The Influence of Rootstock Family and Scion Genotype on Graft Incompatibility in Araucaria cunninghammii Ait. ex D. Don

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Summary

On the basis of compatibility patterns on a range of full-sib rootstock families, the scion clones involved in this study can be separated into "compatible", "early incompatible" and "delayed incompatible" classes.

The evidence gathered offers some support for the hypothesis that there is a factor which must be either present in both scion and rootstock, or absent in both scion and rootstock, to confer compatibility. The "early incompatibility factor" appears to be common to clones of this group, with little evidence available for relatedness conferring compatibility additional to that for a scion class × rootstock family group.

The experimental data suggest that the early and delayed forms of compatibility are controlled by different factors and different genes.

Potential practical approaches to the problem, and areas for further research, are discussed.

Key words: Araucaria cunninghamii, graft, incompatibility, scion, rootstock.

Introduction

Araucaria cunninghamii (hoop pine) is an important plantation conifer in Queensland, and potentially also in other tropical areas (Nikles, 1980). The species has been the subject of an active breeding program (Nikles and Newton, 1983) for approximately 35 years. All planting stock now used is raised from seed collected in clonal seed orchards. Graft incompatibility has long been recognised as a problem, but recently has been of particular concern in relation to the development of biclonal orchards for the mass production of superior full-sib families (Haines and Nikles, 1987a; Haines and Nikles, 1987b). Clones whose representation in such orchards is highly desirable include the outstanding parent "HG", which cannot be included because of a known high incidence of delayed incompatibility. Recent second generation selections among HG progeny also warrant inclusion, but there are concerns that these may display a high incidence of incompatibility also.

A recent study (Haines and Dieters, 1990) provided some justification for separation of incompatibility into distinct "early" and "delayed" forms on the basis of the extent of scion elongation prior to the appearance of symptoms, although no sharp chronological distinction is apparent. It was hypothesized that early and delayed incompatibility may involve different genes. The distribution within the plus tree population of each of these forms of incompatibility is distinctly bimodal — clones tend to be either highly compatible or highly incompatible. Approximately 8% of clones are severely affected by early incompatibility, while a smaller proportion is severely affected by delayed incompatibility. For early incompatibility at least, the distribution of the incidence within the population is consistent with the hypothesis that compatibility is dependent on the presence of a particular factor (or the absence of the factor) in both rootstock and scion. The possibilities of a very simple genetic control mechanism or of a threshold effect were raised. However, significant differences among clones within the compatibility status groups suggested that other factors probably are involved.

This article is aimed at a review of graft incompatibility in hoop pine in the light of scion clone × rootstock family interactions.

Materials and Methods

The data reported here come from two experiments established in hoop pine plantation areas located at latitudes 26°27'S and 26°33'S in Southern Queensland. Rootstocks representing a number of full-sib families were planted respectively in 1969 and 1970, and field grafting of orthotropic scions, using a variation of the chip-budding method (Nikles, 1961), was carried out in 1973 and 1974. Regrafting was undertaken where an initial "take" was not achieved.

Although of similar design, the experiments differed in the number and identity of scion clones and rootstock families represented. Within limits imposed by the availability of seed, the scion clones and rootstock families represented were chosen to include a range with respect to clonal compatibility status. Details of the scion clones and rootstock families represented, together with compatibility status assigned on the basis of performance in clone banks and orchards (where known), are presented in *Figures 1 to 4*.

Each experiment comprised three blocks with three (occasionally four) ramets of each scion clone × rootstock family combination per block. Each scion clone × rootstock family combination was thus represented by a total of nine to ten ramets. In each block, rootstock families were established as row plots, within which scion clones were allocated at random to stock plants. Each experiment was made up of over 700 grafts in total.

Height measurements and visual health assessments, were conducted at intervals of one to three years unitil 14 years after grafting. Incompatibility was diagnosed on the basis of health assessments, and the extent of scion elongation prior to the manifestation of incompatibility symptoms used to distinguish the early and delayed forms — 67 cm being the demarcation point employed (Haines and Dieters, 1990).

Early compatibility of each stock/scion combination was calculated as the number of early compatible ramets expressed as a percentage of the number of takes. Overall compatibility was calculated as the final number of com-

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patible ramets expressed as a percentage of the number of takes.

Results

Early and overall compatibility levels for the scion clone — rootstock combinations of Experiment 1 are presented in *Figures 1* and *2* respectively. The corresponding data for Experiment 2 are presented in *Figures 3* and *4*[2]). On the basis of broad patterns of compatibility with rootstock families, scion clones in Experiments 1 and 2 can be arranged in the groups described in *Tables 1* and *2* respectively. Within these groups, however, are some differences among clones, in particular:

- H73 is highly compatible on H73 x H6, while the other three clones of the group display quite low levels of compatibility on this family. H73 is possibly also more compatible than the others on H60 x H62 and on H73 x H67 (Experiment 1).
- H59 is less compatible than the other three clones of the group on HJ x H15 (Experiment 1).
- HJ is less compatible than the other clones of its group on H6 x H28 (Experiment 2).

The patterns of responses on rootstock families are consistent with the following broad classification of scion clones[3]) in these experiments, within-class variation (par-

Root Stock Family	Comp.* of Parent	SCION CLONE H6 (C)*	HJ (C)	H73 (C)	H59 (E)	H23 (E)	H45 (E)	I105 (D)	Mean
HJ x HJ	C x C	89	78	89	100	34	12	100	71
HJ x H15	C x C	100	100	100	56	0	0	100	65
X16 x X15	C x C	90	100	100	90	0	0	89	67
H73 x H6	C x C	40	78	100	89	0	0	90	57
H73 x H67	C x C	56	56	78	56	0	0	78	46
H60 x H62	C x C	67	90	100	89	22	22	90	68
H42 x H45	C x E	100	100	78	67	100	89	78	87
H45 x H54	E x C	100	78	88	78	78	33	78	76
H23 x H23	E x E	100	90	70	78	89	100	100	90
I105 x H15	D x C	90	78	56	56	0	0	90	53
I105 x X5	D x D	44	78	89	80	22	22	90	60
	Mean	80	84	86	76	31	25	89	

% Compatibility: 0-20 21-40 41-60 61-80 81-100

*) classification on the basis of clone bank records, C, E, D = Compatible, Early Incompatible and Delayed Incompatible respectively.

Figure 1. — Early compatibility, Expt. 1.

Root Stock Family	Comp.* of Parent	SCION CLONE H6 (C)*	HJ (C)	H73 (C)	H59 (E)	H23 (E)	H45 (E)	I105 (D)	Mean
HJ x HJ	C x C	78	78	89	100	22	11	0	54
HJ x H15	C x C	100	100	90	44	0	0	11	49
X16 x X15	C x C	90	100	100	90	0	0	0	54
H73 x H6	C x C	40	11	100	11	0	0	0	23
H73 x H67	C x C	56	11	78	11	0	0	11	24
H60 x H62	C x C	67	44	89	33	10	11	0	36
H42 x H45	C x E	44	33	44	11	80	78	0	42
H45 x H54	E x C	33	44	44	44	66	33	0	38
H23 x H23	E x E	0	0	0	0	89	100	0	27
I105 x H15	D x C	78	67	33	44	0	0	33	36
I105 x X5	D x D	44	67	89	80	0	0	33	44
	Mean	57	50	69	42	24	21	8	

% Compatibility: 0-20 21-40 41-60 61-80 81-100

*) Classification on the basis of clone bank records, C, E, D = Compatible, Early Incompatible and Delayed Incompatible respectively.

Figure 2. — Overall compatibility Expt. 1.

Root Stock Family	Comp.* of Parent	SCION CLONE H6 (C)*	HJ (C)	H28 (C)	X14A (C?)	H10 (E)	H23 (E)	H80 (E)	Mean
H8 X H28	C x C	100	100	100	89	0	11	0	57
HJ X HJ	C x C	100	100	100	100	0	11	11	60
H6 X H28	C x C	100	89	100	78	0	44	0	59
H24 X H61	C x C	100	100	100	89	0	0	0	55
H28 X H29	C x ?	100	100	100	100	0	22	0	60
H10 X H15	E x C	100	89	100	78	0	0	0	52
H23 X H20	E x C	100	89	100	89	0	67	25	67
H6 X H62	C x C	89	100	100	100	44	67	33	76
H23 X H28	E x C	100	100	100	100	90	100	75	95
H23 X H2	E x C	100	100	100	22	78	67	100	81
	Mean	99	97	100	85	21	39	24	

% Compatibility: 0-20 21-40 41-60 61-80 81-100

*) Classification on the basis of clone bank records, C, E, D ? = Compatible, Early Incompatible, Delayed Incompatible and Unknown respectively.

Figure 3. — Early compatibility, Expt. 2.

[2]) In all of these figures, scion clones have been arranged according to the apparent response groups described in *Tables 1* and *2* and rootstock families according to the groupings presented in *Tables 3* and *4*.

[3]) It should be noted that this involves the reclassification of H59 which, on the basis of a small sample from a clone bank, had been classified as an early incompatible clone.

Root Stock Family	Comp.* of Parent	SCION CLONE H6 (C)*	HJ (C)	H28 (C)	X14A (C?)	H10 (E)	H23 (E)	H80 (E)	Mean
HB X H28	C x C	89	100	100	89	0	0	0	54
HJ X HJ	C x C	89	100	78	89	0	11	0	52
H6 X H28	C x C	100	44	100	78	0	33	0	51
H24 X H61	C x C	100	100	100	89	0	0	0	56
H28 X H29	C x ?	100	100	100	100	0	0	0	57
H10 X H15	E x C	100	89	100	78	0	0	0	52
H23 X H20	E x C	100	89	89	89	0	56	25	64
H6 X H62	C x C	78	100	89	100	44	67	33	73
H23 X H28	E x C	100	100	100	89	56	89	75	87
H23 X H2	E x C	56	44	44	11	78	67	33	48
	Mean	91	87	90	81	18	32	17	

% Compatibility: 0-20 21-40 41-60 61-80 81-100

*) Classification on the basis of clone bank records, C, E, D ? = Compatible, Early Incompatible, Delayed Incompatible and Unknown respectively.

Figure 4. — Overall compatibility, Expt. 2.

ticularly within the first group) notwithstanding:

- the "compatible" clones H6, HJ, H73, H59, H28, X14a
- the "early incompatible" clones H23, H45, H10 and H80
- the "delayed incompatible" clone I105

On the basis of pattern of compatibility with scion clones, the rootstock families in Experiments 1 and 2 can be arranged into the groups described in *Tables 3* and *4* respectively. Once again, however, within group variations are apparent.

In general, the evidence for relatedness conferring compatibility higher than that for the scion clone class × rootstock family group is very limited. The H73 case mentioned above is a possible example. On the other hand, H23 displays no pronounced superiority over the other incompatible scion clones with respect to compatibility on the H23 families of Experiment 2; the compatibility of H10 is equally as low as that of H23 and H80 on H10 x H15 in Experiment 2; and H45 is no more compatible than H23 on the H45 families of Experiment 1.

The families included in this experiment represent a number of combinations of parental scion compatibility classes. These combinations and the types of families generated (in terms of their compatibility patterns as rootstocks) are presented in *Table 5*. Marked variation with respect to compatibility patterns of progeny as rootstocks is evident within class combinations (e. g. within the compatible × compatible group).

A major difference between the early and overall compatibility patterns (see *Figures 1* to *4*) lies in the responses of several of the rootstock families of which one or both parents is an early incompatible clone. Although the incidence of incompatibility in these families in combination with scions of the compatible class is quite high, scion elongation is such that much of the incompatibility has been defined here as delayed.

Discussion

The unavoidably low replication (of clones within compatibility class and genotypes within family) in these

Table 1. — Scion clone response groups in experiment 1.

Group	Clones	Response patterns
1	H6, HJ, H73, H59	Generally compatible on HJ x HJ and X16 x X15
		Low to moderate compatibility on H42 x H45 and H45 x H54
		Zero compatibility on H23 x H23
		Much of the incompatibility is delayed, in particular that on H23 x H23
2	H23, H45	Very low compatibility on HJ x HJ, HJ x H15, X16 x X15, H73 x H6, H73 x H67, H60 x H62, I105 x H15 and I105 x X5
		Highly compatible on H42 x H45 and H23 x H23
		Most of the incompatibility is early
3	I105	Moderately compatible with I105 x H15 and I105 x X5
		Negligible compatibility with all other families
		Most of the incompatibility is delayed

Table 2. — Scion clone response groups in experiment 2.

Group	Clones	Response patterns
1	H6, HJ, H28, X14a	Highly compatible on HB x H28, HJ x HJ, H24 x H61, H28 x H29, H10 x H15, H23 x H20, H6 x H62, and H23 x H28 Much lower compatibility on H23 x H2 Incompatibility, to the extent that it occurs, is mostly delayed
2	H10, H23, HB0	Generally very low compatibility on HB x H28, HJ x HJ, H6 x H28, H24 x H61, H28 x H29, and H10 x H15 More moderate compatibility on H6 x H62 Moderate to high compatibility on H23 x H28 Incompatibility is mostly early

Table 3. — Rootstock family response groups in experiment 1.

Group	Families	Compatibility with compatible scion clones	Compatibility with early incompatible scion clones	Compatibility with I105	Nature of incompatibility with compatible scion clones	Nature of incompatibility with early incompatible scion clones	Nature of incompatibility with I105
1	HJ x HJ, HJ x H15 and X16 x X15	generally high	very low	very low	–	mainly early	mainly delayed
2	H73 x H6, H73 x H67 and H60 x H62	variable	very low	very low	both early and delayed	mainly early	mainly delayed
3	H42 x H45 and H45 x H54	low to moderate	moderate to high	zero	mainly delayed	mainly early	mainly delayed
4	H23 x H23	zero	very high	zero	mainly delayed	–	mainly delayed
5	I105 x H15 and I105 x X5	moderate to high	zero	moderate	both early and delayed	mainly early	mainly delayed

Table 4. — Rootstock family response groups in experiment 2.

Group	Families	Compatibility with compatible scion clones	Compatibility with early incompatible scion clones	Nature of incompatibility with compatible scion clones	Nature of incompatibility with early incompatible scion clones
1	HB x H28, HJ x HJ, H6 x H28, H24 x H61, H28 x H29, H10 x H15 and H23 x H20	generally high	very low	–	mainly early
2	H6 x H62 and H23 x H28	high	moderate to high	–	both early and delayed
3	H23 x H2	generally moderate	moderate to high	mainly delayed (except with X14a)	both early and delayed

experiments has led to some difficulties in delineating response types with complete accuracy. In spite of this fact, and ignoring the possible existence of genotype × environment interaction, the response patterns in these experiments are sufficiently striking to warrant speculation.

Table 5. — Rootstock family response groups in relation to parental compatibility classes.

Parental Compatibility Class	Rootstock Family Compatibility Response Types	Number of Cases
"C" x "C"	High with "C" scion clones Low with "E" scion clones Low with "D" scion clone (where tested)	8
	High with "C" scion clones At least moderate with "E" scion clones	1
	Variable with "C" scion clones Very low with "E" scion clones Very low with "D" scion clone	3
"C" x "E" (or "E" x "C")	High with "C" scion clones Low with "E" scion clones	2
	High with "C" scion clones At least moderate with "E" scion clones	1
	Low to moderate with "C" scion clones Moderate to high with "E" scion clones	3
"E" x "E"	Zero with "C" scion clones Very high with "E" scion clones Zero with "D" scion clone	1
"D" x "C"	Moderate to high with "C" scion clones Zero with "E" scion clones Moderate with "D" scion clone	2

Scion clones can be divided into broad classes on the basis of compatibility patterns. To some extent, rootstock families which are highly compatible with one class of scion clone tend to display a lower level of compatibility with other classes. This pattern is consistent with the hypothesis that there is a factor which must be present in both scion and rootstock (or absent in both scion and rootstock) to confer compatibility. A similar mechanism has been proposed also for *Pinus patula* (VAN DER SIJDE, 1974).

An increase in compatibility levels through the use of related rootstocks has been demonstrated for a range of species, including *Eucalyptus grandis* (VAN WYK, 1977), *Pseudotsuga menziesii* (COPES, 1973), *Pinus caribaea* (SLEE and SPIDY, 1970) and *P. patula* (BARNES, 1969). A simple comparison of related with a broad mixture of unrelated rootstocks would yield a similar result for hoop pine. In this species, however, clones of the early incompatible class appear to have a factor in common and, there is little evidence for relatedess conferring compatibility additional to that for a scion class × rootstock family group. Similarly, a study involving two highly incompatible scion clones of *P. patula*, and their rootstock progeny, revealed cross compatibility between the clones (VAN DER SIJDE, 1974).

The absence of cross compatibility between I105 and the early incompatible clones with respect to scion clone × rootstock family responses suggests that these types of incompatibility are controlled by different factors and by different genes.

The following matters indicate that the mechanism is not quite as simple as the above, and that additional factors exist which modify or suppress the incompatibility reaction in some circumstances:

— the variation among clones within groups with respect to their compatibility patterns on rootstock families,
— the existence of families which apparently include substantial numbers of genotypes which are compatible with both the compatible and early incompatible scion clones, and
— the greater elongation of the scion when the early incompatibility factor is in the rootstock rather than in the scion.

Variation in proportions of compatibility types within compatible × compatible, or early incompatible × compatible families emphasizes that clones within a compatibility class (the "compatible" class at least) are not genetically identical with respect to a compatibility factor. The representation of genotypes in each rootstock family in these experiments is insufficient for the detailed analysis of ratios which would permit speculation as to whether an early incompatibility factor might be inherited as a simple Mendelian trait or as a quantitative character with a threshold.

The relationships observed in this study indicate that the use of rootstocks which are the progeny of the scion clones would reduce the incidence of incompatibility in clone banks and seed orchards of hoop pine, as it has for the other forest species noted above. Such specific matching of scions and rootstocks, however, involves practical difficulties and adds to the lead times between selection and grafting, and is not a desirable strategy to apply in practice. The use of more broadly compatible rootstocks would offer substantial practical advantages.

On the basis of the nature of the response observed here, the breeding of highly compatible rootstock families through the selection and crossing of highly compatible parents, as employed for Douglas fir (COPES, 1981), would not be a suitable approach to overcoming the early incompatibility problem in poop pine. The evidence for hoop pine suggests that crossing among the highly compatible scion clones generally would give rise to progeny which, as rootstocks, would be highly incompatible with the incompatible scion clones. Approaches which could be considered are:

- the segregation of compatible and early incompatible clones, and the use of appropriate rootstocks for each. For the compatible clones, a broad mixture of compatible x compatible progenies would be a situable and very convencient choice. For the early incompatible clones, rootstocks should comprise families or clones resulting from incompatible x incompatible matings.
- the identification and production of the broadly compatible rootstock families and clones which apparently exist. This approach, circumventing the need for the segregation of clones, would be preferable and is worthy of further investigation.

The extent to which a delayed incompatibility factor is common to I105 and HG (the delayed incompatible clone not represented in these experiments) would be of considerable interest. Only a modest improvement in the compatibility of I105 has been achieved by grafting onto progeny arising from crossing I105 whith a compatible clone. In the light of the pattern observed for early incompatible clones, the use of rootstock progeny resulting from the crossing of I105 and HG, or the selfing of these clones, warrants investigation.

Progeny arising from the crossing of I105 and compatible clones have produced only a minor proportion of genotypes carrying the postulated incompatibility factor as rootstocks. It might be speculated therefore that second generation selections made among HG progenies would include a similarly modest proportion of genotypes with the incompatibility factor as scions. On this basis, these selections should not be excluded from the breeding or propagation programs without prior testing of their compatibility status.

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Response of Norway spruce (Picea abies [L.] Karst.) Annual Increments to Drought for Various Provenances and Locations

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Summary

Annual diameter increments were measured for the years 1976 to 1985, which include the drought years 1982 to 1984, on 17 Norway spruce (*Picea abies* [L.] KARST.) provenances growing at four locations of a trial established in 1969.

Spruce responds to drought with reduced diameter growth. Variation in annual increment at individual locations is explicable by the weather conditions in the given year and place. The lowest increments were observed in the second year of drought and not in the year of lowest precipitation, which would indicate the importance of ground water. Differences between blocks and significant interactions between blocks and other parameters indicate that microsite variation is important in determining diameter growth response to drought.

Spruce populations, regardless of origin, react to drought similarly (weak genotype x environment interaction) thus one should not expect any benefits of selection for drought resistance in spruce. Variation in the interaction pattern of some provenances with different weather conditions was observed. Rare severe droughts of long duration may be responsible for the absence of natural stands of Norway spruce in northwestern Poland.