SPRING NEEDLE-CAST OF *PINUS RADIATA* IN TASMANIA: II. EFFECTS OF FERTILISERS AND THINNING ON DISEASE SEVERITY, AND THE IMPACT OF DISEASE ON GROWTH*

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ABSTRACT

Four field experiments were established in closed stands of *Pinus radiata* D. Don in north-western Tasmania to test the effectiveness of soil applications of nitrogen, phosphorus, sulphur, and a comprehensive fertiliser formulation in correcting or preventing the development of the defoliating disease "spring needle-cast" (SNC). They provided no support for hypotheses that chronic nutrient deficiencies contribute to the disease. The possibility that seasonal but ephemeral deficiency in one or more nutrients might predispose susceptible individuals to SNC remains to be tested.

Over a 4-year period, between 9 and 13 years after planting, the diameter growth of SNC-affected trees in an unthinned stand was reduced by 14% for each 10% increase in defoliation. This is comparable to that reported for Dothistroma needle blight and Cyclaneusma needle-cast in New Zealand. In a younger stand the impact on diameter growth was less but increased over successive measurement intervals. In stands thinned prior to the onset of SNC the development of significant disease was delayed by 2–5 years.

Keywords: needle-cast; growth impact; fertiliser; etiology; management; *Pinus radiata*.

INTRODUCTION

The symptoms, distribution, and etiology of the disease, spring needle-cast (SNC), which results in premature and heavy casting of 1-year-old needles in some Tasmanian plantations of *Pinus radiata*, have been discussed in the previous paper (Podger & Wardlaw 1990).

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In this paper we describe four field experiments in north-western Tasmania (Fig. 1) which test hypotheses that nutrient deficiencies or imbalances among nutrient levels are either the direct cause of the disease, or predispose genetically susceptible individuals to secondary pathogens. Nitrogen, phosphorus, and sulphur were tested because of their relevance to several hypotheses proposed by earlier workers and referred to in greater detail below. A comprehensive fertiliser formulation was tested as an exploratory measure. Two experiments with pairs of diseased and resistant trees were designed to determine if fertiliser applications could cure established disease. Two others using small stands as experimental units were designed to determine whether fertilisers applied shortly before first onset of SNC might prevent development of the disease. The fourth of these experiments included a heavy thinning treatment to explore the influence of canopy density on the severity of SNC. Although all four experiments were incomplete at the time of first appearance of *Dothistroma septospora* Morelet in the region (Podger 1984), at no stage did defoliation due to Dothistroma needle blight exceed trace levels in any of the experimental stands.

Data derived from these experiments have been used to estimate the impact of the disease on growth of individual trees.

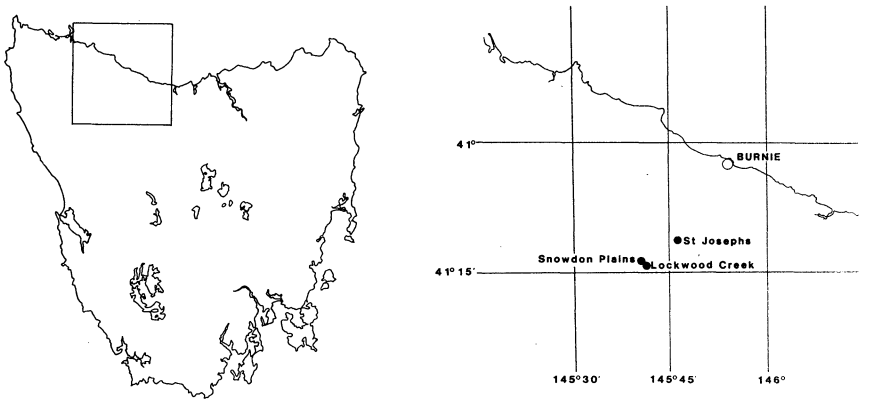

FIG. 1–Location of experimental stands

MATERIALS AND METHODS

Measurement of Disease Severity

We have used two estimates of severity of defoliation. In the experiments with paired trees we derived a measure of the degree of defoliation which we refer to as the "SNC index". It was computed according to the formula

$$\text{SNC index} = \{(H_d - H_s) / (H_t - H_s)\} \times 100\%$$

where, H_d = height to the uppermost level of substantial yellowing or casting of 1-year-old needles

H_s = height to the base of the living crown of surrounding healthy trees (a measure of the effects of shading due to canopy closure)

H_t = total tree height

In the experiments with large numbers of trees we made a subjective estimate of the level of defoliation in each tree. This has been called the "SNC score"; although it is related to the SNC index, it is not to be equated with it. It is a visual assessment of the loss of volume of potentially live crown due to SNC expressed on a scale of 0–5, each step on the scale between 1 and 5 representing an increase of 20% from no trace of SNC.

To obtain a measure of the reliability of estimate of the SNC score we measured the SNC index of all trees in Experiment 4 in March 1986 and then immediately after, without reference to that record, assessed the SNC scores of the same 1200 trees. A simple linear regression of SNC index on SNC score (Fig. 1) accounted for significant ($p<0.001$) variation in SNC ($r = -0.92$) and took the form

$$\text{SNC score} = 7.23 - 0.069(\text{SNC index})$$

The 95% confidence interval for this regression indicates that only differences of 2 or more units can be considered real. Because of this, we classify a tree as SNC-affected when it is scored at 2 or more. We use the term "incidence of SNC" to indicate the frequency of SNC-affected trees within plots, and SNC score to indicate severity in individual trees.

Experimental Tests of Hypotheses of Nutrient Deficiencies

Four experiments at several locations were conducted in young, densely stocked plantations on former improved-pasturelands on krasnozem soils on basalts of Tertiary origin in Associated Forest Holdings Pty Ltd properties in north-western Tasmania (Fig. 2). Fertiliser

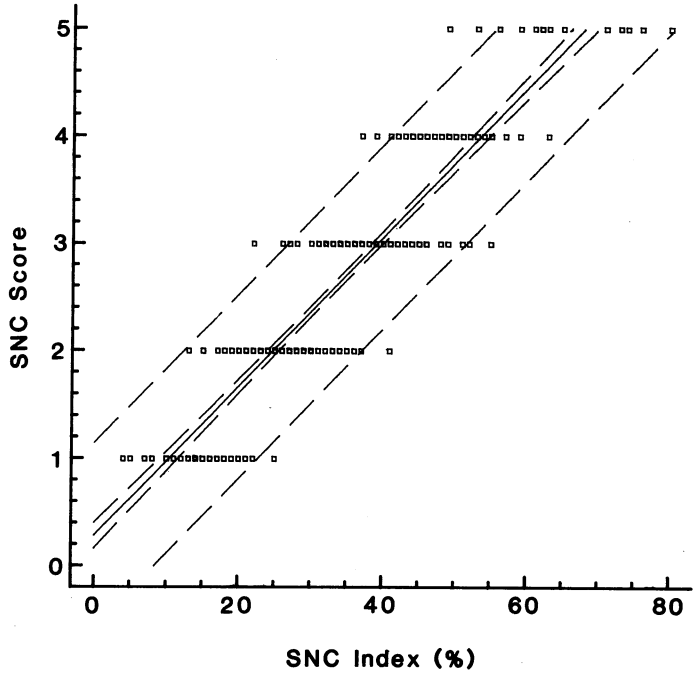

FIG. 2–Linear regression of SNC score on SNC index with 95% confidence intervals for the prediction indicated (outer two curves).

formulations were recommended by Mr W.A. Nielsen (Forestry Commission, Tasmania) and Dr J. Turner (Forestry Commission of New South Wales) and are based on their experience of the nutrition of *P. radiata* on krasnozem soils.

Effects of Soil Applications of Nitrogen and Phosphorus on Disease Levels

Hypothesis for test: An experiment was conducted to test whether SNC symptoms could be alleviated by soil applications of nitrogen and phosphorus fertiliser. Nitrogen was selected because the late Mr J.W. Gilmour and Dr R.D. Burdon had suggested (pers. comm.) that heavy premature casting of needles which occurred annually in plantations of *P. radiata* in the central North Island of New Zealand was a consequence of a severe but ephemeral deficiency of foliar nitrogen during spring. This was thought to be due to a high level of nutrient demand in rapidly expanding new foliage which exceeded uptake by relatively inactive roots in cool soils. Such a hypothesis seemed to be consistent with the Tasmanian occurrence of SNC in cloudy climates at high altitudes and its rapid development in densely stocked stands at the time of canopy closure. Phosphorus was selected because (a) SNC symptoms bear a resemblance to some of the symptoms in the A.C.T. which Fielding & Brown (1961) had attributed to phosphorus deficiency (e.g., their Fig. 7), and (b) Bowen (1970) had reported that phosphorus uptake is seriously impeded when root growth is depressed at low temperatures on phosphate-poor soils. Although the basaltic soils are not low in total phosphorus, their ability to bond phosphorus in forms unavailable to plants is well documented (Stephens 1937).

Experiment 1 – St Josephs Plantation: a paired-tree trial with urea and rock phosphate

Design, location, and site description: A 2 × 2 factorial was employed using four pairs of resistant (R) and diseased (D) trees in each of seven randomised blocks. The experiment was established in June 1980 in a SNC-affected stand at 400 m elevation in Cpt 14, St Josephs Plantation. The compartment was machine planted in 1971 with 1/0 seedlings at a density of 1156 trees/ha.

Selection, treatment, and measurement of subject trees: All trees in the stand were pruned to 1.7 m to facilitate selection of experimental trees. Twenty-eight pairs of D and R trees were selected according to the following criteria: (a) trees of any pair were both locally codominant and no further than 2 m apart; (b) trees were well-formed, single-stemmed, and had well-balanced crowns; (c) R trees carried healthy foliage throughout the unpruned part of the crown and D trees had shed all 1-year-old foliage in more than 20% of the crown; (d) the diameter of any tree was within 10% of the mean of all trees. All pruning-slash and litter were cleared from 7 × 7 m about each pair of subject trees, to minimise diversion of fertiliser to litter breakdown processes. One pair of trees within each block was randomly assigned to each of four fertiliser treatments: N_1P_1, N_1P_0, N_0P_1, and N_0P_0. Fertiliser was applied on 20 July 1980 at the rates of 360 kg urea/ha (N_1) and 700 kg rock phosphate/ha (P_1). Stem diameter over bark at breast height, total tree height, height to base of live crown, and length of diseased crown were measured on 22 July 1980, 16 September 1981, 20 August 1982, and after felling on 26 October 1984.

Analysis of treatment effects: The significance of differences among treatments and blocks and between resistant and diseased tree was tested by analysis of variance of the variables diameter, height, and SNC index for each measurement occasion.

Effects of Soil Applications of Nitrogen and Sulphur on Disease Levels

Hypothesis for test: In a series of papers Lambert and her colleagues (Lambert *et al.* 1976; Lambert & Turner 1977, 1978; Turner & Lambert 1978; Lambert 1986) developed a hypothesis which proposed that the ratio of sulphur-containing to sulphur-free amino acids in the host is an important determinant of resistance to foliar diseases. They had observed that a number of diseases of *P. radiata* are most prevalent on sulphur-deficient, igneous substrates (Eldridge *et al.* 1981; Turner & Lambert 1986). The common occurrence of SNC on Tertiary basalts and Devonian granites in Tasmania encouraged us to conduct experiments to test for evidence that this hypothesis might explain SNC. We conducted two experiments with combinations of sulphur and nitrogen to determine whether the treatment could (a) ameliorate established SNC (Experiment 2), or (b) prevent the onset of SNC (Experiment 3). In both experiments a comprehensive fertiliser treatment was also included as an exploratory measure.

Experiment 2 – Lockwood Creek: a paired-tree trial with soil applications of nitrogen, sulphur, and a comprehensive mix of fertilisers

Design, location, and site description: A randomised block design was employed using five fertiliser treatments (N_1S_1, N_1S_0, N_0S_1, N_0S_0, and ALL) and five replications. The experiment was established in December 1983 in Cpt RB9, Lockwood Creek Plantation, at 460 m elevation. The compartment had been planted in 1975 with 1/0 seedling stock at a density of 1156 trees/ha.

Selection, treatment, and measurement of subject trees: The 25 pairs of R and D trees were selected and prepared in the same manner as in Experiment 1 except that no tree in any of the five blocks varied by more than 0.5 cm about the mean diameter for the block or more than 5% of block mean height. As it was not always possible to find R and D trees of the required size as close as 2 m, fertiliser was applied around each subject tree in a circle 1 m in radius. Within each block, pairs were randomly assigned to each of the five fertiliser treatments. Fertilisers were applied in December 1983 and again in August 1984: sulphur as gypsum (2000 kg/ha), nitrogen as ammonium nitrate (400 kg/ha). The comprehensive mix included sulphur and nitrogen at the same rates, plus phosphorus and molybdenum as molybdenum superphosphate (750 kg/ha), potassium as potassium chloride (200 kg/ha), boron as borax (44 kg/ha), magnesium as magnesium sulphate (40 kg/ha), zinc as zinc sulphate (10 kg/ha), and copper as copper sulphate (5 kg/ha). The same variables as those in Experiment 1 were measured at the commencement of the experiment and again immediately after felling in March 1986.

Analysis of treatment effects: The significance of differences was tested by analysis of variance for the variables SNC index, height to the base of green crown, diameter, and height. Tests of the significance of differences between treatments were based on plot mean values (n=5) and those between R and D trees on individual tree pairs (n=25).

Experiment 3 – Snowdon Plains: a trial at stand level with nitrogen, sulphur, and a comprehensive fertiliser mix

Design, location, and site description: A randomised block design was employed using the same five fertiliser treatments as in Experiment 2, each with five replications. The 25 rectangular plots each contained 30 subject trees selected within plots of c. 60 trees. The site is located in Nisbetts Block (Cam, Cpt 5) at 530 m elevation on a domed ridge of slope c. 5°. The stand was machine planted in 1978 at a density of 1400 trees/ha. At commencement, in August 1984, the stand was at the point of canopy closure and was free of SNC.

Selection, treatment, and measurement of subject trees: The 30 subject trees were as evenly spaced as was consistent with the requirements that they should be codominant, single-stemmed, and have a well-balanced crown. Fertiliser treatments were applied in September 1984. In March 1986 and February 1989 diameters at breast height were measured and all subject trees assigned a SNC score.

Analysis of treatment effects: Significance of differences among treatments and blocks was tested using analysis of variance of the plot mean values for the variables diameter, diameter increment, incidence of SNC, and SNC score, for each measurement occasion.

Effects of Early Thinning and Comprehensive Fertiliser on Disease Levels

Hypothesis for test: In the Oonah district there are substantial areas of Forestry Commission plantations which are managed principally for sawlog production under regimes of early pruning and heavy thinning. We have observed that the incidence of SNC in these stands is much lower than in nearby plantations of Associated Forest Holdings which are managed principally for pulpwood production and subject to later and less severe thinning regimes. It was not clear to what extent this difference was due to some degree of deliberate culling of SNC-affected trees or to the effects of thinning regimes unbiased by considerations of SNC status. An experiment was designed therefore to test the effect of thinning just prior to first appearance of disease symptoms. It included a comprehensive fertiliser treatment to test for possible interaction between thinning and fertiliser applications.

Experiment 4 – Snowdon Plains: a stand-based trial using a comprehensive fertiliser mix and thinning

Design, location, and site description: A 2×2 factorial design was employed using thinning and comprehensive fertiliser in three randomised blocks each with four plots of 100 subject trees. The site is adjacent to Experiment 3 on a west-facing aspect just below the summit of the ridge-line and exposed to prevailing winds.

Selection, treatment, and measurement of subject trees: Subject trees were selected among approximately 325 trees in 12 parallel rows of 27 trees normal to the axis of the ridge and at least three rows inside a north-south aligned fire break. The basis for selection was a compromise between maintenance of even spacing and desirable silvicultural characteristics in retained trees. On plots assigned for thinning, all but 100 subject trees were felled during August-September 1984 and their crowns dismembered. In unthinned plots, subject trees

were selected on the same basis and were numbered for subsequent identification and measurement. In each treatment all detritus and litter within a 1-m radius of subject trees were removed. Fertiliser was spread over a 1-m radius around the base of each subject tree in late September 1984.

Analysis of treatment effects: Significance of differences among treatments and blocks was tested by analysis of variance of the plot mean values for the variables diameter, height, incidence of SNC, and SNC score, for each measurement occasion. At the level of plot means an analysis of covariance, using initial diameter (at the commencement of each increment period) and SNC score (at the end of the increment period) as covariates, showed that covariates did not contribute significantly to differences among blocks or treatments for diameter increment in either increment period. At the level of individual tree values a multiple linear regression analysis showed that the interactions of these covariates with the factors block, thinning, and fertiliser were minor compared to the main effects of the covariates and factors. We therefore used an analysis of variance to test for significance of differences in the variables diameter, height, incidence of SNC, and SNC score, at each measurement. The Genstat statistical program (Payne *et al.* 1988) was used for all three analyses.

Impact of SNC on Growth of Individual Trees

Direct assessment of the impact of SNC on the growth of stands is virtually impossible. In the region of occurrence of SNC we have been unable to find, for comparative analysis, closed stands which are disease free or have even very low levels of disease. An alternative approach, experimental manipulation of the proportions of resistant and susceptible trees in stands by thinning, has been considered but is not feasible because of the effect of stand density on disease incidence demonstrated in Experiment 4.

For these reasons the impact of disease on growth has been restricted so far to comparisons of the growth of resistant and susceptible individuals using regression analyses of data derived from three of the four experiments described here.

Data from Experiment 1

A multiple linear regression of the dependent variable diameter increment (1980–84) was calculated for the independent variables SNC index (1980) and initial diameter (1980) using data from all 56 trees.

Data from Experiment 3

A multiple linear regression of the dependent variable diameter increment (1986–89) was calculated for the independent variables SNC score (1989) and initial diameter (1986) using data from the 739 trees alive in 1989.

Data from Experiment 4

Multiple linear regressions of the dependent variable diameter increment were calculated for the independent variables SNC score (at the end of the appropriate increment period), diameter (measured at the start of the appropriate increment period), and the thinning effect using data from the 1171 trees living in 1989. Regressions were calculated for the increment periods 1984–86 and 1986–89.

RESULTS

Effects of Experimental Treatments on Disease Levels

Experiment 1

There was no effect of fertiliser treatment on SNC index of diseased or resistant trees at any stage of this experiment. The over-all mean of SNC index for D trees increased from an initial level of 36% to 61% and 73% over successive measurement intervals. Except for one tree which increased from 0% to 55% between the 1982 and 1984, the SNC index of R trees remained at 0%.

The rank of differences in height and diameter ($p<0.001$) among blocks evident in 1980 persisted for the duration of the experiment. None of the fertiliser treatments had any significant effect on either diameter or height on any of the three measurement occasions.

Mean values of SNC index, diameter, and height at three measurement occasions for R and D trees are summarised in Table 1. In 1980 the diameters of paired R and D trees were not significantly different. Thereafter R trees had significantly ($p<0.001$) greater diameters than D trees. The heights of R and D trees were not significantly different except for the last (1984) measurement when R trees were taller than D trees ($p<0.01$).

TABLE 1–Experiment 1 (St Josephs). Effects of disease status (resistant (R) or diseased (D), with mean values of SNC index indicated) upon stem diameter at breast height over bark (dbhob) and height at each of three measurements. Values which are not significantly different ($p<0.05$) have common subscripts. Standard errors for differences (s.e.diff.) are indicated.

	1980			1982			1984		
	R	D	s.e.diff. (n=28)	R	D	s.e.diff. (n=28)	R	D	s.e.diff. (n=28)
SNC index	0_a	36_b	3.32	0_a	61_b	4.24	2_a	73_b	5.36
Dbhob (cm)	14.7_a	14.6_a	4.94	18.1_a	16.6_b	6.71	21.4_a	17.7_b	9.13
Height (m)	10.7_a	10.6_a	2.70	13.1_a	12.8_a	3.91	16.3_a	15.3_a	5.80

Experiment 2

Although none of the fertiliser treatments had an effect on SNC index, there were significant ($p<0.01$) responses in diameter growth, with the nitrogen-plus-sulphur and comprehensive fertiliser treatments showing significantly better diameter growth than the other fertiliser treatments (Table 2). There was no effect of treatment on tree height.

TABLE 2–Experiment 2 (Lockwood Creek). Effects of fertiliser treatments on SNC-affected trees for the variables SNC-index, dbhob, and total height. Values which are not significantly different have subscripts in common. Standard errors refer to the pooled data for SNC-affected trees of all fertiliser treatments.

Variable	s.e.diff.	Treatment				
	(n=5)	All*	N+S	N	S	Control
SNC index (%)	5.26	74.0_a	77.2_a	72.1_a	74.6_a	64.4_a
Dbhob 1986 (cm)	0.57	20.9_{ab}	21.1_a	19.5_c	19.8_{bc}	18.8_c
Height 1986 (m)	0.48	12.9_a	13.2_a	12.6_a	12.6_a	12.7_a

* All = comprehensive fertiliser mix

There were significant differences ($p<0.001$) between R and D trees for SNC index and for diameter (Table 3). There was no signficant difference in height between R and D trees.

TABLE 3–Experiment 2 (Lockwood Creek) Comparisons of mean values for 1986 measurements of SNC index, dbhob, and total height in two groups of 28 trees rated resistant or diseased in 1983 (mean values of SNC index indicated). Values which are not significantly different have subscripts in common. Standard errors for differences (s.e.diff.) are indicated.

Variable	s.e.diff.	Disease class	
	(n=25)	R	D
SNC index (%)	2.74	01.8_a	53.3_b
Diameter 1986 (cm)	0.24	20.5_a	19.5_b
Height 1986 (m)	0.33	12.7_a	12.9_a

Experiment 3

Treatment and block means for SNC incidence, SNC score, diameter, and diameter increment are summarised in Table 4. No fertiliser treatment had any effect on the incidence or SNC score of disease at any stage. Except for a small ($p<0.05$) adverse effect of sulphur alone on diameter, there was no effect of fertiliser treatment on growth. A difference among blocks ($p<0.001$) in tree diameters apparent in 1986 was not evident in 1989.

Experiment 4

The mean values within treatments (thinning and fertiliser); within blocks, and over-all of five variables (SNC incidence, SNC score, diameter, diameter increment, and height) for each measurement interval are summarised in Table 5. Gradients of increasing SNC incidence ($p<0.01$) and higher SNC scores ($p<0.05$) from Block 1 to Block 3 corresponded with decreasing elevation and exposure and with increasing tree height and diameter.

The averages of SNC incidence and score were significantly lower in thinned treatments at both the 1986 ($p<0.001$ for both SNC incidence and SNC score) and 1989 ($p<0.01$ for SNC incidence and $p<0.001$ for SNC score) assessments. However, when SNC scores of affected trees only were considered there was no significant difference between thinned (2.46) and unthinned plots (2.59) at the 1989 measurement. The incidence of disease in thinned plots increased by an order of magnitude between the two assessments, but by only 26% in the unthinned plots. This result indicates that the effect of thinning is to delay the onset of SNC and that the effect is short-lived. This interpretation has been confirmed by wider observation in clearwood stands (Neilsen 1979) inspected at various times since thinning.

Although fertiliser application caused a small but significant ($p<0.001$) increase in diameter increment in the first interval, it had no significant effect on SNC incidence or score at any stage.

Impact of SNC on Growth of Individual Trees

Experiment 1 – St Josephs

Initial diameter (in 1980) did not contribute significantly to variation in diameter increment (between 1980 and 1984) when included in a multiple linear regression model

TABLE 4–Experiment 3 (Snowdon Plains). Effects of treatment (five fertiliser regimes) and block (five randomised) on mean values of SNC incidence, SNC score (calculated for diseased trees only), and diameter (at breast height over bark) at each of two measurements. Values which are not significantly different ($p<0.05$) have common subscripts. Standard errors for differences are indicated.

Variable	s.e.diff.	Treatment					Block				
	(n=150)	All	N+S	N	S	Control	A	B	C	D	E
Incidence 1986 (%)	5.48	25 $_{a}$	37 $_{a}$	39 $_{a}$	36 $_{a}$	42 $_{a}$	34 $_{a}$	35 $_{a}$	24 $_{a}$	41 $_{a}$	46 $_{a}$
Incidence 1989 (%)	5.68	58 $_{a}$	63 $_{a}$	64 $_{a}$	64 $_{a}$	61 $_{a}$	62 $_{ab}$	69 $_{b}$	46 $_{a}$	62 $_{ab}$	71 $_{b}$
SNC score 1986	0.21	2.6_{a}	2.7_{a}	2.9_{a}	2.6_{a}	2.9_{a}	2.9_{a}	2.7_{a}	2.9_{a}	2.6_{a}	2.8_{a}
SNC score 1989	0.30	3.3_{a}	3.3_{a}	3.5_{a}	3.4_{a}	3.5_{a}	3.5_{a}	3.3_{a}	3.4_{a}	3.2_{a}	3.6_{a}
Diameter 1986 (cm)	2.52	14.8_{a}	14.5_{ab}	14.4_{ab}	14.0_{b}	14.9_{a}	13.9_{a}	14.1_{ab}	14.7_{abc}	15.0_{c}	14.9_{bc}
Diameter 1989 (cm)	4.41	19.6_{a}	19.1_{a}	19.0_{a}	18.5_{a}	19.5_{a}	18.7_{a}	18.7_{a}	19.4_{a}	19.6_{a}	19.3_{a}
Increment (cm)	3.17	4.9_{a}	4.6_{a}	4.6_{a}	4.6_{a}	4.9_{a}	4.9_{a}	4.6_{a}	4.9_{a}	4.7_{a}	4.4_{a}

TABLE 5–Experiment 4 (Snowdon Plains). Effects of thinning (0=unthinned, 1=thinned) and fertiliser (0=without, 1=with) treatments (in a 2×2 factorial randomised block experiment (with three replications) upon SNC incidence, SNC, score and tree height at each of two measurements, on diameter at breast height over bark at three measurements, and diameter increment for the two measurement intervals. Values which are not significantly different ($p<0.05$) have subscripts in common. Standard errors for differences are indicated.

	s.e.diff.	Thinning		Fertiliser		s.e.diff.	Block			Over-all
	(n-600)	0	1	0	1	(n=400)	1	2	3	(n=1200)
Incidence 1986 (%)	1.91	37 $_{a}$	3 $_{b}$	21 $_{a}$	19 $_{a}$	2.34	16 $_{a}$	18 $_{a}$	26 $_{b}$	20
Incidence 1989 (%)	3.25	50 $_{a}$	33 $_{b}$	43 $_{a}$	40 $_{b}$	3.98	37 $_{a}$	38 $_{a}$	50 $_{b}$	41
SNC score 1986	0.125	1.2_{a}	0.1_{b}	0.7_{a}	0.6_{a}	0.15	0.5_{a}	0.6_{ab}	0.9_{b}	0.6
SNC score 1989	0.06	1.6_{a}	1.0_{b}	1.4_{a}	1.3_{a}	0.07	1.2_{a}	1.2_{a}	1.7_{b}	1.3
Diameter 1984 (cm)	0.09	11.2_{a}	10.8_{a}	11.2_{a}	10.9_{a}	0.11	10.5_{a}	11.1_{ab}	11.5_{b}	11.0
Diameter 1986 (cm)	0.17	15.4_{a}	17.1_{b}	16.2_{a}	16.3_{a}	0.21	15.6_{a}	16.3_{ab}	16.8_{b}	16.3
Diameter 1989 (cm)	0.28	20.4_{a}	24.8_{b}	22.4_{a}	22.8_{a}	0.35	22.2_{a}	22.8_{a}	22.9_{a}	22.6
Increment 1984-86 (cm)	0.14	4.2_{a}	6.3_{b}	5.1_{a}	5.4_{b}	0.17	5.2_{a}	5.2_{a}	5.3_{a}	5.2
Increment 1986-89 (cm)	0.26	5.1_{a}	7.6_{b}	6.2_{a}	6.5_{a}	0.32	6.5_{a}	6.4_{a}	6.1_{a}	6.3
Height (1984) (m)	0.092	5.8_{a}	5.8_{a}	5.9_{a}	5.8_{a}	0.112	5.6_{a}	5.8_{ab}	6.1_{b}	5.8
Height (1986) (m)	0.111	8.5_{a}	8.2_{b}	8.4_{a}	8.3_{a}	0.136	7.9_{a}	8.4_{a}	8.6_{a}	8.3

containing SNC index (1980). A simple linear model of diameter increment (1980–84) on SNC index (1980) was therefore calculated. The model

Diameter increment = 64.8 – 0.89(SNC $index_{80}$)

accounted for significant ($p<0.001$) variation in diameter increment ($r = -0.74$, error mean square = 225 with 54 degrees of freedom). This model indicates that diameter increment was reduced by 14% for each 10% increase in SNC index.

Experiment 3 – Snowdon Plains

Both initial diameter (1986) and SNC score (1989) accounted for significant ($p<0.001$) variation in diameter increment. The multiple linear regression model

Diameter increment = 1.8 + 0.12(Diameter 1986) – 0.15(SNC score 1989)

explained 33% of variation in diameter increment (error mean square = 329 with 737 degrees of freedom). This model indicates that a tree of over-all mean diameter suffered a reduction of increment of 10% for each increase of 1 unit in SNC score (approximately 20% increase in defoliation).

Experiment 4 – Snowdon Plains

For both the 1984–86 and 1986–89 increment periods, regressions of initial diameter (measured at the start of each increment period), SNC score (measured at the end of each increment period), and thinning effect, accounted for significant ($p<0.001$) variation in diameter increment. The multiple linear regression models are

(1) Diameter increment (1984–86) = a + 0.12(initial diameter) – 0.15(SNC score)

where "a" takes the value 3.0 in unthinned stands and 5.0 in thinned.

The regression accounts for 66% of the variation in diameter increment (error mean square = 0.59 with 1167 degrees of freedom). It indicates that trees of mean initial diameter (1984) in unthinned stands produced 3.5% less (than the increment of an unaffected mean tree) for each increase of 1 unit in SNC score.

(2) Diameter increment (1986–89) = a + 0.23(initial diameter) – 0.49(SNC score)

where "a" takes the value 1.8 in unthinned stands and 3.6 in thinned.

The regression accounts for 54% of the variation in diameter increment (error mean square = 2.18 with 1167 degrees of freedom). It indicates that trees of mean initial diameter (1984) in unthinned stands produced 8.4% less increment for each increase of 1 unit in SNC score.

DISCUSSION

Relevance to the Etiology of SNC

The experiments reported in this paper, which are relevant only to the nutrient deficiency hypotheses outlined above, provide no evidence of response of SNC to any of the wide range of elements applied. The growth responses to fertiliser treatment in Experiment 2 (Lockwood Creek) and in the first measurement interval of Experiment 4 are the only evidence that nutrient uptake might have occurred. There is no such evidence of uptake in the second measurement interval of Experiment 4 and none at any stage in Experiments 1 and 3. This

is consistent with the failure of nitrogen effects to persist beyond 1 year (Knight *et al.* 1983) and contrasts with much longer residual effects for phosphorus. We have no explanation for this widely based lack of response, though it is noted that the result of Knight *et al.* was obtained on non-binding, deeply weathered sediments. As already noted, all the experiments reported here were established on basaltic soils well known for their capacity to fix phosphorus. More direct methods of manipulating foliar nutrient levels, such as stem injection, have yet to be attempted.

Though these results might be taken as prima facie evidence for rejection of the hypotheses of chronic nutrient deficiency, they provide no basis to reject hypotheses of ephemeral but critical nutrient deficiency. Such deficiencies might occur as the result of a failure of uptake of nutrients due to the action of other factors. One possibility (suggested by J.W. Gilmour and by R.D. Burdon pers. comm.) is that the phenology of root and shoot activity might in some circumstances be temporarily out-of-phase. In densely stocked stands at higher altitudes, where SNC mainly occurs, warming of the root zone during spring may lag substantially behind warming of the canopy. Nambiar *et al.* (1979) have demonstrated that the processes of root initiation and elongation are greatly retarded below a critical root temperature between 11° and 14°C. No adequate set of soil temperature measurements is available for SNC-affected stands of *P. radiata* but measurements made under undisturbed rainforest of lower canopy density and at lower elevation (Podger & Brown 1989) in Tasmania suggest that temperatures at 5 cm depth might not exceed 11°C until late spring. Such a hypothesis is also consistent with the response to thinning in Experiment 4 and might explain the absence of SNC in stands in the high rainfall areas of the West Coast. These occur at lower elevation and have a lower canopy density than stands affected by SNC. Further examination of this hypothesis will require a more detailed knowledge of seasonal trends in (a) foliar nutrient levels, (b) soil to canopy temperature differentials, and (c) the phenology of endophytic fungi as well as their pathogenic capabilities in both stressed and unstressed host tissues.

Management Considerations

The impact of SNC on diameter growth of individual trees in Experiment 1 (St Josephs) appears to be of similar magnitude and kind to that of the impact on volume increment after defoliation by *D. septospora* (van der Pas 1981) and *C. minus* (van der Pas *et al.* 1984) in New Zealand. In all three the relationship between the measures of defoliation and growth are linear and close to a slope of 1:1. For each 10% increase in defoliation the losses of increment in the three diseases were respectively 13.8, 9.8, and 8.0 %. However, it is likely that the real impact of any particular level of defoliation due to SNC at St Josephs is greater than that of either of the other diseases in New Zealand, as our method of rating defoliation is more conservative than that on which the New Zealand studies were based (Kershaw *et al.* 1982). The latter method rates defoliation on all age-classes of needles, so that, for example, some trees with between 10 and 20% loss of crown volume but with no casting of 1-year-old needles would rate 0 on our scale.

The regressions derived from the data of Experiments 3 and 4 (Snowdon Plains) predict a less severe impact of SNC on diameter increment. However, these data are derived from young stands, at a much earlier stage in the development of SNC than at St. Josephs. In these younger stands, both disease incidence and its impact are still clearly increasing as indicated in the analysis of the two increment periods for Experiment 4.

The effect of SNC on stand growth is likely to be less than that due to severe epidemics of *D. septospora* because of the much greater incidence of affected trees in the latter. Comparisons between SNC and Cyclaneusma needle-cast in New Zealand are not possible from the published data (van der Pas *et al.* 1984) in which estimates of disease incidence are not based directly on the frequencies of resistant and susceptible trees. Although SNC has been shown to cause considerable reduction in growth of susceptible trees, its impact on stand growth may not necessarily be a simple summation of individual tree effects as van der Pas *et al.* (1984) assumed in their analysis of the impact of Cyclaneusma needle-cast. We have not yet attempted such stand-based assessments of impact because we have no information on the extent to which SNC-resistant trees are able to take advantage of poor performance by susceptible trees. Alternative approaches to the quantification of impact might include (a) the establishment of clonal stands with varying proportions of resistant and susceptible stock, (b) fungicidal control of disease, (c) analysis of tree growth in groups containing varying proportions of diseased and resistant trees.

The short-term effect of thinning and pruning in reducing SNC levels is similar to that reported by van der Pas *et al.* (1984) for *D. septospora* in New Zealand. In Victoria, Marks & Smith (1987) have also found that increased crown separation greatly reduces infection by *D. septospora.*

Under clearwood management regimes, SNC is not likely to be as serious a problem as it is for stands managed for pulpwood. The early first thinning may delay the onset of severe SNC by 2–5 years and there are opportunities to select for resistance to SNC at subsequent thinning. Unfortunately, in the areas most severely affected by SNC it is not possible to delay first thinning and associated pruning until after the onset of SNC. The advantage of early selection for resistance to SNC to be obtained from delayed thinning is likely to be offset by unacceptably large knotty cores.

As there is clear evidence that resistance to SNC is genetically based (Podger & Wardlaw 1990), programmes of selection may offer the best option to reduce the impact of SNC in the longer-term, particularly in stands managed for pulpwood. The high frequency of resistant individuals in populations should permit such selection without sacrifice of other desirable traits such as improved form and resistance to *D. septospora*, both of which would be desirable in the SNC-affected areas of Tasmania. If the strong genotype × site interaction noted for Cyclaneusma needle-cast in New Zealand (S. Carson pers. comm.) should also apply to SNC, the stability of such selections may not be as great as that evident in resistance to *D. septospora.*

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