SPRING NEEDLE-CAST OF *PINUS RADIATA* IN TASMANIA:
I. SYMPTOMS, DISTRIBUTION, AND ASSOCIATION WITH *CYCLANEUSMA MINUS* *

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ABSTRACT

"Spring needle-cast" (SNC) is an undiagnosed disease of *Pinus radiata* D. Don which causes a rapid browning and collapse of mesophyll tissues of 1-year-old needles in spring and is followed by premature and heavy casting of needles. It first appears about the time of canopy closure and affects between 40% and 80% of trees randomly distributed in closed stands in areas of Tasmania which receive between 1200 and 2000 mm annual rainfall. The incidence and severity of disease appear not to be highly sensitive to local topographic variation and remain relatively constant from year to year. SNC is distinguished from other foliar diseases and disorders of *P. radiata* in Tasmania, including *Dothistroma septospora* Morelet, on the basis of gross symptoms and the phenology of their development. Three common needle-inhabiting fungi, *Cyclaneusma minus* (Butin) DiCosmo Peredo & Minter, *Lophodermium pinastri* (Schard. ex Fr.) Chev., and *Strasseria geniculata* (Berk. & Br.) Hohn., were ubiquitous on fallen dead needles, but none was constantly associated with recently cast needles on SNC-affected trees. Complete foliar sprays with chlorothalinol (500 g a.i./*l*) at intervals of 6 weeks for the first 6 months of one growing season markedly improved needle retention.

It is postulated that SNC is due to the secondary pathogenic activity of one or a suite of endophytic fungi following as yet unidentified seasonal but ephemeral stress.

Keywords: needle-cast; climate; etiology; Tasmania; *Cyclaneusma minus*; *Pinus radiata*

INTRODUCTION

Episodes of premature and heavy shedding of foliage of *Pinus radiata* have been reported over much of the range of exotic cultivation of this industrially important species (Gibson

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1972; Edwards & Walker 1978; Gadgil 1984). The species is capable of retaining the needle production of as many as 6 consecutive years, but most commonly carries that of 2 to 4. Retention of less than this level is considered to be abnormal.

A number of physical and biotic factors which have caused excessive needle loss in *Pinus* have been documented (Sinclair *et al.* 1987). The most severe cases in *P. radiata* are usually attributed to infection by needle-inhabiting fungi such as *Dothistroma septospora* and *Cyclaneusma minus*.

In 1976 we first observed a case of severe needle-casting of 1-year-old needles among a high proportion of trees in closed canopy stands (usually 6 years and older) of *P. radiata* in highly productive plantations in moist environments in north-western Tasmania. A search of unpublished documents of the Forestry Commission, Tasmania, indicated that records of severe defoliation, of what is almost certainly the same problem, were made in 1964, 1968, and 1971; all of these refer to severe symptoms in October. Regular observation since 1976 has indicated that the disease is endemic over some thousands of hectares in closely planted stands. Its incidence and severity appear to be less sensitive to variability in weather conditions and terrain than might be expected of epidemic behaviour of a primary foliar pathogen.

In earlier unpublished correspondence this disease has been referred to as "spring yellows", a name which has caused some confusion for reasons outlined below. We now prefer the name "spring needle-cast".

In this paper we describe the symptoms of SNC and its geographic and climatic distribution, and discuss the possible role of needle-inhabiting fungi, particularly *C. minus*, in its etiology.

MATERIALS AND METHODS

Location of Study Sites

The stands of *P. radiata* selected to survey the distributions of SNC and of *C. minus* were located so that the Tasmanian range of climatic and geological variation of the host was fully represented. Sites referred to in the text are indicated in Fig. 1.

Distinction of SNC Symptoms from Other Foliar Conditions

Description of the symptoms of SNC and their relationship to those of other diseases and disorders of *P. radiata* observed by us in Tasmania are based upon repeated observations in the experiments described by Podger & Wardlaw (1990), and by opportunistic observations made over more than a decade since 1976 in plantations throughout the State.

Needle colours were classified according to the Munsell classification (Anon. 1977). Effects on needle structure were examined microscopically on transverse thin sections.

Resistance and Susceptibility Within Populations of *P. radiata*

Data on the stability of symptom expression were derived from two sources. The first source was the clonal seed orchard at Upper Natone which is the only orchard of suitable age

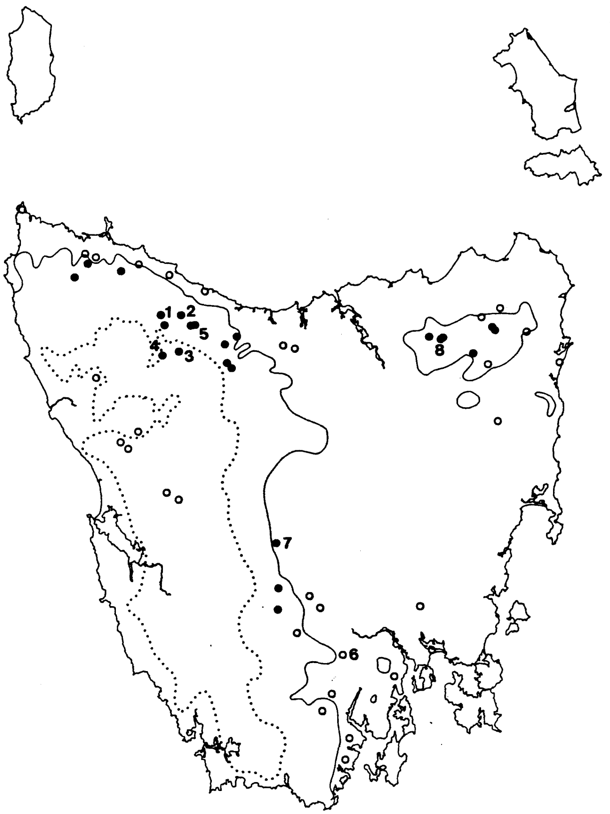

FIG. 1–Location of stands of *P. radiata* in Tasmania with (•) and without (○) spring needle-cast; 1200-mm (——) and 2000-mm (.....) isohyets are indicated. Sites referred to in the text are (1) Snowdon Plains, Lockwood Creek, and Atkinsons Road, (2) St Josephs, (3) Peak Plains, (4) Parrawe, (5) Upper Natone Seed Orchard, (6) Mt Lloyd, (7) Tarraleah, and (8) East Diddleum.

in the region of severe SNC. It was established in 1973 as an unbalanced, randomised, block design and was heavily thinned in 1985. Because of the reduction in disease severity which follows thinning (Podger & Wardlaw 1990) levels of SNC were not as high as in neighbouring unthinned stands. Disease levels were therefore rated on a scale of 0–5, with 5 taken as the most severe level of SNC observed in the orchard. All trees in a sample of 10 blocks were assessed in November 1988. This included four to 10 trees (mean and median seven) in each of 53 clones. The data were subjected to an analysis of variance for unbalanced designs using a computer program developed by Harvey (1977) to calculate clonal repeatability (genetic variance/total variance). Scatter diagrams relating average SNC score to other attributes for genetic selection, viz basal area, height, stem straightness, branch size, and internode length, were plotted for inspection of possible correlations.

The second source of data was repeated visual assessments of the crown health of trees made over several years in four field trials (*see* Podger & Wardlaw 1990 for details).

Patterns of Disease Distribution

Geographic

Fifty-three sites were selected to represent the geographical range of *P. radiata* in Tasmania. The requirements for selection of sites were that the canopy of each stand be closed and that at least 50 codominant or dominant trees, buffered on all sides by at least one row of trees, be available for assessment. A tree was considered to be SNC-affected if shedding of 1-year-old needles was occurring in the unsuppressed part of the tree crown. Each stand was classified as SNC "affected" or "unaffected" on the basis of a visual assessment of retention of 1-year-old needles on a sample of at least 50 internal codominant or dominant trees.

Stands were classified as SNC-affected if 2% or more of the sample trees displayed typical symptoms. Disease incidence in almost all stands which had been affected for 1 year or more exceeded 30% and often more. Those few stands with a single or very few affected trees were excluded from comparative studies of affected and unaffected stands.

There was a geographic bias in the sample which reflects that inherent in land available for plantation forestry. The sample does not therefore represent a complete and balanced sample of Tasmanian climates and geological substrates. It provides nonetheless a comprehensive, if unbalanced, sample of the occurrence of plantation-grown *P. radiata* in Tasmania.

Climatic

The computer program BIOCLIM (Busby 1986; Hutchinson 1983; Nix 1986), which was developed to analyse climatic characteristics of biological distributions, has been applied to a Tasmanian study of climatic constraints on the occurrence of root-rot disease in native vegetation (Podger *et al.* 1990). It has been applied, with further modification here, to discriminate between the climatic envelope for SNC and that for the over-all distribution of *P. radiata* in Tasmania.

The latitude, longitude, and elevation of each of the 53 stands sampled was used as input to BIOCLIM to obtain for each stand values of each of 16 climatic indices which are calculated from estimates of mean monthly rainfall and temperature. The indices describe mean, seasonal, and extreme values. These data were subjected to principal components analysis to determine which of the climatic indices would be most useful for discriminating between the climatic envelope for SNC and that for the Tasmanian distribution of *P. radiata*.

Relationship to variation in exposure to wind and solar radiation

Because we had observed, throughout the range of SNC, that there appeared to be a much lower incidence of defoliation along edge rows than in the interior of stands, we assessed the incidence and severity of SNC in relation to exposure and aspect in and around a severely affected 10-year-old stand at Parrawe. Assessments were made in eight single-row transects (range 50–100 trees per transect). All dominant and codominant trees in each transect were assigned a SNC score (on a scale of 0–5 as defined by Podger & Wardlaw 1990). The number of trees affected by SNC (those with an SNC score of more than 1) and the average SNC score of trees affected by SNC were calculated for each transect.

Distribution of SNC within stands

The apparent randomness in the distribution of SNC within stands and the variability in its severity among affected trees are clearly evident from low-flying aircraft (particularly during October and November). After reconnaissance flights at a range of altitudes, aerial colour-transparency photographs, at a scale of 1:2000, were obtained in October 1980 on 12 transects selected to cover a range of SNC severity as well as several stands with symptoms of other disorders. Ground-truth was assessed in February 1981.

The distribution of SNC inside closed-canopy stands was also assessed by ground survey at three sites. In 1982, 262 contiguous trees in a 10-year-old stand at Lockwood Creek were rated as either "affected" or "unaffected". In 1989, at both Peak Plains and Upper Guide Road, 200 contiguous trees were rated for SNC score in stands aged 20 and 30 years respectively. Runs of diseased and healthy trees were tested for randomness by the methods of Vithayasai (1971).

Patterns of needle-cast within trees

In June 1980 the patterns of foliar retention were described on each of 28 healthy and 28 diseased trees in an 8-year-old stand in St Josephs Block which had shown symptoms for 2 years. The trees had been pruned to 2 m prior to assessment. Height above ground of the point of attachment of each whorl to the main stem was measured and the number of needle-bearing annual increments in each of the first, second, or greater orders of branching was counted. Comparisons were made on whorls at two levels. These were that nearest 2.2 m (the mean of the lowest living whorl on all healthy trees) and that nearest 5.2 m (the mean of the upper level of defoliation for all diseased trees). Two healthy trees and three diseased trees which had no whorl beneath 3.5 m were excluded.

In October 1984 three severely diseased and three healthy trees were felled and all green needles harvested and weighed. Subsamples were taken for calculation of oven-dry weight.

Relationship Between Vigour and Susceptibility to Disease

The extent to which susceptibility to disease might be influenced by vigour was examined by an analysis of the data for 239 "affected" trees in Experiment 4 of Podger & Wardlaw (1990). A simple linear regression was used to examine the relationship between SNC score in 1986, a measure of susceptibility, and diameter in 1984, a measure of vigour prior to onset of disease.

Role of Fungi

Fungi associated with senescent needles

We have made no attempt to survey in detail the endophytic flora nor to study the phenology of endophytic colonisation of living needles. Our survey has been restricted to the fungi fruiting on senescent needles.

On-site inspection of recently shed needles was made at each of the 53 sites of the geographic survey. At each of these sites the presence of *Cyclaneusma* sp. fruiting bodies was determined. At 17 SNC-affected sites samples were retained for a more detailed microscopic examination of fruiting body and spore morphology.

Measurements of the length of between 50 and 200 *Cyclaneusma* apothecia were made on needles collected from each of 15 SNC-affected and 15 unaffected sites. Analyses of variance were performed to test for differences in apothecial length (a) between SNC-affected and unaffected sites, and (b) between those sites receiving >1200 mm annual rainfall and those receiving <1200 mm.

Fungicidal control

Two experiments were performed: one, an attempt at corrective treatment by complete immersion of single shoot units; the second, an attempt at preventative spray treatments of whole trees.

At Lockwood Creek three susceptible trees were selected on the edge row of a 15-m-wide firebreak so that shoots could be treated from the ground. In each tree five sets of four second-order shoots, of the 1981–82 season and of uniform size, were selected. In each set one shoot was randomly assigned to each of four treatments: (a) control, (b) copper oxychloride dip, (c) Benlate dip, (d) Benlate-Difolitan dip—all at the manufacturers' recommended concentrations. Treatments commenced in late-August and were repeated at intervals of 6 weeks until March 1983. The treatments were assessed in November 1983 as counts of the proportion of fascicles retained among a sample of 100 contiguous original fascicles (determined by counts of attachment scars on the shoot axis).

The whole-tree spray experiment was conducted at Atkinsons Road inside a 7-year-old stand. In August 1983, prior to the first onset of disease, three rows, each separated by a buffer row, were selected. Within each row two lines of 11 adjacent trees were selected as experimental subjects. The two sets within each row were separated by three buffer trees. At intervals of 6 weeks between August 1983 and April 1984 the entire foliage of each subject tree in three of the six sets was sprayed to run-off with chlorothalonil (500 g a.i./*l*) applied with an Echo SHR 200E power sprayer. In November 1984 SNC score was assessed on all trees.

RESULTS

Symptoms of SNC and Their Distinction from Other Foliar Conditions

Symptoms

The gross diagnostic feature of SNC is heavy casting of 1-year-old needles which affects the lower, middle, and in some trees all but the uppermost parts of the crown. Extensive disease is first evident in the populations during spring of the first year after canopy closure, though very occasional trees may exhibit typical symptoms of SNC in the year before canopy closure. During September-October the middle 50–60% of the needle length of previously healthy, 1-year-old needles rapidly collapsed and turned yellow-brown. Microscopic examination of cross-sections of shrunken sections showed that all parenchymatous cells of the transfusion tissue had collapsed about the vascular bundles, the endodermis was distorted and flattened with few chloroplasts, and the mesophyll had very few chloroplasts remaining and was completely collapsed and disorganised. Initially the proximal and distal ends of the needle remained turgid and green. Chlorosis then progressed from the collapsed central portion towards the distal end of the needle and finally from the base upwards before the needles began to shed in November. In some instances the needles of SNC-affected trees showed an acropetal gradient of chlorosis or, less commonly, mottled chlorotic spotting over the entire needle. However, these last two symptoms were also seen in older needles in stands unaffected by SNC.

During April-May in years following first onset of the disease, current season's needles of many affected trees exhibited a strong basipetal gradient of needle chlorosis (Table 1). This symptom became less obvious during the spring and was not apparent at the time of needle casting (November). Marked basal needle chlorosis has not been observed in unaffected trees. A uniform needle chlorosis sometimes occurred in stands affected by incipient nutrient deficiencies (*see* Table 1, the data for Mt Lloyd).

Repeated annual episodes of defoliation on first-order laterals resulted in a thin tufted appearance in the affected parts of the crown. A few of these weakened shoots suffered dieback though the majority persisted, possibly because of improved light conditions in the lower crown.

TABLE 1–Comparison of needle colours on terminal shoots of first-order branches in mid-crown of SNC-affected and unaffected trees within several Tasmanian stands of *P. radiata* (based on Munsell Color subdivisions of green-yellow hue) and assessed on samples of 10 (East Diddleum, Tarraleah, Mt. Lloyd) or 30 needles (Peak Plains and Snowdon Plains).

	Location on needle		
	Tip	Middle	Base
Affected trees			
Peak Plains	5.5	4.0	2.8
Snowdon Plains	6.7	5.3	3.6
East Diddleum	5.8	5.0	4.3
Unaffected trees			
Tarraleah	7.5	7.5	7.3
Mt Lloyd	5.8	5.8	5.5
East Diddleum	6.3	7.5	5.4

Distinction from other foliar conditions

We have encountered 10 distinct foliar conditions (including SNC) involving yellowing or needle-casting of *P. radiata* during the course of investigations of SNC in Tasmania. They include one certain case of primary fungal parasitism, two cases of what may constitute normal senescence, three cases of nutritional deficiency, and four cases of possible fungal parasitism.

These conditions differ in seasonality of their appearance, their duration, extent, severity, and other characters. Some have been mistakenly reported to us as additional occurrences of SNC, the disease which, until recently, we had referred to as "spring yellows". Brief accounts of their more distinctive characteristics which are necessary circumscription of our definition of SNC are given in Appendix 1. Of the 10 conditions, all but Dothistroma needle blight have been observed since the beginning of the investigation.

Resistance and Susceptibility Within Populations of *P. radiata*

The clonal repeatability (gross heritability or genetic repeatability) for SNC score in the Upper Natone clonal seed orchard was 0.256, a reasonably high value compared to that for many growth traits (C. Raymond pers. comm.). None of the five silvicultural attributes showed any evidence of correlation with SNC score.

Evidence from three experiments reported by Podger & Wardlaw (1990) indicates that the incidence and severity of disease is largely stabilised within the first few years of its onset. Between July 1980 and October 1984 only two of 56 trees at St Josephs changed their classification. No tree among 50 assessed at Lockwood Creek changed between affected and unaffected classifications during the period December 1983 to March 1986. At these two sites the disease had been established for at least 1–2 years prior to initial assessment. At Snowdon Plains where the first assessment in October 1986 was a year closer to first onset, the incidence of SNC among 558 trees in an unthinned stand increased from 40% to 53% by March 1989. Between 1986 and 1989 only 13% of trees were recorded as having an increased SNC score of 2 or more units. Almost without exception they were trees rated as unaffected in 1986. No tree improved in health by more than 1 unit of disease severity (Table 2). An increase or decrease of 2 units of SNC score is the minimum change for confidence that there is a real difference (Podger & Wardlaw 1990).

TABLE 2–Changes in disease severity (percentages of all trees for which the 1989 SNC score differed from the 1986 score by 1, 2, or more units), among 558 trees in an unthinned stand of *P. radiata*. Data are derived from SNC scores assigned in the unthinned treatments of Experiment 4 described by Podger & Wardlaw (1990).

	Change in SNC Score						
	Less disease				More disease		
Number of units of change	>2	2	1	0	1	2	>2
Percentage of trees	0	0	5	60	21	10	3

Patterns of Disease Distribution

Geographic

The distribution of stands selected for climatic analysis and the subset of stands which were affected by SNC is shown in Fig. 1. Twenty-three of the 53 sites were assessed as having SNC.

The distribution reflects a biased sample of the range of sites in Tasmania. In lowland areas (<400 m) the majority of *P. radiata* plantations occur in lower rainfall areas (<1000 mm rainfall per annum) on soils of low fertility because of competition for land for agriculture. At higher elevations (>400 m) there is a preference for establishing plantations on sites of moderate to high fertility in areas receiving more than 1200 mm rainfall per annum. There were few localities in the West Coast region which met the requirements of selection; all sites but the Strahan Plantation in that region were small trial plots.

These factors have contributed to a preponderance of plantations on igneous substrates within the range of occurrence of SNC. The soils are principally krasnozems on Tertiary basalts and light-coloured gradational soils on Devonian granites. However, there are also occurrences of severe SNC on duplex soils (mainly yellow podsolics) on Ordovician metasediments and limestone and Cambrian sediments and metasediments.

Climatic

The minimum and maximum values of each of the 16 indices for the 53 *P. radiata* stands sampled are given in Table 3, together with the values of the subset affected by SNC.

TABLE 3–Range of elevation, and ranges of 16 climatic indices (derived by the computer program BIOCLIM) for the Tasmanian occurrence of *P. radiata* (p) and for that of SNC (s).

Parameter	Min_p	Min_s	Max_s	Max_p
Elevation (m)	5	140	820	820
Mean annual temperature (°C)	7.9	7.9	11.7	12.9
Mean minimum coolest month	–0.3	–0.3	5.2	6.1
Mean maximum warmest month	18.7	18.7	21.0	23.3
Temperature span*	14.7	15.5	19.1	20.4
Mean temperature coolest quarter	3.6	3.6	8.6	9.6
Mean temperature warmest quarter	12.2	12.2	15.5	17.0
Mean temperature wettest quarter	4.1	4.1	8.6	13.1
Mean temperature driest quarter	8.1	12.1	15.5	16.7
Mean annual rainfall (mm)	563	1247	2007	2898
Rainfall wettest month	59	130	256	321
Rainfall driest month	39	57	93	148
Rainfall coefficient of variation†	12.3	21.7	38.2	38.2
Mean rainfall wettest quarter	165	380	711	895
Mean rainfall driest quarter	126	192	291	505
Mean rainfall coolest quarter	133	376	711	895
Mean rainfall warmest quarter	126	192	291	505

* Calculated as the mean annual maximum – minimum.

† An index of the seasonality of rainfall: seasonality of rainfall increases as the coefficient of variation increases.

The first axis of the principal components analysis explained 56% of the variation between all 53 sites. This axis was weighted equally by elevation, rainfall, and temperature and described the trend of increasing rainfall and decreasing temperature with increasing elevation. BIOCLIM parameters based on rainfall were strongly correlated with one another, as were parameters based on temperature, and elevation was correlated with both sets of parameters (positively with rainfall and negatively with temperature). Because of these strong correlations it was considered that satisfactory representations of the climatic envelopes for *P. radiata* and for SNC could be achieved using mean annual temperature and mean annual rainfall.

The scatter plot of mean annual temperature against mean annual rainfall (Fig. 2) shows that *P. radiata* occupies sites within the range of mean annual temperature 8–13°C and mean annual rainfall 500–3000 mm, while SNC is restricted by rainfall to within the range 1200–2000 mm and mean annual temperatures 8–11.5°C.

Relationship to variation in exposure to wind and solar radiation

Differences in exposure were associated with large differences in disease incidence, but had little effect on severity. The position of each transect in the stand at Parrawe and its exposure to prevailing winds are shown in Fig. 3. Boundaries exposed to the dominant wind directions (north, south, and west) had considerably lower incidence of SNC than any of the edge trees in the protected eastern boundary, or those on narrow (<10 m) internal roads, or

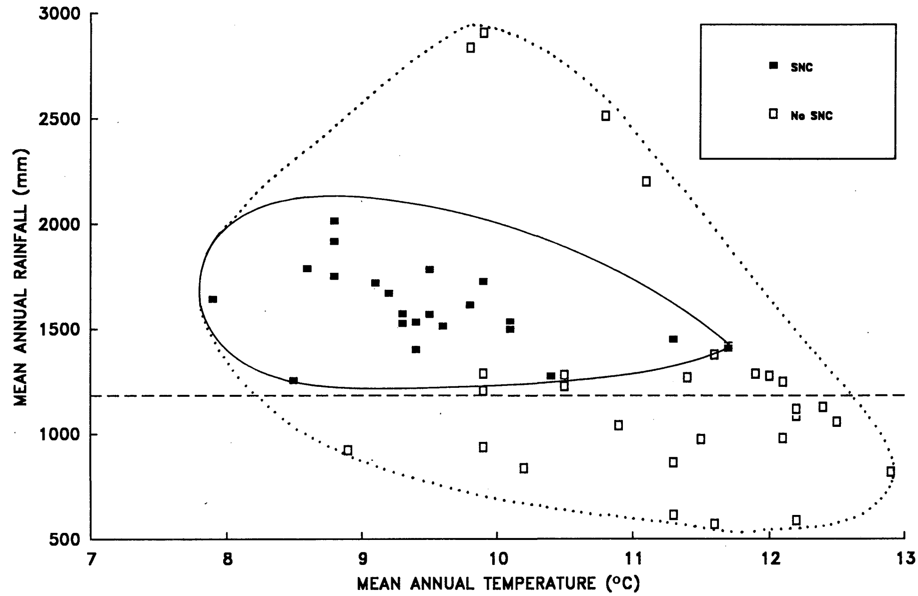

FIG. 2–Plot of mean annual rainfall against mean annual temperature for sites with (■) and without (□) spring needle-cast, indicating climatic envelopes for spring needle-cast (——) and *P. radiata* (equivalent to distribution of *C. minus*) (.....) in Tasmania.

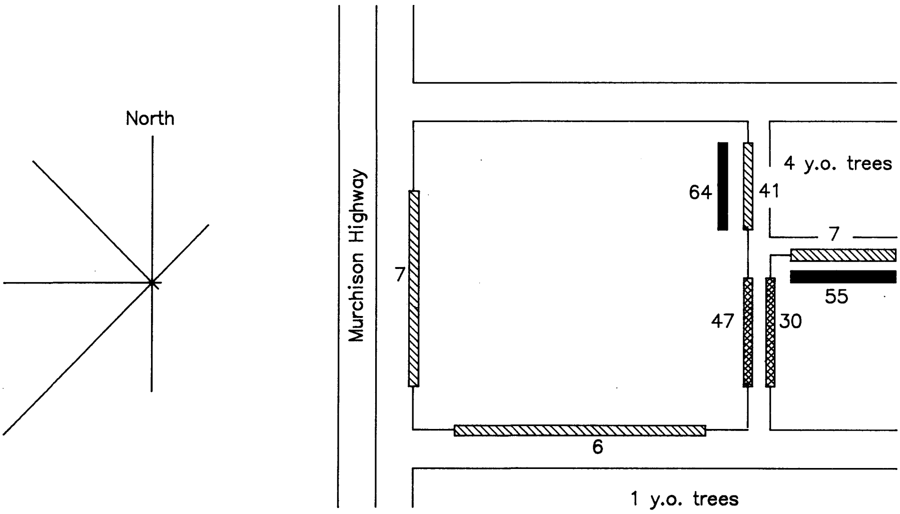

FIG. 3–Transect locations (not drawn to scale) in a 10-year-old stand of *P. radiata* at Parrawe indicating the incidence of SNC (expressed as percentage of trees affected) within stands (solid boxes) and in exposed (diagonally hatched) and internal (cross-hatched) boundaries. The wind rose indicates the dominant wind directions for Waratah (12 km south-west of survey area).

trees inside the stand. The severity of disease (measured by the SNC score) of affected trees on the exposed boundaries was slightly less than but not significantly different from affected trees on protected boundaries (eastern or internal boundaries) or trees inside the stand.

Distribution of SNC within stands

Both the incidence of disease within stands and its severity within individual trees were clearly defined on colour aerial photographs at a scale of 1:2000 as confirmed by ground inspection. On the photographs SNC was readily distinguished from other conditions such as animal damage and putative nitrogen and phosphorus deficiency. In all of the SNC-affected stands the distribution of affected trees appeared to be random. The last observation is supported by the data from Lockwood Creek (Table 4) and Peak Plains; both had non-significant Chi-squared values indicating that the disease is distributed randomly within the stands. For the Upper Guide Road data, Chi-squared values were significantly different ($p<0.05$) from those to be expected of a random distribution. Despite this there was no clear evidence of clumping.

TABLE 4—Contingency tables for unbroken runs of various length of healthy and diseased trees encountered in single row transects totalling 262 trees in an unthinned 8-year-old stand of *P. radiata* at Lockwood Creek. Expected values are calculated according to Vithayasai (1971).

Run length	Diseased		Healthy	
	Observed	Expected	Observed	Expected
1	33	32.73	27	32.22
2	16	15.99	19	15.74
3	8	7.81	7	7.69
4	2	3.82	4	3.76
5	3	1.95	4	1.84
>6	2	1.70	2	1.75

Patterns of needle-cast within trees

The lowest whorls (mean 2.2 m above ground) of 25 diseased and 25 healthy trees exhibited large differences in needle retention. Sixteen of the healthy trees retained 4 years of needles at this level and 10 trees 3 years of needles. By contrast, seven diseased trees retained no needles at this level, one tree retained only 3-year-old needles, and 17 carried no 2-year-old needles. Of these 17 trees, six held 1-year-old needles only and 11 had combinations of 1- with 3- and/or 4-year-old needles.

The differences between diseased and healthy trees were less consistent on the uppermost diseased whorl (mean height 5.2 m, range 3.3–6.9). There was no defoliation on first-order branches on nine diseased trees, 10 trees retained only 1- and 2-year-old needles, and five trees had 1-year-old needles only. On second-order branches defoliation was much more common; all but three of the 25 diseased trees retained only 1-year-old foliage. In healthy trees, by contrast, all age-classes of foliage (1–3 years) which had been produced on whorls originating near 5.2 m were vigorous and healthy.

Needle retention on each of three healthy trees was 10-fold or more greater than that on three diseased trees. The oven-dry weight of foliage retained at October 1984 is shown in

Table 5 together with tree heights, diameters, and the degree of crown defoliation expressed as SNC rating.

Relationship between vigour and susceptibility to disease

The linear regression of SNC score (for affected trees assessed in 1986) on diameter (prior to onset of disease in 1984) had an r^2 value of less than 1%, indicating that disease severity was not correlated with diameter at onset. It is concluded that susceptibility to SNC is unrelated to inherent vigour.

Role of Fungi

Fungi associated with senescent needles

Three fungi—*Cyclneusma minus, Lopherdium pinastri* (with its *Leptostroma* stage (Minter 1980)), and *Strasseria geniculata*—were ubiquitous on fallen needles at sites both affected and unaffected by SNC. The identity of these fungi was determined on (a) the morphology of the ascocarp and the presence of displaced epidermal cells on the ascocarp floor for *L. pinastri,* (b) the distinctive filiform conidial appendage in *S. geniculata,* and (c) ascocarp length in *C. minus* (Fig. 4); the last was confirmed by Dr Minter of the Commonwealth Mycological Institute (IMI numbers 305028–305032).

In many areas of severe SNC no fungal fruiting bodies could be found on attached needles, dead or alive. In some trees *L. pinastri* and *S. geniculata* were found fruiting on necrotic areas of live attached needles or on needles of formerly vigorous shoots which had been detached by pruning or natural breakage. *Lophodermium pinastri* was the most common fungus

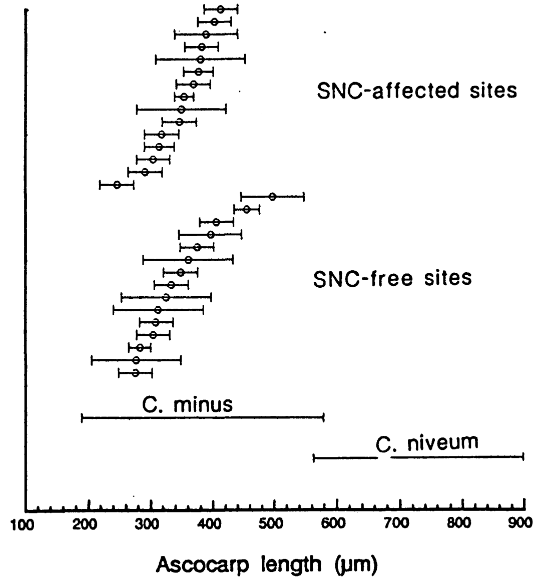

FIG. 4–Mean ascocarp lengths and their 95% confidence intervals for 15 sites with and 15 without spring needle-cast. Ranges for ascocarp length of *C. minus* and *C. niveum* based on Butin (1973) are shown.

TABLE 5–Diameters, heights, and their increments (1980–84) together with 1984 values of componentsof SNC index for each of three healthy and three severely diseased trees at St. Josephs

Tree No.	Diameter 1980 (cm)	Diameter increment 1980–84 (cm)	Height 1980 (m)	Height increment 1980–84 (m)	Measures of defoliation (1984)				
					H_t (m)	H_s (m)	H_d (m)	SNC index	Needle o.d.wt (g)
SNC-affected									
3-1 S	13.2	2.2	9.9	4.0	13.9	4.5	11.7	77	803
3-3 S	12.3	2.2	9.1	4.9	14.0	4.5	12.3	84	229
3-4 S	13.5	0.9	10.7	4.0	14.7	4.5	13.9	93	114
Healthy									
2-3 C	14.7	5.9	10.3	5.8	16.1	6.2	6.2	0	8718
5-1 C	14.5	7.0	11.0	6.2	17.2	7.0	7.0	0	7385
6-4 C	14.5	7.3	10.6	5.0	15.6	5.6	5.6	0	4189

H_t = total tree height
H_s = height to the top of the suppressed part of the crown determined from nearest healthy neighbours
H_d = height to the uppermost level of casting of 1-year-old needles
SNC index = calculated according to the formula $((H_d - H_s)/(H_t - H_s)) \times 100$

fruiting on dead attached needles of suppressed lower branches. *Strasseria geniculata* was the only fungus fruiting on attached needles with the mid-needle collapse symptom exhibited by trees affected by SNC. The presence of fruiting bodies of *S. geniculata*, however, was not consistent and in many areas of severe SNC no fungal fruiting bodies of any kind could be found on attached needles.

Cyclaneusma minus was not found fruiting on attached live needles. Its fruiting bodies occurred on senescent needles with uniform or mottled yellow-brown colour. The means and 95% confidence intervals for ascocarp lengths in each of the 15 SNC-affected and 15 unaffected stands are shown in Fig. 4 together with the range of values due to Butin (1973) for each of *C. minus* and *C. niveum*. All Tasmanian populations are circumscribed for ascocarp length by Butin's *C. minus* values.

The length of apothecia from SNC-affected populations was not significantly different from those in unaffected stands. There was some evidence ($p<0.05$) that apothecia from stands receiving >1200 mm annual rainfall were longer than those from stands receiving <1200 mm annual rainfall.

Fungicidal control

None of the single-shoot dipping experiments produced evidence of a strong treatment response. However, whole-tree spraying with chlorothalonil substantially reduced disease levels (Table 6).

TABLE 6–Numbers of trees in each of 6 classes of disease severity (SNC score) among 33 trees sprayed with chlorothalonil and 33 unsprayed control trees.

	SNC score						Over-all mean SNC score
	0	1	2	3	4	5	(n = 33)
Sprayed	31	–	2	–	–	–	0.12
Control	16	1	7	6	2	1	1.29

DISCUSSION

Climatic Relationships

In contrast to earlier reports of the climatic preference of *Cyclaneusma* (as *Naemacyclus niveus*) in Australia (Stahl 1966; D. Edwards pers. comm.), which referred to its more frequent occurrence during dry seasons or at dry localities, SNC in Tasmania is clearly a disease of cool humid environments. Our examination of the distribution of Cyclaneusma needle-cast in New Zealand (van der Pas *et al.* 1984) in relation to climatic conditions there, as summarised in the klimadiagrams of Walter & Leith (1960), indicates that disease due to *C. minus* occurs in a much wider variety of climates there than SNC does in Tasmania. The absence of SNC in areas of low rainfall (<1200 mm) in Tasmania and its lower incidence in thinned stands and at exposed boundaries is consistent with the environmental response expected of a foliar pathogen which requires periods of leaf wetness for infection. This interpretation is supported by the reduced incidence of disease after fungicidal treatment. However, the absence of SNC in the limited sample available within the high rainfall region of western Tasmania, its low sensitivity to both topographic variation and year-to-year climatic fluctuation, and the regular presence of severe defoliation in the uppermost and well-aerated parts of the canopy of severely affected codominant trees are all features inconsistent with such an hypothesis.

Possible Role of *C. minus*

The identity and pathogenicity of the two species of *Cyclaneusma* have been the subject of confusion. The description of *Cyclaneusma* in this study as *C. minus* rests on measurements of the length of apothecia and the diagnosis of Dr Minter. The statistically significant differences in length of apothecia between populations from high and low rainfall areas in Tasmania suggests that this character may be influenced by environmental factors. The only qualitative character of value for diagnosis is conidial shape. We have not seen conidia *in vivo* and nor has Dr Minter (pers. comm. 27.June.1986). Nor have we produced them in culture. Butin (1973) suggested that the two species of *Cyclaneusma* were host-specific and Gadgil (1984) has referred to this in assigning his specimens in *P. radiata* to *C. minus*. Millar & Minter (1980) and Minter & Millar (1980) noted that *C. niveum* is restricted to Europe, but J.A. Simpson (pers. comm.) has recorded this fungus (DAR 63546) on *P. radiata* in New South Wales. The supposed host specificity of the two *Cyclaneusma* species (Butin 1973) is not supported in the host lists of Millar & Minter (1980) and Minter & Millar (1980) where both species are listed for *P. mugo* Turra, *P. nigra* Arn., and *P. ponderosa* P.& C. Lawson. Inoculation experiments with a range of isolates of both species on a range of hosts, which might clarify the influence which a host exerts upon the dimensions of reproductive structures, appear not to have been attempted.

Minter & Millar (1980) stated that *C. niveum* is probably only a weak parasite and Magnani (1972) has reported its failure to infect *P. radiata* in inoculation trials. However, Martinez (1942), Stahl (1966), and Merrill & Kistler (1974) all reported evidence that it can sometimes act as a primary pathogen.

Cyclaneusma minus is regarded as a primary pathogen of some species of *Pinus* by Millar & Minter (1980) and its pathogenicity has been demonstrated experimentally for *P. sylvestris* L. by Merrill & Kistler (1974) and Karadzic (1981). Although Gadgil (1984) demonstrated that inoculation with *C. minus* reproduced the symptoms of mottling typical of field infection, this was expressed only on needles older than 1 year.

Comparison of SNC with Other Diseases

Despite similarities with other previously described diseases, no other syndrome is entirely consistent with that of SNC. The symptomatology and epidemiology of Dothistroma needle blight are clearly very different from those of SNC (Table 7). SNC more closely resembles the descriptions of Cyclaneusma needle-cast in New Zealand (Gadgil 1984; van der Pas *et al.* 1984). However, SNC and Cyclaneusma differ in the development of symptoms on the needles prior to shedding. Gadgil (1984) described a chlorotic spotting which developed into a mottled yellow-brown coloration uniformly along the entire length of 1-year-old and older needles. Choi & Simpson (in press) described the same symptoms on *P. radiata* in New South Wales but only on 2-year-old and older needles. This contrasts markedly with the rapid collapse of the midsection of needles in SNC, subsequent chlorosis of the distal and then the proximal segments of the needle, and ultimately the uniform yellow-

TABLE 7–Epidemiological characteristics of spring needle-cast, Dothistroma needle blight, and Cyclaneusma needle-cast

Character	Spring needle-cast	Dothistroma needle blight	Cyclaneusma needle-cast
Age of host susceptibility	>6–7 years	<1–15 (occ. 35) years	>6–35 (+?) years
First appearance of disease in stands	Sudden/general	Localised/spreading	Sudden/general?
Year to year variability in disease severity	Low	High	Low?
Spatial distribution	General/random	Patchy/contagious	General/random?
Frequency of resistance in affected stands	>40%	<0.1%	?
Incubation period	<52 weeks	5–18 weeks	5–48 months
Fruiting bodies on live needles	Occasional fungi	In necrotic bands on live needles	None (cast needles only)
Age range for peak infection	11–20 years	2–8 years	?
Response to fungicides	Yes	Yes	Yes
Response to thinning	Yes	Yes	?

brown coloration just prior to casting. In Tasmania the mottled, yellow-brown coloration typical of *C. minus* infection was most often evident on 3- to 4-year-old and rarely observed on 1-year-old needles.

The rapid collapse and discoloration of needles in SNC more closely resemble those associated with *Lophodermium seditiosum* Minter, Staley & Millar infection of *P. sylvestris* (Rack 1981). But that pathogen kills needles in their first year on both seedlings and mature trees (Martinsson 1979) and the fungus is not known to sporulate on attached needles.

Another feature in which SNC differs from many other needle-cast diseases is the very rapid development of crown symptoms to relatively stable levels of disease severity. In this respect it more closely resembles Cyclaneusma needle-cast in *P. sylvestris* which Merrill *et al.* (1980) found to be usually uniform over the crown. They noted the contrasts with other needle-casts where the severity usually decreases from the lower to upper crown.

The symptoms of neither SNC nor Cyclaneusma needle-cast are consistent with those of epidemics of local lesion diseases caused by primary pathogens such as *D. septospora* and *Mycosphaerella dearnessii* Barr. (syn. *Scirrhia acicola*), both of which produce distinct necrotic lesions with sharp boundaries in living tissue.

There are also other features of the disease which do not fit the behaviour expected of a primary foliar pathogen. The very rapid appearance of SNC symptoms in most susceptible trees and the low variability in disease levels year to year differ from the pattern of epidemic development from discrete loci of infection typical of known primary pathogens such as *D. septospora* and *L. seditiosum.* The severity of these diseases fluctuates widely from year to year in response to climatic variation (Martinsson 1979; Kurkela 1979; van der Pas 1981). In these respects it more closely resembles the behaviour of Cyclaneusma needle-cast reported by van der Pas *et al.* (1984). Although van der Pas *et al.* stated in introduction that disease severity varies from year to year, they indicated (in their Table 1) that the longer term assessments between 1977 and 1982 showed no significant variation.

Fungi Associated with Senescent Needles

Because we have found no constant association between SNC and any unequivocal primary pathogen we consider it is necessary that the possible role of necrotrophic secondary pathogens be addressed. Although three fungal endophytes, *C. minus, L. pinastri,* and *S. geniculata*, are common on recently senesced needles, it seems to us unlikely that any of them, either singly or in combination, are acting as primary pathogens in SNC. We have found no report which demonstrates that any of these fungi is a primary cause of needle-casting of 1-year-old needles of *P. radiata.*

Demonstration that *C. minus* is an early and extensive endophytic colonist of *P. radiata* (e.g., Gadgil 1984) cannot be taken as undisputed evidence of its causal role in needle disease. Rack & Scheidemann (1987) considered *C. minus* to be a harmless endophyte in *P. sylvestris*. Fungal endophytism is almost universal among higher plants (Carroll 1986; Petrini 1986) and the symbiosis may be mutualistic, antagonistic, or neutral (Petrini 1986; Sieber 1988, 1989). A very large and taxonomically diverse endophytic fungal flora exists in varying degrees of intimacy and nutritional dependency with hosts (Petrini 1986). Endophytes have been defined (Carroll 1986) as "those fungi which cause unapparent asymptomatic infections entirely within the tissues of plants". In that definition proven primary pathogens are excluded including, presumably, those which spend significant time as latent infections. In *D. septospora* infection of *P. radiata,* for example, the time required to complete a single spore-to-spore cycle under field conditions may vary from 5 to 18 weeks depending upon environmental conditions (Gilmour & Noorderhaven 1969). Even this lengthy period of latency is short compared to the 40 weeks to several years of latency required if Cyclaneusma is to be proposed as the primary cause of the needle-casts of *P. radiata* with which it is associated.

The response to chlorothalonil cannot be taken as evidence that the disease is the result of primary pathogenic action by any particular endophyte. Such a response might be due to the control of secondary effects of individual endophytes such as *C. minus* or even suites of endophytes after preconditioning by some other primary factor. It might be attributed to the effects of some component or breakdown product of chlorothalonil on the nutritional status of the host. It has been suggested by van der Pas *et al.* (1984) that some of the remedial effect of chlorothalonil may be due to nitrogen supplementation. Injection of Cyclaneusma-infected trees with non-fungicidal compounds rich in nitrogen has achieved the same increase in needle retention as that obtained with nitrogen-containing fungicides (Hood & Vanner 1984; I.A. Hood unpubl. data).

An Alternative Hypothesis

We postulate that environmental conditions, which have yet to be defined, seasonally induce ephemeral stress which stimulates a ubiquitous endophyte or a complex of endophytes to secondary pathogenic activity. In SNC this stress must operate in the first year of the life of needles and occur before October. Sinclair *et al.* (1987) have observed that it is unusual for severe needle-casting to occur in spring unless the preceding growing season or winter was particularly stressful. Carroll (1986) stated that fungi known to be potential pathogens can live for a period as neutral endophytes and cause symptoms only after onset of appropriate ecological and physiological conditions. They have suggested that some potential pathogens of conifer needles could behave in this way. A gradient of severity would be expected for any of the possible agencies of stress and a concomitant gradient in the severity in the resulting disease.

We consider that SNC is the extreme condition in a continuum which extends from the casting of 1-year-old needles through to that of 3- to 4-year-old needles. Among possible predisposing factors which have been suggested are stress induced by inadequate winter irradiance or ephemeral deficiencies of nutrients or imbalances among them.

The irradiance hypothesis was suggested by Burdon (1978) in relation to the needle-casting condition on *P. radiata* in New Zealand then called "yellows" and now referred to as Cyclaneusma. This hypothesis has also been suggested for the British Isles (Everard & Fourt 1974), Brittany, north-west Spain, and Italy (Burdon 1978) in areas subject to mild cloudy weather during winter. It is thought to result from inadequate light to support the foliar growth promoted by mild winter temperatures (Burdon 1978). On first consideration this hypothesis might be consistent with evidence from the bioclimatic analysis. However, disease is not present in the high rainfall areas of the West Coast Region of Tasmania which have a high incidence of cloud cover.

Experiments designed to test the validity of nutrient deficiency hypotheses are considered separately (Podger & Wardlaw 1990).

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APPENDIX 1

CHARACTERISTICS OF NINE FOLIAR CONDITIONS OF *P. RADIATA* WHICH HAVE BEEN OBSERVED IN TASMANIA

Primary pathogens

(1) Dothistroma needle blight. The causal fungus of this defoliating local-lesion disease, *D. septospora,* was first recorded in Tasmania in 1984 (Podger 1984). Before the autumn of 1989 it occurred at very low levels in most plantations within its limited range in Tasmania, except for localised severe defoliation in topographic "hot-spots", usually less than 1 ha in extent. By September 1989 it had become more widely distributed in the north-west region and had caused moderate to severe defoliation over a wider range of topographic situations. In the most severely affected stands almost all trees, including those previously seen to be resistant to SNC, were affected. The disease syndrome and its detailed symptoms in Tasmania are very similar to those reported for New Zealand (Gilmour 1967) and New South Wales (Edwards & Walker 1978). This disease affects trees from seedling age to c. 15 years and its severity is sensitive to microtopographic variation and seasonal fluctuations in rainfall. The presence of red bands 3–5 mm long with characteristic erumpent black stromata on living needles is diagnostic.

"Normal" shedding of needles

(2) Spring and autumn casting of older needles. Marked yellowing and subsequent needle-cast in trees are very common in all closed stands including edge trees. Symptoms which appear each autumn and spring are restricted to 3-, 4-, or 5-year-old needles. Affected needles exhibit mottled chlorotic spotting which progresses from the tip until the entire needle is uniformly yellow or yellow with brown mottles. Large numbers of *Cyclaneusma* sp. fruiting bodes are usually produced on these needles after casting.

(3) Main stem needle yellows. This condition is most noticeable in scattered trees in vigorous 4- to 5-year-old stands. One-, 2-, and 3-year-old needles on the main stem turn uniformly bright yellow in striking contrast to the bright green healthy foliage on the branches.

Nutritional deficiencies

(4) Chronic symptoms of severe nitrogen deficiency. The spindle stand symptom of thin branching and shortened yellow-green needles throughout the crown described by Turner *et al.* (1979) occurs widely in Tasmania on poor soils in low-rainfall areas. Within the range of occurrence of SNC this symptom is restricted to patches (c. 0.5 ha) of trees on shallow soils over Devonian granites at Star of Peace plantation and on scalped krasnozems over Tertiary basalts at Lockwood Creek. Needles are not usually cast until year 4 or 5 but canopy development is always poor.

(5) Symptoms of phosphorus deficiency. Throughout Tasmania, stands on extensive areas of infertile podsolic and heavy clay soils on sediments, metasediments, and dolerites exhibit a range of symptoms usually associated with phosphorus deficiency. These include poor growth, open canopy, spindle symptoms, and shedding of 2- to 4-year-old

needles in addition to those symptoms described by Turner *et al.* (1979) and Nielsen *et al.* (1981) for severe deficiency of phosphorus. In some stands on substrates of intermediate fertility less severe symptoms may occur around 20–25 years of age (W.A. Nielsen pers. comm.). Remission of symptoms has followed applications of superphosphate and rock phosphate (Nielsen *et al.* 1981).

(6) Symptoms of potassium and magnesium deficiency. These symptoms may occur in all trees in patches of several hectares in extent from at least 2 to 12 years of age. They are common in stands on krasnozems on former pasture and cropping land not treated with fertiliser at plantation establishment. The symptoms are similar to those described by Raupach & Clark (1967) but not as severe as those described by Hall & Raupach (1963).

Localised minor, possibly pathogenic conditions

(7) "Mid-crown yellows". In this condition one or a few first-order branches in the upper third of the tree exhibit strong yellowing in 1- and 2-year needles, usually during autumn. Dieback of the shoot often follows.

(8) Foliar blight. Vigorous shoots of first- and second-order branches in the lower canopy of fast-growing closed-canopy stands develop a strongly bleached appearance in early spring. The bleaching is seen on most needles in the affected shoots, initially in the basal parts. At this stage most of the needles in a shoot are bound by a vigorous hyaline mycelium which spreads epiphytically and distally along the surface of the apparently healthy portion of the needle. The condition superficially resembles foliar blights associated with infection by *Phacidium* sp. (Sinclair *et al.* 1987) and *Rosellinia* sp. (Francis 1986).

(9) Undiagnosed needle-tip necrosis. Highly variable proportions of 2-year-old needles on some shoots exhibit necrosis for 20–40% of the distal end of needles whilst still attached. In September the necrotic tissue is grey and is almost invariably subtended by a dark red (Munsell—10R 3/6) band <10 mm in length. Between this and the normal green of the proximal portion of the needle is a yellow (Munsell—2.5 GY 8/8) band 1–2 mm long. No fungal fruiting bodies have been observed in the red bands, but typical black hysterothecia of *Lophodermium pinastri* are common in the necrotic portion.