Many forks were observed where there was no indication of pathological or mechanical damage. It seems quite likely that many forks resulted from physiological control of apical dominance, in the absence of injury. On that basis, the relatively strong negative correlation between branch angle and number of forks at a whorl may indicate that the buds that potentially can produce the most steeply inclined branches, have the greatest tendency to become forks. The negative correlation between number of forks and number of branches per whorl lends support to this interpretation.

Genetic control of forking is necessarily related to causal the factors for forking. Insect resistance and frost hardiness are genetically influenced traits which were directly related to the incidence of forking. Genetic control in that case would be indirect. Physiological factors which affect the incidence of forking may be under more direct genetic control. Considering the diversity of causal factors and related genetic systems, genetic control of forking by a few major genes is not likely. It is more likely that genetic control of this trait is quantitative in nature.

Summary

Multinodality, branching, and forking were studied in six wind- and nine control-pollinated families of *Pinus* contorta var. murrayana ENEGLM. This species typically produces multinodal annual shoots by (1) formation of multinodal winter buds, (2) late-season flushing, and (3) sprouting of latent buds. The first, or major, annual whorl in a season has more branches, and steeper-angled branches than minor whorls produced later in the season. Major whorls contained 80 percent of all forks observed.

Branches had steeper angles in their first growing season than in subsequent seasons. This flattening phenomenon caused some very small branches in minor whorls to be classified as forks in the first season and reclassified as high-angled branches in the second season. Branches produced in each succeeding year had flatter angles than those produced in previous years.

Average number of forks per tree doubled annually from the second through the fifth year. Insects caused a significant but small proportion of the forks: about 10 percent in 1963. Frost injury was the apparent cause of a large proportion of forks, but the cause of many forks was not apparent. Lack of apical dominance due to physiological conditions was hypothesized as a probable cause of forking.

Genetic control of branching traits and forking was indicated by large amounts of variation associated with families. Nonparametric tests of data on families for presence or absence of forks also indicated genetic control of forking.

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The incidence of graft incompatibility with related stock in Pinus çaribaea Mor. var. hondurensis B. et G.

By M. U. SLEE[1] [2] and T. SPIDY[1]

Introduction

Some grafted scions do not develop satisfactorily even though they appear to have become successfully established on the stock plants. This phenomenon is known as incompatibility or uncongeniality and has received considerable study from horticulturists (see MAHLSTEDE and HABER, 1957; HARTMANN and KESTER, 1959; MOSSE, 1962 and numerous others).

Failures due to incompatibility are a more serious problem in forestry than in horticulture. In horticultural practice grafts are made between scions of one clone and stock plants of another clone, and when particular combinations of clones prove incompatible other compatible combinations with the same attributes can be used instead. However, the forester usually propagates selected breeding trees by grafting these not onto clonal stocks, but onto stock plants raised from seed. In these circumstances the proportions of grafts that become incompatible vary from clone to clone. Severely affected clunes may have to be omitted from the breeding Programme, and such omissions are serious losses. In less severe cases the development of incompatibility also presents problems; incompatible grafts cannot be detected for some time after establishment, and their occurrence modifies irrevocably a planned graft lay-

[1]) Queensland Department of Forestry.
[2]) Present address: — Department of Forestry, Australian National University, Canberra, A.C.T.

out, disturbs individual clone representation in that layout, and reduces seed yield.

The proportions of incompatible grafts that have occurred in individual clones of selected breeding trees of Honduras Caribbean Pine *(Pinus caribaea* MOR. var. *hondurensis* B. & G.) in Queensland are given in *Table 1.* A grafted seed orchard of this species was established in early 1968 and some trees, e. g. C46 and C53, had such a regularly high incidence of graft-incompatibility that they could not be considered for inclusion. In addition, some minor losses are expected within the seed orchard due to the development of incompatibility in the clones that have been included.

Table 1. — The incidence of graft-incompatibility in clones of selected breeding trees of *Pinus caribaea* var. *hondurensis* determined from grafts made over the period 1960—1964 in Queensland.

Clone	% grafts incompatible	Clone	% grafts incompatible
(i) Clones lightly or moderately incompatible			
C1	25	C57	26
C40	39	C58	20
C41	23	C59	13
C51	30	C60	7
C54	2	C61	8
C55	17	C63	Nil
C56	6	CF	46
CD	39		
(ii) Clones severely incompatible			
C19	78		
C22	70		
C45	89		
C46		Both so severely incompatible that only one successful graft has been established from numerous attempts in both clones.	
C53			

Graft incompatibility may take several forms. Many authors regard any failure in graft development as incompatibility (WEBBER, 1926; ROBERTS, 1949 and GARNER, 1958) but others, such as MOSSE (1962), feel that incompatibility should refer solely to situations where a clean break develops at the union between stock and scion.

In Queensland three different categories of graft failure are recognized as incompatibility in Honduras Caribbean Pine. The first is similar to that described by DUFFIELD and WHEAT (1964) for *Pseudotsuga menzeseii* (MIRB.) FRANCO. Although normal xylem continuity is maintained between stock and scion the development of a phloem blockage at the union results in a faster rate of stem growth on the scion than on the stock. The different growth rates lead to a loss of mechanical balance after about three years and the graft bends over or breaks at the union. In the second category some growth follows grafting but resin exudation and swelling occurs at the union with breakage and death when the scion is about two feet tall. In the third category the scion remains alive but makes very little growth and continual trimming of the stock branches is necessary to prevent their overtopping and killing the scion. The scion eventually dies.

An abnormality which is not associated with failure to survive is not regarded as incompatibility (GARNER, 1958). For example, WEBBER (1926) has noted that the development of a larger stem diameter on the stock than on the scion does not affect graft survival unless the difference is excessive. Accordingly grafts developing this feature are not regarded as incompatible.

The causes of incompatibility have been discussed by MOSSE (1962). These are not fully understood, but it is probable that several different causal agents can be operative, all producing similar morphological symptoms. Viruses, toxic to one unit of the combination but not the other, biochemical or physological disorders, structural differences and environmental effects have all been suggested as possible causal agents, but the phloem blocks that commonly occur are generally regarded as a symptom of incompatibility rather than a cause.

Consideration of the possible causes of incompatibility suggested that if some genetic or other affinity were to exist between the stock and the scion then the incidence of incompatibility might be reduced. This paper records the results of trials in Queensland in which two selected breeding trees of known incompatibility were grafted onto related and unrelated stock plants. Comparisons were made of initial grafting success and later of the incidence of incompatibility. Graft development was closely studied to determine the earliest age at which incompatibility could be detected from external morphological appearance.

Material and Method

Grafts were made of two trees of which one, C46, was severely graft-incompatible and the other, CF, moderately so *(Table 1).* From October 1963 to January 1965 grafts in both clones were made onto closely related and onto unrelated stock plants established both in the field and in the nursery at Bowenia in coastal Central Queensland (Latitude 22° 50', Altitude 50'). The related stock plants were from wind-pollinated seed collected from the ortets of the individual clones and the unrelated stock plants from seed imported from British Honduras.

The stock plants were raised according to the usual nursery procedure for *P. caribaea* in Queensland, outlined by ROGERS (1957). All originated from a March sowing at Bowenia followed by an August tubing. Those for field grafting were outplanted in the summer (December-January) and grafted approximately twelve months later. For the nursery grafting potted stocks were used. The stock plants were selected for sturdiness from tubed material available at the usual planting time (December). They were potted at this time and grafted later the following year. Thus when grafted the stock plants used for both field and nursery grafting were aged up to twenty-one months from sowing.

Scions were collected from both the ortets and established grafts and grafted on the same day. The top-cleft method of grafting was used following the usual Queensland procedure described by NIKLES (1962) and SLEE (1967). Binding was with plastic tape, no sealer was used and a suitable post-grafting environment was provided by the use of a plastic bag enclosing the scion. In the field an additional calico bag provided shelter from the sun, whilst in the nursery newly made grafts were kept under shade. All bags were removed between four and six weeks after grafting and the binding later as the union strengthened. Potted grafts were hardened off and outplanted as soon as possible after grafting (see *Table 2).*

To determine when incompatibility could first be detected with certainty the development of the successful grafts was closely studied, with particular attention being paid to the development of colour differences in the foliage, the occurrence of different rates of girth growth above and

Table 2. — The initial results of grafting clones CF and C46 onto related and unrelated stock plants.

Clone	Scion origin	Month[1]) grafted	Number of grafts made	successful	Month outplanted[1])
CF (related stock plants)					
	Ramets	8,10/64	7	7	12/64
	Ramets	12/64	14	10	Field
	Ortet	12/64	5	5	Field
Total			26	22 (85%)	
CF (Unrelated stock plants)					
	Ramets	8,10/64	7	7	12/64
	Ramets	12/64	15	11	Field
	Ortet	12/64	5	5	Field
Total			27	23 (85%)	
C46 (related stock plants)					
	Ortet	10/63	10	10	2/64
	Ramets	5/64	4	4	8/64
	Ortet	1/65	20	13	Field
Total			34	27 (80%)	
C46 (unrelated stock plants)					
	Ortet	1/64	5	5	2/64
	Ramet	5/64	4	4	8/64
	Ortet	1/65	20	15	Field
Total			29	24 (83%)	

[1]) Month/Year. Field = Field grafting.

below the union and the presence of resin exudation at the union. To determine whether a decrease in height increment was detectable in incompatible grafts before other morphological symptoms were apparent, total height measures were made on all grafts each January and July. At the conclusion of the study the mean six-monthly height increments were calculated for compatible and incompatible grafts omitting those that had died or had never attained vigorous growth. No account was taken of stock plant parentage, but comparisons were restricted to scions with the same origin that had been grafted at the same time in the same location (nursery or field). Unfortunately so few compatible grafts were produced on clone C46 that meaningful comparisons could only be made within the one other clone, CF.

By October, 1967, the grafts had developed sufficiently for the incidence of incompatibility to be assessed and each was classified subjectively according to the following scale: —

(a) *Compatible grafts* Vigorous and healthy graft. Diameters of stock and scion immediately adjacent to the union equal or else stock diameter exceeds scion diameter.

(b) *Incompatible grafts* (i) Vigorous graft usually of healthy appearance, scion diameter exceeds stock diameter.

(ii) Dead, broken off at union. Swelling and resin flow associated with the break.

(iii) No vigorous scion growth ever attained, stock branches frequently overtopped scion and had to be trimmed back. Scion possibly dead before assessment.

Results

The results of the several graftings accorded well with those usually achieved in Queensland. The two clones, C46 and CF, grafted well, with grafting success unaffected by the scion origins or by the use of related stock plants; scion material collected from ortets gave equally as good and sometimes better results than that from ramets and approximately equal proportions of grafts were obtained successfully on both related and unrelated stock plants (*Table 2*).

Symptoms of incompatibilty were evident after about twelve months in incompatibility classes (ii) and (iii), but they were not in evidence in class (i) until twentyfour months, and sometimes thirtythree months from the date of establishment in the field. In grafts that eventually developed incompatibility of class (i) it was possible to observe a very slight dulling of the colour of the foliage after six months but this was so slight that the presence of a healthy graft of the same clone alongside was necessary for its detection.

Height increment cannot be used to distinguish incompatible grafts at an early age. In one of the three vigour comparisons made in clone CF (*Figure 1*) mean differences in rate of height growth were not apparent between compatible and incompatible grafts until thirty months after grafting and even after thirtysix months some incompatible grafts were still growing faster than their compatible counterparts. In the other comparisons slight mean differences were usually apparent at an early age, but again some incompatible grafts were growing faster than some compatible grafts thirty months after establishment.

Differences in the incidence of incompatibility between the clones were well illustrated (*Table 3*). There was a far lower proportion of incompatible grafts in clone CF than in C46 in accord with the general pattern usual in Queensland (*Table 1*).

In both clones the proportion of incompatible grafts was dependent on the relationship of the stock plants to the ortet of the clone. When related stock plants were used incompatibility decreased from 48% to 9% in clone CF and from 100% to 81% in clone C46 (*Table 3*). The difference in clone CF was significant at the 5% level with a χ^2 test, but this same test could not be meaningfully applied to clone C46 where the expected incidence of compatible grafts was too low.

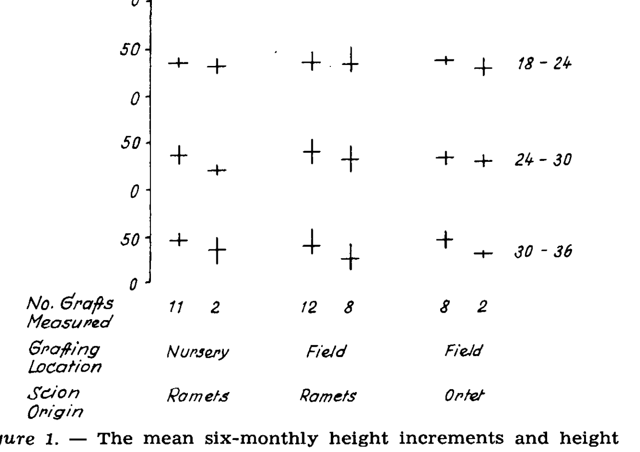

Figure 1. — The mean six-monthly height increments and height increment ranges compared for compatible and incompatible grafts of clone CF in three trials.

Table 3. — The incidence of incompatibility on related and unrelated stock plants in clones CF and C46.

Date established[1])	No. of grafts	No. compatible	No. incompatible in categories[2]) (i)	(ii)	(iii)
CF grafts (related stock plants)					
12/64	7	7	—	—	—
12/64	10	8	2	—	—
12/64	5	5	—	—	—
Total	*22*	*20 (91%)*	*2*	*0*	*0*
CF grafts (unrelated stock plants)					
12/64	7	4	2	—	1
12/64	11	5	5	—	1
12/64	5	3	2	—	—
Total	*23*	*12 (52%)*	*9*	*0*	*2*
C46 grafts (related stock plants)					
2/64	10	2	5	—	3
8/64	4	1	2	—	1
1/65	13	2	8	3	0
Total	*27*	*5 (19%)*	*15*	*3*	*4*
C46 grafts (unrelated stock plants)					
2/64	5	—	3	1	1
8/64	4	—	2	—	2
1/65	15	—	9	4	2
Total	*24*	*0 (0%)*	*14*	*5*	*5*

[1]) Month/Year.
[2]) For description of assessment categories see text.

Discussion

There appears to be no simple external morphological method for the early detection of graft incompatibility in Honduras Caribbean Pine. The colour differences evident some six months after grafting are too slight to be a reliable guide, and the incidence of incompatibility is not clearly defined in the species until between two and three years from field establishment. At this age, however incompatibility can possibly be detected with some certainty for although in some horticultural species incompatibility may develop on older grafts (Hartmann and Kester, 1959; Mosse, 1962 and others) this has not occurred on Honduras Caribbean Pine in Queensland, where the oldest grafts are now aged 13 years and are over 60 feet high.

The use of related stock plants markedly reduced the incidence of incompatibility in the moderately incompatible clone, but in the severely incompatible clone the effect was much less pronounced. Several different causal agents of incompatibility (e. g. viruses, structural differences etc.) may be operative in one graft simultaneously (Mosse, 1962) and it is suggested that severely incompatible clones may be affected by more causal agents than their more compatible counterparts. If the agents active in a moderately incompatible clone are mostly controlled by stock-scion affinities the use of related stock plants will reduce incompatibility in these clones to negligible proportions. In contrast, in severely incompatible clones the greater number of active causal agents will probably include some unaffected by the relationship between stock and scion, and the gain from the use of related stocks will be limited.

For practical purposes there may be some advantages in the use of related stocks for the establishment of grafts for breeding purposes. Such a procedure does not affect initial grafting success and could reduce the incidence of incompatibility to negligible proportions in some clones. However, the reduction in severely incompatible clones would probably be only slight and incompatibility thus remains a major practical problem.

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Summary

Grafting success and the incidence of graft incompatibility were studied in two clones of *Pinus caribaea* Mor. var. *hondurensis* B. & G. grafted onto related and unrelated stock plants. One of the clones used was known to be generally moderately graft incompatible and the other severely so.

No differences were observed in the grafting successes obtained with related and unrelated stock plants in either clone.

External morphological symptoms of graft incompatibility did not become evident for two or three years following grafting, and incompatible grafts frequently showed no early loss of vigour. The use of closely related stock plants reduced the incidence of graft incompatibility markedly in the moderately incompatible clone but only slightly in the severely affected clone.

It is suggested that several types of incompatibility may be operative in the species. The partial improvement in compatibility obtained by the use of related stocks may have been due to some, but not all, of these types having been rendered inoperative in the genetically similar material.

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