Genetic Control of Propagation Effects and the Importance of Stock Plant Age and Source on Early Growth in Cuttings of *Pinus radiata*

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Abstract

The genetic control of propagation effects and the impact of stock-plant age and source was examined in 9 month-old *Pinus radiata* cuttings. The cuttings investigated were propagated from stock-plants aged between 2 and 5 years, and microcuttings propagated from 12 week old stock-plants. The design included 20 families, with seven clones per family and an average of seven ramets per clone. Five traits: height, root score, root-shoot ratio, root weight and shoot weight, were measured at nine months after planting (setting). Early growth in cuttings was found to be affected by genotype and stock-plant age and an interaction between these two effects. Cutting performance was found to decline with increasing stock-plant age, with the cuttings taken from 2 year old stock-plants showing superior growth for all traits. Cuttings harvested from stock-plants raised as seedlings showed superior growth compared to cuttings propagated from stock-plants raised as harvested seedling stock plants (seedling stock plants previously harvested for microcuttings) and stock-plants raised as microcuttings. Seedlings displayed superior growth compared to microcuttings. Heritabilities were moderate for height and root-shoot ratio, and low for root and shoot weight and root score. The ranking of families was found to vary with increasing stock plant age. It is recommended that selection and deployment of genetic material is made using cuttings from the same stock-plant ages to ensure that family or clonal ranking is not adversely affected.

Key words: cuttings, stock-plant age, heritabilities, *Pinus radiata.*

Introduction

Forest managers have been using cuttings of *Pinus radiata* in their plantations for well over a decade in Australia. In 1999 approximately 9.7 million cuttings were deployed by 10 forestry companies in Australia. The advantages of deploying cuttings rather than seedlings include increased growth rates and improved form, additional genetic gain from selection, improved uniformity of crop, and faster multiplication of genetically improved material (SWEET and WELLS, 1974).

The success of a plantation deployment system utilising cuttings is influenced by the minimisation of non-genetic variation caused by C-effects and c-effects (FOSTER *et al.,* 1984). C-effects are the non-genetic effects that are common to members of a group of relatives such as a family or clone (LERNER, 1958), while c-effects are related to the individual propagule or ramet (LIBBY and JUND, 1962). These effects have environmental causes. For example, stock plants may be growing in different environments, or are in different stages of maturation, so that the cuttings taken from them are in different maturational or developmental states (CANNELL *et al.,* 1988). C-effects are problematic as they may contribute to the differences between groups of relatives and thus inflate the total genetic variance and other genetic parameters such as heritabilities, correlations among traits and genetic gains (FRAMPTON and FOSTER, 1993). Overestimation of genetic variance is more common in traits measured shortly after propagation (LIBBY and JUND, 1962). Furthermore, c-effects may contribute to the differences among propagules within a group of relatives and inflate the variance among propagules within a group of relatives (BURDON *et al.*, 1992).

The effect of maturation and physiological age on cutting performance has been studied with considerable interest for *P. radiata.* As the age of the stock plant increases the rooting of cuttings becomes more difficult and unreliable, from 93% survival in cuttings propagated from 1 year-old stock plants to 8% in cuttings from 17 year-old stock plants (BROWN, 1974). Early height and diameter growth in cuttings is also reduced (SWEET, 1973; SWEET and WELLS, 1974; MENZIES and KLOMP, 1988), a consequence of a less vigorous root system on cuttings from older stock plants (GREENWOOD, 1993). However, stem and branch form improve (FIELDING, 1970; SWEET, 1973; TUFUOR and LIBBY, 1973; THULIN and FAULDS, 1973; MENZIES *et al.,* 1988).

Shearing the stock plants to form low hedges has been found to reduce the speed of maturation and prolong juvenile characteristics in the stock plants (LIBBY *et al.,* 1972) and therefore the cuttings propagated from these stock plants also retain juvenile characteristics (FRAMPTON and FOSTER, 1993). However, some forestry companies are establishing their stool beds with microcuttings (small cuttings) rather than seedlings as it enables mass propagation of small quantities of elite control pollinated seed. A serial propagation program using microcuttings involves raising seedlings from control pollinated seeds in the glasshouse and harvesting each seedling for microcuttings when they reach 15 cm height (approximately 12 weeks of age). The microcuttings taken are 5 cm long with a basal diameter of 1.5 mm to 2 mm, and are grown in the glasshouse for 12 weeks before hardening off and planting out in stool bed nurseries (Australian Paper Plantations, 1999). The cuttings taken from these microcutting stock plants are known as secondary cuttings. It is not known how the history of the stock plant (i.e. whether it is raised as a seedling or microcutting) affects the growth of the cuttings taken from them.

The level of genetic control of growth and rooting traits in cuttings, and the interaction between genotype and stock plant age, is also not well known for *P. radiata.* Significant interactions between genotype and stock plant age could cause variation in family or clonal rankings. For example, a family or clone with cuttings taken from stock plants aged 1 year may display superior growth compared to others, but when the same family or clone is propagated from older stock plants its growth may be less than average. This has important implica-

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tions for breeding programs if selection and deployment is made with propagules from different stock plant ages.

This study was designed to examine early growth in cuttings of *P. radiata* taken from stock plants up to 5 years of age. The study was conducted in two stages with the aim to follow closely the techniques currently employed operationally by some forestry companies.

The first experiment (a nursery experiment) investigated cuttings taken from hedged stock plants aged between 2 and 5 years. The aims of this experiment were to examine the levels of genetic control of early growth in cuttings, identify any trends in cutting growth with increasing stock plant age, and determine the effect of stock plant history on cutting growth.

The second experiment, a glasshouse experiment, compared the growth of seedlings and microcuttings raised in the glasshouse.

Materials and Methods

Plant Material

Nursery experiment

The cuttings used in the nursery experiment were harvested from hedged stock plants aged 2 to 5 years. Stock plants aged 3 to 5 years were all propagated as seedlings. The 2 year-old stock plants were propagated either as: seedlings; seedlings which have been previously harvested for microcuttings prior to planting out in the stool beds (harvested seedlings); or the microcuttings themselves.

Each cutting harvested from these hedged stock plants was approximately 13 cm in length with a basal diameter of 4 mm to 6 mm. The cuttings were immediately inserted (or 'set') in alluvial soil at Australian Paper Plantation's Richmond Nursery, Cowwarr, Victoria (Australia). The cuttings were raised under mist irrigation, with initially 1 to 3 minutes of mist, 8 times a day, and then reducing the time after roots have been adequately developed (approximately four months). Herbicide (e.g. *Agraprop* at 1 kg/ha plus *Dacthal* at 10 kg/ha) was applied approximately every 8 weeks to prevent weed competition. Fungicide (*Ridomil 50 G* at 10 kg/ha) was applied approximately 8 weeks after setting the cuttings to control *Phytopthora* and *Pithium* species. The cuttings were also inoculated with macerated fruiting bodies of *Rhizopogon luteolus* at 0.7 kg/ha approximately three weeks after fungicide application. The experiment was conducted in July 1996.

Glasshouse experiment

Seedlings and seedling stock plants for the glasshouse experiment were raised in grow tubes (volume approximately 225 ml) in potting mix comprising 40% copra peat (composted pine bark and coir fibre), 20% coarse sand, 20% perlite, 20% vermiculite, with slow release fertiliser (*Osmocote Plus* at 4 g/L) and soil wetting agent (*Saturaid* at 1 g/L).

Stock plants were harvested when they reached 15 cm height (approximately 12 weeks of age). The cuttings harvested were 5 cm in length with a basal diameter of 1.5 mm to 2 mm. Each was dipped in a rooting hormone powder (8% IBA) prior to insertion in the potting mix described above.

Seedlings, stock plants and microcuttings were raised on heated beds at a constant 20°C, under mist, and maintained with fortnightly applications of fertiliser (*Aquasol* at 1 g/l), fungicide every three weeks (alternating between *Bravo* at 1 g/l, *Ridomil MZ WP* at 1 g/l, *Fongarid at* 1.3 g/l and *Previcur* at 10 ml/l), and innoculated with macerated fruiting bodies of *Rhizopogon luteolus* at 0.6 g/l two days after every second application of fungicide.

Table 1. – Treatment combinations for the nursery and glasshouse experiments.

Family	Glasshouse Experiment		Nursery Experiment					
	Seedling	Micro-cutting	Stock plant age (years) for cuttings					
			2			3	4	5
			S[1]	HS[2]	M[3]			
A	✓	✓	✓					✓
B				✓	✓	✓		✓
C							✓	✓
D	✓	✓	✓	✓	✓			✓
E						✓		✓
F	✓	✓	✓					✓
G				✓	✓	✓		✓
H				✓	✓	✓		
I				✓	✓	✓		✓
J				✓	✓	✓		✓
K	✓	✓	✓	✓	✓		✓	✓
L							✓	✓
M							✓	✓
N	✓	✓	✓	✓	✓			✓
O	✓	✓	✓					✓
P	✓	✓	✓				✓	✓
Q	✓	✓	✓	✓	✓		✓	✓
R	✓	✓	✓					✓
S	✓	✓	✓	✓	✓		✓	✓
T							✓	✓

[1]) seedling stock plants.
[2]) harvested seedling stock plants, ie seedlings which have been previously harvested for microcuttings prior to establishment in stool beds.
[3]) microcutting stock plants.

Design

The treatment combinations for both experiments are outlined in *table 1.* Twenty full-sib families were represented in the nursery experiment and ten full-sib families in the glasshouse experiment. Each family treatment was replicated across seven blocks, with each block representing a different clone, or seedling (glasshouse experiment), from a given family. Where possible, ten cuttings (ramets) were represented for each clone and, in addition, seven seedlings were raised for each family. For some treatment combinations 10 cuttings were not available for harvest, and therefore the average number of cuttings represented for each clone treatment combination was seven.

Measurements

All cuttings and seedlings were assessed at nine months after setting/sowing. The following attributes were measured:

- total height growth (for cuttings only);
- root score – based on the number of quadrants the root system occupies, where 1 refers to one quadrant being occupied and four is all quadrants being occupied;
- oven dry root weight;
- oven dry shoot weight;
- root-shoot ratio (oven dry weight).

Statistical Analysis

Data was analysed using ASReml, which estimates variance components under a general mixed model by restricted maximum likelihood (GILMOUR *et al.,* 1999). The variance components and heritabilities for the nursery trial were estimated using the following model:

$$y_{ij} = \mu + B_j + a_i + m_k + a.m_{ik} + e_{ijkl}$$

where y represents an individual tree observation (height, root score, root weight, shoot weight or root-shoot ratio); μ is the overall mean for the trait; B_j is the fixed effect of the jth block; a_i is the additive genetic effect of the ith clone; m_k is the effect of kth stock plant age (maturation state); $a.m_{ik}$ is the genotype-age interaction, and e_{ijkl} is the unexplained residual of the lth ramet in the ith clone at the kth stock plant age in the jth block.

Individual heritabilities of cuttings were calculated as:

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_M^2 + \sigma_{A.M}^2 + \sigma_E^2}$$

where σ^2_A is the variance for genetic effects, σ^2_M is the variance for stock plant age effects, $\sigma^2_{A.M}$ is the variance for the interaction between genetic and stock plant age effects, and σ^2_E is the residual variance. No specific combining ability effects were considered because separation of additive and dominance genetic effects was difficult as only a few parents were in common between families.

Means and standard errors were obtained from the ASReml analysis. Differences between means were tested using the SAS GLM procedure with the Tukeys standardised range test option (SAS Institute Inc., 1989). The difference between means for seedlings and microcuttings, and stock plant sources, was tested using the following model:

$$y_{il} = \mu + B_j + f_i + t_k + e_{ijkl}$$

where y represents an individual observation (total height, root score, etc); μ is the overall mean for the trait; B_j is the effect of the jth block; f_i is the effect of the ith family; t_k is the effect of the kth propagule type, or kth stock plant source; and e_{ijkl} is the unexplained residual of the lth ramet in the ith clone from the kth type/source in the jth block.

The effect of stock plant age and the interaction between family and stock plant age for each trait was tested using the following model:

$$y_{il} = \mu + B_j + f_i + m_k + f.m_{ik} + e_{ijkl}$$

where m_k is the effect of the kth age (maturation state) and $f.m_{ik}$ is the effect of the interaction between the ith family and kth age.

Results

Comparison of Means for Each Propagation Type

Seedlings versus microcuttings (Glasshouse experiment)

A comparison of seedling and microcutting means for each trait is presented in *figure 1.* Compared to cuttings, seedlings had a greater root score (38%), a greater root-shoot ratio (16%), greater root weight (34%) and a greater shoot weight (28%). All differences were significant at the 0.05 level.

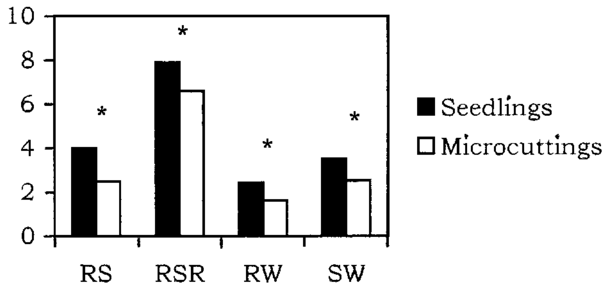

Figure 1. – Means of seedlings and microcuttings for each trait. RS = root score (1 to 4), RSR = root-shoot ratio (x10), RW = root weight (g), SW = shoot weight (g). *denotes a statistically significant difference between means (p = 0.05).

Cuttings from stock plants aged 2 to 5 years (nursery experiment)

The unit change in each trait as the age of the stock plant increases by one year is presented in *table 2.* The trend was a general decline in growth of all traits as the stock plant age increased by one year, with total height decreasing by 1.36 cm, root score decreasing by 0.10 units, root weight decreasing by 0.16 g, shoot weight decreasing by 0.34 g, and root-shoot ratio decreasing by 0.01 units. This effect of stock plant age was found to be highly significant for all traits (p>0.001).

The Effect of Stock Plant History on Cutting Performance

The trait means for cuttings derived from the three different two-year-old stock plant sources (seedlings, harvested seedlings, and microcuttings) and raised in the nursery are presented in *figure 2.* The effect of stock plant source was found to be important for all traits. Stock plants derived from seedlings were found to produce significantly taller cuttings with higher root scores and greater shoot weights than the stock plants derived from harvested seedlings and microcuttings. The root weights of cuttings propagated from seedling and harvested seedling stock plants were both significantly larger than root weights of cuttings propagated from microcutting stock plants.

Table 2. – The effect of stock plant age and the interaction between stock plant age and family on cutting growth for each trait.

Trait	Stock plant age effect			Stock plant age x family interaction
	mean	Slope[1]	Significance (P)	Significance (P)
Total height (cm)	30.02	-1.36	0.0001	0.0001
Root score (1-4)	2.49	-0.10	0.0001	0.0001
Root weight (g)	2.10	-0.16	0.0001	0.0001
Shoot weight (g)	6.03	-0.34	0.0001	0.0001
Root-shoot ratio	0.34	-0.01	0.001	0.0001

[1]) represents the unit change in each trait as the age of the stock plant increases by one year.

Table 2. – Variances and heritabilities of cuttings from stock plants aged 2 to 5 years. σ^2_A is the additive genetic variance; σ^2_M is the variance of stock plant age; $\sigma^2_{A.M}$ is the variance of the interaction between genotype and stock plant age; σ^2_E is the residual variance; h^2 is individual heritability. Standard errors are shown in parentheses.

Trait	σ^2_A	σ^2_M	σ^2_{AM}	σ^2_E	h^2
Height	16.83 (5.74)	5.35 (5.25)	7.71 (4.73)	32.63 (1.14)	0.27 (0.09)
Root Score	0.045 (0.040)	0.033 (0.034)	0.066 (0.038)	0.649 (0.022)	0.06 (0.05)
Root Weight	0.184 (0.098)	0.039 (0.046)	0.135 (0.083)	1.090 (0.038)	0.13 (0.07)
Shoot Weight	0.719 (0.636)	0.384 (0.412)	1.062 (0.580)	4.458 (0.155)	0.11 (0.09)
Root-shoot Ratio	0.641 (0.142)	0.007 (0.021)	0.091 (0.089)	1.276 (0.044)	0.32 (0.06)

For root-shoot ratio, there was no significant difference between cuttings propagated from seedling and harvested seedling, and also no difference between cuttings propagated from seedling and microcutting stock plants, but there was a significant difference between harvested seedling and microcutting stock plants. The performance of cuttings derived from harvested seedlings and microcuttings were not significantly different from each other for height, root score and shoot weight.

Genetic Control of Propagation Effects

The variances and individual heritabilities of cuttings from stock plants aged 2 to 5 years are presented in *table 2.* Comparisons were made between cuttings taken from seedling stock plants only. Variances were apportioned between additive genetic effects, stock plant age effects, effects of the interaction between genotype and stock plant age, and residual effects. The individual heritabilities for each trait were variable. Moderate heritabilities were found for height (0.27) and root-shoot ratio (0.32). Low heritability was found for root score (0.05). Root weight and shoot weight had intermediate heritabilities of 0.13 and 0.11 respectively.

The effect of stock plant age was not as large as genetic effects, accounting for 9% of the total variation for total height, 4% for root score, 3% for root weight; 6% for shoot weight and 1% for root-shoot ratio. The interaction between genotype and stock plant age was found to be larger than the effect of age alone for all traits. This interaction was also larger than the effect of genotype alone for root score (8% of the total variation for the genotype-age interaction compared to 6% for genotype) and shoot weight (16% of the total variation for the genotype-age interaction compared to 11% for genotype).

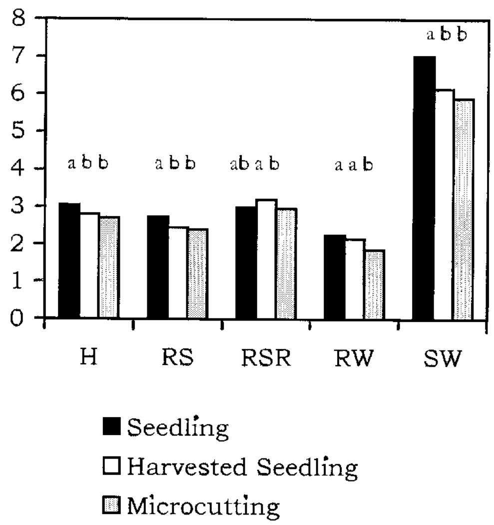

Figure 2. – Trait means for 9-month-old cuttings derived from different types of stock plants: seedlings; seedlings which have been previously harvested for microcuttings (harvested seedlings); and microcuttings. H = total height (cm^{-1}), RS = root score (1 to 4), RSR = root-shoot ratio (x10), RW = root weight (g), SW = shoot weight (g). Different letters denote a significant difference between means (p=0.05).

The interaction between stock plant age and family was found to be significant for all traits studied ($p = 0.0001$) (*Table 2*). This interaction is illustrated in *figure 3* for shoot weight with four families which were propagated from seedling stock plants aged 2, 4 and 5 years. The ranking of families was variable. Family S had the largest shoot weight in cuttings propagated from 2 year-old plants, but was not different to the other families for cuttings propagated from 5 year-old plants. Family P was the lowest ranking family in cuttings propagated from 2 year-old plants and 4 year-old plants, but was equally ranked with the other three families in cuttings propagated from 5 year-old plants.

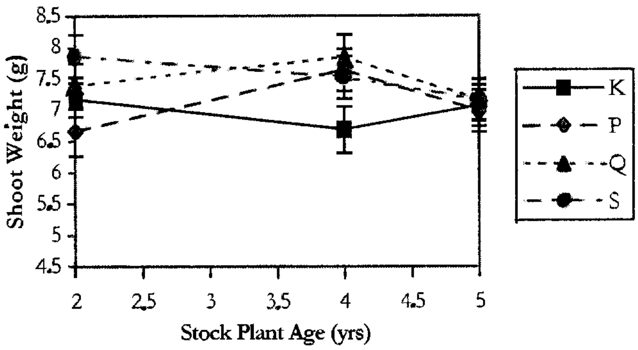

Figure 3. – The interaction between shoot weight and stock plant age for four families propagated from seedling stock plants.

Discussion

Propagation Effects

Stock plant age was found to have a significant effect on the early growth and rooting characteristics in cuttings of *P. radiata*. There was a decline in cutting performance with increasing stock plant age. Thus the cuttings propagated from the 2 and 3 year-old stock plants were generally superior to those propagated from the 4 and 5 year-old stock plants. This trend is consistent with studies by FIELDING (1970), THULIN and FAULDS (1968), SWEET (1973). Even though the stock plants used in this study were hedged, a procedure which has been found to delay maturation (LIBBY *et al.,* 1972), significant differences between the cuttings taken from increasing aged material were still apparent. The differences are possibly less dramatic than those between unhedged stock plants of the same ages undergoing a normal ageing process.

Seedlings raised in the glasshouse displayed superior growth compared to microcuttings for all four traits measured at 9 months of age. The main factors causing a difference in performance between the two propagule types are the smaller root mass and distribution of roots in the microcuttings. This may reflect a lag time in root production for the microcuttings.

Stock plant history also showed a significant impact on the early growth of cuttings raised in the nursery. The cuttings propagated from seedling stock plants displayed consistently superior growth compared to the cuttings propagated from harvested seedling stock plants and cuttings harvested from microcutting stock plants at 9 months of age.

Interpretation of Variances

The individual heritabilities for the 9 month-old *P. radiata* cuttings were found to be moderate for height and root-shoot ratio and low for the other traits, especially for root score, indicating moderate to low genetic control of these traits. Cutting performance in this study was influenced by genetic and stock plant age effects, with significant variation attributable to the interaction between genotype and stock plant age: family rank was found to vary with increasing stock plant ages. This has important implications for breeding programs if selection and deployment is made with propagules taken from different stock plant ages.

The variation due to stock plant age represents the so called c-effects, that is, the non-genetic effects that increase the differences between individual propagules (cuttings), and the interaction between genotype and stock plant age represent C-effects, that is, the non-genetic effects that affect the differences between groups of relatives such as families or clones. These effects can have significant impacts on estimates of individual heritability (h^2), clonal heritability (H^2), family or clonal means, genetic correlations between traits and estimates of genetic gain depending on the type of plant material being compared. For example, we may be interested in comparing a group of relatives (family or clone) which is represented by vegetative propagules derived from 5 year old stock plants, with another group of relatives which is represented by vegetative propagules derived from 1 year old stock plants. If the variance for stock-plant age or the interaction between genotype and stock plant age is large, the magnitude of the difference between their means will be affected. In addition, the genetic effects will be confounded by stock plant age effects, and therefore the estimates of heritability (individual or clonal), correlations between traits, and genetic gain will all be inflated.

Alternatively, we may be comparing groups of relatives which are represented by vegetative propagules derived from stock plants of mixed ages ranging from 1 to 5 years. In this case, the variation between individual propagules will be large, and therefore the mean for each group is unlikely to be affected but the error of estimates will be larger, because the larger within-group-error.

The results of this study indicate that the effect of the interaction between genotype and age is much larger than age effects alone in all traits studied, and larger than genetic effects for root score and shoot weight. Therefore it is important to ensure that families or clones are compared using cuttings of the same age or similar position on the plant. For example, one group of relatives may display faster growth than another group when represented by cuttings propagated from 1 year old stock plants, but slower growth when represented by cuttings propagated from 3 year old stock plants, and equal growth when represented by cuttings propagated 5 year old stock plants.

If selections are made based on the performance of cuttings taken from 4 year old stock plants, and deployment of cuttings from stock plants aged only 2 years is undertaken, then family and clonal rankings may be quite different.

Recommendations

It is recommended that selection and deployment of genetic material is made using cuttings from the same stock plant ages to ensure that family or clonal ranking is not adversely affected. If these trends are expected to have an impact on later performance, or if selection is carried out at young ages, the results suggest that age of stock plants can affect the efficiency of breeding programs.

It is also recommended that cuttings are propagated from stock plants less than 4 years-of-age to achieve higher growth rates and superior rooting characteristics.

The results of this study are an indication of the growth of cuttings at only 9 months of age. Further investigation into the trends after a longer period of growth is essential to determine how long these effects persist.

Conclusions

Early growth in cuttings was found to be influenced by genotype and stock plant age, the interaction between these two effects, and stock plant source:

- Cutting growth was found to decline with increasing stock plant age (between 2 to 5 years);
- Cuttings taken from stock plants raised as seedlings displayed superior growth compared to the cuttings taken from seedling mother plants and microcutting stock plants;
- Early growth in seedlings was superior to microcuttings;
- The levels of genetic control in cuttings was moderate for height and root-shoot ratio, and low for root weight, shoot weight and very low for root score;
- There was a significant interaction between genotype and stock plant age causing variation in family ranking with increasing stock plant age.

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