninjurious handling of herbaceous plant material reduces growth. Heuchert and Mitchell (1983) demonstrated growth inhibition in tomato and several other herbaceous species by mechanical shaking, and showed the growth retardation effects to be reversible once the stress was discontinued. Shaking trunks of young sweet gum (*Liquidambar styraciflua*) reduced elongation growth, increased lateral growth, and hastened terminal (dormant) bud set (Neel and Harris, 1971).

2.2.1.1 Species and cultivar response

Species and cultivars differ in growth response to mechanically stress. Barley (*Hordeum vulgare* L.), wild hop (*Bryonia dioica* Jacq.), cucumber (*Cucumis sativa* L.), kidney bean (*Phaseolus vulgaris* L.), and castor bean (*Ricinus communis* L.) were significantly retarded in stem elongation by rubbing. However, rubbing did not affect stem elongation of pumpkin (*Cucubita pepo* L.), pea (*Pisum sativum* L.), and wheat (*Triticum aestivum* L.) (Jaffe, 1973). Shoot dry weight and leaf area of cauliflower (*Brassica oleracea* L.), lettuce (*Lactuca sativa* L.) and celery (*Apium graveolens* L.) seedlings were reduced by brushing. The reduction in leaf weight was greatest in cauliflower and least of lettuce and celery (Biddington and Dearman, 1985a). These responses related to differences in natural growth habit of the individual species.

The degree of growth retardation of transplants of four Japanese cucumber cultivars in response to brushing corresponded to the cultivars' normal vigor and growth habit (Latimer et al., 1991). Cucumber cultivars with naturally short internodes exhibited less growth reduction than did cultivars with typically longer internodes relative to their respective untreated controls. Four tomato (*Lycopersicon esculentum* Mill.) cultivars differing in internode length and vigor showed similar responses; hybrids between these cultivars responded in a manner similar to the maternal parent (Latimer et al., 1991). However, four cultivars of chrysanthemum responded similarly to an automated mechanical stress treatment relative to their respective untreated controls (Beyl and Mitchell, 1977a).

2.2.1.2 Physiological response

Neel and Harris (1971) reported the effects of shaking on growth of *Liquidambar* seedlings, and quoted experiments showing reduced growth of vine leaves subjected to breeze. Such a reduction could be caused by partial drying of the leaves through two known mechanisms. Lowered turgor could prevent cell expansion directly. Stomatal closure could also occur, with a reduction in photosynthesis. All of the stress-induced decline in dry weight gain can be attributed to reduce photosynthetic surface (Biddington and Dearman, 1985b; Biddington and Dearman, 1987a). The long-term reduction in dry matter accumulation initially suggested metabolic involvement in mechanical stress-induced growth retardation. Either an elevated rate of respiration or a depressed rate of photosynthesis could have accounted for the observed dry weight reduction. Mitchell et al. (1977) demonstrated noninjurious mechanical stress inhibited dry weight accumulation by tomato plants, although this effect was the result rather than the cause of the growth reduction. Grace et al. (1982) examined that the effects of shaking on the growth and water relation of *Festuca arundinacea* Schreb. These authors found that extension growth was reduced by shaking, and shaken plants displayed a higher stomatal conductance and a lower water potential than the controls. However, shaking reduced extension growth of *Pinus contorta* even though there was no effect on water potential (Rees and Grace, 1980).

Studies have been conducted on a general hormone-mediated mechanism of growth inhibition (Mitchell, 1977), or the role of individual plant growth substances in response to mechanical stress (Biddington and Dearman, 1987b; Latimer, 1991). Ethylene has been implicated in many mechanical stress responses (Biro and Jaffe, 1984; Pressman et al., 1984; Takahashi and Jaffe, 1984). Shortening and swelling of internodes have been reported to be caused by ethylene (Biddington, 1986). Mechanical stress induces increased ethylene production in pea epicotyls and *Lilium* stems (Hiraki and Ota, 1975). Jaffe and Biro (1979) showed that mechanical disturbance induces the production of ethylene in beans. Latimer (1991b) reviewed mechanical disturbance and how it affects the production of growth promoters and inhibitors. Reductions in gibberellin-like promoters, demonstrated for shaken sunflower (Beyl and Mitchell, 1983) and brushed bean (Suge, 1978), may be responsible for reductions in stem elongation and leaf expansion. Rubbing or shaking inhibited polar auxin transport in pea stems (Mitchell, 1977). Abscisic acid or other inhibitors increased in rubbed bean (Erner and Jaffe, 1982), brushed rice (*Oryza sativa* L.) (Jeong and Ota, 1980), and shaken or rubbed sunflower (Beyl and Mitchell, 1983), but was unchanged in eggplant by 3 days of shaking (Latimer and Mitchell, 1988).

2.2.1.3 Growth equilibrium between shoot and root

Mechanical stress generally reduces root growth less than shoot growth, resulting in increased root:shoot ratios. Biddington and Dearman (1985a) reported cauliflower, lettuce and celery shoot fresh and dry weights and leaf area were reduced following brushing. Root length and the number of branches per root system were also reduced in all three species. Root dry weight was reduced and the root:shoot dry weight ratio was increased in lettuce, reduced in celery and unaffected in cauliflower. The reduction in shoot weight and root weight have also been reported for four cultivars of cucumber (*Cucumis sativus* L.) (Latimer et al., 1991). Dry weights of shoot components were reduced by brushing in each cultivar. However, root dry weight was affected by brushing only in one of four cultivars. Turgeon and Webb (1971) found no effect on root weight following handling of *Cucurbita melopepo* petioles and leaves. Akers and Mitchell (1984) also found that shaking caused significant reduction in all growth parameters of pea (*Pisum sativum* L. cv. Alaska) except root dry weight and leaf number.

2.2.2 Injurious mechanically stress

Previous research evaluating pruning of woody plants has shown that shoot pruning suppressed root growth (Randolph and Wiest, 1981; Young and Werner, 1982). Fordham

(1972), working with tea (*Camellia sinensis* L.), showed that periods of maximum shoot growth are associated with minimal root growth. Pruning stimulated rapid shoot growth, which was accompanied by the cessation of root growth on both young and mature tea (Fordham, 1972). The stagnation in root growth on young tea plants following pruning, considered it to be caused by a diminished supply of assimilates to the roots. It is possible that the observed alternations in root and shoot growth in tea are related to competition for assimilates.

Mertens and Wright (1978) reported that 'Helleri' and 'Rotundifolia' holly growth is episodic, with active root growth preceding a shoot flush by one to two weeks, indicating a competitive inhibition of root growth by rapid new shoot growth. Gilliam et al. (1986) demonstrated that shoot pruning of *Ilex crenata* 'Compacta' liners at potting reduces root growth and causes vigorous shoot growth, especially during the first 4-6 weeks after potting. This vigorous shoot growth coupled with suppressed root growth during a time of year when environmental conditions are conducive to water stress may adversely affect plant development. Leiser et al. (1972) compared the effects of pruning and staking on shoot and root development of young trees. They found that shoot pruning treatments had a greater influence in root weight than staking. The removal of laterals decreased root weight about 30% compared with the no pruning treatment.

2.3 Root modification

2.3.1. Interactions of environmental factors on plant roots

Plant roots are plastic in their development (Klepper, 1991). They respond to a wide variety of environmental stimulation and stressful environments. Roots modify and interact with each environmental factor. However, the most significant environmental parameter in terms of root growth and development is the edaphic environment (Eshel and Waisel, 1996).

Physical stress of the soil directly influence the root growth and mass. In compact soils the spaces (pores) between soil particles are reduced, either in number or in size. Root penetration into these pores may be attendant upon changes in the structural characteristics of impeded roots (Bengough and Mullins, 1990). In compact soils, root growth rates are typically reduced and roots are often thickened. Branching patterns are modified greatly, with lateral roots often differentiating uncharacteristically close to the apex (Feldman, 1984). Shoot growth is often more reduced than root growth when plants are grown with a restricted rooting volume or on compacted soils. Andrade et al. (1993) reported relative leaf expansion rate of sunflower (*Helianthus annuus* L.) decreased linearly with increasing soil strength. Smaller plant size in compacted treatments was due not only to slower expansion rates, but also to smaller maximum size of individual leaves. Sensitivity of leaf expansion to soil strength was best illustrated by a reduction in relative leaf expansion rate and maximum size of the first leaf to emerge in a treatment with only the lower 10-20 cm of the profile compacted (bulk density of 1.7 g cm^{-3}). Root growth was less affected than shoot growth by compaction and root:shoot ratios of compacted treatments were significantly higher than the control.

The effect of soil temperature in root growth has received considerable attention (Fitter, 1991). McMichael and Burke (1996) indicated that the soil temperature of ridge tilled plots tended to be higher, which resulted in root growth rates of 80-100% of maximum. The growth of a plant root system is very sensitive to changes in soil temperature with each species having an optimum temperature range for maximum root development. In general, the growth of roots increases as the temperature increases up to the optimum, and the decreases as the temperature continues to increase. At a depth of 50 cm, i.e. within the rooting range of many plant species, the temperature remains essentially constant by day, although still varying with season. However, steep and rapidly changing positive or negative temperature gradients can exist along the length of a root, affecting both structure and function.

Root growth is dependent on moisture (Klepper, 1990). All the physical factors in the soil are modified by water (Fitter, 1996). Different components of the soil water potential near the root surface affect different processes in root growth and function. Steep gradients of content and potential are common in soils and are a prime cause of gradients in both physical and chemical environmental factors along the length of the root. Roots interact with soil water by exudation and absorption, but also by shrinking or swelling and so varying the area of their contact with the soil. Since water is transported to roots down a gradient of soil water potential, instrumentation that would enable potential gradients to be measured close to roots without significantly altering the flow or affecting the environment would advance the pace of research on plant water relations (Lake, 1987). By virtue of their water content, roots will be relatively good conductors of heat compared with the surround soil if it is dry, but their heat capacity will be relatively small, so root and soil temperatures are unlikely to differ greatly. Changes in water content can impact soil temperature changes and subsequently root growth. An increase in soil water content can reduce soil heating both by evaporative cooling of the soil surface and by increasing soil heat capacity (Fitter, 1996). A larger interaction of roots with their thermal environment results from the effects of root activity in changing the structure and water content of the surrounding soil.

Bevington and Castle (1985) examined annual root growth pattern of young citrus trees (*Citrus sinensis* L.) in relation to shoot growth, soil temperature and soil water content. They found that the most intense root growth occurred when soil temperatures were above 27°C, and was limited at soil temperatures below 22°C. No root growth was evident at soil temperatures below 14°C. When the soil water content was decreased intentionally, root growth was checked at a soil matric potential of -0.05 MPa. Root growth was very limited at a soil water potential -0.75 to -0.80 MPa After rewatering, there was a lag period of two days before root growth increased. Root growth was cyclic. During periods of shoot elongation, the number of growing roots and the rate of root elongation declined. Shoot growth was a major factor controlling the intensity of root growth when soil temperature and soil water content were nonlimiting.

2.3.2 Noninjurious root restriction (container design or container effects)

The physical restriction of plant roots growing in containers induces a variety of responses. Results are mixed with respect to the design of the container and its ultimate effects on shoot growth. Some researchers found little or no effect (Carmi and Shalhevet, 1983; Ruff et al., 1987), while others saw much improved top growth in container designs which stimulate more fibrous root systems and reduce shoot vegetative growth. Studies of the effects of root restriction on plant growth can be investigated widely growth response, ranging from no response to enhanced harvest index through to slow decline and death of plants (Tschaplinski and Blake, 1985). Privett and Hummel (1992) reported that root growth of cotoneaster and Leyland cypress (*X. Cupressocyparis leylandii*) were greatly suppressed by container design. Shoot growth of 'Coral Beauty' cotoneaster was greater in the porous container than in the nonporous smooth-walled container, while shoot growth of Leyland cypress was not affected by container design. When roots in the porous walled containers reached the periphery of the root ball they stopped growing, resulting in a fine, fibrous root mass at the periphery of the rootball. Generally, increased container size results in increased canopy growth (Biran and Eliassaf, 1980; Gilliam et al., 1984). Bilderback (1985) also found that larger Leyland cypress were produced in 11.4-litre than 3.8- or 7.6-litre containers after two growing seasons, although after the first season, container size had no effect on growth indexes. Beeson (1993) found that in the absence of root restriction, pine (*Pinus elliottii* Engelm) grown in small containers had faster shoot growth than their counterparts grown in larger containers. However, after the roots filled the containers, root restriction was observed on plants grown in containers < 10 litres (Beeson, 1993). Plants remaining in the smaller containers were probably water stressed. Limited available moisture in the container, in conjunction with root restriction, reduced growth rates.

After observing a 39 per cent reduction in root dry weight and a consequent comparable (34 per cent) reduction in top dry weight of container-grown peach (*Prunus persica* Batsch) seedlings, Richard and Rowe (1977) suggested that the root regulated the growth top. These authors concluded that growth in small containers was restricted by a reduction in supply of cytokinins from root apices. A hormonal equilibrium, with continuous activity of hormone-producing root meristems, is required for normal shoot growth. Fluctuations in this production, possibly resulting from root restriction, can limit plant growth independently of nutrient and water uptake (Richard and Rowe, 1977).

Although internal regulation of root and shoot growth can be overruled by exogenous application of growth substance (Richards, 1980; Carmi and Heuer, 1981), the modification is usually short-lived, with the plant returning to its pre-treatment balance between root and shoot growth even when exogenous hormone supply is maintained (Thuantavee, 1991).

2.3.3 Injurious restriction (Root pruning)

Root modification of shoot growth has been attributed to control of nutrient and water uptake or hormone synthesis (Richards and Rowe, 1977). It is not clear whether reduced shoot growth following root pruning results from interference with nutrient or water uptake. Resumption of shoot growth following cytokinin application to pruned roots indicated hormones may exert a regulatory influence (Richards et al., 1979; Dawkins et al., 1983). Nonpruned roots has been postulated to be localised in root tips since they are sites of high rates of nutrient and water uptake and of synthesis of cytokinins and gibberellins supplied to the shoot. Mertens and Wright (1978) proposed a theory that employs a source-sink concept to explain rhythmic growth of woody plants. As N is absorbed in roots, it reacts with carbohydrates to promote their development. Eventually, nutrient absorption exceeds root need, and surplus is transported to the shoot where it combines with carbohydrates to form protein and promote shoot growth. Since carbohydrates are used preferentially in the shoot, fewer are available to the roots, resulting in reduced growth of roots and ultimately shoot growth. As shoot growth slows, carbohydrates become available for translocation to the root, and the cycle repeats.

Maggs (1964) reported an increase in net photosynthesis after root pruning of apple trees, but in other plants, net photosynthesis was reduced or was found to return to normal rates after an initial decrease (Geisler and Ferree, 1984). Root removal induced water stress in maize (Brevedan and Hodges, 1978) and holly (Randolph and Wiest, 1981), but water uptake recovered after ten days in peach seedlings (Richards and Rowe, 1977). Shortly after root pruning, assimilates were redistributed in favour of the roots and new roots were initiated in close proximity to the cut (Maggs, 1964; Randolph and Wiest, 1981). Geisler and

Ferree (1984) also confirmed vegetative growth of young apple trees can be reduced by root pruning, but the pruning must be severe and the reduction in growth is only temporary. The growth reductions are likely closely related to the changed moisture status of the trees due to removal of part of the root system. Later reductions in shoot growth, however, can be attributed to an increased allocation of photosynthate to the roots and to hormone imbalances. The trees re-establish their root/shoot balance by enhancing root regrowth at the expense of shoot growth. With the development of new roots, water balance in the tree improves, and net photosynthesis and shoot growth rates increase.

Bentz et al. (1985) examined changes in primary root number, root dry weight, and shoot dry weight in seven woody ornamental plants after root removal treatments. Their results showed root and shoot were reduced in all species and each species produce a different maximum root number. The implication is that a minimum root number is required for the onset of shoot growth. Young and Werner (1982) examined the effects on early root and shoot growth in 'Golden Delicious' apple trees of both shoot and root pruning. Shoot pruning stimulated rapid new shoot growth and resulted in the highest new shoot relative growth rate and new shoot/total shoot dry weight ratio. Also, shoot pruning, with and without root pruning, resulted in very little root dry weight increase up to eight weeks after planting, indicating a competitive inhibition of root growth by rapid new shoot growth. Root pruning, with and without shoot pruning, stimulated the greatest amount of new, white root formation soon after planting, but these contributed very little to root dry weight. Shoot-root-pruned trees had the lowest shoot and root dry weights.

Chapter three: Materials and methods

3.1 Experimental site

Experiments were undertaken at the Plant Growth Unit, Massey University, Palmerston North, New Zealand (Lat. 40° 23′S, Long. 175° 37′E) from September 1997 to February 1998. They were set up in the temperature controlled greenhouse where air temperature was maintained between a minimum of 16°C and a maximum of 25°C.

3.2 Plant Materials and Production Conditions

Four species were chosen as they were expected to show contrasting sensitivity to experimental treatments. Plants of *Camellia × saluenensis* cultivar 'Donation' were supplied by Duncan and Davies Nursery, New Plymouth. Plants were 20 months old from stem cutting and 25 to 30 cm high. They had been grown for 6 to 9 months in a bark-based growing medium held in rigid plastic pots (0.5 litre). Plants of *Pittosporum tenuifolium* cultivar 'Kohuhu' were supplied by Lyndale Nurseries Auckland Ltd. They were approximately 6 to 9 months from stem cutting and had been grown in a bark-based growing medium held in 7.0 × 7.0 ×10.0 cm liner tubes.

Pumpkin (*Cucurbita pepo* cultivar 'Crown Hybrid') plants were raised from seed germinated under mist in a plant propagation room of the greenhouse for approximately ten days. Air temperature was maintained at 27°C/17°C (day/night). Seedlings were transplanted to 5.0 × 5.0 × 8.0 cm tapered tubes when the cotyledons were fully expanded, grown on in the propagation room for two weeks and moved to the experimental greenhouse for one week. Plants were 10.5 ± 0.5 cm tall. During the early growth stage, the seedling were grown in a 2 peat: 1 pumice (by volume) medium amended with PG Mix (14-7-15 NPK + trace elements, 2 g/L, Windmill, Holland), 3 g/L Dolomite, and 3 g/L 8-9 month controlled release Osmocote (Scootts). Shoot tip cuttings of coleus (*Coleus blumei*), 5-6 cm tall, were rooted in the same sized container and medium as the pumpkin seedlings. After two weeks, rooted plants were moved from the propagation area to the greenhouse for another week. Plants were 6.0 ± 0.8 cm tall.

3.3 Experimental

3.3.1 Experimental treatments

Two experiments were conducted in November and December 1997. Two methods (root shaking and root washing by hand) were used to remove growing medium (bare-rooted) as experimental treatments. The first experiment (root shaking) examined the influence of mechanical stress on plant growth recovery and compared species and shaking conditions, durations and frequencies effects on root cleanness. This was a preliminary experiment to establish treatment conditions for the next experiment.

The second experiment (root washing), the main experiment, examined the effects of root washing on plant vegetative and reproductive growth. The degree of root damage was determined on four species with six durations during root washing procedure. The effectiveness of root cleaning and growth recovery were compared between species and durations.

3.3.1.1 Root shaking

Plants of coleus and pumpkin were shaken in dry (shaking under ambient) and wet (shaking with root ball suspended under water) conditions using a Griffin flask shaker (S36-670). Plants were watered to container capacity, then lifted from their containers and weighed before treatments were applied. Plant stems were protected by bubble plastic and mounted on the shaker located on the bench. Then, they were shaken in dry or wet conditions for three durations (30, 60, and 120 s) at four frequency levels: 1 (90 rocking oscillations per minute-rpm), 2 (120 rpm), 3 (150 rpm), and 4 (180 rpm). There were 144 plants used in this experiment (2 species × 2 shaking conditions × 3 durations × 4 frequencies × 3 blocks).

Plants with medium remaining after shaking were reweighed to determine the weight of removal of growing medium. Plants were potted immediately into 0.5 L plastic pots containing 2 peat: 1 pumice (by volume) medium amended with PG Mix, dolomite, and 8 - 9 month controlled release Osmocote at the rates specified in Section 3.2. All plants were then watered and moved to the temperature controlled greenhouse.

3.3.1.2 Root washing

Root systems of each species were hand washed (Plate 3.1) for six durations (0, 3, 10, 30, 100, and 300 s) and then potted into rigid plastic pots (2.5 L for camellia, and 1 L for pittosporum, coleus, and pumpkin) using the same growing medium specified in Section 3.2. Control plants (0 s washing) were transplanted from their original containers into the new pots as above with as little disturbance as possible. Root-washed plants were weighed before washing (at container capacity) and after washing to determine the approximate mass of growing medium removed. Root fragments from each plant were collected immediately after washing and kept in water in a cool store at 1°C. After potting, the treated plants were returned to the greenhouse (Plate 3.2).

3.3.2 Experimental design

A randomised complete block design (RCB) was used in both the root shaking and root washing experiments. In the root shaking experiment, the treatments consisted of two washing conditions at four levels of frequency for three durations and two species, i.e. coleus and pumpkin, were arranged in three blocks. Treatments and species were randomly allocated to positions within each block.

Eight blocks were used in the root washing experiment to account for possible variation in light and air temperature profiles within the greenhouse (Roberts et al., 1986). The four plant species and six washing treatment times were randomly allocated within their blocks. Each block consisted of two replications of each species in six durations. In total, 48 plants were used in each block.

3.4 Data collected

3.4.1 Medium removed

The percentage of medium removed (PMR) was used to determine medium loss in root shaking and root washing experiments. PMR was calculated from following equation:

$$\text{PMR} = (\text{FW} - \text{SW}) / (\text{FW} - \text{PW}) \times 100\%$$

FW (first weight): the initial weight of plant before treatment application.
SW (second weight): the weight of plant after treatment.
PW (plant weight): the mean of five plants each species.

3.4.2 Root loss measurement

The lengths of root fragments detached from root systems were recorded using a Comair Root Length Scanner (Commonwealth Aircraft Co., Melbourne, Australia). Dry weight of root fragments were measured after 24 hours at 80°C in a air drying oven.

3.4.3 Vegetative growth

The vegetative growth was quantified by non-destructive and destructive methods. Non-destructive measurement, i.e. plant height, shoot height, the number of shoots and leaves, were used in the root washing experiment during the growth period. Leaf area and dry weights of leaf, stem, and root were determined by destructive harvest at the end of the growth period.

3.4.3.1 Non-destructive measurement

Shoot growth parameters were measured in all plants varied according to the factors that were most practicable, i.e. pittosporum height; camellia bud break, height and number of shoot; the width of first true pumpkin leaf and the number of leaves; coleus plant width (tip-to-tip distance across lowest pair of leaves on the cutting). These measurements were recorded from the day after the washing treatment to the harvest day every ten days during the observed growth period for each species (40 days for coleus and pumpkin, and 50 for pittosporum).

The morphological changes in response to root-washing treatments were recorded each week (Table 3.1).

Table 3.1 The degree of plant under treatment stress

Degree	Phenomenon	Survival possibility
Low	tip-top shoot bending and leaves in bottom of stem wilted	plants recovered in couples of days
Middle	top shoots bending and leaves in bottom of branches wilted	some plants died, others survived
High	all shoots and leaves dry wilted completely	plants died

3.4.3.2 Destructive harvest

Five plants of each species were harvested at the start of each experiment to determine initial plant height, leaf area, leaf dry weight, root length and root dry mass of the experimental population.

Pumpkin plant leaf area of was measured destructively 12 days after treatment in root shaking experiment.

In root washing experiment, each herbaceous species was harvested 40 days after treatment, and pittosporum after 50 days. Total leaf area was measured with a LI-COR LI-3100 leaf area meter (Lambda Instruments Co., Lincoln, NE, USA). Plant dry weight for all components (leaf, stem, and root) were weighed on a Mettler PC4400 (Delta Range) electronic balance after oven drying at 80°C for 24 hours.

3.4.4 Reproductive growth

Floral bud numbers on each camellia plant were recorded 16 weeks after the root washing treatment when the buds were approaching maturity and readily distinguished from vegetative buds. Flower and floral bud numbers per pumpkin plant were recorded during destructive harvesting. Pittosporum and coleus plants did not produce any flower buds during this study.

3.5 Statistical analysis

All data were analysed as a randomised complete block design. Analysis of variance (ANOVA) was performed using Statistical Analysis Systems (SAS) software (SAS Institute, Cary, N.C). Mean comparisons were carried out using the Duncan's multiple range test at 5% level of significance.

Plate 3.1 Root washing by hand as used in root washing experiment.

Plate 3.2 A view of the plants in the root washing experiment.

Chapter four: Results

4.1 Root shaking

The herbaceous species, pumpkin and coleus, were used to determine the effects of mechanical root disturbance. The measurements included the growing medium removal and the plant response to the treatments.

4.1.1 The effectiveness of medium removal

The percentage of medium removed (PMR %) from the root ball was used to determine effectiveness of medium removed or root cleanness and compared with root washing.

The percentage of medium removal was influenced significantly by species ($P < 0.0001$), treatment ($P < 0.01$), duration ($P < 0.01$), and frequency ($P < 0.0001$). Less medium was removed from pumpkin plants (87.9%) than from coleus plants (92.3%). More medium was removed under wet conditions (91.8%) than under dry conditions (88.4%). More medium was removed as shaking duration increased: 30 s (88.0%) < 60 s (90.1%) < 120 s (92.2%). Similarly, the medium removal increased as the frequency increased: 1 (82.7%) < 3 (91.0%) = 2 (91.2%) < 4 (95.6%). Treatment interacted with species ($P < 0.01$), and also with frequency ($P < 0.05$).

Coleus was sensitive to the treatment conditions, and lost significantly more medium was during shaking under wet condition than under dry condition (Fig. 4.1). In the contrast, there was no significant difference in medium removal between the treatment conditions in pumpkin; extent of medium removal was similar to coleus under dry condition.

At lowest shaking frequency (1), the medium removed under dry condition was significantly less than under wet condition (Fig. 4.2). As the frequency increased, the difference was progressively reduced between the two conditions until the medium removal at highest frequency (4) was exactly same in both treatments with average 95.6%.

In coleus plants, the three factors significantly influenced PMR % from plants and treatment interacted with frequency (Table 4.1). The lower PMR% was found at the shortest duration (30 s) than at other two durations. The lower PMR% was also found at the lowest frequency (1) than at other three frequencies. The difference of PMR% between dry and wet conditions was reduced as frequency increased, although the PMR% in dry conditions was consistently lower than in wet conditions (Fig. 4.3). Overall, coleus was quite sensitive to the increase of duration and frequency, but only at initial stage.

In pumpkin, only duration and frequency had significant effects on PMR% from plants (Table 4.1). More medium was removed at the highest duration (120 s) than at the other two durations. The PMR% increased as the frequency increased and the highest PMR% occurred at the highest frequency (4). Overall, pumpkin was also sensitive to the increase in duration and frequency, but had a slower response to increasing duration.

4.1.2 Plant response to treatment

Mechanical disturbance had no effect on plant survival for plants of both herbaceous species as all plants survived. However, mechanical disturbance influenced growth of pumpkin plants as the leaf area was reduced when measured after two weeks compared with controls.

Leaf area production in pumpkin plants was significantly different between wet and dry shaking treatments (Table 4.2). Leaf area of pumpkin plants in wet shaking treatment was significantly higher than dry shaking treatment in all durations and frequencies. There were no significant difference between shaking durations. There was only a significant difference between shaking frequencies, and this was mainly in the dry condition. No interaction existed between all factors. The overall average leaf area was about 200 cm^2 in the dry disturbance condition and 280 cm^2 in the wet one. Therefore, the plants recovered better or faster in the wet shaking conditions than in dry shaking conditions.

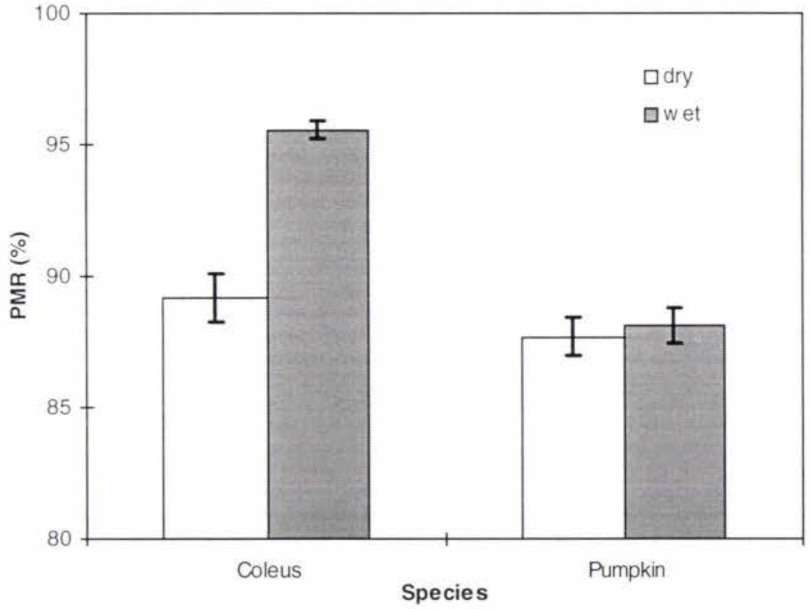

Fig. 4.1 The medium removal between species under dry and wet shaking conditions (vertical bars indicate s.e.m.)

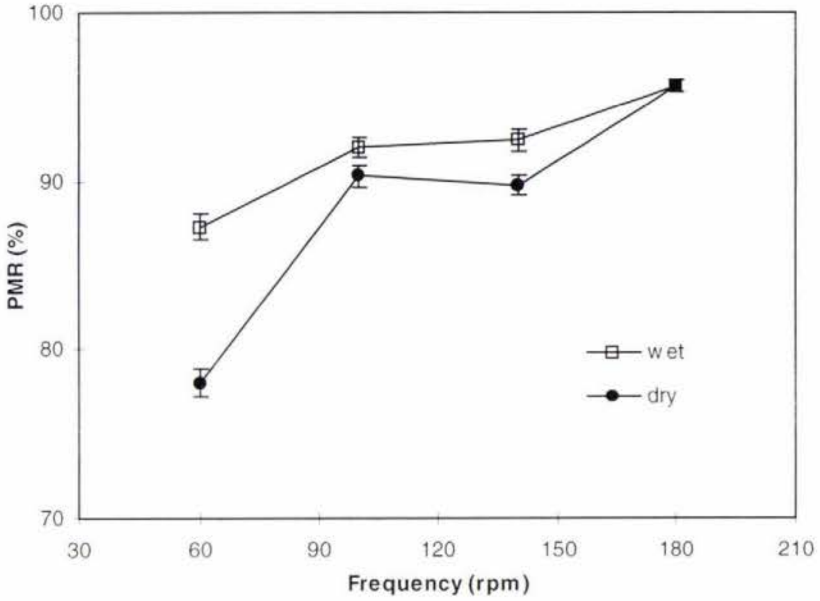

Fig. 4.2 The effect of frequency on the medium removal from plants under dry and wet shaking conditions (vertical bars indicate s.e.m.).

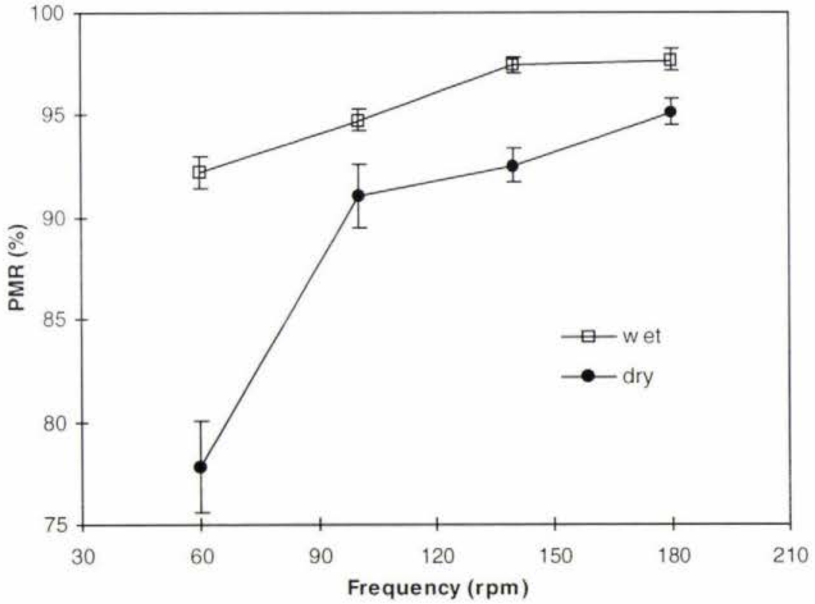

Fig. 4.3 PMR% from coleus in dry and wet shaking conditions at different levels of frequency (vertical bars indicate s.e.m.).

Table 4.1 Influence of root shaking treatments on percentage of medium removed (PMR%) from the plants of coleus and pumpkin.

Factor	Level	Coleus	Pumpkin
Treatment	dry	89.1 b	88.1 a
n = 36	wet	95.5 a	87.8 a
Duration (second)	30	89.6 b	86.4 b
n = 24	60	93.8 a	86.5 b
	120	93.6 a	90.8 a
Frequency (rpm)	60	85.0 b	80.3 c
n = 18	100	92.9 a	89.4 b
	140	95.0 a	87.0 b
	180	96.4 a	94.8 a
Interaction			
Treatment vs Frequency		*	ns
Treatment vs Duration		ns	ns
Frequency vs Duration		ns	ns
Treatment vs Frequency vs		ns	ns

the means in each factor with same letter are not significantly different ($P < 0.05$); rpm: rock/minute; ns: nonsignificant; *: significant at $P < 0.05$.

Table 4.2 Influence of root mechanical root shaking treatments on pumpkin leaf area (cm^2).

Treatments	Dry shaking	Wet shaking
Duration (second)		ns
30	202.7 a	269.4 a
60	203.2 a	303.1 a
120	199.1 a	274.8 a
Frequency (rpm)		*
60	200.4 b	294.3 a
100	248.7 a	288.9 ab
140	184.9 c	262.2 b
180	172.7 c	284.3 ab
Treatment		***
Interaction		
Treatment vs Duration		ns
Treatment vs Frequency		ns
Duration vs Frequency		ns
Treatment vs Duration vs		ns

the means with same letter between levels in each condition are not significantly different ($P < 0.05$); rpm: rock/minute; ns: nonsignificant; * and ***: significant at $P < 0.05$ and $P < 0.0001$, respectively.

4.2 Root washing

Four species were used for root washing, including two woody species, camellia and pittosporum, two herbaceous species, coleus and pumpkin. Root cleanness and root loss data were collected.

4.2.1 Root cleanness

The effectiveness of root cleaning by washing was determined by the percentage of removed medium (PMR%) from growing medium. The two factors, species and duration, have significantly influence on PMR% ($P < 0.0001$), and there was also a significant interaction with each other ($P < 0.0001$).

There were significant differences in the root cleanness between the four species at all washing durations from 3 to 300 seconds (Table 4.3). At same time, there were also significant differences between the durations within each species.

The PMR% of four species were significantly increased by extending the washing time. Pittosporum, coleus and pumpkin roots were typically much cleaner than camellia roots. PMR% from camellia was only about was 87.% even after the longest duration of root washing (300 s) while PMR% from other three species were up to 95% only after one hundred seconds (Fig. 4.4). This is probably a reflection of the structure of the individual root systems.

The medium was removed very quickly from coleus. More than 80% of the growing medium was removed just after three second washing (Plate 4.3). Little additional change occurred after 30 second washing and PMR% were as high as 98.8% after 300 second washing time.

Growing medium removal was also rapid in pittosporum. More than half of the medium had been removed from the plants after three second washing (Plate 4.2). Thereafter, it gradually caught up to the PMR% for coleus. At the longest washing time (300 s), almost no growing medium was left on plant roots (PMR% 99.5%), which was slightly cleaner than coleus.

About one third of the medium was removed from pumpkin plants after three second washing. PMR% increased to 87% after 30 second washing and up to 95% after 300 second washing, similar final value with above species.

The poorest cleanness was found in camellia. Only about one fifth of the medium fell off their roots after three second washing. Even after 300 second washing, more than 20% of the growing medium was still on the roots (Plate 4.1). It may take another 300 seconds to be comparable with the cleanness with other three species. The denser fibrous mass of camellia roots prevented easy removal of growing medium in this species.

Plate 4.1 Root cleanness of camellia in six durations of root washing.

Plate 4.2 Root cleanness of pittosporum in six durations of root washing.

Plate 4.3 Root cleanness of coleus (top) and pumpkin (bottom) in six durations of root washing.

4.2.2 Root loss

Root fragments were found in the removed medium from pittosporum, and pumpkin during all durations (3, 10, 30, 100, and 300 seconds) of root washing. However, root loss of camellia and coleus occurred only with the three higher washing durations (30, 100, and 300 seconds) and no root fragments were found in the removed medium after 3 and 10 second washing.

There were significant effects ($P < 0.05$) of root washing on root loss of camellia, pittosporum, and pumpkin between the durations of washing time. Root loss increased as washing time increased for each of three species with the highest root loss in the 300 second duration (Fig. 4.5).

The length of roots lost from camellia after 30 second washing was only 0.6 m. It increased consistently to 2.1 m after 300 second washing. In the contrast, the length of roots lost from pittosporum was 0.4 m just after 3 second washing and increased to 2.6 m after 100 second washing, Then, the rate of increase deceased from 100 to 300 second washing as only 0.5 m more roots were removed during this period.

The length of lost roots from pumpkin after 3 second washing was 0.2 m. And it increased gradually to 1.0 m as the washing time up to 300 seconds. Comparably, much less roots were washed off from coleus. Only 0.2 m was removed after washing for 300 seconds. There was no significant ($P > 0.05$) difference in coleus root loss between all washing durations from 3 to 300 seconds (Table 4.4).

There were significant root losses in each species when washing for 300 seconds. However, root losses from four species at the longest duration (300 s) were significantly different ($P < 0.05$). Pittosporum root loss was the highest, and losing 15% (3.2 m from 21.1 m) of the total root length. A much less proportion was lost in the other species, camellia, pumpkin, and coleus had 2.6% (2.1 m from 81.8 m), 3.4% (1.0 m from 30.4 m), and 5.9% (0.2 m from 3.0 m) respectively (Fig. 4.6a, b).

4.2.3 Plant survival

All camellia, pumpkin, and coleus plants survived all washing treatments. However, the washing treatment had significant influence on pittosporum survival rates. Increased washing time increased root loss and reduced survival rates (Fig. 4.7). Survival rates decreased from 100% after 3 and 10 second washing to 94% (30 seconds), 81% (100 seconds) and 62% (300 seconds). A negative relationship was found between root loss and survival rate (Fig. 4.8). The survival rates decreased as the root loss increased.

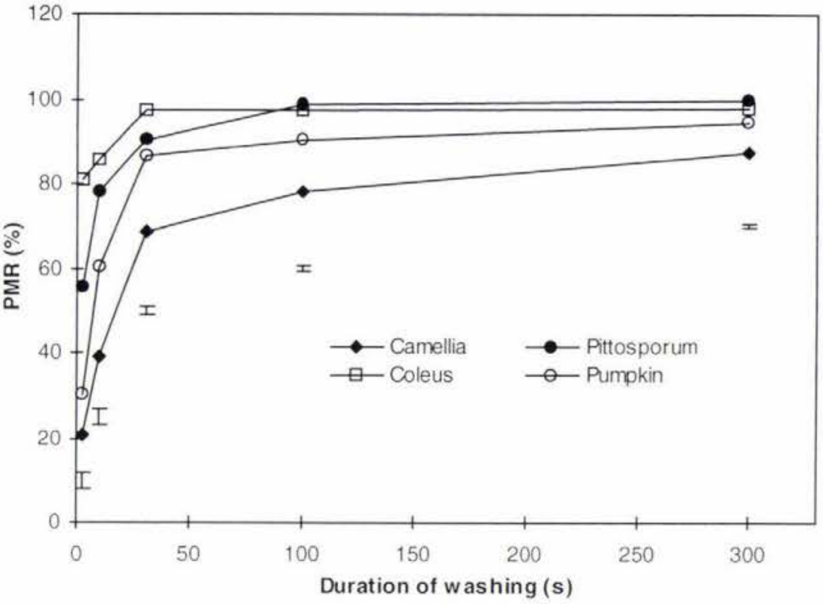

Fig. 4.4 Effect of root washing on the percentage of growing medium removal (vertical bars indicate s.e.m.).

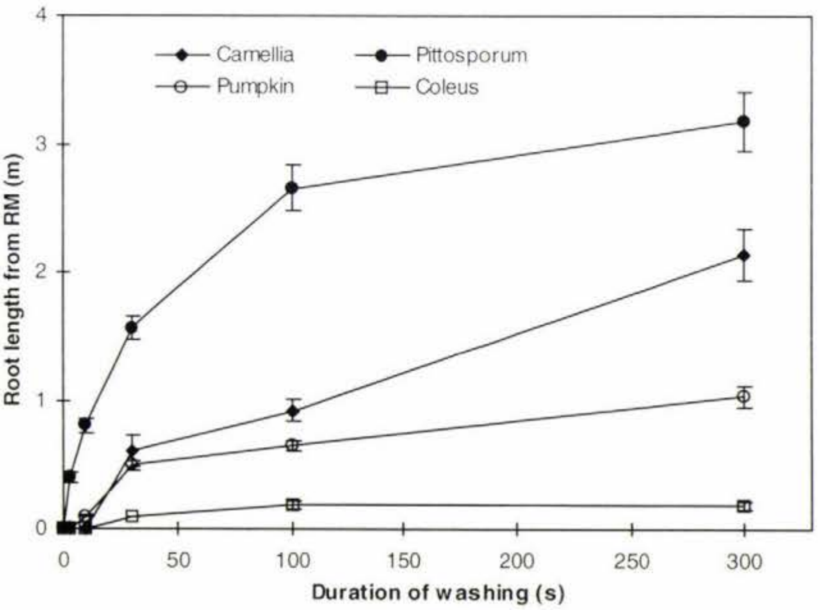

Fig. 4.5 Effect of root washing on root loss from plants (RM: removed medium; vertical bars indicate s.e.m.).

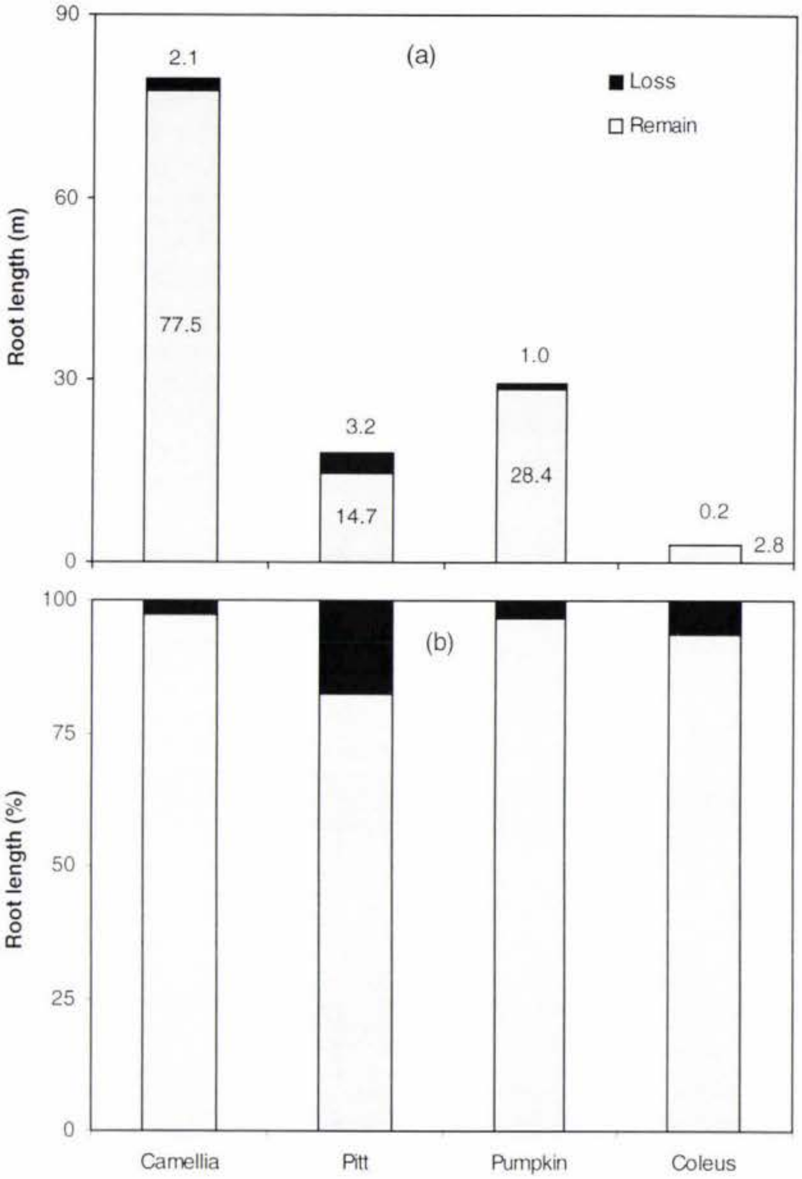

Fig. 4.6 Root loss from various species plants at longest root washing duration (300 s): (a) length, and (b) the percentage.

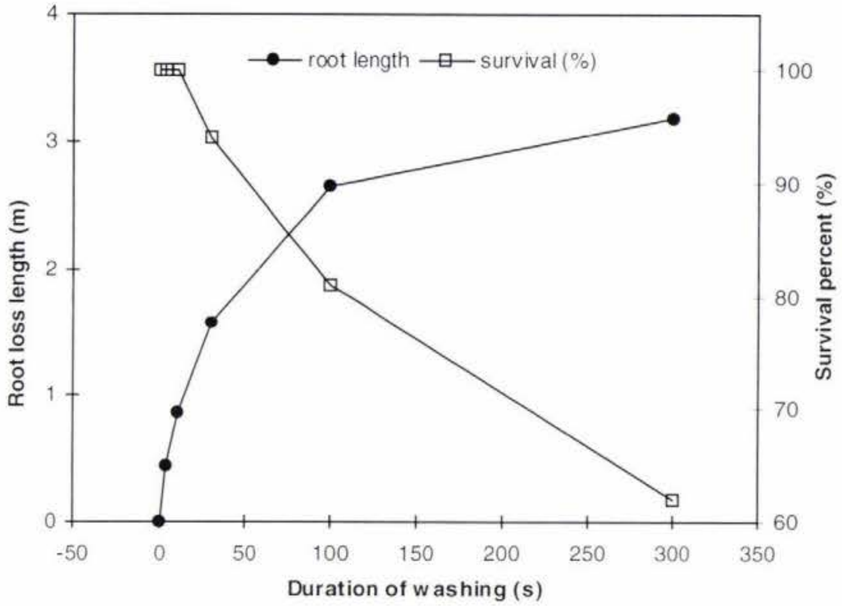

Fig. 4.7 Root loss and survival of pittosporum with increasing root washing.

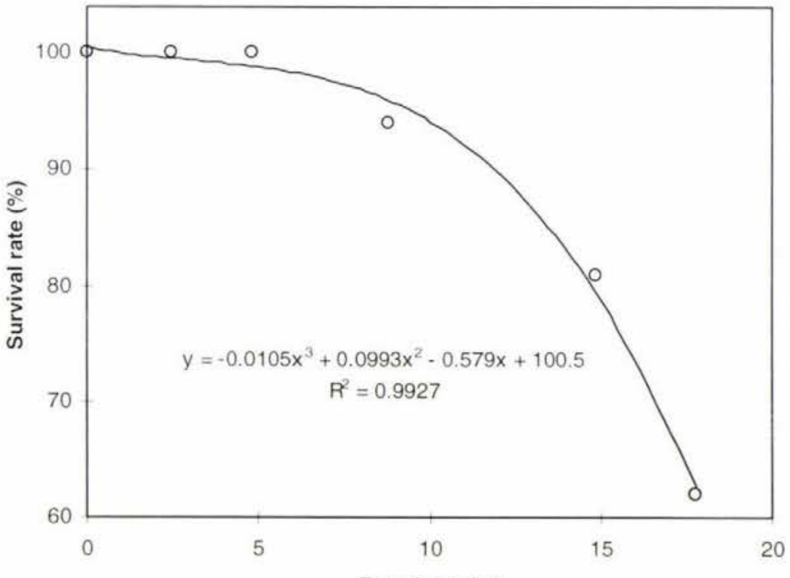

Fig. 4.8 The relationship between pittosporum root loss and survival rate.

Table 4.3 Effect of root washing on the percentage of growing medium removal.

Duration (second)	Camellia	Pittosporum	Coleus	Pumpkin	s.e.m.	Significant
3	20.8	55.3	80.7	30.0	3.8	***
10	39.2	78.3	85.5	60.1	3.5	***
30	68.9	90.2	97.2	86.5	2.1	***
100	78.1	98.7	97.4	90.4	1.3	**
300	87.6	99.5	98.8	94.6	0.7	*
s.e.m.	3.2	2.4	1.6	3.4	---	---
Significant	***	***	***	***	---	---

*, **, *** significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 4.4 Effect of root washing on root loss from plants (unit: m).

Duration (second)	Camellia	Pittosporum	Coleus	Pumpkin
3	–	0.4	–	–
10	–	0.8	–	0.1
30	0.6	1.5	0.1	0.4
100	0.9	2.6	0.2	0.6
300	2.1	3.1	0.2	1.0
s.e.m.	0.24	0.19	0.03	0.07
Significant	***	***	ns	***

ns, *** Nonsignificant or significant at $P \leq 0.10$, or 0.001, respectively; – no root fragments found.

4.2.4 Shoot and root growth

The shoot and root growth was monitored after root washing. In camellia, bud break and new shoot growth were monitored and measured whereas in pittosporum shoot growth, root length, node number, leaf area and oven dry biomass weight were measured. Pumpkin leaf number, nodes and flowers, plant height, and oven dry biomass were measured. In coleus, node number, shoot height, leaf area, root length and oven dry biomass.

4.2.4.1 Camellia

Bud break in camellia occurred two weeks after replanting in middle of December 1997 (Table 4.5). The new flushing shoot following bud break grew rapidly and the fast growth last about three weeks. Then, the growth slowed down and eventually stopped.

The number of bud breaks and new shoot was significant difference between all durations of root washing ($P < 0.001$), even after a few second washing (Table 4.6). There were 17 new shoots in the control plants and it was reduced to 9 only after 3 second washing. Just 5 new shoots were found on the plants after 300 second washing.

New shoot growth was also obviously affected by root washing. The height of new shoot was significant ($P < 0.007$) reduced by increasing washing time (Table 4.6, Fig. 4.9). Maximum shoot height appeared in control (27 cm) and minimum was in the highest washing times (10 cm), 100 and 300 seconds. Two deepest reductions happened between 3 to 10 seconds and 30 to 100 seconds. In addition, the percentage of new shoots in total shoots had similar trend. Twenty eight percent of total shoots was new flushing in the control and reduced to 13% after 3 second washing. Eventually, only 8% after 300 second washing.

There was no significant effect of root washing treatment on camellia flower bud number ($P > 0.05$), although flower buds appeared one month later after root washing in all treatment plants (Table 4.6).

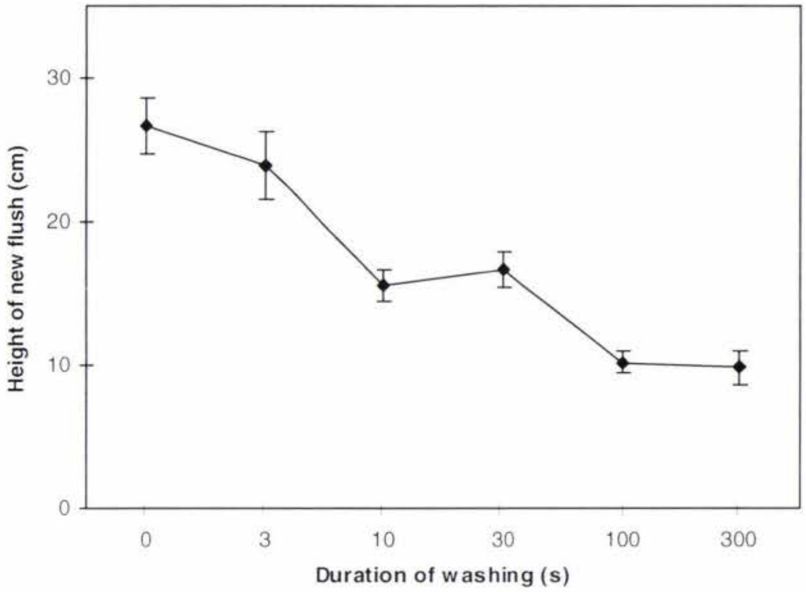

Fig. 4.9 Effect of root washing on camellia shoot growth after 8 weeks (vertical bars indicate s.e.m.).

Table 4.5 Effect of root washing on bud break and number of new shoots growing (NSG) in camellia.

Date \ Duration (s)	0	3	10	30	100	300
12/12/97	0	0	0	0	0	0
22/12/97	2	0	1	0	0	0
2/1/98	4	1	0	0	0	0
12/1/98	3	2	2	3	1	1
22/1/98	2	4	2	2	2	2
2/2/98	3	0	0	0	1	0
16/2/98	3	2	2	1	2	2
Number of new	17	9	7	6	6	5
Total shoot	62	71	71	62	70	62

Table 4.6 Effects of root washing on the length and percentage of new shoots growing (NSG), and the flower bud number per plant in camellia.

Duration of root washing (s)	New shoot length (cm)	NSG in the total shoots (%)	Flower bud number
0	26.6	28.1	17.4
3	23.8	13.0	17.4
10	15.5	10.0	17.8
30	16.6	9.9	17.0
100	10.1	10.1	18.1
300	9.8	8.0	16.7
s.e.m	1.8	1.9	0.6
Significance	**	***	ns

ns, **, *** Nonsignificant or significant at $P \le 0.10$, 0.01, or 0.001, respectively.

4.2.4.2 Pittosporum

Pittosporum shoot and root growth was significantly affected by root washing (Plates 4.4 and 4.5), even with very short time washing, such as three seconds. These effects were determined by a range of significant parameters, which included shoot height, leaf area, root length, and biomass dry weight of all plant components.

Shoot growth was significantly different at evaluation date (Table 4.7). Differences of shoot height between treatments increased with time. Ten days after replanting, plants in control and with the shortest washing treatment (three seconds) had increased in the height more rapidly than the other treatments. The plants with the longest washing treatment were 23 cm, which was unchanged from the plant height before root washing (Fig. 4.10). After 50 days, the difference in plant height was more marked, 27 cm in the plants with longest washing treatment compared with about 40 cm in the control and with the shortest washing treatment.

There were significant differences in number of node and stem length between the six washing times (Table 4.8), but no difference in mean node length. There were about 40 nodes in the control plants and the ones with three second washing. The node number decreased steadily down to 26 as the washing time increased from 3 to 300 seconds (Fig. 4.13a).

Plant leaf area was significantly different ($P < 0.0001$) between the treatments. Leaf area decreased as root washing time increased (Fig. 4.11). Leaf area of the control plants, about 400 cm^2, was significantly higher than all washed plants. The leaf area decreased from 312 cm^2 (about 78% of the control) to 166 cm^2 (about 41% of the control) as the washing time increased from 3 to 300 seconds (Table 4.8).

The root length was also significantly reduced by root washing ($P < 0.01$). Root length in the control plants was approximately 35 m (Fig. 4.12, Table 4.8), and decreased to 29 m in the three second washing treatment and 19 m in 300 second washing treatment.

A positive linear relationship occurred between leaf area and stem length. Within the plants at the lowest washing duration (3 seconds), the more the leaf area, the higher the plant (Fig. 4.14a). Similar trend was also found in other durations, such as at the highest duration though the slope was deeper (Fig. 4.14b). Furthermore, the trend was also same on the means of the six washing treatment times (Fig. 4.14c).

Root washing had significant ($P < 0.001$) effect on the dry weight of leaf, stem, and root components (Fig. 4.13). The highest biomass and highest the individual plant component dry weight was always in the control plants (Table 4.8). The dry weight was reduced as the washing time increased. Even after 3 second washing, the shoot dry weight of plants was reduced to 88% of the control plant. After the longest washing, it was reduced to only 43% of the control plants.

Although the significant differences existed in root and shoot respectively, the root washing treatment did not affect on root:shoot ratio ($P > 0.05$).

A negative relationship existed between the length of lost root and leaf area (Fig. 4.15). As more roots were lost, less leaf area was correlated with the loss. On the other hand, several other factors were highly correlated with roots this included total root length and total leaf area (Fig. 4.16), total root length and plant height (Fig. 4.17) and root dry weight and shoot dry weight (Fig. 4.18). The more the total root amount, the more the these three performances.

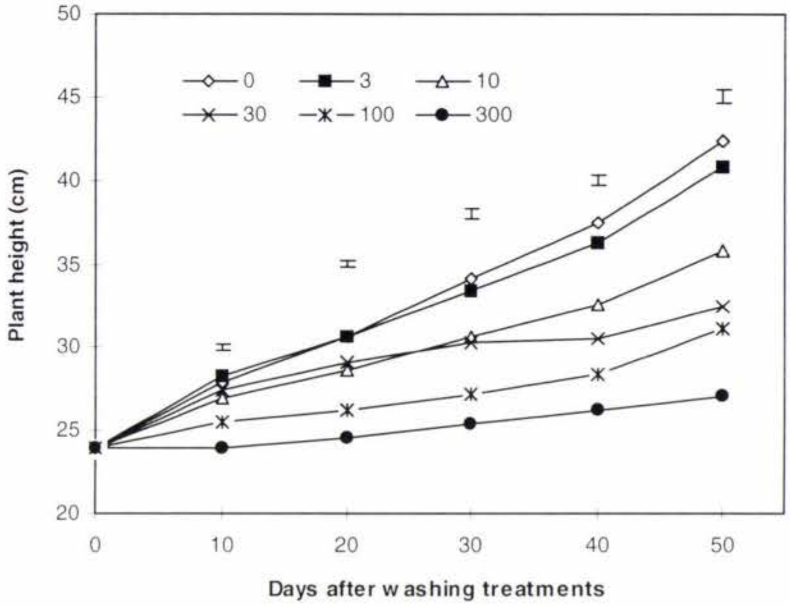

Fig. 4.10 Effect of root washing on growth and development of pittosporum shoots (vertical bars indicate s.e.m.).

Table 4.7 Influence of root washing on the change of shoot height (cm) in pittosporum.

Duration of washing	12/12/97	22/12/97	2/1/98	12/1/98	22/1/98
0 (control)	27.9	30.6	34.1	37.4	42.3
3 s	28.2	30.5	33.4	36.2	40.8
10 s	26.9	28.6	30.5	32.5	35.7
30 s	27.4	29.1	30.3	30.4	32.4
100 s	25.4	26.2	27.1	28.4	31.1
300 s	23.9	24.5	25.4	26.2	27.1
s.e.m.	0.17	0.21	0.26	0.31	0.4
Significance	***	***	***	***	***

*** significant at $P \leq 0.001$.

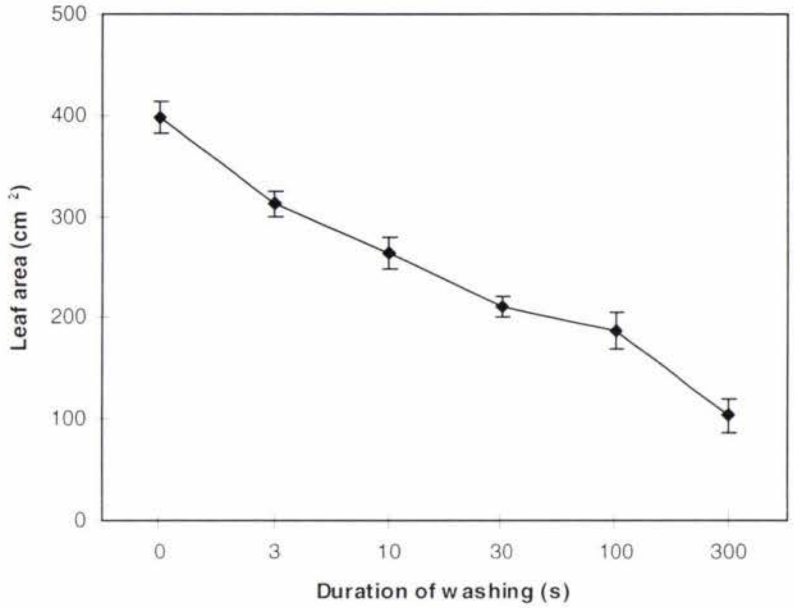

Fig. 4.11 Leaf area of pittosporum plants two months after root washing and replanting (vertical bars indicate s.e.m.).

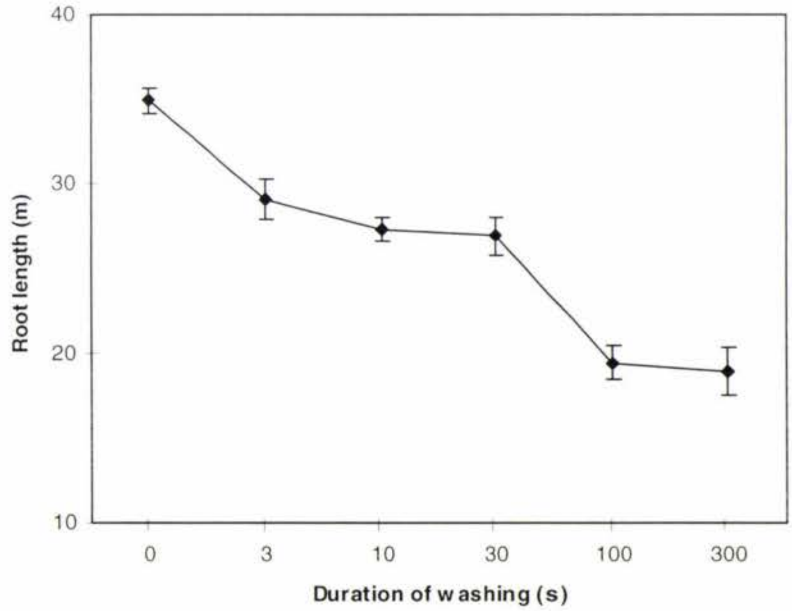

Fig. 4.12 Root length of pittosporum plants two months after root washing and replanting (vertical bars indicate s.e.m.).

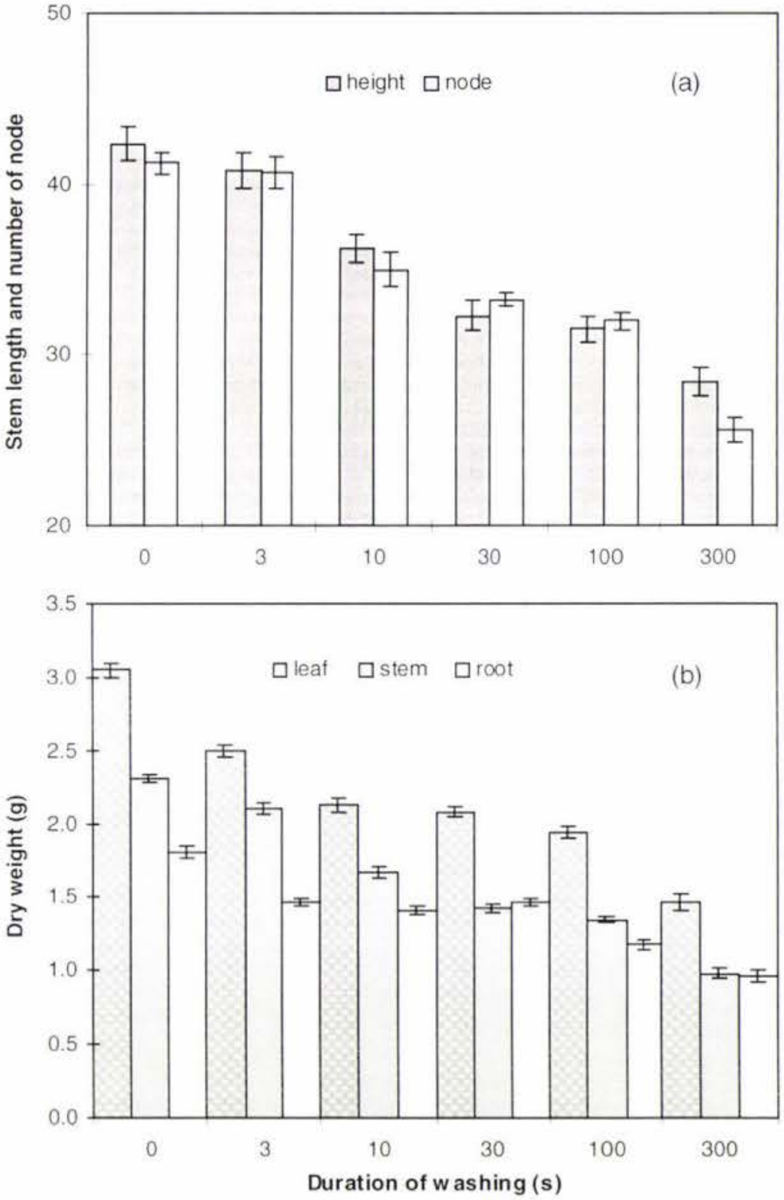

Fig. 4.13 Effect of root washing on the growth of pittosporum components: (a) stem length and number of node. (b) leaf, stem and root dry weight (vertical bars indicate s.e.m.).

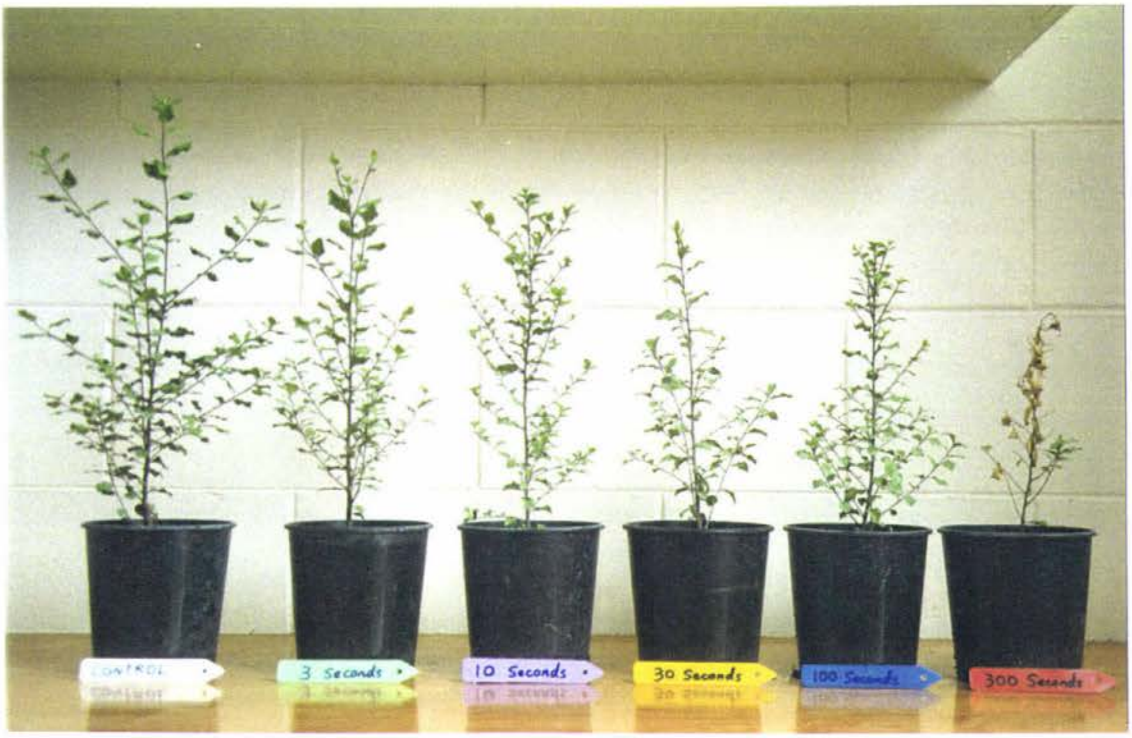

Plate 4.4 Comparison of pittosporum shoot growth in six durations of root washing.

Plate 4.5 Comparison of pittosporum root growth in six durations of root washing.

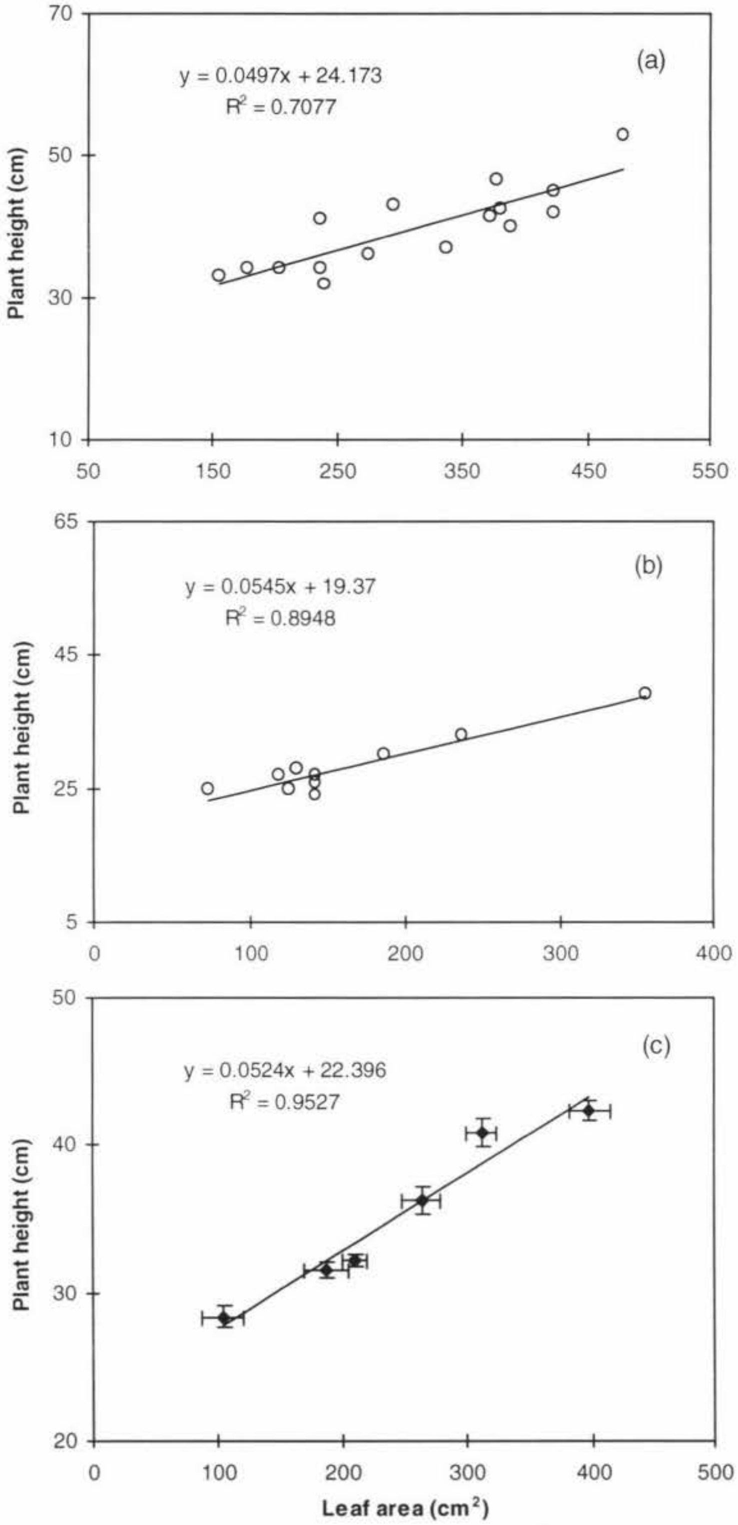

Fig. 4.14 Relationship between plant height and total leaf area for pittosporum plants. (a) at the shortest duration (b) at highest duration (c) the mean of six durations (horizontal and vertical bars indicate s.e.m.).

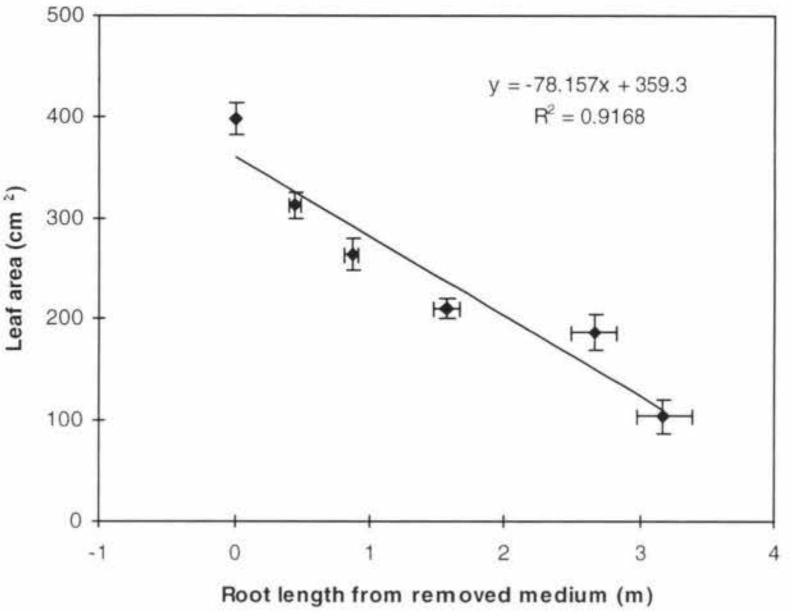

Fig. 4.15 Relationship between root loss length from removed medium and total leaf area for pittosporum plant (horizontal and vertical bars indicate s.e.m.).

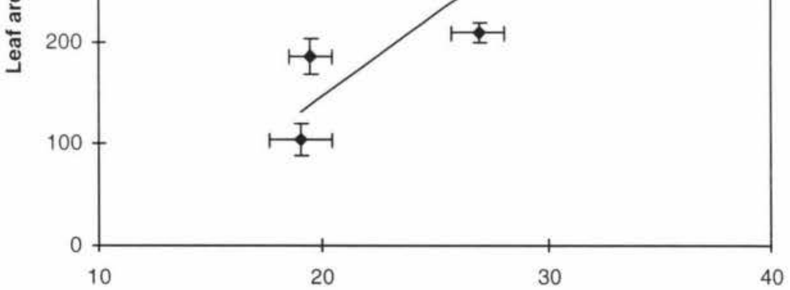

Fig. 4.16 Relationship between total root length and total leaf area of pittosporum plants 50 days after washing and replanting (horizontal and vertical bars indicate s.e.m.).

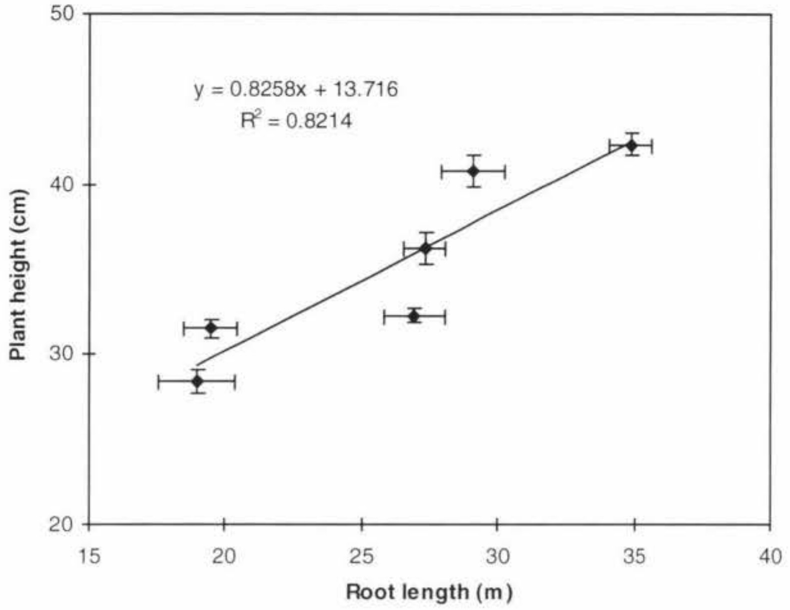

Fig. 4.17 Relationship between total root length and plant height of pittosporum plants 50 days after washing and replanting (horizontal and vertical bars indicate s.e.m.).

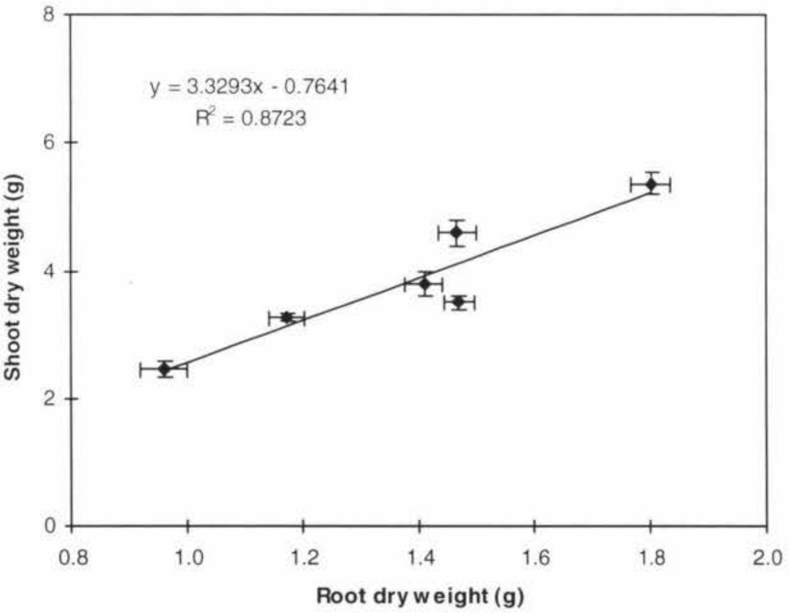

Fig. 4.18 Relationship between shoot dry weight and root dry weight of pittosporum plants 50 days after washing and replant (horizontal and vertical bars indicate s.e.m.).

Table 4.8 The effects of root washing on the growth of pittosporum components.

Duration of washing (second)	Stem length (cm)	Number of node	Leaf area (cm^2)	Leaf dry weight (g)	Stem dry weight (g)	Root dry weight	Shoot dry weight	Shoot: root ratio	Root length (m)
0	42.3	41.1	397.9	3.0	2.3	1.8	5.4	3.1	34.8
3	40.8	40.6	312.0	2.4	2.1	1.5	4.5	2.9	29.0
10	36.2	35.0	263.8	2.1	1.6	1.4	3.7	2.8	27.2
30	32.2	33.2	224.4	2.0	1.4	1.4	3.4	2.7	26.9
100	31.5	32.0	229.9	1.9	1.3	1.1	3.2	2.4	19.4
300	28.4	25.6	165.8	1.4	0.9	0.9	2.3	2.3	18.9
s.e.m.	1.6	0.18	30.8	0.16	0.12	0.1	0.38	0.21	0.1
Significance	***	*	***	***	***	***	***	ns	**

ns, *, **, *** Nonsignificant or significant at $P \leq 0.10$, 0.05, 0.01, or 0.001, respectively.

4.2.4.3 Pumpkin

Root washing treatment had significantly influenced on the number of node, leaf and flower, stem length, leaf dry weight, and stem dry weight ($P < 0.05$).

The leaf number was significant different between durations of root washing throughout the forty day course of the experiment ($P < 0.05$). Plant leaf number increased in control and with the shortest washing treatment even only 10 days after replanting, but no change in the other treatments (Fig. 4.19). After 40 days, there were 16 leaves on the plants in the control and with three second washing treatment, only about 13 leaves on the plants with 300 second washing treatment (Table 4.9).

Plants in control had the highest stem length, leaf area, the number of node and the dry weight of each component. On the contrary, plants in the longest washing treatment had lowest values on these plant performances (Table 4.10, Fig. 20, 21).

Leaf area and the number of flower buds were not affected by the washing treatments (Table 4.10). However, the flower number was significantly affected by the treatments (Fig. 4.21, Table 4.10). More flowers were found on control plants than on other washed plants. And less flowers were found on the plants with higher washing treatments (i.e. 100 and 300 seconds) than on the ones with lower washing treatments (i.e. 3, 10 and 30 seconds).

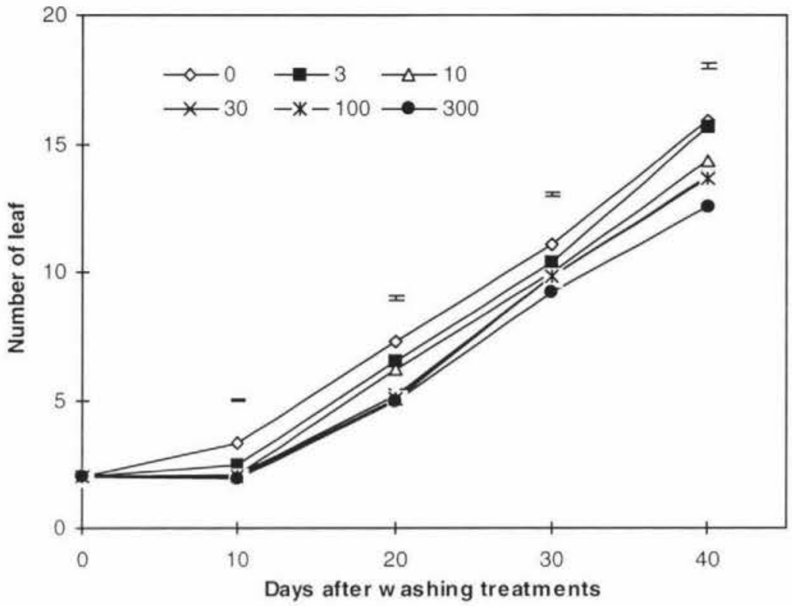

Fig. 4.19 Effects of root washing on pumpkin leaf number (vertical bars indicate s.e.m.).

Table 4.9 Influence of root washing on pumpkin leaf number.

Duration of washing (s)	12/12/97	22/12/97	2/1/98	12/1/98
control	3.3	7.2	11.0	15.8
3 s	2.5	6.5	10.3	15.6
10 s	2.1	6.1	10.0	14.3
30 s	2.1	5.1	9.8	13.6
100 s	2.0	5.0	9.1	13.6
300 s	1.9	5.0	9.8	12.5
s.e.m.	0.08	0.14	0.18	0.24
Significant	***	***	***	***

*** significant at $P < 0.001$.

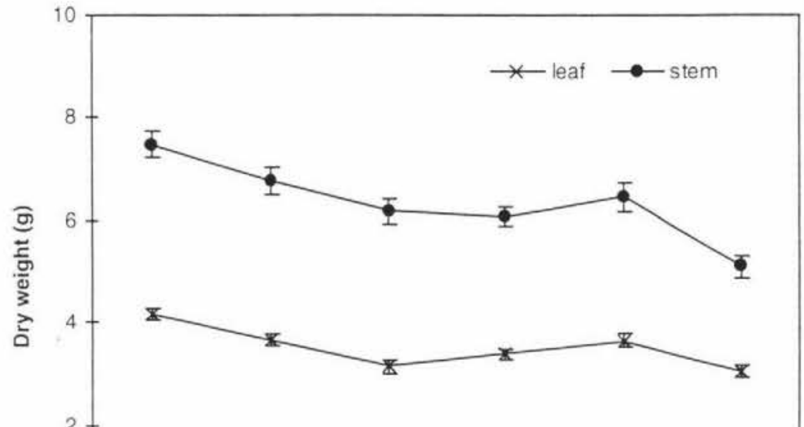

Fig. 4.20 The leaf and stem biomass of pumpkin plants 40 days after root washing and replanting (vertical bars indicate s.e.m.).

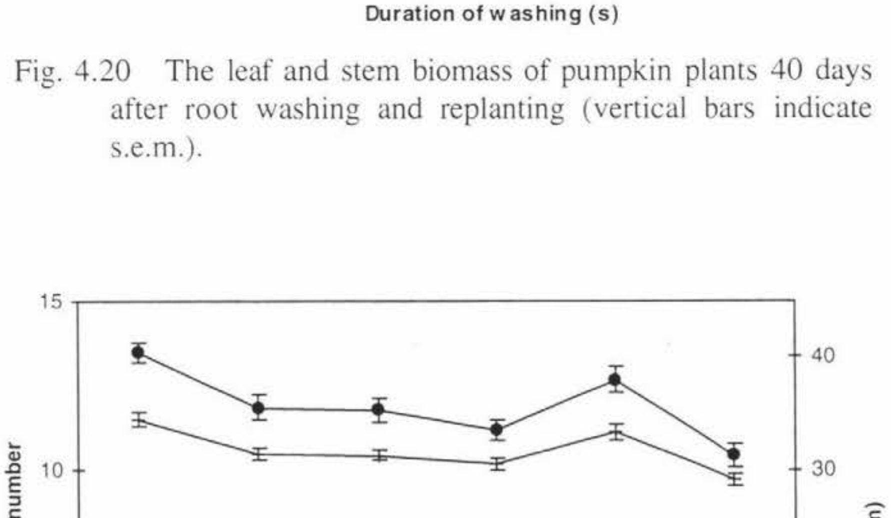

Fig. 4.21 Pumpkin performance 40 days after root washing and replanting (vertical bars indicate s.e.m.).

Table 4.10 Effects of root washing on the growth of pumpkin components 40 days after washing and replanting.

Duration of washing (second)	Stem length (cm)	Number of node	Leaf area (cm^2)	Leaf dry weight (g)	Stem dry weight (g)	Shoot dry weight (g)	Number of flower	Number of flower bud
0	40.4	11.5	732.7	4.17	7.48	11.6	6.5	7.5
3	35.5	10.5	661.5	3.65	6.77	10.4	5.2	7.3
10	35.3	10.4	619.1	3.14	6.18	9.3	5.5	7.6
30	33.5	10.1	629.8	3.37	6.06	9.4	5.2	8.2
100	38.0	11.1	703.1	3.63	6.45	10.0	3.9	8.6
300	31.3	9.75	595.9	3.04	5.09	8.1	4.4	7.5
s.e.m.	0.86	0.16	20.2	0.1	0.21	0.17	0.22	0.21
significant	**	***	ns	***	***	***	**	ns

ns, **, *** Nonsignificant or significant at $P \leq 0.10$, 0.01, or 0.001, respectively.

4.2.4.4 Coleus

Root washing treatments had significant effects on shoot height growth throughout the 40 day course of the experiment ($P < 0.01$) (Table 4.11). Shoot height increased in all treatments only 10 days after replanting. Plants in shorter washing time (3 and 10 seconds) and control treatment were higher then others (Fig. 4.22). After 40 days, the stem length was significantly different ($P < 0.01$) between the treatments. Plants with the longest washing treatment had the shortest stem length (Fig. 4.23). The evident change occurred between 10 and 30 second washing, and there were no difference between the plants with washing time under 10 seconds or above 30 seconds.

Root washing treatments had no significant effects ($P \geq 0.05$) on other plant performances, which included the number of node, leaf area, the oven dry weight of leaf, stem, and root, shoot:root ratio, and root length (Table 4.12).

Table 4.11 Effects of root washing on coleus shoot height (cm).

Duration of washing (s)	12/12/97	22/12/97	2/1/98	12/1/98
0	3.8	7.4	11.0	14.8
3	3.8	7.7	12.4	15.2
10	3.7	7.2	11.2	15.0
30	3.7	6.6	9.5	13.0
100	3.5	5.7	8.7	12.4
300	3.6	5.8	9.0	12.6
s.e.m.	0.11	0.17	0.26	0.32
Significance	ns	***	***	**

ns, **, *** Nonsignificant or significant at $P \leq 0.10$, 0.01, or 0.001, respectively.

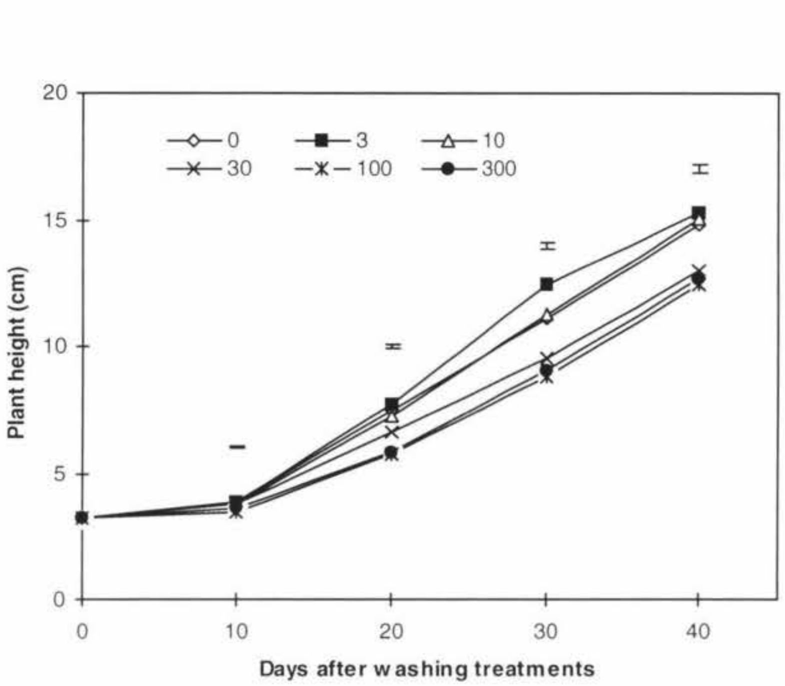

Fig. 4.22 Effect of root washing on coleus shoot growth and development (unit: second; vertical bars indicate s.e.m.).

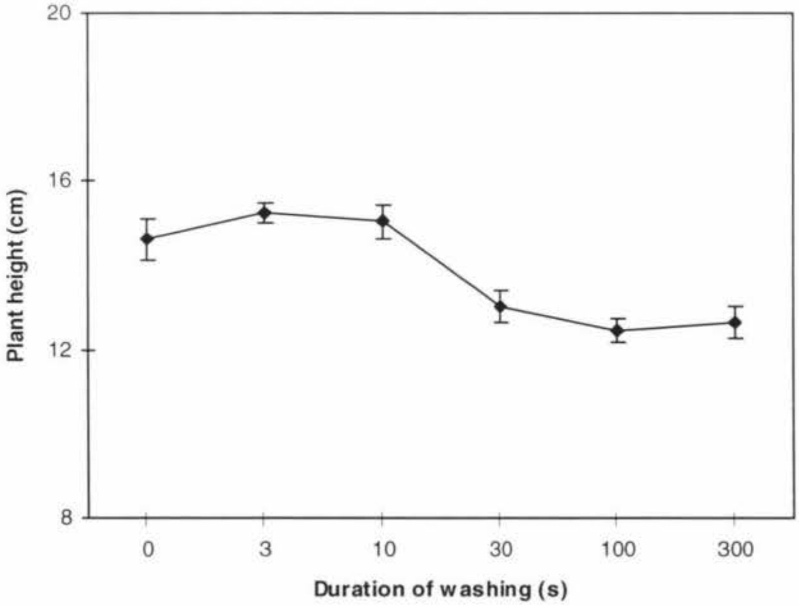

Fig. 4.23 Coleus height 40 days after root washing and replanting (vertical bars indicate s.e.m.).

Table 4.12 Effects of root washing on the growth of coleus components 40 days after root washing and replanting.

Duration of washing (second)	Stem length (cm)	Number of node	Leaf area (cm^2)	Leaf dry weight (g)	Stem dry weight (g)	Shoot:root ratio	root length (m)	root dry weight (g)
0	14.6	8.2	728.2	1.62	0.56	5.9	31.1	0.40
3	15.2	7.9	821.1	1.84	0.57	6.4	34.7	0.45
10	15.0	8.0	636.6	1.62	0.52	4.7	29.7	0.38
30	13.0	8.0	621.9	1.41	0.44	5.6	28.0	0.36
100	12.4	7.8	566.8	1.28	0.41	5.5	26.7	0.34
300	12.6	7.6	632.4	1.31	0.38	5.6	26.5	0.32
s.e.m.	0.32	0.08	28.5	0.06	0.03	0.23	1.60	0.02
significance	**	ns	ns	ns	ns	ns	ns	ns

ns, **, Nonsignificant or significant at $P \leq 0.10$, or 0.01, respectively.

Chapter five: Discussion

5.1 Mechanical disturbance

5.1.1 The effectiveness of root cleaning

The difference between two species of plant in their media removal percentage was found in the shaking experiment (Table 4.1). Coleus plants were more easily cleaned than pumpkin plants. The reason was probably because of a difference in root morphology between the species (Zobel, 1996). Coleus with a fibrous root system was unbranched in early stages and total root length was only about three meters per plant (Fig. 4.6a). However, pumpkin had a tap root system which was much longer and had more branches (Plate 4.3).

Shaking conditions, duration of shaking time and shaking frequency also affected percentage of medium removed. Shaking the plants root system under water (wet condition) produced much cleaner roots than under ambient (dry shaking) in both species. The components of medium were easily removed from root system by shaking in water. In both dry and wet conditions, the degree of root cleaning was improved with increased cleaning time and increased shaking frequency (Table 4.1). Up to 90% of the growing medium was already removed before using high level frequencies and longer duration, for example frequency level 3 or 4, for 120 seconds. However, shaking the plant at high frequencies and extending the shaking time would cause more physical damage to plant or plant parts and produce increased mechanical stress. Therefore, the results of this study suggested shaking plants at frequency level 2 (120 rpm) and for 1 minute of shaking time would be considered the suitable application of root cleaning.

5.1.2 Plants response to mechanical stress

The shaken plants in both dry and wet conditions suffered a reduction in the growth rate of their leaves compared to the unshaken controls. Reduction in leaf growth following shaking of pumpkin seedlings in this study is similar to previous findings with other species (chrysanthemum, tomato, pea etc.) (Beyl and Mitchell, 1977a; Heuchert et al., 1983; Akers and Mitchell, 1985). The mechanism of the mechanical stress in growth inhibition has been explained by physiological effects and the role of plant growth substances (Latmer, 1991b).

Some studies have presented evidence that mechanical stress (including stress caused by rubbing, bending, and shaking) alters the growth of plants by causing changes in concentration of the following growth regulators: ethylene (Hiraki and Ota, 1975; Mitchell, 1977; Biddington and Dearman, 1986), gibberellins (Suge, 1978; Beyl an Mitchell, 1983), auxin (Mitchell, 1977; Erner and Jaffe, 1982; Boyer et al., 1983), and cytokinins and growth inhibitors (Beyl and Mitchell, 1983). For instance, mechanically-induced stress retards growth by lowering endogenous gibberellin levels (Suge, 1978; Beyl and Mitchell, 1983; Biddington and Dearman, 1987b). Ethylene production increases in several species with mechanically-induced stress and in *Prunus vulgaris*, exogenous ethylene reduced elongation and increased radial growth of stems in a manner similar to mechanically-induced stress. The turgor potential is the cellular parameter most responsive to mechanical stress (Grace et al., 1982). Therefore, assimilative, hormonal, and cellular growth factors all have been implicated in the mechanism of growth responses to mechanical stress.

The effect of shaking action on plant growth was split into two components by Heuchert and Mitchell (1983). One is the physical stress resulting from bending, displacement or damage of plant tissues. Another is alteration of leaf microclimate and gas exchange following. Growth reduction may result from both components of shaking action. Plant growth responses to shaking may involve changes in water relations, tissue temperature, and even CO_2 availability. Grace et al. (1982) demonstrated shaken plants had lower water potentials than the controls. Therefore, the shaken plants would have transpired more water than unshaken control plants. Normally, an increase in water flux through the plant is accompanied by a decline in the leaf water potential. One interpretation of the response to shaking was this higher transpiration rate produced a lower water potential, that was associated with reduced extension growth. Reduction of photosynthetic activity producing less fixed carbon, would play a significant role in reducing plant growth. Growth reduction in tomato plants was related to reduced leaf growth, temporary reduction in stomatal aperture, and retarded carbon assimilation (Mitchell et al., 1977). Many plants grown in controlled environment facilities were shortened by normal handling and management procedures relative to control plants (pers. com. C.B. Christie). These findings are supported by short periods of shaking (vibration) that caused temporary photosynthetic inhibition in chrysanthemum plants (Beyl and Mitchell, 1977a). Reduced photosynthetic productivity was the result, rather than the cause of growth reduction. Net photosynthetic productivity may be lower in shaken plants due to reduced leaf area.

5.2 Root washing

5.2.1 Root cleanness

The effectiveness of root cleaning varied between species in the root washing experiment. The four species had different root types, root development stages, root sizes, and root morphology. Camellia had well developed fibrous root systems that were more difficult to clean than the other three species, even after the longest washing time to remove 87%. Up to 90% of the growing medium was removed from other three species in 60 seconds or less. For these species, it would not be necessary to extend the duration of washing beyond 60 seconds.

When comparing the two washing methods used, shaking and root washing, root washing was normally more effective than shaking for root cleaning, although both methods reduced growth parameters. It was expected that shaking whole plant would cause more mechanical stress and damage to the shoot and root system than root washing, which only really disturbed the plant root system, with rather less shaking of the shoot growth. The roots were generally much cleaner using the root washing procedure instead of plant shaking.

5.2.2 Plant response

Some physical damage occurred to root systems in all species after root washing. Pumpkin roots exhibited more damage than coleus after the same treatment, and pittosporum was more damaged than camellia. Overall, pittosporum was the most easily damaged species by root washing treatment.

Differences in root morphology may account for differences in damage between the species or cultivar (Jaffe, 1973; Bentz et al., 1985; Biddington and Dearman, 1988). This was supported by the present study that showed differences in plant survival and shoot growth following root washing.

Jaffe (1973) reported that two closely relate plants, cucumber (*Cucumis sativus*) and pumpkin (*Cucurbita pepo*), reacted completely differently to the stimulus. When cucumber plants were given a gentle mechanical stimulus by rubbing the internodes for about 10 seconds once or twice daily, elongation was significantly retarded. Plants of pumpkin did not exhibit any such response. Bentz et al. (1985) examined the change in primary root number, root dry weight and shoot dry weight on seven woody ornamental plants after either no root removal or partial root removal. Their results showed that species significantly differed in maximum root number, root dry weight and shoot dry weight, but varied in time of achievement. For instance, root number of *Ligustrum* increased over 12 weeks, whereas root number of *Buxus*, *Prunus*, *Vitis* and *Weigela* did not change. In this study, each species differed in their response to treatment stress by root washing and varied in the degree of root damage indicated by the amount of root loss.

The duration of root washing also affected the amount of damage which was closely related to plant survival (Fig. 4.8). Longer washing times increased pittosporum mortality (Fig. 4.7) and reduced the growth of roots and shoots of all species plants (Tables 4.5; 4.8; 4.10; 4.12). The longest root washing treatment was the most damaging treatment. Thirty-eight percent of pittosporum plants did not survive in the longest duration, these plants lost about 18% of their total root mass (Fig. 4.6b; 4.8). The extent of root damage was linked to increased the root mortality and plant death.

The plant growth response to root washing was rapid, even as short as 3 seconds produced an effect on subsequent development. The recovery of normal growth by the plant occurred gradually over a period of time after treatment. Some plants, such as pittosporum, with higher degree of damage never recovered. Following repotting, root development of treated plants involved the death and decomposition of old or injurious roots and recovery which presented the regeneration of new roots. Abod and Webster (1989) demonstrated that a large proportion of the transplanted root system of apple (*Malus*) trees was lost through death and decomposition soon after transplanting. Mortality of roots increased significantly with time. The total length of the transplanted root system decreased at about 20% per 15 days in the first 45 days after planting. At 120 days after planting, only 25% of the original length remained. Any damage to the roots after lifting from the nursery and transplanting is likely to increase the root mortality (Insley and Buckley, 1985). Taking into account that only a small proportion of the root systems are lifted with trees when they are transplanted, further losses many prove fatal to newly-transplanted trees unless efforts are made to reduce root mortality and increase the rate of root regeneration (Watson and Himelick, 1982; Watson, 1987). Current techniques for establishing large scale tree plantations favour the use of bare-rooted stocks. Insley and Buckley (1985) have cautioned that the roots of bare-rooted planting stock must be well protected from desiccation to ensure successful establishment. Damage of roots by lifting from growing medium, besides reducing moisture uptake, reduced the proportion of stored root carbohydrate available, root regeneration and shoot growth.

Insley and Buckley (1985) demonstrated that loss of lateral roots during plant handling might account for 20-40% of the total root carbohydrate, with important differences occurring between species. However, there was usually sufficient carbohydrate to allow recovery and rapid growth of less severely pruned and desiccated *Fraxinus* and *Betula* seedlings. Root losses appeared to stimulate the production of new lateral roots, improving soil contact and allowing rapid uptake of water and nutrients.

The physiological processes influencing plant survival and growth at early and late planting times may also differ although there is an interaction between the root and shoot in their growth and function (Abod and Webster, 1989). The reduced root growth of root-washed plants could be due either to direct damage to the original root system or to the water stress which occurs after planting or some contribution of these factors. However, increased water stress after planting, especially in plants which subsequently died, suggests interference with water uptake is a major factor preventing the growth of new roots and leading to the death of long-time-washed plants. Reduced drought resistance following washing in plants may be caused by the plants losing more water relative to the absorbing capacity of the root system. Compared to unwashed controls, root loss from root tip in washed roots reduced more the absolute size of the root system. This is similar to results showing that root pruning increased stomatal resistance to water loss (Arnold and Struve, 1989). Reduced leaf water potential can be expected when a root system is pruned as reported in cotton (Stansell et al., 1974), holly (Randolph and Wiest, 1981), apple (Geisler and Ferree, 1984) and maize (Brevedan and Hodges, 1978). Abod et al. (1979) proposed that root pruning of pine induces water stress which causes reduced turgor and stomatal closure, thus leading to reduced CO_2 uptake and decreased transpiration.

Loss of leaf turgor due to water stress caused by root pruning is generally only temporary. In peas, wilting occurred immediately after root pruning, but plants quickly recovered (McDavid et al., 1973). Geisler and Ferree (1984) found the water potential recovered after one day, and although root pruned apple trees still had lower water potentials than untreated trees 7 and 10 days following pruning. However, water uptake recovered after 7 weeks in

Norway spruce (Parviainen, 1979, cited in Geisler and Ferree, 1984) and after 10 days in peach seedlings (Richards and Rowe, 1977). Future recovery in leaf water potential could have been induced by new roots enhancing water uptake and correlated with the regeneration of the root system. Abod and Webster (1989) found survival of late-planted *Malus* trees lost about 40% of their transplanted roots, and made almost no root growth in the first month after transplanting. This may be attributed to a functional imbalance between the water absorbing surface of the roots and the transpiring surface of the leaves.

Root pruning also reduced in net photosynthesis, transpiration and stomatal conductance, but all plants recovered after root regeneration (Arnold and Struve, 1989). Geisler and Ferree (1984) suggested that stomatal closure resulting in reduced CO_2 uptake probably caused the immediate decrease in net photosynthesis. Improved water uptake due to new root growth reversed this situation followed by the recovery of photosynthesis. Reduction in net photosynthesis appeared related to reduced in demand for assimilates and reduced translocation of assimilates from the leaves to the roots. As new roots developed, the proportion of photosynthates translocated to the root increased and was correlated with increased rate of photosynthesis. Plants re-established their root/shoot growth balance, with the development of new roots, water relations in the plant improve, and net photosynthesis and shoot growth rates increase.

5.2.3 Shoot and root regrowth (vegetative growth)

Both root and shoot growth were inhibited by prolonged root washing, but did not influence the balance of root and shoot growth as treatment stress did not affect root:shoot ratio. Each species had a different reduction rates on root and shoot growth in root washing experiment. Pittosporum was more sensitive to stress after washing treatment. Shoot and root growth ceased, even after very short initial washing, such as three seconds (Fig. 4.11, 4.12, 4.13). As a result, inhibition of shoot extension growth could occur simultaneously with the lowest root rate of root extension. This growth pattern was consistent with the concept of a functional relationship with inherent in competition between roots and shoots for available assimilates, with developing shoots being the stronger sink, and in the inhibition of root growth by auxin produced during periods of shoot extension (Milligan and Dale, 1988).

The relationship between the shoot and the root is a complex homeostatic balance in which root:shoot ratio (Watts et al., 1981), this is optimised so that size and activity of both sub-systems are maintained at values most appropriate to external conditions (Richards, 1980). When a change in the environment occurs, the rate of growth of one sub-systems changes relative to that of the other so that the functional equilibrium is maintained. Conversely, if the environment is kept constant but the root:shoot ratio is altered experimentally differential growth rates can be established which lead to a return to the original ratio over a periods of a few days (Spek and Oijen, 1989). Johnson et al. (1987) has suggested that the basis of such control lies in the maintenance of a constant carbon-nitrogen ratio so that as nitrogen availability from the soil increases, leaf expansion is promoted and carbon fixation increases, root growth is promoted leading to enhanced nitrogen uptake.

A nutritional correlation between periods of root and shoot growth was proposed by Mertens and Wright (1978) where N absorbed by plant roots tends to react first with carbohydrates in the root. As the root system develops to the extent that it can absorb higher levels of fertiliser, nutrients in excess of what is needed for root growth are translocated to the shoots where they are used in conjunction with carbohydrates there for protein synthesis and shoot growth. Consequently, less carbohydrate is available for translocation to the roots, and root growth is then limited relative to the shoot growth. Since root growth, and hence nutrient absorption, is at a low level, new shoot growth eventually depletes the nutrient level within the plant, and growth of the plant top ceases. Carbohydrates become available again for translocation to the root, root growth and nutrient absorption begin again, and the cycle repeats itself. Gilliam and Wright (1978) have shown that in 'Helleri' holly tissue N concentration of the plant top is at its highest level when shoot growth begins and at its lowest level when shoot growth ceases. Although no plant nutritional data were collected in this root washing experiment, a correlation between periods of root and shoot growth and nutritional status may be worthy of further investigation and could also explain why there was a 1 - 2 month period in which little or no shoot growth occurred in root-washed plants.

Root loss from the roots in the root washing experiment reduced the absolute size of the root system and the number of root tips. Root tips are sites of synthesis of gibberellin-like and cytokinin-like hormones (Buttrose and Mullins, 1968; Crozier and Reid 1971; Richards and Rowe, 1977; Richards et al., 1979; Beck and Wagner, 1994). As a group, gibberellins are involved in several responses frequently touted as evidence of cytokinin involvement. Exogenous gibberellins applied to promote leaf expansion in bean (Brock and Cleland, 1990) and apple leaves (Steffens et al., 1985). In contrast, Thuantavee (1991) reported increases in only stem length and dry biomass accumulation in tomato plants with foliage or roots treated with Gibberellin acid (GA_3). It is possible that gibberellins act in concert with cytokinins in leaf growth; applying both gibberellin and cytokinin to root-restricted bean plants was necessary to restore the growth of leaves and stems (Carmi and Heuer, 1981). These reports indicated shoot tissues are also significant producers of gibberellins (MacMillan, 1987) to the extent that shoots may be self-sufficient in their production makes the idea of root-sourced gibberellins playing a major role in root-shoot communication considerably less tenable than that postulated for other hormones (Brock and Cleland, 1990; Carmi and Heuer, 1981; Kuiper et al., 1989; Thuantavee, 1991).

Short and Torrey (1972) suggested that high cytokinins concentrations inhibit lateral root formation. Stenlid (1982) also suggested that the cytokinin should be considered as a possible natural inhibitor and regulator of root growth. Cytokinins have been implicated in control of shoot growth through their involvement in regulation of cell division and elongation, leaf protein metabolism and axillary shoot growth (Skene, 1975; Stenlid, 1982). Roots are also linked with primitive effects on shoot growth. Reduction of cytokinin supply to the shoot after root removal or reduction in root size has been linked with shoot stunting (Buttrose and Mullins, 1968; Richards and Rowe, 1977; Richards et al., 1979; Skene, 1975). In *Prunus persica*, reduced shoot growth followed root restriction or pruning and was a function of lowered root tip number (Richards and Rowe, 1977; Richards et al., 1979). Cytokinin application to leaves overcame this reduction (Richards and Rowe, 1977; Richards et al., 1979; Richards, 1980). In the current study, the reduction in root tips preceded shoot and root growth. Perhaps the activity of root-produced factors, such as a critical level of growth substance, is regulated by the number of root tips. This could be responsible for maintenance of balanced root and shoot growth, which is perturbed by root restriction (or root washing). Under condition where nutrients, oxygen, and water uptake and transport are not limiting, restricting root growth results in a balanced reduction in root and shoot growth. Shoot:root ratios are similar, irrespective of the level of root loss or root damage.

5.2.4 Reproductive growth

Root washing treatment reduced flower development in pumpkin. Washed plants developed fewer flowers than did unwashed plants, the longer the washing duration, the fewer the flowers (Fig. 4.21). However, there were no differences in numbers of floral bud, but rather in the number of flowers that matured. Akers and Mitchell (1984) reported a similar result that shaking delayed anthesis on pea (*Pisum sativum* L. cv. Alaska), but no influence on the number of fruits set. Latimer et al. (1991) found long-term brushing reduced cucumber yield reduction, but had no effects on fruit weight, dimensions, or quality. Brushing potted soybean during various periods of vegetative and reproductive development did not affect seed yield (Latimer et al., 1986; Umezaki and Mataumoto, 1990, cited in Latimer, 1991b). Brushing affected broccoli transplant growth but not yield (Latimer, 1990). Buitelaar (1989) reported that twice-daily shaking of tomato plants during fruit production in the greenhouse reduced yields 18%, but shaking on alternate days did not affect yield. The current study did not provide any evidence of root washing effects on fruit number as the pumpkin plants were not grown to maturity. There was no difference on the number of flower buds between different washing times when pumpkin plants were harvested 40 days after repotting (Table 4.10). It may show that the washed plants had fully recovered and no further difference on fruit set and production would be expected.

The changes in reproductive growth caused by root washing could have resulted indirectly from altered rates of vegetative growth or from altered partitioning of assimilates (Akers and Mitchell, 1984). Injurious and non-injurious mechanical stress altered hormone levels in shoot and root tips (Beyl and Mitchell, 1983; Richards and Rowe, 1977; Skene, 1975; Stenlid, 1982). Root damage may influence the initiation or development of flowers, or shoots and would have the potential to limit crop yield.

Root washing had no effect on reproductive growth of camellia, which differed from pumpkin plant. Although root washing tended to reduce vegetative growth, the number of floral buds on washed camellia plants were similar to those than on unwashed plants. The treatment stress did not influence initiation and development of flowers. Due to the longevity and growth cycle of most woody plants, the influence on their reproductive growth is more complex than on the reproductive growth of herbaceous plants. The effects of treatment stress of woody plant on reproductive growth are less well characterised than those on vegetative growth. The floral buds could has been initiated before the washing treatment was applied. The repressive effects on vegetative growth may only influence the reproductive growth in following season or year. Hence, long-term studies, such as a full growth cycle, would be required to determine the contribution of root washing action to limitation of reproductive growth.

Chapter six: Conclusions

This study has examined the morphological and physiological aspects of plant response to root disturbance by shaking and root washing. The response to shaking or root washing is immediate, but the recovery of normal growth by the plant occurs gradually over a period after treatment. Growth readjustments of this kind are relatively slow. Thus it seems that treatment stress is a very real phenomenon in plants, which affects many aspects of their growth and development. Treatments applied to roots affect their capacity for water and nutrition uptake, water stress; shoot-root nutritional correlation has been invoked as being responsible for such effects. It is important to note that the nature and extent of the response depend on the species or variety, as well as the physiological and hormonal mechanism operating in the plant when it is stressed by root damage or root loss.

The results of this study indicated the shoot-root regrowth capacity related to the relative degree of root damage, but there was a general lack of explanations of physiological mechanism, for example root washing caused reduction of both root and shoot growth via water stress or that reduced photosynthetic rates resulted in lower total plant biomass. Furthermore, there is strong circumstantial evidence of a negative growth involved cytokinins or other hormones as corespondents that influence shoot growth in response to root restriction.

The present study demonstrated that root washing as technique may be of value for nursery bare-root production or in the export across trade barriers of plants free of growing medium. Although the reduction in growth induced by root washing occurred, they might be negligible or temporary, in species or variety which have a high root regeneration potential or high capacity of regrowth under non-injurious and injurious root restriction. This should not be a serious problem. For example, both shoot and root extension growth or dry biomass were reduced by root washing in pittosporum plants. Root washing only inhibited shoot growth of coleus plants, but not root growth. Pumpkin reproductive growth declined after root washing treatment. However, the washing treatments had no effect on camellia reproductive growth during the four month experimental period.

The growth reductions are likely related to the changed moisture status of the plant due to shaking or washing the root system. Delayed reduction in shoot growth of two woody species plants may be attributed to a changed allocation of photosynthate to the root and to hormone imbalances. Therefore, further research is required to assess how root washing influences in long-term vegetative growth and development of two woody species, camellia and pittosporum, as well as reproductive growth in camellia.

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