GRAFT INCOMPATIBILITY IN RADIATA PINE IN NEW ZEALAND

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ABSTRACT

It has been generally considered that the incidence of graft incompatibility in **Pinus** is low compared with other genera. This paper cites an example of a sudden increase to more than 50% incompatibility in a 14-year-old seed orchard of **Pinus radiata** D. Don. The types of incompatibility present are examined and the implications for New Zealand's clonal seed orchard programme are discussed.

INTRODUCTION

The use of grafts has been important for the production of genetically improved seed of radiata pine (*Pinus radiata* D. Don) in New Zealand. Suitable tip-cleft grafting techniques were developed for this species some 20 yr ago (Thulin, 1957) and over the last 10 yr there has been an average of 10 000 grafts made per year at the Forest Research Institute. A large proportion of these have been used for the establishment of seed orchards of which there are now close to 200 ha in New Zealand.

The problem of incompatibility between root stock and scion has been known and studied by horticulturists for a long time (*see* e.g. Mosse, 1962) and foresters too are well aware of it. In species such as Douglas fir it is particularly serious, and largely because of this tree-breeders in one major Douglas fir area of Canada have changed from clonal to seedling seed orchards (Heaman, 1967). In *Pinus* the problem is generally regarded as less severe but it has been observed in Europe, North America, and Australasia and recorded in the literature by a number of authors, e.g. Perry, 1960; North Carolina State University, 1963, 1970; Brown, 1971. Probably the majority of the world's tree improvement programmes in *Pinus* currently utilise grafted seed orchards, and are therefore potentially liable to problems of incompatibility. To date the emphasis has been on the word potentially, and as recently as last year Brown (1971) in Australia reported ". . . it appears that graft incompatibility in *Pinus radiata* is of little practical significance. . . ." Such a statement could correctly have been made in New Zealand in 1970, but not in 1971.

THE NATURE OF GRAFT INCOMPATIBILITY

Perhaps one of the major characteristics of incompatibility is its variability, both in occurrence and in symptoms. It may occur almost immediately after grafting, but alternatively there may be no symptoms for many years; and while incompatibility may lead to rapid death of the plant, it does not necessarily do so. Great variation in the incidence of incompatibility may occur between clones of the one species, and even

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within a very incompatible clone it is rare for all ramets to show symptoms. Examples have been published of site and mineral nutrient levels affecting incompatibility, and Mosse (1962) has suggested that there may in fact be no clear-cut demarcation between compatible and incompatible graft combinations: rather external factors may often control the balance.

A number of horticultural workers have attempted to classify different types of incompatibility. Of these probably the simplest classification is that of Mosse (1962) who recognised only two types, viz. localised incompatibility and translocated incompatibility. In the former the incompatibility reaction appears to depend on contact, because it can be overcome by a mutually-compatible intermediate stock. With localised incompatibility either the cambium and vascular cylinder of the stock and scion do not join, or at some stage after joining disorganisation develops and continuity is lost: as a result stem breakage at the union occurs very readily. With translocated incompatibility in contrast, vascular and cambial continuity is normal at the union, and the major indication of incompatibility is phloem degeneration. Grafts with this sort of incompatibility rarely die from stem breakage at the union.

INCOMPATIBILITY IN RADIATA PINE

For radiata pine in New Zealand, the earliest signs of incompatibility occur during the first growing season after grafting. Such incompatibility is not widespread and is essentially restricted to a few clones. At the Forest Research Institute it has been particularly bad in only one clone where approximately half of all grafts made die within the first two years. By leaving foliage on the rootstock death is prevented, indicating that mortality in that clone is caused by the inability of carbohydrates to reach the root system. There is evidence from radioactive-tracer studies that in the grafts which do die, the secondary phloem of scion and rootstock fails to form a functional union (Cameron and Thomson, 1971).

The establishment of Gwavas seed orchard in Hawke's Bay has taken place over a number of years, and from counts made in 1971 it has been possible to note for that site changes in the incidence of graft incompatibility with time. Sampling in 1971 showed that the incidence of trees dead or with clear signs of ill-health was 11% in 13-yr-old plantings, 5% in 7-yr-old plantings and 3% and 1% in 5- and 3-yr-old plantings respectively. There was a strong clonal effect, with quite a high proportion of the dead and dying trees belonging to five or six clones only: many of these trees displayed symptoms of incompatibility, of a type which will be described later.

Until 1971 this level of mortality was regarded as typical of that found in radiata pine seed orchards in New Zealand, and it compares with the 7% mortality at age nine recorded from New South Wales by Brown (1971). However, in 1971 at the 1957-58-established Kaingaroa seed orchard (*ca.* 90 miles from Gwavas) the incidence of mortality was seen to increase very rapidly. This is illustrated by Table 1 which compares by clones the percentage of trees dead or with clear signs of incompatibility in 1971 at Kaingaroa and Gwavas. At age 14 more than 50% of the Kaingaroa trees were either dead or dying with the values ranging from 23% in the most-compatible to 81% in the least-compatible clone.

TABLE 1—Percentage of trees dead or with clear signs of ill-health in 1971

Clone No.	Kaingaroa (planted 1957/58)	Gwavas (planted 1958)
7	46	1
19	28	1
37	26	7
55	61	15
80	81	13
82	71	16
88	74	5
89	35	1
90	31	3
91	57	6
96	47	25
97	79	32
99	62	8
121	23	12
	—	—
Mean	53	11
	—	—
No. of trees in sample	826	1360

Examination of the dead and dying trees showed varying symptoms of incompatibility. Perhaps the most common type involved the development of abnormalities which appeared to commence in the phloem and subsequently to affect the cambium and xylem. Fig. 1 illustrates such a graft union: the "pitting" shown in the xylem is, of course, also present in the phloem in reverse relief. Microscopic examination of this type of union suggests that the rootstock phloem elements appear to remain functional for a much shorter time after differentiation than do the phloem elements of the scion. Thus, the width of functional phloem narrows sharply and suddenly at the graft union (Fig. 2, centre). No such narrowing is evident at a compatible graft union (Fig. 2, left). In the ridges of the "pitted" areas the width of the zone of phloem is markedly increased radially; but generally the width of *functional* phloem is no greater than in any other area of the rootstock. The orientation of the phloem elements may be very far removed from vertical (Fig. 2, right), so that useful conduction by the sieve tubes may be limited. A second type of symptom is shown in Fig. 3: there the cambium at the graft union apparently becomes inactive forming a zone of discontinuity, with xylem and phloem "pitting" above and below the union. Fig. 4 illustrates a combination of the previous two types with, in addition, the rootstock xylem showing a number of resin pockets. The bark below the graft union is considerably thicker than that above in this

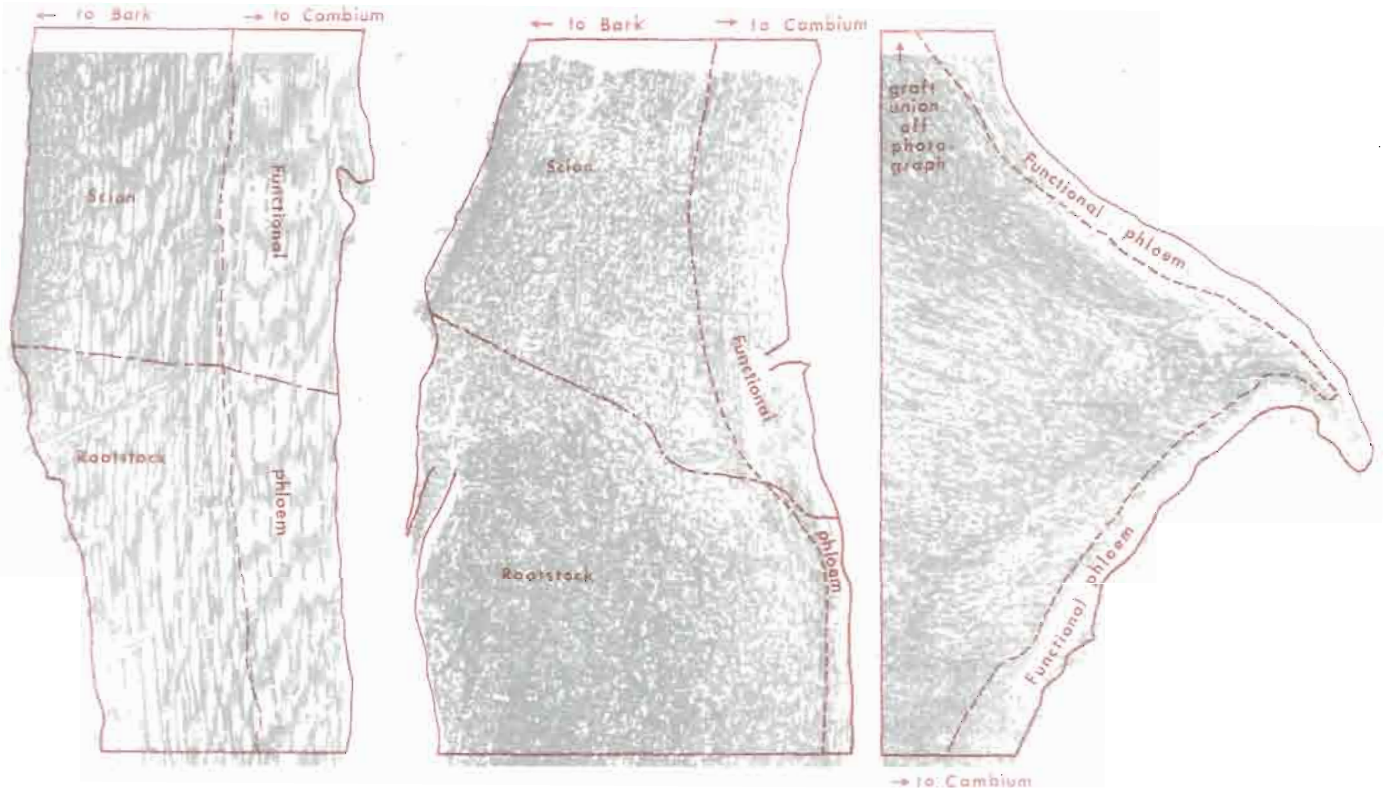

FIG. 2—Radial longitudinal sections of a compatible graft union (left, × 2), an incompatible union (centre, × 7) and a ridge in the "pitted" area of the phloem (right, × 10). Overlay indicates position of the graft union and zones of functional phloem.

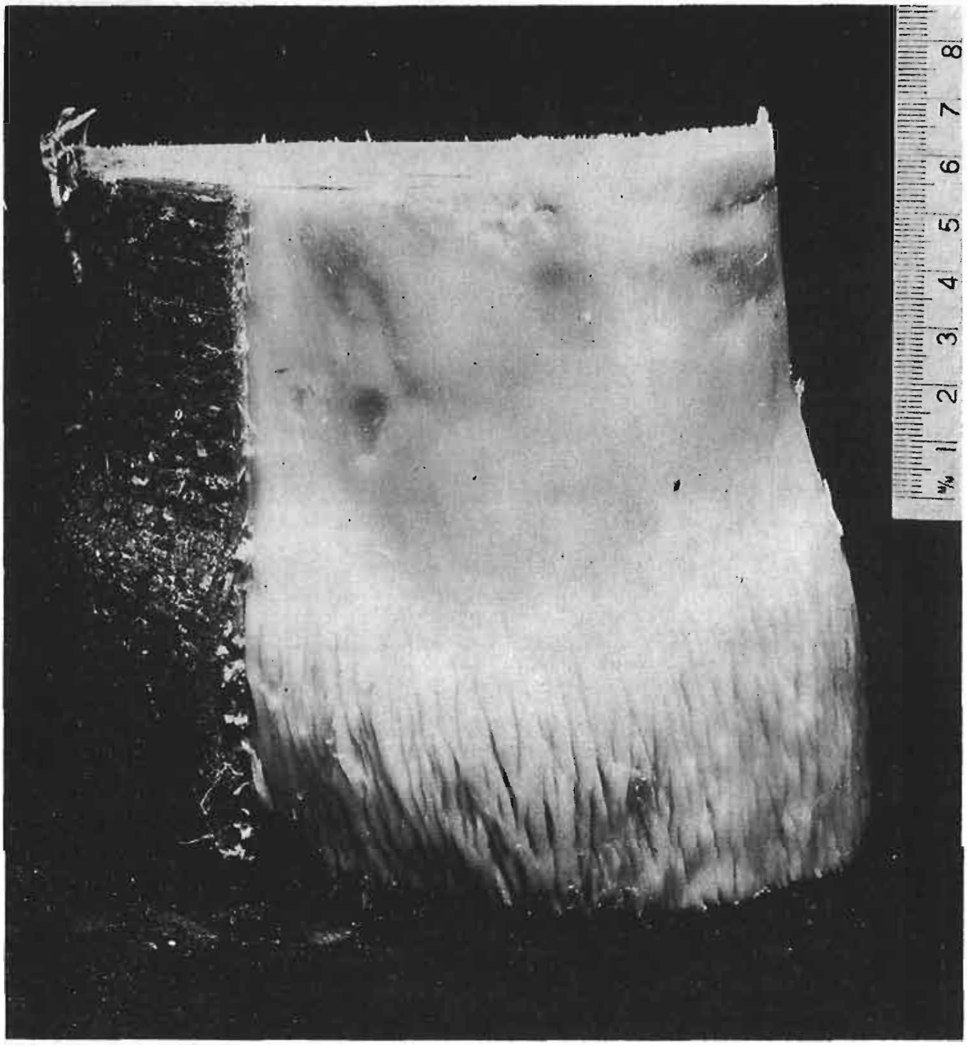

FIG. 1—A very typical form of graft incompatibility in radiata pine. The xylem pitting occurs only below the graft union.

graft also, a factor typical of a number of incompatible unions examined. Overall, the patterns seen in radiata pine probably best fit Mosse's category of translocated incompatibility.

It has not so far proved possible to detect any signs of incompatibility which were present more than two (or at the most three) years before the death of the tree, and these earliest symptoms have been detected only by sectioning of the stem. They show up then in the form of abnormal tissue at the junction of the stock and scion. External indications such as the change of stem diameter at the point of graft union do not of necessity reflect developing incompatibility (*see* Fig. 5) and at present we know of no way that the death of an individual graft through incompatibility can be predicted prior to the first signs of ill-health.

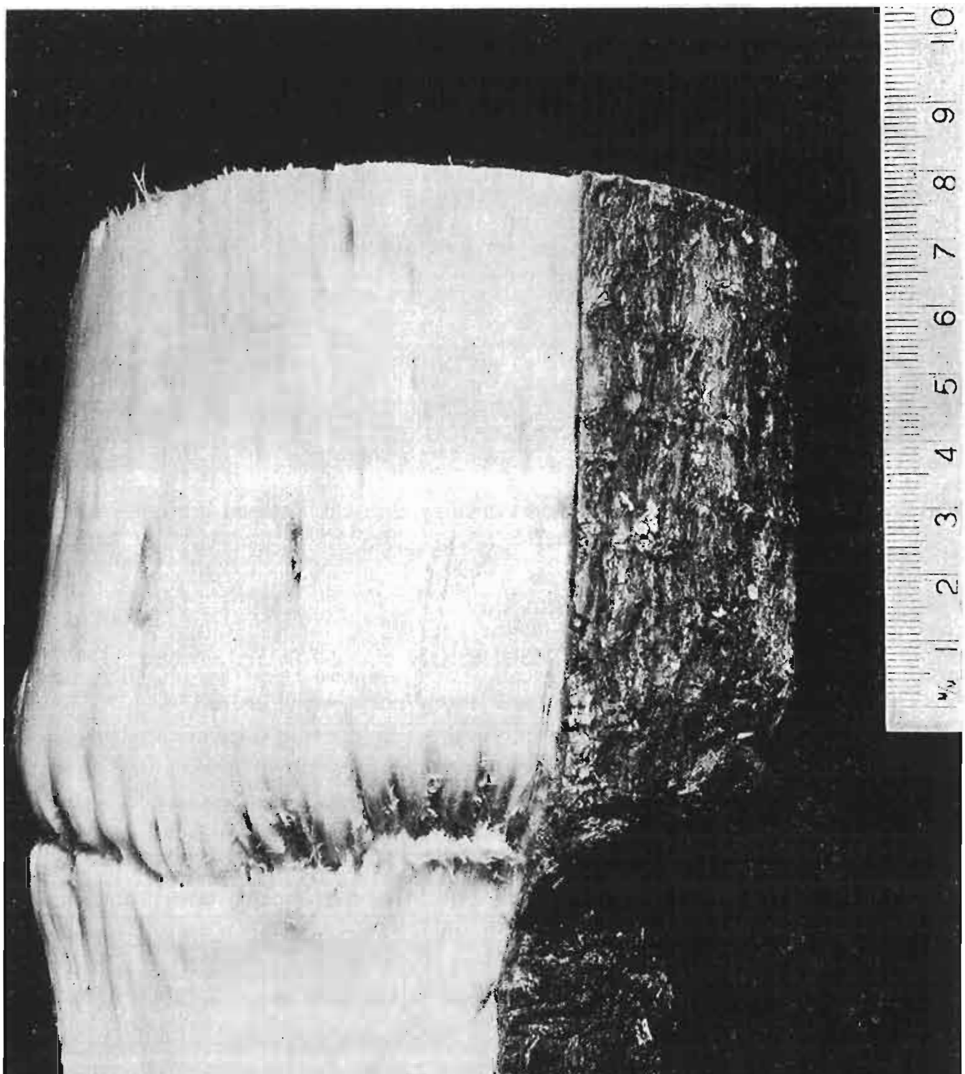

FIG. 3—The position of the union of this incompatible graft is shown by the restricted cambial activity. There is some overgrowth of the scion and "pitting" is present both above and below the union.

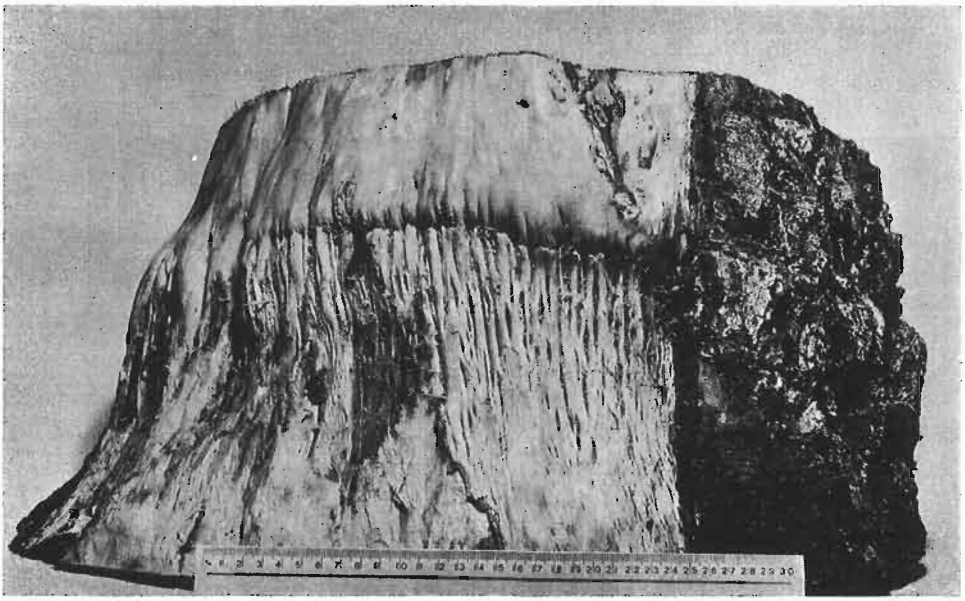

FIG. 4—Incompatibility in a graft of approximately 15-yr-old. Cambial growth is restricted at the graft union, and "pitting" is present. The large scars below the union were filled with resin.

DISCUSSION

The causes of graft incompatibility are largely unknown (Mosse, 1962). In Douglas fir, Copes (1967a) has shown that the physical act of grafting does not lead to incompatibility, and neither do differences between stock and scion in growth rate or in the timing of growth initiation. It seems probable that these statements are also true for radiata pine. Various types of biochemical antagonism (such as antigen: antibody reactions) have been suggested in the literature as being causal, and a number of biochemical differences between incompatible graft combinations have been documented. Differences between rootstock and scion in their susceptibility to viruses transmitted from the scion have also been recorded. There is no information available as to which, if any, of these constitute the causal mechanism in radiata pine.

The literature suggests no easy prospect for preventing incompatibility in radiata pine seed orchards from becoming serious, and neither do our own studies show any immediate prospect of using early detection methods to minimise the problems, as recommended by Copes (1967b) for Douglas fir. The fact that the Gwavas seed orchard at a comparable age to that of Kaingaroa has not shown a big upsurge in incompatibility may imply regional variation either in the occurrence or in the timing of the problem, and we certainly do have evidence that individual grafts may grow actively and remain healthy for at least 20 yr. However, following the sudden increase in the incidence of incompatibility at Kaingaroa we are accepting in our planning that a high level of graft failure of all seed orchards could occur prior to their reaching the age of 18 yr,

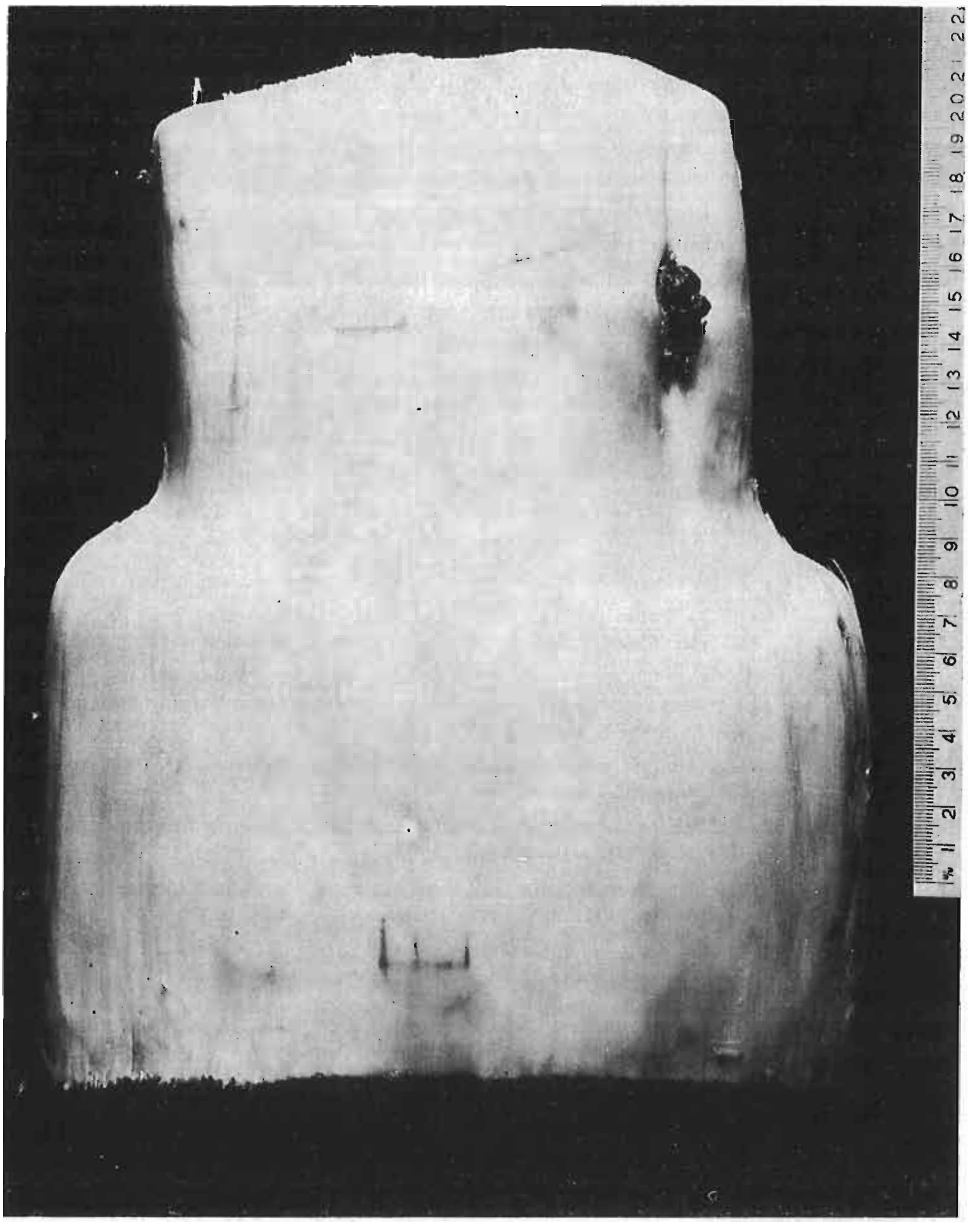

FIG. 5—A scion of **Pinus elliottii** on a **P. radiata** rootstock illustrates that large changes of diameter at the graft union need not be associated with incompatibility.

at which time it was originally planned to clear-fell and replant. As it is the final years that are particularly productive in terms of cone yield, this acceptance necessitates consideration of a change of strategy for our clonal seed orchard areas.

It is fortunate that successful techniques have been developed for rooting cuttings of radiata pine from trees of a wide range of ages (Thulin and Faulds, 1968), and thus it is possible to consider establishing clonal seed orchards with rooted cuttings. Recent work by Sweet (in press) suggests it to be unlikely that either the growth rate or the flowering behaviour of cuttings from mature ortets will vary greatly from those of grafts, and on current planning it is therefore intended to replace the older orchards after clear-felling, with rooted cuttings. In the interim, however, orchards being planted on new sites will still be established with grafts. An attempt will be made to reduce the effect of incompatibility by grafting each clone onto specific seedling rootstocks raised from open-pollinated seed collected from ramets of that clone. Recent work by Lantz (1970) with loblolly pine suggests that such a procedure could result in a substantial reduction in the incidence of incompatibility.

ACKNOWLEDGMENT

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