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DEVELOPMENT OF INTERNAL GRAFT INCOMPATIBILITY SYMPTOMS IN *PINUS RADIATA* D. DON

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Detailed anatomical study of **P. radiata** grafts revealed that phloem tissues of incompatible grafts are abnormally thick. Grafts with thick phloem often displayed "pitted" stems. Thickened bark resulted jointly from overproduction of sieve cells and underproduction of tracheids. Normal pattern of phloem differentiation was altered and phloem areas formed which lacked axial parenchyma. Other internal symptoms in union zones of some incompatible grafts were suberisation and necrosis of cortex cells, excessive tannin accumulation indicated by abnormally darkly-stained bark tissues, formation of abnormal parenchyma in the xylem, and atypical dilation of horizontal ray cells and axial parenchyma. Increasingly more grafts developed symptoms of incompatibility as graft age increased: 10%, 24%, 35%, 54%, and 72% of 1-, 3-, 5-, 8-, and 13- to 18-year-old grafts, respectively. Possible interactions between occult viruses and true stock-scion incompatibility may be responsible for the graft survival and vigour problems.

INTRODUCTION

Graft incompatibility problems in seed orchards result in lost or reduced seed production and, consequently, fewer logged areas being replanted with genetically improved seedlings. Severe incompatibility losses may prompt geneticists to change from using grafted orchards to seedling or cutting orchards. Such a change is often time-consuming and not always desirable because of reduced genetic gain or difficulty in rooting some clones. Tree improvement workers were forced to make this change in New Zealand when they found that over 50% of 14-year-old trees in one grafted seed orchard were either dead or displayed external symptoms of graft incompatibility (Sweet & Thulin 1973). Similar but less severe incompatibility problems have also been reported in Australia (Pederick & Brown 1976) and there may be some stock-scion problems in Tanzania where *P. patula* scions were grafted on *P. radiata* stocks (Dyson 1975).

Some research on the incompatability problems was done by Cameron & Thomson (1971). Radioactive tracer studies of translocation in 1st year grafts indicated early mortality of scions occurred because the grafts failed to form functional phloem unions. Sweet & Thulin's (1973) study of older grafts suggested that incompatibility may have occurred because of premature degeneration of sieve cells. The sieve cells in unions of incompatible grafts were disoriented from the normal axial direction, and an unusual "stem pitting" symptom was shown in their photographs.

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Efficient rogueing of incompatible grafts before planting in orchards is not possible because many incompatible grafts cannot be identified by external symptoms alone. However, detailed anatomical study might reveal additional information on development of internal symptoms and permit earlier identification of problem grafts or allow accurate selection of highly graft-compatible trees for use as parents in a breeding programme for better stocks.

In this report, the primary objective of an anatomical study was to determine the development of internal symptoms of incompatibility in 3-month-old, 1-, 3-, 5-, and 8-year-old grafted *P. radiata* trees. A second objective was to utilise the anatomical data and external distress symptoms in a survey of older grafts growing in orchards at 2 different sites. This survey was made to obtain more accurate estimates of potential long-term losses. Results of this study will aid tree improvement workers in managing existing orchards and in planning future clonal orchards.

METHODS

Grafting was done by propagators of the Forest Research Institute in Rotorua, New Zealand. Tip-cleft grafts were made during spring on 1-year-old *P. radiata* stocks growing in nursery beds (Thulin & Faulds 1966). All foliage was removed from the stocks during late summer of the year of grafting, and the ramets were planted in clonal archives at Rotorua the following winter.

Selections of grafts for external and internal study were confined to 3-month-old, 1-, 3-, 5-, and 8-year-old grafts. Single grafts of 80 different 3-month-old clones, 80 grafts of 3 1-year-old clones, and approximately 10 grafts of each of 13 to 20 3-, 5-, and 8-year-old clones were examined. Clones within the 3-, 5-, and 8-year-old age classes were selected at random in the clonal archives; ramets within those clones were sampled systematically within the rows of 10 to 20 ramets. Ramets of 3-month-old and 1-year-old clones were collected from the nursery beds where they had been grafted.

Ramets were examined for both external and internal symptoms of ill health. External symptom indicators of low vigour and possible graft incompatibility were needle chlorosis, short slender needles, abundant resin flow from the lower bole, reduced leader growth, and dead or "spike" tops. Before cutting off the unions, an estimate based on external appearance was made to decide whether the grafted tree was compatible or incompatible.

Two types of samples were collected for anatomical examinations: phloem and xylem. Phloem samples were taken from all unions; xylem samples of unions were only studied in 20 8-year-old grafts and in 80 3-month-old and 80 1-year-old grafts. Xylem sampling was less intensive because it required the destruction of the entire graft.

Phloem samples consisted of 2 × 4 cm strips of bark cut from the union zones where the stock and scion tissues joined. The samples separated along the cambial interface, so phloem samples contained all tissues from the inner phloem to the outer phellem. Bark thickness was measured to the nearest millimetre with a millimetre ruler. Only the thickness of the living bark was measured.

Bark and xylem samples were killed and fixed in FAA solution and later were sliced into 25 to 50 μm-thick sections on a sliding microtome. General microtechnique procedures used are described by Gnose & Copes (1975). Both traverse (XS) and radial (RS) sections were cut from each bark sample of 3-, 5-, and 8-year-old grafts. Xylem samples from 8-year-old grafts were also microtomed into tangential sections (TS) as well as XS and RS. All sections were stained with safranin 0 and fast green FCF.

Incompatibility surveys of 122 Kaingaroa and 162 Gwavas seed orchard trees were made in 1979. The grafts were 18 years old at Kaingaroa and 15 years old at Gwavas. Only external symptoms and the presence of "pitting" in union zones were examined.

RESULTS

Ramets of 8-year-old grafts with well-defined external and internal incompatibility symptoms were examined first. Further study was made later on progressively younger ramets. This reverse order of study made it possible to determine which systems, tissues, or cells were altered in incompatible grafts and it allowed the detection of minute changes in younger grafts which otherwise would have been undetected. Results are presented in order of youngest to oldest grafts for the reader's convenience.

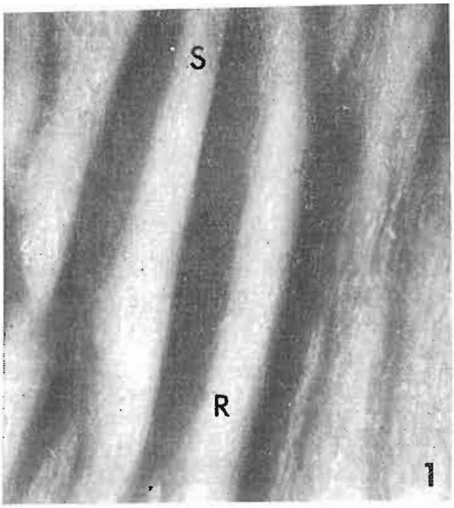
Development of external incompatibility symptoms

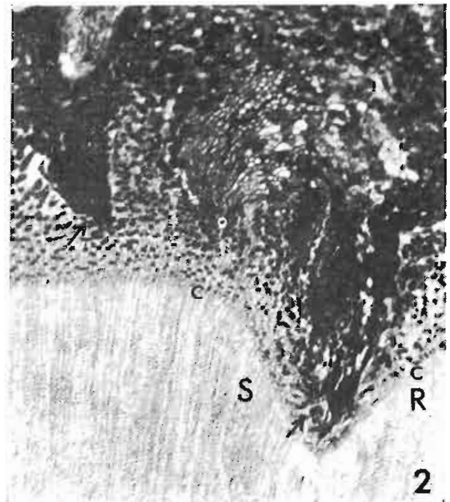
No external incompatibility symptoms were seen in 3-month-old grafts. Propagators at the Forest Research Institute state that a few 1-year-old grafts exhibit marked needle chlorosis, and a small percentage of 1-year-old grafts die each year. It is not always possible to determine if they die from graft incompatibility or from root rot because the external stress symptoms of both are similar.

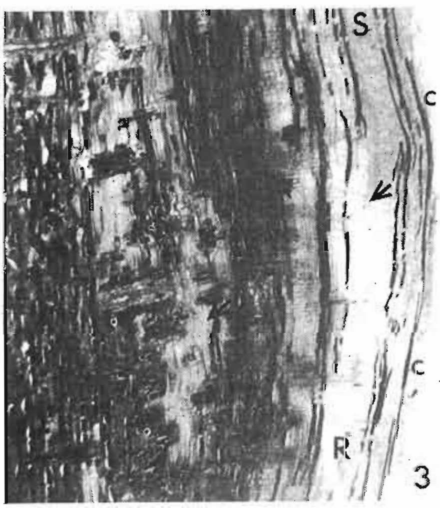
The first external symptom of incompatibility to appear with regularity in 3- to 8-year-old grafts was the presence of abnormally short, slender needles. This condition usually began on a few isolated branches of each tree; the remaining foliage on the tree appeared normal. Older trees generally had a greater proportion of the crown displaying the short, slender needle symptom. A trained observer was able to identify most 8-year-old incompatible grafts when all areas of the bole and crown could be closely examined for colour, length, and thickness of needles, resin flow from the bole, and dead tops or branch flagging. Assessment of taller orchard trees was not as accurate because the crown of each tree could not be examined closely. External assessment of 3- and 5-year-old trees was also not as accurate because many trees had not yet developed external symptoms.

An unusual malformation of the inner bark tissues and the outer xylem surface, termed "stem pitting", was first seen in several 3-year-old graft unions (Fig. 1). Pitted areas of the stems were visible only when a segment of the bark was removed. Severely pitted tissue was characterised by the convoluted series of longitudinal ridges and sunken areas. Excellent photographs of this abnormality were published by Sweet & Thulin (1973). Pitting deformed areas in both the inner bark and the outer xylem. When pitting was sparse, the individual pits appeared as slight longitudinal depressions on an otherwise smooth xylem cylinder. The inner bark from the same areas appeared as small mountain-like projections which extended into the sunken xylem area.

The extent or proportion of the stem which was pitted also varied within ramets of the same clone. Pitting was usually restricted to the union area in grafts and only very small areas were affected. As the pitting became more severe, additional areas







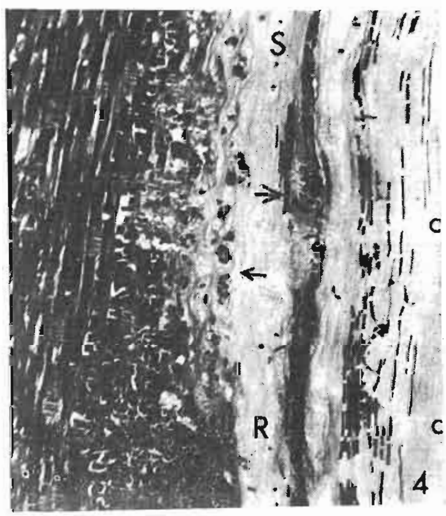


FIG. 1—Effect of stem pitting is shown by the ridged surface of the inner phloem of an 8-year-old incompatible graft. TS. ×10. (XS = transverse section; HS = radial section; TS = tangential section; R = stock; S = scion; C = cambial zone)

FIG. 2—V-shaped groups of unusually darkly-stained cortex and phloem cells in the bark of a 1-year-old union. An invaginated xylem area formed where tracheid differentiation or initiation was abnormally slow. XS. ×25. (For abbreviations see Fig. 1.)

FIG. 3—Thickened bark from a pitted 3-year-old union containing an excessive number of pitted collapsed sieve cells and abnormally few axial parenchyma. RS. ×25. (For abbreviations see Fig. 1.)

FIG. 4—"Laminate" pattern of lightly- and darkly-stained phloem tissues in a 5-year-old incompatible graft. The beginning of the central area or core of one pit is located at the larger arrow. The "wavy" pattern of degenerated sieve cells and axial parenchyma is near the centre of the photograph. RS. ×25. (For abbreviations see Fig. 1.)

of the lower bole became pitted. A few grafts were discovered with sporadic pitting 20–40 cm below the union, and occasionally pitting extended into the roots. Scion tissues were less pitted than stock tissues of the same ramet. Pitting of scion tissues was always restricted to grafts which also had severely pitted union and graft tissues. About 50% of the trees with deeply pitted stock tissues also had pits in the scions. Incidence of pitting in the scion decreased as distance from the union increased, but a few grafts were found with pitted stems 30–50 cm above the union. Pitted tissues were also found in large branches close to the union.

Some trees with pitted unions had extremely chlorotic needles and grew slowly; other trees with similar degrees of pitting had no external symptoms of distress and grew normally. A larger area of the stem becomes pitted as graft age increases, and it is likely that most trees with pitted trunks will also develop external symptoms of distress as tree vigour declines. There was a large increase in the percentage of trees with pitted stems between years 5 and 8 (Table 1).

TABLE 1—Percentage of trees with graft incompatibility symptoms and average thickness of living bark at various graft ages

Graft age	Number of scion clones	Number of grafts	Dead from incompatibility (%)	Pitted stems (%)	No stem pitting, but internal incompatibility symptoms (%)	Total incompatibility (%)	Bark thickness* (mm)	
							Incompatible	Compatible
3 months	80	80	0	0	0	0	—	—
1 year	3	80	0	0	10	10	—	—
3 years	13	108	7	3	14	24	3.9	3.4
5 years	13	108	7	6	22	35	5.0	3.9
8 years	20	242	10	27	15	52	8.4	4.1

*Thickness of living bark measured 1 cm below the union

Thickness of living bark 1 cm below the graft union was directly correlated with stem pitting or incompatibility (Table 2). In 8-year-old grafts the correlation between pitting and living bark thickness was $r = 0.69$. The living bark of such incompatible trees was thicker than bark from similar areas of compatible trees. The bark thickness relationship was consistent even when stem diameters were different. All but 3 of the 20 8-year-old incompatible clones at the Rotorua test site had living bark which was thicker than 6.5 mm (Table 2). Measurements of living bark thickness in 3- and 5-year-old compatible and incompatible grafts showed a similar thick-thin relationship, but living bark thickness was less in older grafts because of periderm formation, so detection of incompatibility was less certain (Table 1).

Development of internal incompatibility symptoms

No internal indications of present or future graft rejection problems could be identified in 3-month-old unions. Of the unions from 1-year-old trees, 10% displayed internal symptoms of stock-scion disharmony. These symptoms occurred in grafts of just 1 of the 3 clones examined at that graft age. The symptoms were union zones with deeply invaginated xylem areas (Fig. 2). Abnormally darkly-stained cortex and phloem cells in both union and adjacent non-union areas were also found.

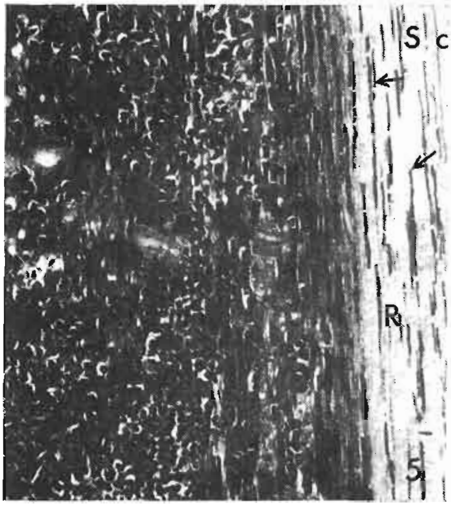
Microscopic study of the 3- to 8-year-old unions showed the same abnormal conditions but a greater percentage of the older grafts was affected. The incompatible grafts formed an excessively large number of sieve cells which probably did not remain functional for long in such areas since they were soon pushed to the exterior and crushed by the profusion of later-formed sieve cells. Collapsed sieve cells did not stain as darkly as non-collapsed cells. The non-functional sieve cells appeared as very light-coloured bands when viewed in RS (Figs 3 and 4). The phloem area of compatible grafts of similar age lacked the broad areas of squashed sieve cells (Fig. 5).

The formation of thickened phloem in the bark of incompatible unions was correlated with decreased tracheid production on the other side of the cambial zone. Incompatibility factors appeared to alter the normal differentiation in the cambium and promoted sieve cell production at the expense of tracheid production. This inhibition was very localised.

The light-coloured zones of squashed non-functional sieve cells were interspersed in RS between darkly-stained zones containing axial parenchyma, horizontal rays, and sieve cells (Fig. 3). Cells of these areas accumulated tannins. Continuity of vertical columns of axial parenchyma in the stem was often incomplete across pitted areas. Phloem elements usually showed a slight horizontal displacement. Areas completely lacking axial parenchyma were often found at the basipetal end of areas with greatly accelerated phloem sieve cell production; a more normal alignment and distribution of axial parenchyma was found on the acropetal end of such areas. Formation of zones of lightly- and darkly-stained cells produced a characteristic "laminated" pattern in RS (Fig. 4). This unusual alteration in the normal cell differentiation pattern did not occur in compatible grafts (Fig. 5). Normal phloem organisation in compatible graft unions was 4–8 sieve cells in a radial file for each axial parenchyma cell. Compatible unions showed no tendency to form wide zones of squashed sieve cells (Fig. 4).

The "laminated" pattern observed near the cambial zone changed as the zones were displaced from the cambial area. Meristematic activity and cell dilation of adjacent axial parenchyma and horizontal ray cells caused the vertically oriented tissues to be laterally displaced. This resulted in characteristic wavy bands of collapsed cells in RS (Figs 4 and 6).

Examination of xylem development in 8-year-old unions revealed the chronological history of the graft. Sunken zones, which later became the first pits in the union area, formed when some grafts were only 3–5 years old (Fig. 13). Traumatic resin canals developed at about the same time (Fig. 14). Epithelial cells surrounding the traumatic canals stained darker than the resin canals formed before pit formation (Fig. 14). Xylem of some incompatibles contained zones of darkly-stained, atypical parenchyma; these areas were found in approximately the middle of a year's xylem increment (Figs 12 and 15). Such zones of atypical parenchyma were only found where the stock and



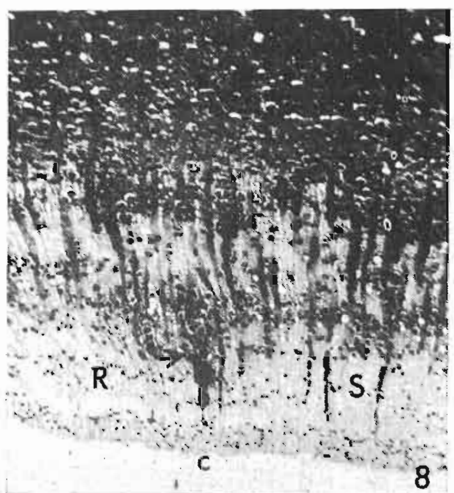


FIG. 5—Bark from a compatible 5-year-old graft containing a narrow zone of functional phloem. Axial parenchyma is distributed uniformly along the radial files of sieve cells. RS. ×25. (For abbreviations see Fig. 1.)

FIG. 6—A characteristic "wavy" pattern was seen at the arrows in the outer phloem of a pitted 5-year-old graft. RS. ×50. (For abbreviations see Fig. 1.)

FIG. 7—Tannin-filled parenchyma forms an irregular mass or core in the centre of one pit in a 5-year-old incompatible graft. RS. ×25. (For abbreviations see Fig. 1.)

FIG. 8—Dilation and proliferation of irregular parenchyma indicate a very early stage of incompatibility in a 3-year-old graft. XS. ×25. (For abbreviations see Fig. 1.)

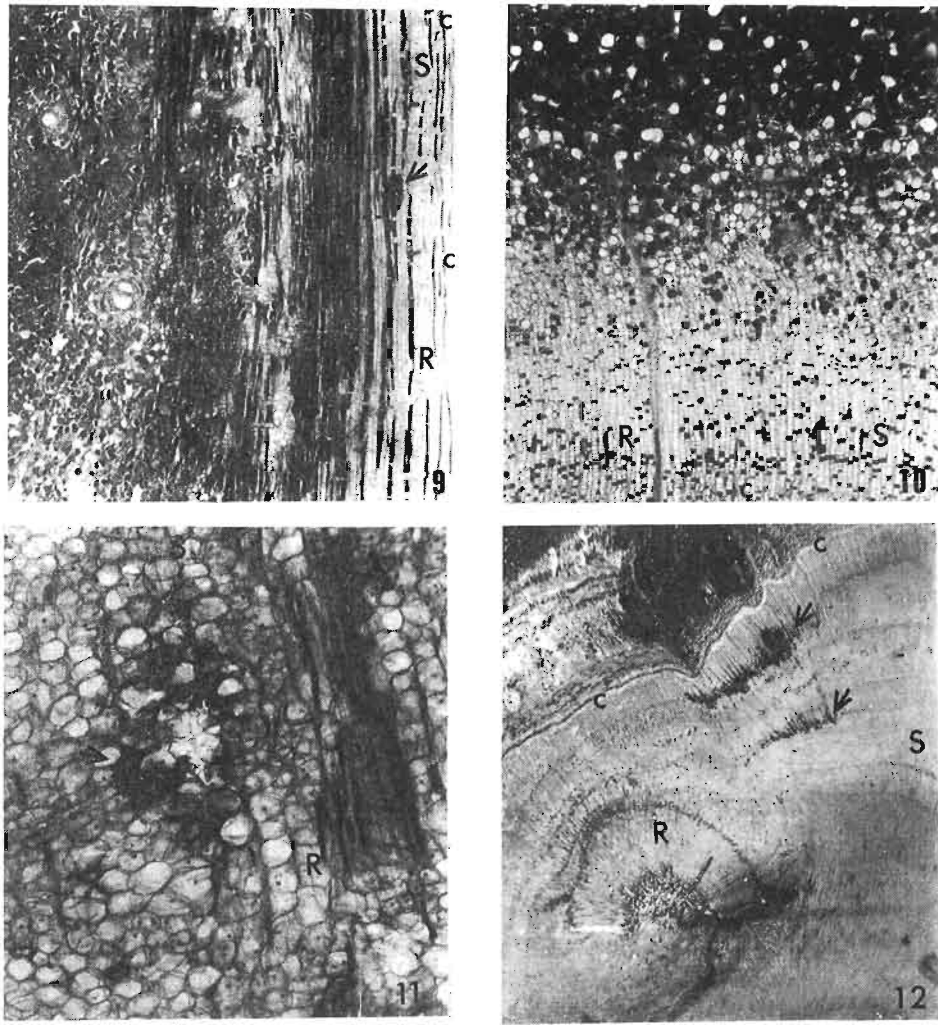
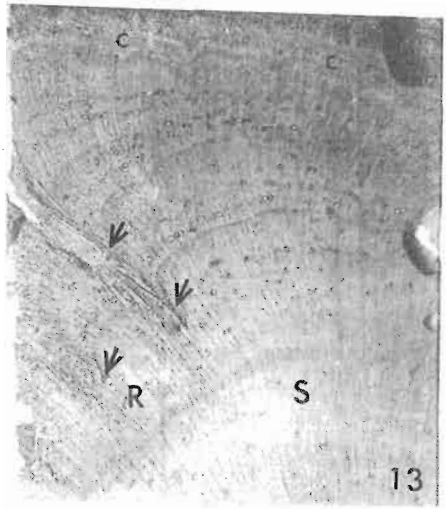


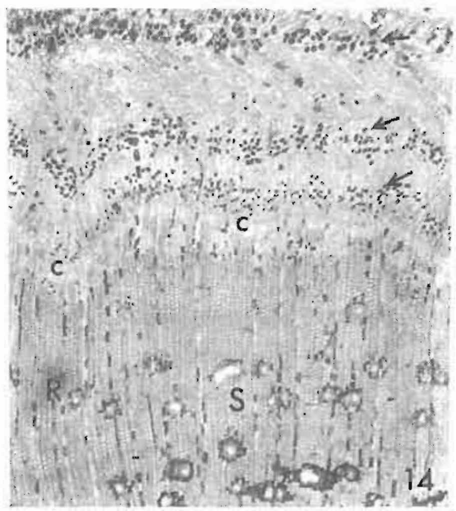
FIG. 9—The first stage in formation of a pit in a 3-year-old graft is shown by the presence of one small group of atypically dilated and tannin-filled cells. RS. ×25. (For abbreviations see Fig. 1.)

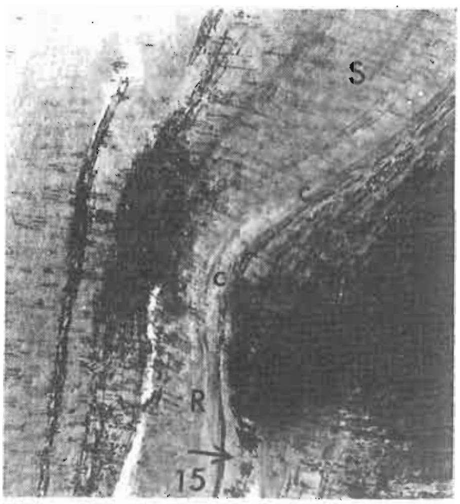
FIG. 10—Bark structure of a typical 5-year-old compatible graft shows the uniform cell distribution pattern and the gradual increase in cell diameter of parenchyma which normally occurs as distance from the cambial zone increases. XS. ×25. (For abbreviations see Fig. 1.)

FIG. 11—Between-cell disharmony in bark of the union of an 8-year-old incompatible graft is indicated by necrosis and suberisation of small groups of cortex cells located along the phloem-cortex interface. FS. ×50. (For abbreviations see Fig. 1.)

FIG. 12—Wound-like masses of tannin-filled parenchyma in the xylem union of a pitted 5-year-old graft. Phloem and cortex cells in and near the union of a 3-year-old incompatible graft stained darker with accumulated tannins than did adjacent non-union areas of the same tree. XS. ×6. (For abbreviations see Fig. 1.)







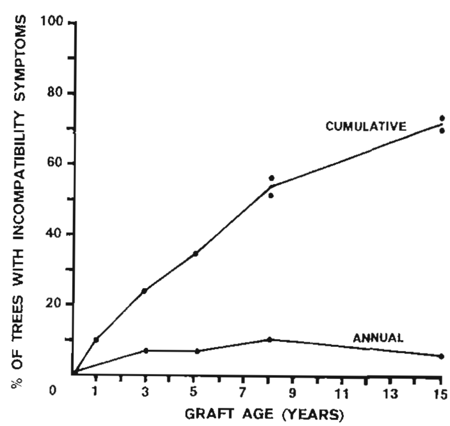


FIG. 13—Traumatic resin canals formed throughout the xylem of a pitted 8-year-old graft. Evidence of previous pit formation is shown at the arrow by the convoluted annual rings. XS. ×6. (For abbreviations see Fig. 1.)

FIG. 14—Abnormally dark-stained epithelial cells surround the traumatic resin canals of an incompatible graft. "Laminated" bands of phloem are visible at the arrows where three zones of darkly-stained parenchyma alternate with the unstained zones of crushed sieve cells. XS. ×25. (For abbreviations see Fig. 1.)

FIG. 15—Parenchyma wound areas in the xylem of an 8-year-old incompatible graft. Note the poor development of axial parenchyma strands at the arrow in the inner phloem and the lack of xylem growth throughout the invaginated area of the pit. RS. ×12. (For abbreviations see Fig. 1.)

FIG. 16—Cumulative percentage of trees which became incompatible and annual rate at which previously compatible grafts developed incompatibility symptoms.

scion cells joined. The youngest graft containing such areas was 3 years old. The areas resembled resin pockets described by Harris & Barnett (1975) and in some grafts they did contain vertical resin canals. Similar areas in other grafts were devoid of resin canals and were composed entirely of parenchyma.

Use of anatomical symptoms in testing the union of 3- to 8-year-old grafts permitted the identification of incompatible stock–scion combinations which would otherwise have been misclassified as compatible. Anatomical testing revealed that 14 to 22% of the 3- to 8-year-old unions, respectively, were incompatible even though they appeared healthy externally (Table 1).

The within-clone variation in grafts with internal symptoms but no external signs of incompatibility is given for 8-year-old grafts in Table 2. The same internal and external symptoms were found in ramets of all clones. Clones differed only in the percentage of ramets which exhibited each type of symptom.

Another unusual condition found in some grafts with pitted stems was a mass of irregularly-shaped parenchyma cells; these cells were filled with tannins and stained darkly (Fig. 7). Tannin-filled horizontal rays extended through such areas, but axial

TABLE 2—Percentage of 8-year-old grafts with various incompatibility symptoms and average thickness of living bark (by clone)

Scion clone no.	Number of ramets examined	Dead from incompatibility (%)	Pitted stems (%)	Internal incompatibility symptoms, but no pitted stem (%)	Total incompatibility (%)	Bark thickness* (mm)	
						Incompatible	Compatible
502	10	10	10	10	30	6.5	3.8
511	9	33	22	22	77	6.9	5.0
521	10	0	0	10	10	—	4.8
522	9	11	56	11	78	7.9	4.5
525	11	18	36	0	54	8.4	3.1
528	11	36	9	18	64	8.5	4.1
531	11	9	0	36	45	7.5	4.5
534	11	0	27	0	27	6.8	3.6
537	13	15	39	31	85	9.4	4.6
541	11	0	0	0	0	—	4.3
544	2	0	0	0	0	—	5.4
547	8	0	50	13	63	6.8	3.6
548	13	31	31	0	62	9.1	4.6
550	12	0	8	8	16	5.0	3.6
553	12	0	8	17	25	5.0	4.0
555	17	0	82	6	88	9.9	5.0
561	12	0	42	25	67	7.7	4.7
565	9	11	56	0	67	9.4	4.3
608	10	0	0	50	50	4.6	3.4
611	10	20	20	30	70	6.5	3.6
Av. (wt.)	11	10	26	15	52	8.4	4.1

* Thickness of living bark measured 1 cm below the union

parenchyma and sieve cells were missing. Development of these areas was initiated by cell dilation and tannin accumulation at random intervals around the circumference of the stem (Figs 8 and 9). Such areas developed into the sunken areas characteristic of "stem pitting". Similar masses of irregular tissues were not found in compatible grafts (Fig. 10).

Other signs of potential stock–scion antagonism were necrosis and the bright red staining of suberised cortex cells in the union zone. This problem was first initiated at the phloem–cortex boundary (Fig. 11), but these symptoms were not seen in all incompatible grafts. Another indicator of incompatibility was the unusually dark staining of stock and scion areas of the union. This colour reaction resulted from excessive tannin accumulation (Fig. 12).

Incompatibility surveys in orchards

Surveys of grafted trees in the Gwavas and Kaingaroa orchards were made to determine the effect of varied site and environment on the percentage of trees which become incompatible and to determine if even more grafts became incompatible when they grew older. The survey of the Kaingaroa orchard was based jointly upon the presence or absence of external distress symptoms and stem pitting. In the Kaingaroa survey, total incompatibility was calculated to be 57 and 73% for the 8- and the 13- to 18-year-old grafts, respectively (Table 3).

A similar external symptom survey was made in the Gwavas orchard, but no testing was done for pitted stems. Estimated incompatibility loss for the Gwavas orchard at age 15 years was 71% (Table 3).

The pattern from the Kaingaroa and Gwavas orchards indicated that the percentage of trees showing incompatibility symptoms increased with graft age. The most rapid cumulative increase occurred through the first 8 years (52–57%) and rose to approxi-

TABLE 3—Seed orchard survey showing percentage of trees exhibiting various stages of incompatibility

Orchard	Graft age (years)	Number of graphs	Dead from incompatibility	External symptoms but no pitting	External symptoms and pitting	No external symptoms but has pitting	No external symptoms and no pitting but internal symptoms	Total incompatibility
Kaingaroa	8	60	10	7	12	13	(15)[1]	57
Kaingaroa	13–18	62	14	8	15	21	(15)	73
Gwavas	15	162	15	20[2]	—	21[3]	(15)	71

[1] Substituted value from 8-year-old grafts from Table 1.

[2] Value was obtained solely from external symptoms: needle colour, resin flow, foliage density, dead top, etc. No bark sample was tested for stem pitting

[3] Substituted value from the 13- to 18-year-old grafts of the Kaingaroa orchard

mately 73–75% by age 15 years (Fig. 16). However, the percentage of previously compatible trees which developed incompatibility symptoms for the first time averaged 8.6% each year and varied from 10.3% at age 8 years to 6.9% at age 15 years.

DISCUSSION

True stock–scion incompatibility occurs in *P. radiata* grafts. Some grafts develop external distress symptoms and die without forming pitted stems. A number of *P. radiata*'s symptoms of ill health resemble common incompatibility symptoms. The invaginated union areas and darkly-stained phloem and cortex cells were found in grafts which had no increase in phloem or bark thickness. Such symptoms are very similar to the incompatibility symptoms found in *P. contorta* grafts (Copes 1975). Signs in 8-year-old unions also suggest that some form of stock–scion disharmony may contribute to ill health. The masses of parenchyma cells within xylem increments resemble the parenchyma areas in *P. ponderosa* grafts caused by incompatibility (Copes 1980). An even more precise indicator of true graft incompatibility is the localised suberisation and necrosis of cortex cells which occurred at the cortex–phloem border in unions of some incompatibility grafts. This type of cell interaction is very similar to the incompatibility reported in *Pseudotsuga menziesii* (Copes 1970).

There is some indication that an additional factor, other than just true stock–scion incompatibility, may be responsible for some of the vigour and survival problems experienced in *P. radiata* grafts. The gradual spread of the pitted stem condition from union to non-union stock tissues and then finally to non-union scion tissues suggests a causal agent other than the biochemical interaction of unlike cells. Biochemical incompatibility normally is typified by a very clearly defined reaction zone separating stock and scion cells. The pitted stem symptom found in *P. radiata* grafts is a highly unusual symptom. Grafts of several woody plants have been reported to develop almost identical pitted stem symptoms: citrus species (Wallace 1951; Schneider 1957), apples (Smith 1954), grapes (Graniti & Martelli 1965), and plums (Mosse & Garner 1954). In each of these plants the symptoms were found to be caused by occult virus infections. Anatomical abnormalities found in bark tissues of pitted orange trees (Schneider 1957) and anatomical abnormalities in *P. radiata* were nearly identical. Both had extensive sieve cell degeneration, abnormal proliferation of one phloem cell-type, hyperplastic rays, and abnormally thick zones of living phloem. The stem pitting condition in orange grafts was again associated with occult viruses. No reports of stem pitting in other conifers are known. The possibility that stem pitting in *P. radiata* grafts may also be caused by occult viruses could not be overlooked since stem pitting has occurred only in species which also contain occult viruses. This possbility will be difficult to prove since there are no known plants for successful virus indexing of conifers and few viruses have even been positively identified in any conifer.

Observations indicated that many extensively pitted 5- to 18-year-old grafts grew normally after pitting first occurred and showed little or no external signs of distress for many years; trees of similar age which contained much smaller areas of pitted tissue quickly lost vigour and died. The main difference between these two conditions was that the trees which died quickly had an abrupt transition or discontinuity of tracheids across the union, whereas the pitted tree which survived with little ill health had no irregular orientation of tracheids across the union. Varied symptoms hint that both biochemical incompatibility and pathogens may interact in the grafts to produce what has been loosely termed "incompatibility".

Internal symptoms of graft incompatibility or ill health may not become detectable until years after grafting, and the related external symptoms are not often visible until even later. This makes tests for early incompatibility detection almost impossible. The most accurate external detection is done at 8 years of age when external symptoms are fairly well defined and thickness of the living bark below the union can be evaluated. Trees with living bark thicker than 6.5 mm are usually incompatible. Bark measurements must be made between winter and early summer before periderm activity causes great variability in bark thickness. It is not known if the same living bark thickness–graft incompatibility relationship persists at different sites or under different growing conditions. Detection surveys based solely on external appearance usually underestimate the actual level of incompatibility since they exclude the unseen components for pitted stems.

Phloem in and around pitted areas may actually hinder phloem translocation. Sweet & Thulin (1973) suggested that the sieve cells of incompatible grafts collapsed prematurely and became non-functional a short distance from the cambial zone. Observations from the present study also support the collapse of the overly abundant sieve cells, but translocation problems are not thought to arise directly from this condition since the functional phloem zone does not appear to differ in width in compatible and incompatible grafts. The actual minimum width of functional phloem required for nearly normal growth is not known (Barnett 1974a).

A more serious problem in grafted trees may be the drastic alteration in the ratio and distribution of cell types in pitted areas of the stem. Such changes could alter the trees' ability to store and mobilise reserves and to transfer photosynthates between the phloem and xylem. Radial files of phloem did not have a normal distribution of sieve cells and axial parenchyma. Normal phloem in RS contained one axial parenchyma cell for every 4–8 sieve cells. The potential effect of 30–50 sieve cells in radial files without axial parenchyma is not known. Barnett (1974b) stated that axial parenchyma functioned as a "constant level" device in the plant. The trees with abnormal sieve cell and axial parenchyma ratios may not be able to effectively regulate the balance of nutrients between the xylem and phloem. The changes in cell distribution and orientation, the overproduction of sieve cells, and the underproduction of xylem tracheids suggest that the normal course of vascular differentiation was altered.

Incidence of stem pitting and other external symptoms of ill health increased steadily with graft age and showed no tendency to cease as grafts aged. If the 8.6% initiation rate continues, only 11% of the original trees will be without symptoms of ill health 25 years after grafting. It is true that only 10% of the trees are dead from incompatibility 8 years after grafting, but another 42% of the original number of grafts contain external or internal incompatibility symptoms. The Gwavas and Kaingaroa 15-year-old orchards appear to be adequately stocked and surviving trees do not show serious signs of early failure or death. Orchard workers have noted that fewer and smaller seeds are produced on incompatible trees. Incompatibility losses have made the job of tree improvement workers more difficult by altering the number and distribution of ramets.

Although the long-term survival and performance of existing *P. radiata* is uncertain, grafted orchards established in the future may be more compatible than present day orchards. Several clones examined in this study and a number of other trees identified in compatibility surveys of grafted clonal archives were found to be free of incompatibility symptoms when they were 8 or 9 years old. It is not certain if such clones are highly graft compatible, if they are free of pathogens, or both. Whichever is true, it may be possible to cross pollinate the selected clones and grow more graft-compatible seedling stock for grafting in new seed orchards.

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