Eur. J. For. Path. 20 (1990) 418–429

ISSN 0300-1237

Forest Research Institute, Rotorua, New Zealand

Changes in needle retention associated with the spread and establishment of Phaeocryptopus gaeumannii in planted Douglas fir

By I. A. Hood, C. J. Sandberg, C. W. Barr, W. A. Holloway, and P. M. Bradbury

Abstract

The needle-infecting fungus *Phaeocryptopus gaeumannii* (Rohde) Petrak spread to stands of Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] in most parts of New Zealand following its first detection in the central North Island in 1959. At Hanmer Forest in the South Island, the percentage of infected needles rose more rapidly in a provenance from northern inland California than in one from Kaingaroa Forest in the North Island. Increase in infection was accompanied by a significant decrease in the proportion of needles retained on shoots of certain age classes, the reduction in the Californian seedlot being greater than in that from Kaingaroa. More older foliage was retained in the Kaingaroa provenance at Hanmer Forest, when infection averaged under 30 %, than at two other locations where mean infection exceeded 90 %. It is suggested that heavily infected production stands of Douglas fir suffer some premature casting of older needles, even when crowns appear healthy.

1 Introduction

The needle fungus *Phaeocryptopus gaeumannii* (Rohde) Petrak is commonly associated with a chronic decline in health of Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] in parts of the world where the host species is planted (e. g., Boyce 1940; Peace 1962; Hood and Kershaw 1975; Skilling 1981). Although inoculation experiments have been used to demonstrate the pathogenicity of the parasite towards Douglas fir seedlings (Strittmatter 1974; Hood 1977), the precise role played by *P. gaeumannii* in the disease syndrome in forests has yet to be clarified by means of rigorous field trials (Hood and van der Pas 1979). The associated symptoms of chlorosis and premature needle shedding vary in intensity in different stands and locations, raising questions as to the exact significance of *P. gaeumannii*, particularly when plantations are often encountered that appear healthy despite the presence of heavy infection throughout tree crowns (Rohde 1937; Peace 1962).

P. gaeumannii was first observed in New Zealand in 1959, and spread throughout Douglas fir in the North Island and the northern end of the South Island over the next fifteen years (Hood and Kershaw 1975). The discovery of trace infection in Hanmer Forest in 1978 afforded an opportunity for a study of the relationship between *P. gaeumannii* and the decline. A decision was made to monitor needle retention in a healthy Douglas fir provenance trial, in order to see if detectable changes in crown health accompanied the anticipated build-up of infection in the stand. Moreover, since this trial is replicated at other localities, it was possible to compare foliage health of a selected seedlot at sites exposed to different intensities of infection. This paper reports the results of the study and considers their implications. It also documents the spread of *P. gaeumannii* in New Zealand Douglas fir subsequent to the first detections in the South Island at Golden Downs Forest (Fig. 1) and nearby Wakefield in 1969 (Hood and Kershaw 1975).

U. S. Copyright Clearance Center Code Statement: 0300-1237/90/2006-0418/$ 02.50/0

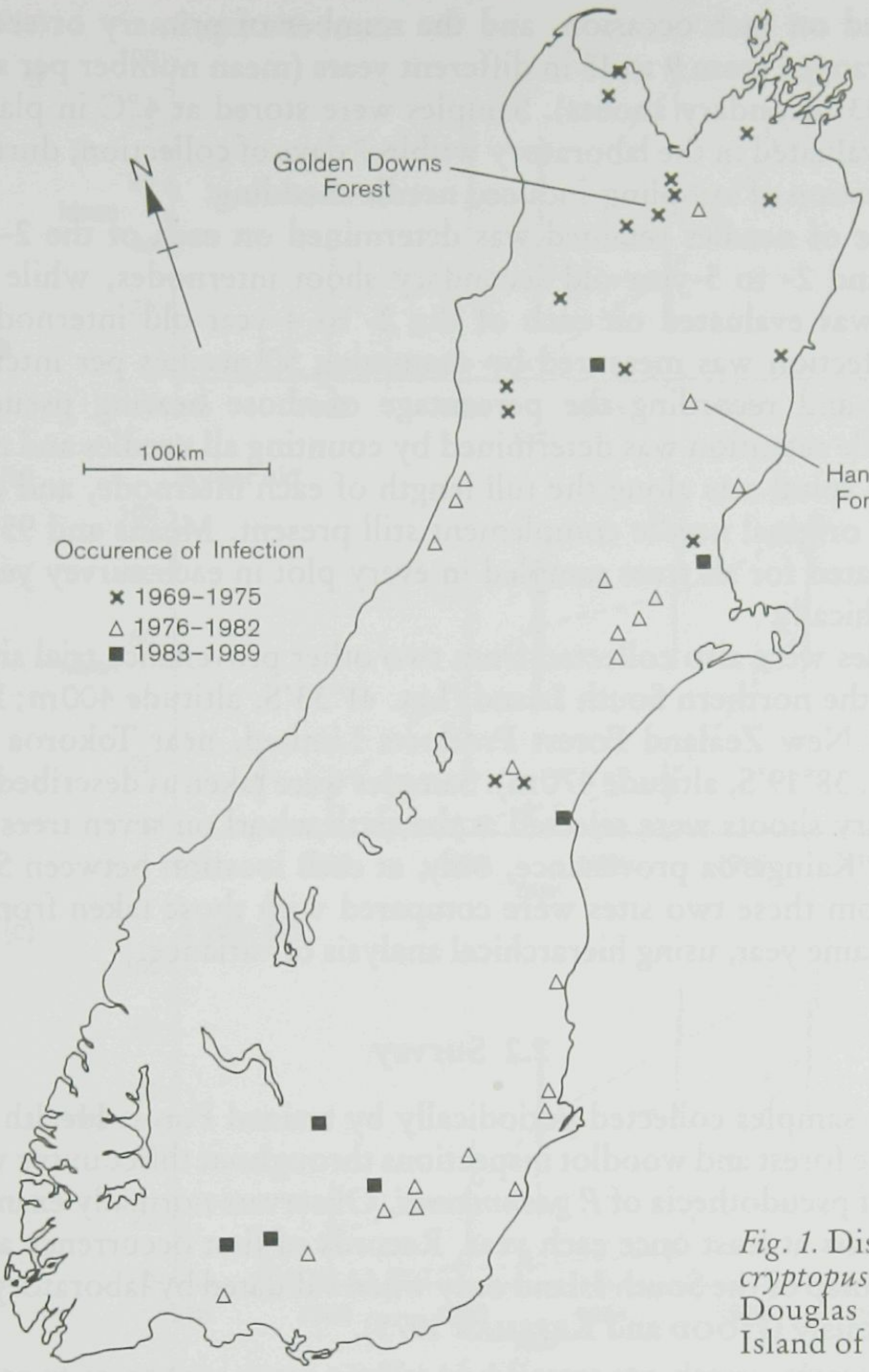

Fig. 1. Distribution of *Phaeocryptopus gaeumannii* on Douglas fir in the South Island of New Zealand

2 Materials and methods

2.1 Needle infection and retention

The Douglas fir provenance trial was established in 1959 and 1960 by the Forest Research Institute (G. B. Sweet 1964, unpublished). It has a randomised block design, and at each site there is normally one plot of each seedlot in each of three blocks. The trial was thinned in 1977 to between 600 and 750 stems per ha at each of the sites used in this sudy, and there was no subsequent treatment. Two plots were selected at the Hanmer Forest site (Lat. 42° 31′S, altitude 490 m; Fig. 1) of provenance 31 (seed source: Kaingaroa Forest, central North Island, New Zealand; coding as in Sweet 1965) and two were chosen in the same two blocks of provenance 23 (Inskip, east of the Sacramento Valley, northern inland California, Lat. 39°59′N, Long. 121°32′W, altitude 1417 m). Fifteen trees were tagged at random in each plot, and were sampled by climbing in early Spring (August–October), immediately prior to budburst. One primary branch of southerly aspect was taken at the sixth whorl down from the top of each tagged tree in each of the years 1979, 1980, 1982 and 1987. One secondary shoot with five internodes was cut from the proximal node of this primary branch (detached or not) in 1979, 1980, 1982, 1983, 1985, and 1987. Not all tagged trees were sampled on each occasion, and the number of primary or secondary shoot samples per plot ranged from 9 to 15 in different years (mean number per survey year: 14 primary shoots; 13 secondary shoots). Samples were stored at 4 °C in plastic or waxed-paper bags, and evaluated in the laboratory within 7 days of collection, during which time there was no indication of sampling-induced needle shedding.

The percentage of needles retained was determined on each of the 2- to 6-year-old primary branch and 2- to 5-year-old secondary shoot internodes, while percentage of needles infected was evaluated on each of the 2- to 4-year-old internodes (secondary shoots, only). Infection was measured by examining 50 needles per internode under a stereomicroscope and recording the percentage of those bearing pseudothecia of *P. gaeumannii*. Needle retention was determined by counting all needles and needle scars on either one or two spiral sets along the full length of each internode, and calculating the percentage of the original needle complement still present. Means and 95 % confidence limits were calculated for all trees sampled in every plot in each survey year, and results were plotted graphically.

In 1985, samples were also collected from two other provenance trial sites, at Golden Downs Forest in the northern South Island (Lat. 41°33′S, altitude 400 m; Fig. 1), and on Rapanui Road of New Zealand Forest Products Limited, near Tokoroa in the central North Island (Lat. 38°19′S, altitude 470 m). Samples were taken as described above, except that only secondary shoots were selected at the sixth whorl on seven trees in each of the three plots of the Kaingaroa provenance, only, at each location between September and October. Data from these two sites were compared with those taken from the Hanmer Forest site in the same year, using hierarchical analysis of variance.

2.2 Survey

Douglas fir shoot samples collected periodically by trained Forest Health Survey observers during routine forest and woodlot inspections throughout the country were examined for the presence of pseudothecia of *P. gaeumannii*. Observers normally examined Douglas fir in all state forests at least once each year. Records of first occurrence at each locality were plotted on a map of the South Island only when validated by laboratory examination, as was done previously (Hood and Kershaw 1975).

3 Results

3.1 Needle infection and retention

In the trial at Hanmer Forest, infection increased between 1979 and 1987 on all three foliage age classes on the provenance from northern inland California (Fig. 2 a–c). The mean percentage rose from less than 20 % to more than 90 % within 9 years. In marked contrast, infection on the Kaingaroa provenance remained low (less than 20 %) until 1984, thereafter rising rapidly to levels exceeding 60 % on all three age classes.

Crowns on all trees in the Hanmer trial were dense and green in 1979, at the start of the study period. Signs of yellowing were first detected in the California provenance in 1985. In 1987 trees of this provenance were distinctly thin-crowned and chlorotic, and samples taken from 12 and 13 trees, respectively, in each plot bore needles with yellow mottling. Trees of the Kaingaroa provenance remained green and healthy throughout the monitoring period, and chlorosis was not present in any foliage collected from this provenance.

Mean needle retention fell significantly on 2- to 5-year-old primary shoots of the California provenance at Hanmer between 1979 and 1987 (Fig. 3 a–d). Retention of two-year-old needles, for instance, decreased from more than 80 % to less than 20 % (Fig. 3 a), and the same trend occurred in other foliage age classes. There was a similar substantial

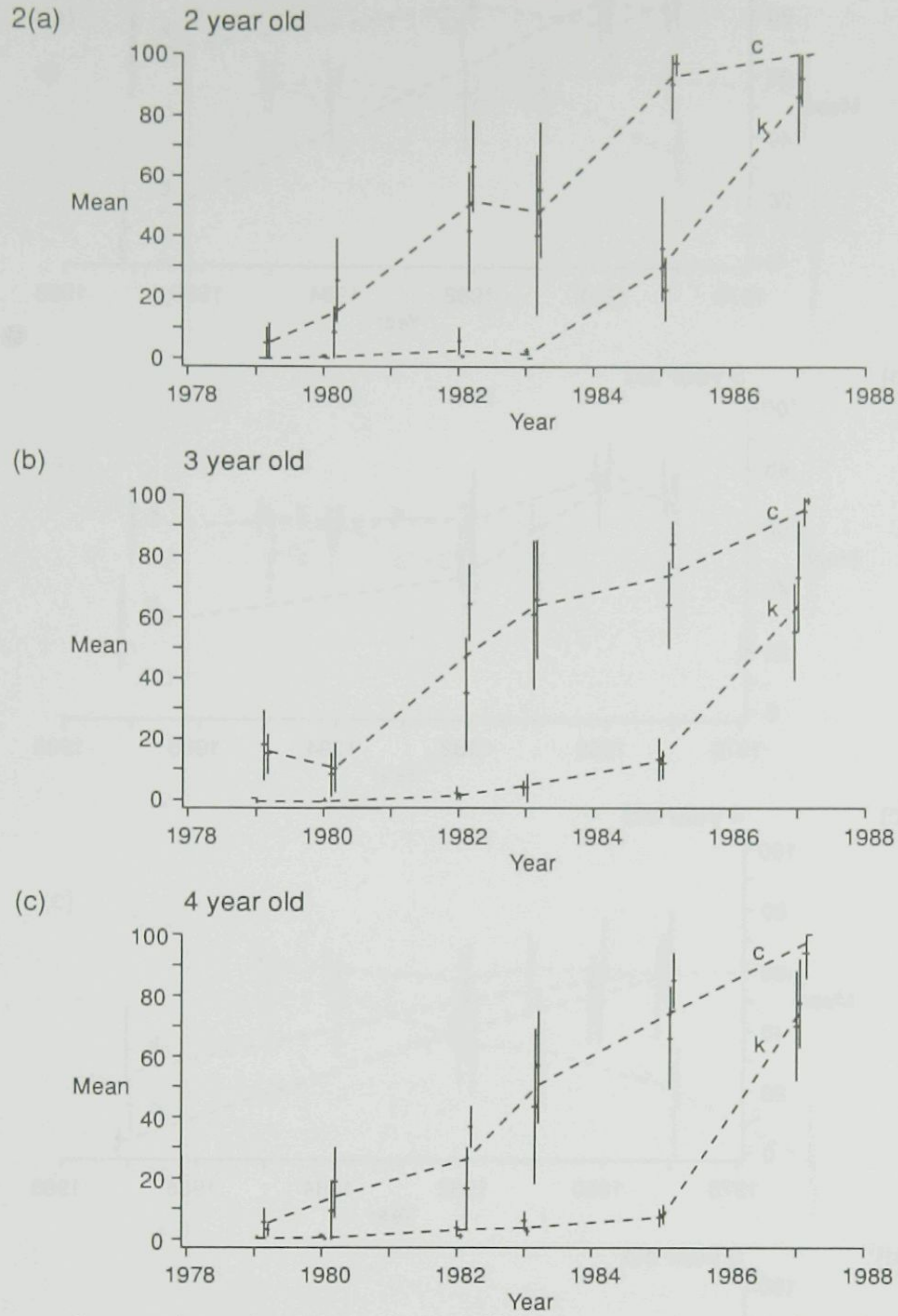

Fig. 2. Percentage of secondary shoot needles of different age classes infected at Hanmer (solid lines denote plot means and 95 % confidence limits; broken lines link provenance means; provenances indicated by k, Kaingaroa, and c, California, respectively)

Table 1. **Mean percentage older needles retained on trees of provenance 31 (Kaingaroa) in 1979 and 1987 at Hanmer**

Shoot/branch order	Age class (years)	Plot No.	1979	1987	Significance[1]
Primary	4	1	58	33	*
		2	66	15	***
	5	1	27	2	**
		2	21	5	***
Secondary	4	1	90	88	NS
		2	92	85	NS
	5	1	73	57	NS
		2	78	62	*

[1] Significance of mean difference between 1979 and 1987, Mann-Whitney test ($p > 0.05$, NS; $p < 0.05$, *; $p < 0.01$, **; $p < 0.001$, ***)

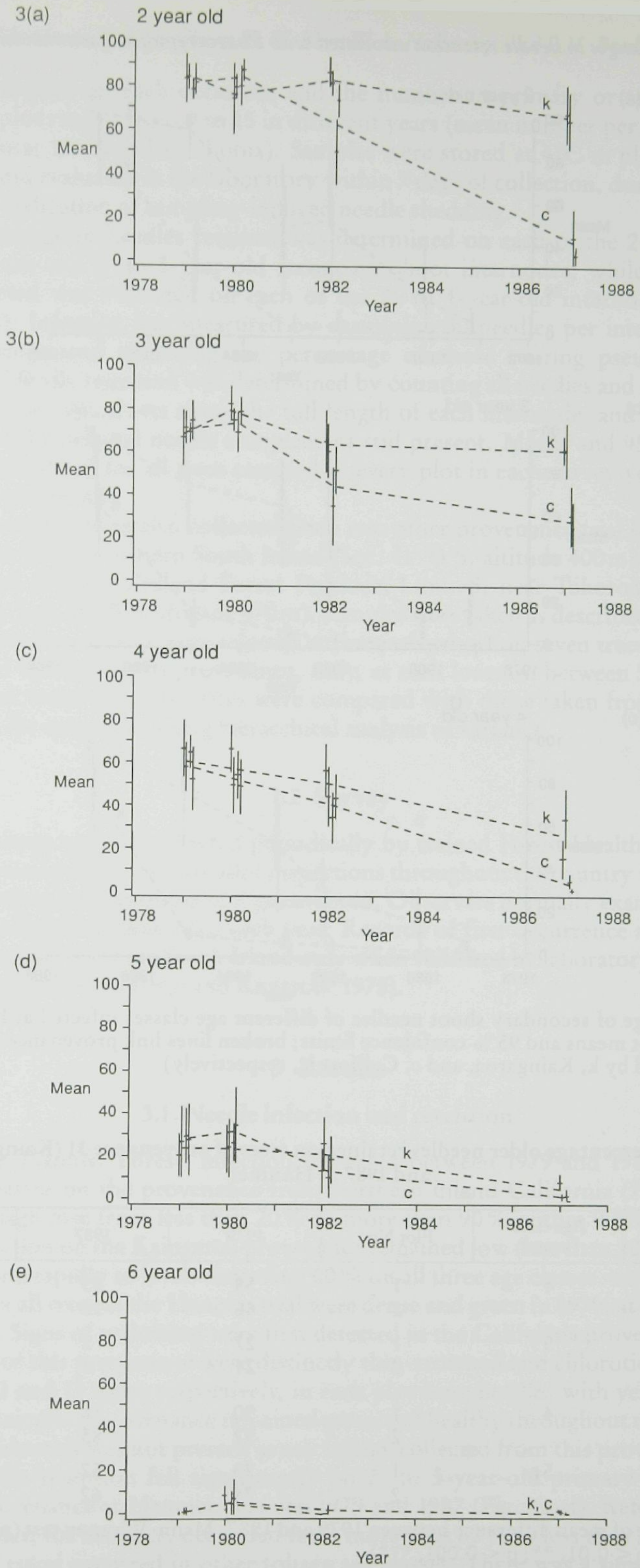

Fig. 3. Percentage of primary shoot needles of different age classes retained at Hanmer (solid lines denote plot means and 95 % confidence limits; broken lines link provenance means; provenances indicated by k, Kaingaroa, and c, California, respectively)

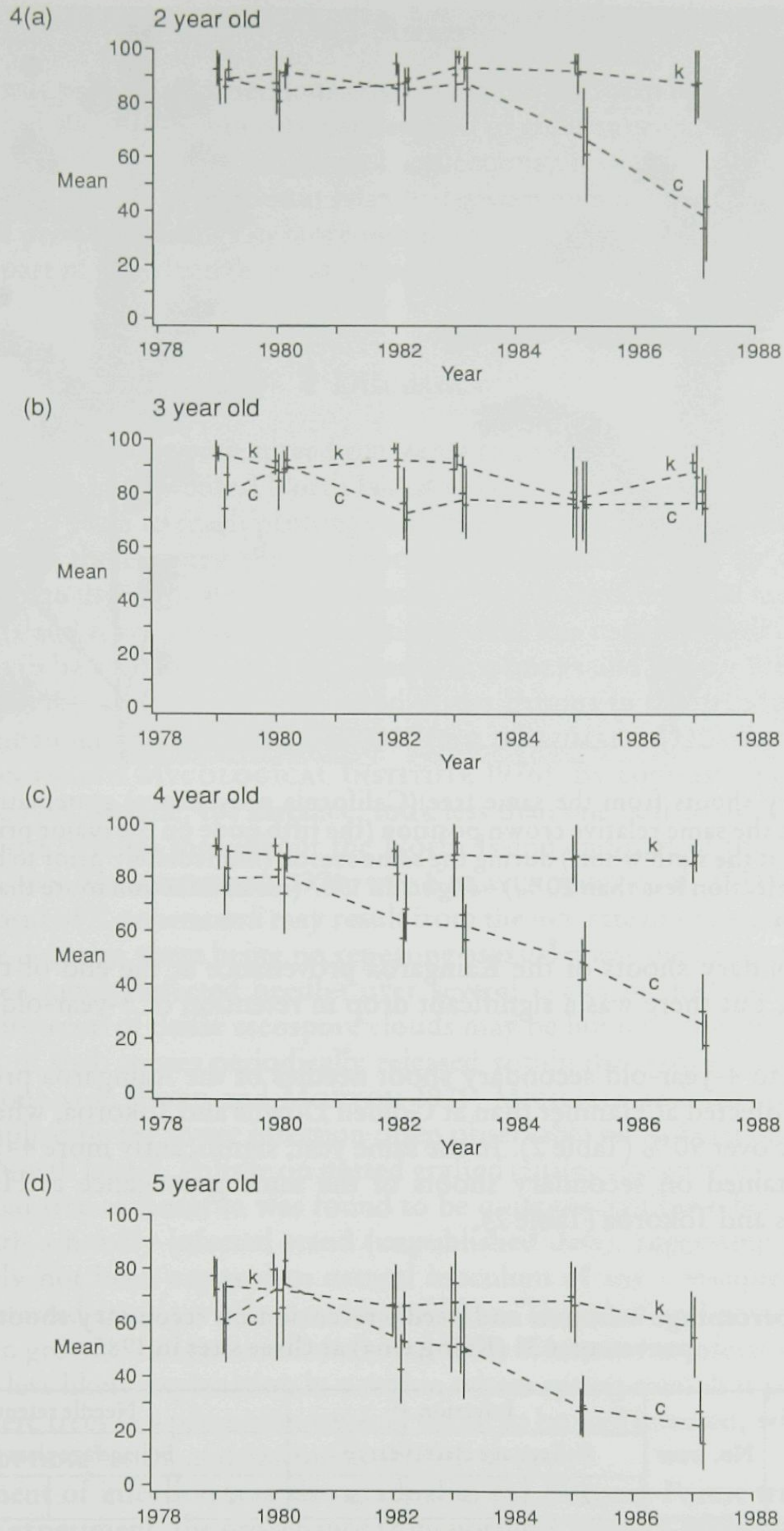

Fig. 4. Percentage of secondary shoot needles of different age classes retained at Hanmer (solid lines denote plot means and 95 % confidence limits; broken lines link provenance means; provenances indicated by k, Kaingaroa, and c, California, respectively)

decrease in retention of 2-, 4- and 5- (but not 3-)year-old foliage on secondary shoots of the same provenance over this period (Fig. 4 a–d; Fig. 5). Needle retention also tended to decrease on primary shoots of the provenance from Kaingaroa during the monitoring period (Fig. 3). The reduction was significant and appreciable for older foliage (Table 1), but of lower magnitude than that of the California provenance. This trend was barely ap-

Fig. 5. Secondary shoots from the same tree (California provenance) systematically selected 8 years apart from the same relative crown position (the fifth node on the major primary branch of southern aspect at the sixth whorl) during the same season (immediately prior to budburst). *Left:* In 1979 (mean infection less than 20 %) – *Right:* In 1987 (mean infection more than 90 %)

parent on secondary shoots of the Kaingaroa provenance at the end of the monitoring period (Fig. 4), but there was a significant drop in retention of 5-year-old foliage in one plot (Table 1).

In 1985, 2- to 4-year-old secondary shoot needles of the Kaingaroa provenance were markedly less infected at Hanmer than at Golden Downs and Tokoroa, where mean infection levels were over 90 % (Table 2). In the same year, significantly more 4- and 5-year-old foliage was retained on secondary shoots of the same provenance at Hanmer than at Golden Downs and Tokoroa (Table 2).

Table 2. **Mean percentage infection and needle retention on secondary shoots from trees of provenance 31 (Kaingaroa) at three sites in 1985**

Site	No. trees	Infection			Needle retention			
		Foliage age class (years)[1]			Foliage age class (years)[1]			
		2	3	4	2	3	4	5
Hanmer	28	29 a	14 a	7 a	94 a	78 a	87 a	68 a
Golden Downs	21	91 b	93 b	100 b	85 a	73 a	32 b	12 b
Tokoroa	21	94 b	96 b	100 b	76 a	53 a	18 b	1 b

[1] Within each column means linked by a common letter subscript are not significantly different (Duncan's test, $p > 0.05$). Variation between plots in forests, not significant, except for 4-year-old foliage retention ($p = 0.03$).

3.2 Survey

P. gaeumannii was present in collections made from the northern half of the South Island during the period 1969–1975, but was not detected in collections taken from sites further south at this time (Fig. 1). In subsequent collections, however, infection was found throughout the full length of the South Island. *P. gaeumannii* has not yet been recorded in certain isolated private plantings in more mountainous terrain east of the Main Divide in the southwest part of the island (e. g., at Queenstown and Wanaka).

4 Discussion

The needle fungus *P. gaeumannii* spread outwards at a steady rate beyond its initial, 1959 focus of distribution in the central North Island of New Zealand, and infection eventually took more than 30 years to reach plantings of Douglas fir in all but a number of the more remote corners of the country (Fig. 1; Hood and Kershaw 1975). Establishment and spread has been equally gradual *within* plantations, as was demonstrated in an earlier study in one North Island forest, in which appreciable time was required for high equilibrium infection levels to be attained within each stand (Stoodley and Hood 1984). This rate of spread is comparable to that which occurred across Europe in the decades following the discovery of the fungus in Switzerland in 1925 (e. g., Gäumann 1930; Thomas 1939; Lyr 1955; Commonwealth Mycological Institute 1976). By contrast, species of the rust genus *Melampsora* Castagne, for instance, took less than one year to infect foliage of susceptible *Populus* L. clones throughout the North Island and part of the South Island of New Zealand (van Kraayenoord 1974; van Kraayenoord et al. 1974). The comparatively slow spread of *P. gaeumannii* may result from the low rate of reproduction (only one infection cycle per year, there being no repeating asexual phase permitting further release of inocula from newly infected needles over several cycles in the one season). It also suggests that dispersal of dense ascospore clouds may be limited, despite the presumably large numbers of such spores periodically released within the crowns of heavily infected stands in the one year (Ford and Morton 1971; Michaels and Chastagner 1984b). This is also implied by the lower infection often observable on isolated open-grown trees in the central North Island. Foliage on potted grafted cuttings taken from a solitary, apparently uninfected tree at Rotorua was found to be quite susceptible when placed for two seasons beneath a heavily infected stand (unpublished data), suggesting that the source tree had simply not been exposed to natural inoculum of any consequence despite the presence of infected stands within a radius of 5 km. That the local environment within crowns of open grown or edge trees is not suitable for at least some infection to occur (Lyr 1955) seems a less likely explanation in a region where spring rainfall is plentiful (Hood 1982), and where trees in a plantation were all found to be well infected, whether they had been thinned or not (Hood and Sandberg 1979).

Establishment of infection was also gradual in the Hanmer Forest trial in the South Island. In this experiment, the provenance from northern inland California was markedly more susceptible to infection than the seedlot from Kaingaroa Forest in the central North Island. Since seedlots used in New Zealand forest plantations since 1926 originated in "the coast ranges of British Columbia, Washington, and Oregon" (Weston 1957), this result is consistent with earlier results from provenance trials in North America (Hood 1982; McDermott and Robinson 1989). However, it is anticipated that expression of resistance to *P. gaeumannii* will be only transitory under the environmental conditions prevailing at Hanmer (mean November–January, 3-monthly-spring-rainfall: 256 mm; New Zealand Meteorological Service 1973). Results indicate that infection levels in both provenances will equilibrate at a high level (over 80 %, Fig. 2), as is already the case in

North Island and northern South Island sites (e. g., Tokoroa, Golden Downs, Table 2) where differences in infection are not known to occur between any seedlot (unpublished data, see HOOD 1982; cf. MARKS and PEDERICK 1975). MCDERMOTT and ROBINSON (1989) raised the possibility that in some provenances susceptibility to *P. gaeumannii* might be induced, as much as intrinsic, due to stress or loss of vigour when seedlots are established outside their natural distribution ranges. Since trees of both provenances evaluated at Hanmer were all vigorous and healthy prior to the advent of *P. gaeumannii*, it is probable that variation in susceptibility is truly inherent in these seedlots. It may be relevant that density of pseudothecia produced on the lower surfaces of infected needles was reported to be a heritable character by NELSON et al. (1989). This does not rule out the possibility of reduced resistance to infection, or of increased symptom expression, when stock is planted on sites particularly unfavourable to the host. It may be that climatic or edaphic stress factors react synergistically with *P. gaeumannii* to produce severely diseased stands of Douglas fir on poor sites.

Needle retention on internodes of certain age classes decreased significantly as infection became established at Hanmer, indirectly supporting the contention that the pathogenicity of *P. gaeumannii* demonstrated in seedling and cutting inoculation experiments also holds true for planted trees. An inverse relationship between intensity of infection and degree of needle retention has previously been observed in diseased Douglas fir plantations (THULIN 1949; MICHAELS and CHASTAGNER 1984 a; NELSON et al. 1989), while CHASTAGNER et al. (1984) found that more heavily infected Douglas fir Christmas trees shed a greater proportion of older needles after cutting and partial drying than did those with less infection. It is not known why foliage was retained longer on 3-year-old secondary internodes of the California provenance than on younger shoots (Fig. 4 b; Fig. 5).

The California provenance was selected from one of several potentially sensitive seedlots believed to be less tolerant of infection, as demonstrated by their markedly poor crown health and growth in trials where mean infection already exceeds 80 % (HOOD 1983). The Kaingaroa provenance was chosen as one likely to indicate the effect of high infection in typical production stands on good sites in New Zealand. As anticipated, needle loss in trees of the Kaingaroa provenance was less severe than in those of the Californian seedlot, and was still barely detectable on secondary shoots at the end of the study period. However, the situation had not stabilised when the study finished, and trends suggest that needle retention will drop further as infection continues to increase to maximum intensity (Fig. 2–4; Table 2). Even so, it is likely that retention levels exceeding 50 % will be maintained on secondary shoots of 1- to 3-year-old foliage on trees of the Kaingaroa seedlot, if one may judge by results at other sites (Table 2), where foliage colour and crown density appear satisfactory despite heavy infection. Well infected production stands in the central North Island are known to retain fewer older age class needles than similar stands in the South Island where there is still only trace, or no infection present (unpublished observations). It therefore seems reasonable to infer that even apparently healthy trees on good sites normally lose older needles prematurely (and perhaps suffer reduced assimilation on still retained foliage; HOOD 1977), if the local environment is such as to permit infection to rise to high equilibrium levels. It is pertinent that a significant, and apparently permanent decrease in growth increments set in during the late 1960s in central North Island Douglas fir, soon after the consolidation of *P. gaeumannii* in forests in this region (BEEKHUIS 1978; B. Manley, unpublished report, 1985). A similar drop in growth increments, also coinciding with the onset of infection, was recorded by MERKLE (1951) in 38-year-old trees sampled in the Federal Republic of Germany.

Acknowledgements

Collections of Douglas fir foliage were made from different parts of New Zealand by members of the Forest Health Survey group. Regional staff of the then New Zealand Forest Service cooperated and assisted actively during the progress of the trial at Hanmer Forest. The manuscript was reviewed by L. BULMAN, M. DICK and P. D. GADGIL. The assistance of these people is gratefully acknowledged.

Summary

The significance of *Phaeocryptopus gaeumannii* (Rohde) Petrak in planted Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] was studied indirectly by monitoring infection and foliage retention in two provenances soon after the appearance of the fungus in Hanmer Forest, New Zealand, in 1978. Infection of secondary shoot foliage on a provenance from northern inland California rose steadily from less than 20 % to more than 90 % needles infected in 9 years. By contrast, in a provenance from production stands in Kaingaroa Forest, New Zealand, infection remained below 20 % for 6 years, before rising rapidly to more than 60 %. Increase in infection in the California provenance was accompanied by the appearance of chlorosis and a decrease in retention of foliage on both primary shoots (2- to 5-year-old needles) and secondary shoots (2-, 4-, and 5-year-old needles). In the Kaingaroa provenance a smaller decrease in needle retention occurred on 4- and 5-year-old primary, but not secondary shoot foliage, and chlorosis was not observed. Retention of 4- and 5-year-old secondary shoot foliage in this provenance was greater at Hanmer (more than 65 %) than at two other sites (less than 20 %) where infection exceeded 90 %, suggesting that retention may decrease further at Hanmer as infection rises to higher levels. It is likely that loss of older age-class needles may be common in heavily infected Douglas fir plantations, even when trees appear healthy.

Résumé

Modification de la persistance des aiguilles en liaison avec l'installation et l'extension de Phaeocryptopus gaeumannii en plantations de Douglas

L'importance de *P. gaeumannii* en plantations de Douglas a été étudiée indirectement en suivant l'infection et la persistance du feuillage chez deux provenances, peu après l'apparition du champignon en forêt de Hanmer (NZ) en 1978. L'infection du feuillage des pousses secondaires d'une provenance intérieure du nord de la Californie, a augmenté régulièrement en 9 ans de moins de 20 % à plus de 90 % des aiguilles. Par contre, chez une provenance d'une forêt productive de Kaingaroa (NZ), l'infection est restée inferieure à 20 % pendant 6 années, avant de croitre rapidement à plus de 60 %. La progression dans la provenance de la Californie s'est accompagnée d'une manifestation chlorotique et d'une baisse de persistance du feuillage, aussi bien chez les pousses primaires (aiguilles de 2 à 5 ans) que secondaires (aiguilles de 2, 4 et 5 ans). Dans la provenance de Kaingaroa une baisse plus faible de la persistance avait lieu pour les aiguilles de 4 et 5 ans des pousses primaires, et pas chez les pousses secondaires; la chlorose n'était pas observée. La rétention des aiguilles de 4 et 5 ans des pousses secondaires chez cette provenance était plus grande à Hanmer (plus de 65 %) que dans deux autres sites (moins de 20 %) où l'infection dépassait 90 %; ceci laisse supposer que la rétention peut diminuer ultérieurement à Hanmer quand l'infection augmentera. Il est probable que la perte des aiguilles plus âgées soit usuelle dans les plantations fortement infectées, même si les arbres semblent sains.

Zusammenfassung

Veränderungen in der Benadelung in Abhängigkeit von Ausbreitung und Manifestierung von Phaeocryptopus gaeumannii in gepflanzten Douglasienbeständen

Die Bedeutung von *Phaeocryptopus gaeumannii* in künstlich begründeten Douglasienbeständen wurde indirekt durch Bonitierung der Infektion und des Benadelungsgrades an zwei Provenienzen untersucht, und zwar bald nach dem Auftreten des Pilzes 1978 im Hanmer Forest, Neuseeland.

Die Infektion der Nadeln von Trieben 2. Ordnung einer Provenienz aus dem Innern Nordkaliforniens stieg in 9 Jahren ständig von weniger als 20 % auf mehr als 90 %. Im Gegensatz dazu blieb der Infektionsgrad in einer Herkunft aus dem Kaingaroa Forest, Neuseeland, während 6 Jahren unter 20 %, bevor er rasch auf über 60 % anstieg. Der Anstieg der Infektion in der kalifornischen Provenienz war von Chlorose und einer Abnahme der Verweildauer der Nadeln an Zweigen 1. Ordnung (2- bis 5jährige Nadeln) und 2. Ordnung (2-, 4- und 5jährige Nadeln) begleitet. Bei der Provenienz aus dem Kaingaroa Forest war eine geringere Abnahme des Benadelungsgrades an 4- und 5jährigen Teilen von Zweigen 1. Ordnung zu beobachten, nicht so bei der Benade-

lung der Zweige 2. Ordnung. Außerdem wurde keine Chlorose festgestellt. Die Benadelung mit 4- und 5jährigen Nadeln an Zweigen 2. Ordnung war bei dieser Provenienz im Hanmer Forest größer (über 65 %) als an zwei anderen Standorten (weniger als 20 %), an denen der Infektionsgrad über 90 % lag, was die Annahme zuläßt, daß der Benadelungsgrad im Hanmer Forest abnehmen wird, wenn der Infektionsgrad ein höheres Niveau erreicht haben wird. Es ist wahrscheinlich, daß der Verlust älterer Nadeljahrgänge in stark infizierten Douglasienpflanzungen normal ist, selbst wenn die Bäume gesund aussehen.

References

BEEKHUIS, J., 1978: Growth decline in Douglas fir. pp. 119–125. In: A review of Douglas fir in New Zealand. New Zealand Forest Research Institute Symposium No. 15, 16–19 September, 1974. Ed. by R. N. JAMES, E. H. BUNN. New Zealand Forest Service (455 pp.).

BOYCE, J. S., 1940: A needle-cast of Douglas fir associated with *Adelopus gäumanni*. Phytopathology **30**, 649–659.

CHASTAGNER, G. A.; BYTHER, R. S.; MACDONALD, J. D.; MICHAELS, E., 1984: Impact of Swiss needle cast on postharvest hydration and needle retention of Douglas-fir Christmas trees. Plant Disease **68**, 192–195.

COMMONWEALTH MYCOLOGICAL INSTITUTE, 1976: Distribution maps of plant diseases, Map No. 42, edition 4 [*Phaeocryptopus gaeumannii* (Rohde) Petrak on *Pseudotsuga menziesii*); 2 pp. Commonwealth Agricultural Bureaux.

FORD, K. F.; MORTON, H. L., 1971: Etiology, impact and distribution of Swiss needle cast on Douglas-fir in Michigan. Phytopathology **61**, 1023.

GÄUMANN, E., 1930: Über eine neue Krankheit der Douglasien. Schweizerische Z. Forstw. **81**, 63–67.

HOOD, I. A., 1977: Inoculation experiments with *Phaeocryptopus gaeumannii* on Douglas fir seedlings. New Zealand J. For. Sci. **7**, 77–82.

– 1982: *Phaeocryptopus gaeumannii* on *Pseudotsuga menziesii* in southern British Columbia, New Zealand J. For. Sci **12**, 415–424.

– 1983: Swiss needle-cast of Douglas fir. Forest Pathology in New Zealand No. **2**. Ed. by P. D. GADGIL. New Zealand Forest Research Institute (4 pp.).

HOOD, I. A.; KERSHAW, D. J., 1975: Distribution and infection period of *Phaeocryptopus gaeumannii* in New Zealand. New Zealand J. For. Sci. **5**, 201–208.

HOOD, I. A.; SANDBERG, C. J., 1979: Changes within tree crowns following thinning of young Douglas fir infected by *Phaeocryptopus gaeumannii*. New Zealand J. For. Sci. **9**, 177–184.

HOOD, I. A.; VAN DER PAS, J. B., 1979: Fungicidal control of *Phaeocryptopus gaeumannii* infection in a 19-year-old Douglas fir stand. New Zealand J. For. Sci. **9**, 272–283.

LYR, H., 1955: Untersuchungen zur Pathologie der Douglasie. Archiv Forstwesen **4**, 533–544.

MCDERMOTT, J. M.; ROBINSON, R. A., 1989: Provenance variation for disease resistance in *Pseudotsuga menziesii* to the Swiss needle-cast pathogen, *Phaeocryptopus gaeumannii*. Canadian J. For. Res. **19**, 244–246.

MARKS, G. C.; PEDERICK, L. A., 1975: Sensitivity of Douglas-fir provenances to Swiss needle cast disease. In: Research activity 75. A summary of research for 1975. Ed. by RHONDA IDCZAK. Forests Commission, Victoria, Australia.

MERKLE, R., 1951: Über die Douglasien-Vorkommen und die Ausbreitung der Adelopus-Nadelschütte in Württemberg-Hohenzollern. Allgemeine Forst- und Jagdzeitung **122**, 161–192.

MICHAELS, E.; CHASTAGNER, G. A., 1984 a: Distribution, severity and impact of Swiss needle cast in Douglas-fir Christmas trees in Washington and Oregon. Plant Disease **68**, 939–942.

– 1984 b: Availability of *Phaeocryptopus gaeumannii* ascospores and conditions which influence their release. Plant Disease **68**, 942–944.

NELSON, E. E., SILEN, R. R.; MANDEL, N. L., 1989: Effects of Douglas-fir parentage on Swiss needlecast expression. Eur. J. For. Path. **19**, 1–6.

NEW ZEALAND METEOROLOGICAL SERVICE, 1973: Rainfall normals for New Zealand 1941 to 1970. Miscellaneous Publication **145**. New Zealand: Ministry of Transport.

PEACE, T. R., 1962: Pathology of trees and shrubs, with special reference to Britain. Oxford: Clarendon Press, 753 pp.

ROHDE, T., 1937: Über die *„Schweizer"* Douglasienschütte und ihren vermuteten Erreger *Adelopus* spec. Mitteilungen Forstw. Forstwiss. **4**, 487–514.

SKILLING, D. D., 1981: Control of Swiss needlecast in Douglas fir Christmas trees. Amer. Christmas Tree Journal **25**, 34–37.

STOODLEY, M. A.; HOOD, I. A., 1984: Distribution of *Phaeocryptopus gaeumannii* on Douglas fir in a New Zealand forest. Australasian Plant Pathology **13**, 62–64.

STRITTMATTER, W., 1974: Ökologische und biologische Studien an der Baumart Douglasie im Zusammenhang mit dem Auftreten von *Phaeocryptopus gäumanni* (Rohde) Petr. Schriftenreihe Landesforstverwaltung Baden-Württemberg **43**, 1–75.

SWEET, G. B., 1965: Provenance differences in Pacific Coast Douglas fir. Silvae Genetica 14, 46–56.

THOMAS, E. A., 1939: Über die Schweizer Douglasienschütte. Schweizerische Z. Forstw. 90, 55–62.

THULIN, I., 1949: Beskadigelser af Douglasgran (*Pseudotsuga taxifolia*) i Danmark i vinteren 1946–47. Det forstlige Forsøgsvaesen 19, 285–329.

VAN KRAAYENOORD, C. W. S., 1974: Melampsora poplar leaf rust in New Zealand. Research report to 31 December 1973. Published by Ministry of Works and Development for National Water and Soil Conservation Organisation, Wellington, New Zealand (9 pp.).

VAN KRAAYENOORD, C. W. S.; LAUNDON, G. F.; SPIERS, A. G., 1974: Poplar rusts invade New Zealand. Plant Disease Rep. 58, 423–427.

WESTON, G. C., 1957: Exotic forest trees in New Zealand. Statement prepared for the 7th British Commonwealth Forestry Conference, Australia and New Zealand, 1957. Bulletin No. 13, New Zealand Forest Service, Wellington, New Zealand, 104 pp.

Authors' addresses: I. A. HOOD, C. J. SANDBERG, Forest Research Institute, Private Bag, Rotorua, New Zealand; C. W. BARR, Ministry of Forestry, P. O. Box 13 40, Rotorua, New Zealand; W. A. HOLLOWAY, 109 Edward Street, Wakefield, Nelson, New Zealand; P. M. BRADBURY, Ministry of Forestry, P. O. Box 25-022, Christchurch, New Zealand

Receipt of ms.: 18. 4. 1990