SEASONAL CHANGES IN FROST TOLERANCE OF PINUS RADIATA SEEDLINGS RAISED IN DIFFERENT NURSERIES

M. I. MENZIES, D. G. HOLDEN*,
Forest Research Institute, New Zealand Forest Service,
Private Bag, Rotorua, New Zealand
L. M. GREEN,
Plant Physiology Division, DSIR, Palmerston North, New Zealand
and D. A. ROOK
Forest Research Institute, New Zealand Forest Service,
Private Bag, Rotorua, New Zealand

(Received for publication 29 October 1980; revision 3 August 1981)

ABSTRACT

Seedlings of **Pinus radiata** D. Don (radiata pine) raised in seven nurseries in New Zealand were subjected to advective frosts in controlled-environment rooms in autumn (May), winter (August), and spring (October) to determine their seasonal patterns of frost tolerance. At each of these times four levels of frost were provided which allowed differences in frost tolerance to be quantified. The seedlings from Kaingaroa and Athol nurseries withstood frosts of -11°, -12°, and -10°C in May, August, and October respectively, whereas Bulls stock tolerated -6°, -9°, and -5.5°C at these times. Stock from Edendale, Rangiora, Te Teko, and Owhata were intermediate in their responses. Although there was general agreement with published work that changes in temperature and daylength appeared to relate to frost tolerance, a more precise relationship could not be found. In fact, generally, the higher the altitude of the nursery the greater was the frost tolerance of the stock produced.

INTRODUCTION

In New Zealand frosts can occur in autumn, winter, and spring, and also in summer at higher altitudes. As land for exotic afforestation becomes more scarce, forests are being established on sites where the frequency and severity of unseasonable frosts are high and on some of these sites severe frost damage to the major exotic species, radiata pine, is common (Washbourn 1978).

Menzies & Holden (1981) examined seasonal frost-tolerance changes in radiata pine seedlings by exposing batches of seedlings to known levels of frost every month for a year. He observed that for radiata pine growing at Palmerston North the summer frost tolerance was approximately –6°C and the seedlings gradually hardened off from March to May when they could withstand about –8°C without serious injury. Maximum winter frost-tolerance (to about –12°C) was reached during late August

* Current address: Forest Research Office, Queensland Department of Forestry, Gympie, Queensland, Australia.

and from September to November the seedlings dehardened again to have a tolerance in December of about –6°C. These seasonal changes in frost tolerance have been confirmed by Green & Warrington (1978) and tie in with seasonal climatic changes (Washbourn 1978).

Climatic conditions of the nursery in which seedlings are raised have a profound effect on planting stock quality. A pilot study showed that differences in frost tolerance may be found in radiata pine stock raised in different nurseries, with seedlings from colder nurseries having greater frost tolerance than seedlings from nurseries on warmer sites (Rook *et al.* 1974). However, that study did not compare the patterns of frost tolerance of seedlings raised at cool and warm sites. For example, seedlings could have had similar maximum frost-tolerances regardless of where they were grown, or they could have shown similar seasonal changes in frost tolerance, with the stock from a cooler nursery having a frost tolerance 2° or 3°C greater than the stock from a warmer location throughout the year.

Alden & Hermann (1971) claim that the frost tolerance of plants is affected by their mineral nutrient status, and correcting nutrient imbalances or changing the ratios between nutrients has improved cold hardiness (Baule & Fricker 1970; Timmis 1974). Seedlings from New Zealand sources are often low enough in nitrogen, phosphorus, potassium, and magnesium to adversely affect both growth and physiological quality (Knight 1978b). Therefore, in this study it was important to take account of differences in the nutrient status of seedlings from different nurseries in comparisons of frost tolerance between nurseries. Although it is recognised that the cultural treatment of the stock, in addition to mineral nutrition, can affect frost hardiness, it is contended that under normal conditions this would account for only some 0.5°C difference in frost tolerance (cf. effect of wrenching in paper by Rook *et al.* 1974) while the effects of climatic conditions can account for much greater differences in frost tolerance (cf. Menzies 1976). The decision was made to accept the normal cultural and conditioning treatments as carried out in each nursery and not to specify any special conditions which might make the stock tested different from normal stock produced by each of these nurseries.

The objectives of this study were to quantify differences in frost tolerance of radiata pine seedlings raised in different nurseries throughout New Zealand at three times of the year, and to relate frost-tolerance level to the environment in which the seedlings were raised.

MATERIAL AND METHODS

The radiata pine seedlings used in this study were 1/0 stock obtained from the N.Z. Forest Service nurseries at Owhata, Kaingaroa, Bulls, Rangiora, and Edendale, the Tasman Pulp & Paper Co. nursery at Te Teko, and the N.Z. Forest Products Ltd nursery at Athol. Their locations are indicated in Fig. 1. Standard production stock was used so that the frost-tolerance results would be applicable to stock that was being planted in the field. Thus the seedlings were conditioned by undercutting and wrenching, but the conditioning regimes and seedbed densities could vary between nurseries. Normally the seedlings were lifted 3 days before being potted up in 1.2-*l* pots, using a 40 : 40 : 20 v/v mixture of soil : peat : pumice. The seedlings were held in a cool-store prior to transplanting except for a period of several hours while they were being transported by truck or air-freighted to Palmerston North. At the time of transplanting, foliage samples were collected for nutrient analyses.

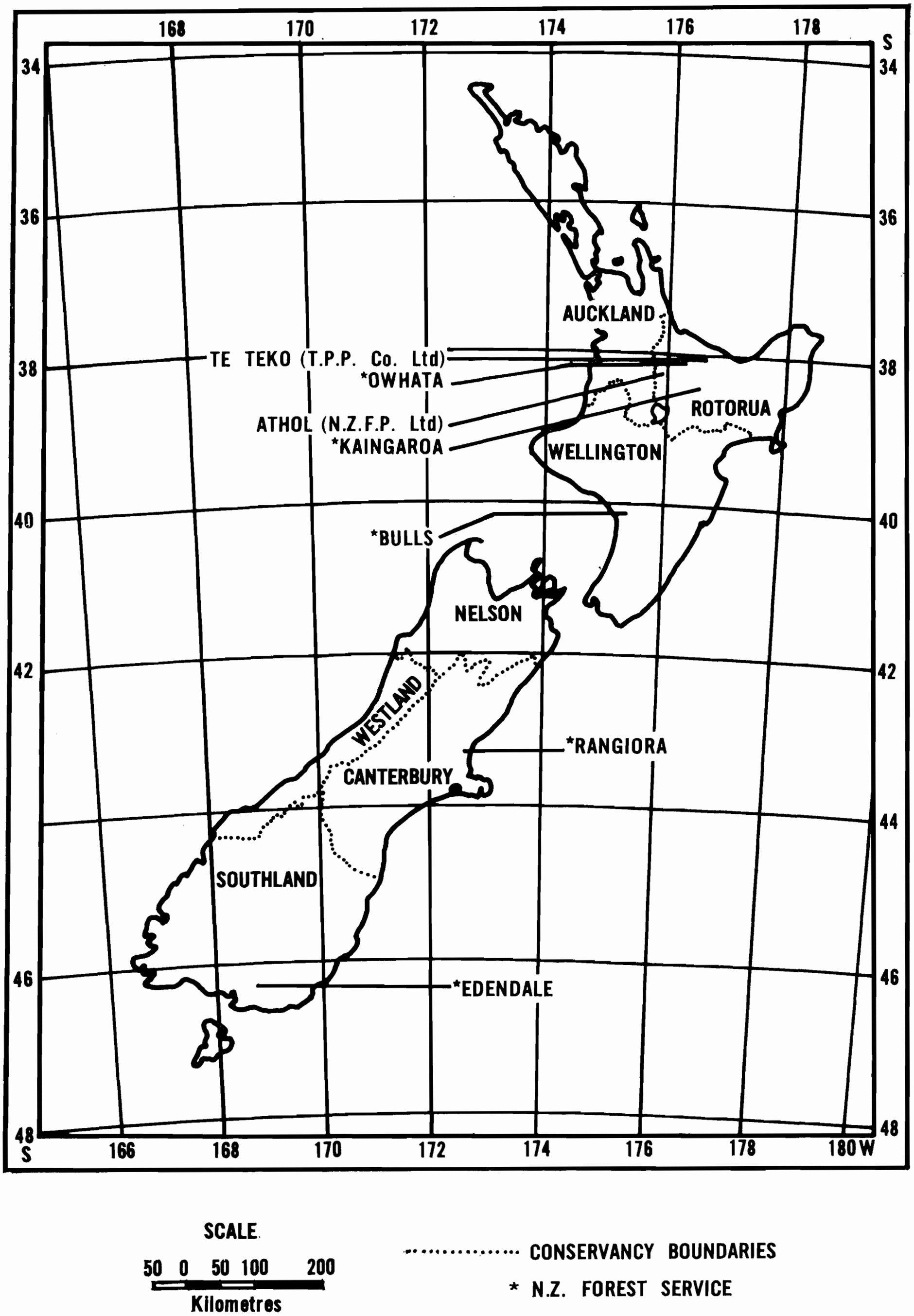

FIG. 1—Locations of the forest nurseries sampled in New Zealand.

To minimise any acclimatisation effects the seedlings were frosted within a week of being lifted from the nursery in which they had been grown. Frost tolerances were determined at three times of the year – autumn (mid May), winter (early August), and spring (mid October). At each of these times of the year four levels of frost, which would be expected to span the range of frost tolerances of the stock from the different nurseries, were programmed using the artificial frost rooms at the DSIR Climate Laboratory, Palmerston North (Robotham *et al.* 1978). The frosts used in May were –6°, –7°, –8°, and –9°C, in August –10°, –12.5°, –14°, and –15°C, and in October –6°, –8°, –10°, and –12°C. Whereas one level of frost could have provided a ranking of frost tolerance of the stock from the different nurseries, the use of a range of frost levels allowed differences in frost tolerances between the stock to be accurately quantified (Warrington & Rook 1980). White advective frosts were provided starting from a +10°C temperature. The temperature decreased over 6 hours to the frost temperature, which was maintained for 6 hours, and then the temperature was increased over 4 hours to +10°C.

The Rangiora seedlings were omitted from the May frosts and from the –12.5°C frost in winter. There were 16 seedlings per frost temperature from the six nurseries examined in May, and 11 or 15 seedlings per frost temperature from all seven nurseries for the other three winter frosts and the four spring frosts. Seedlings from each nursery were randomly allocated to each of four trolleys for each frost run. The seedlings were frosted once only and after being frosted they were transferred outside to an area where they were protected from natural damaging frosts. Approximately 1 month after being frosted the seedlings were visually assessed for frost damage on a 0 to 5 scale (Menzies & Holden 1981) as follows:

0 = no damage
1 = buds undamaged, needles reddening
2 = buds may be damaged, 10% to 30% of needles killed
3 = 40–60% of needles killed
4 = 70–90% of needles killed
5 = all needles killed, stem dead.

Field tests have shown that a seedling will recover from damage rating 2 or less, but consecutive winter frosts will kill a seedling that has a rating of 3 or above. In fact a damage rating of 2 has been used in this study to indicate the lowest temperature that a seedling can be exposed to without being critically injured.

STATISTICAL ANALYSES

Two-factor analyses of variance were used to determine differences in frost tolerance of the seedlings from the seven nurseries at each frosting period, and the significance of any difference is given in brackets. Where there was a significant interaction between main effects, the main effects were tested against the interaction term. The Student-Newman-Keul (SNK) test was used to evaluate significant differences within a main effect, and means with the same subscript were not significantly different at the 5% level.

Multiple linear regression analyses were used to test the relationship between frost tolerance, the environmental conditions in the nursery during the month preceding frost evaluation, and the seedling foliar nutrient levels. The mean frost damage from the four frosts each time was used in the analyses, and the analyses were carried out for each frost period separately and also for the three periods together.

RESULTS

Autumn Frost: The results for the six nurseries are given in Figs 2a and 3a. There was a significant interaction (0.1% level) between nurseries and frost level, a significant difference between nurseries (0.1% level), and a significant difference between frosts (1% level). The significant interaction between nurseries and frost levels was caused by the lack of frost damage at all frost levels in the hardier stock from some nurseries (Athol, Kaingaroa, and Owhata), and the more severe frost damage at –9°C in the stock from Bulls, Edendale, and Te Teko nurseries. The order of increasing frost-tolerance, based on the means from the four frost levels, was Bulls (3.0_a), Edendale (1.6_b), Te Teko (1.1_{bc}), Athol (1.1_{bc}), Kaingaroa (1.0_{bc}), and Owhata (0.8_c).

The percentage of seedlings critically damaged (damage rating >2) for each nursery is given in Fig. 3a. Only in stock from Bulls nursery were more than 20% of the seedlings critically damaged by –6°, –7°, or –8°C frosts, although more than 20% of the seedlings from Bulls, Edendale, and Te Teko were damaged by a –9°C frost.

Generally the frost levels used in the series of autumn frosts were too light and in fact only the Bulls seedlings were severely damaged at the most severe frost level, i.e., –9°C (Fig. 2a).

Winter Frost: The results for the seven nurseries are given in Figs 2b and 3b. As in the autumn frost, there was a significant interaction (0.1% level) between nurseries and frosting level, and significant differences between nurseries and between frosting levels (0.1% level). The order of increasing frost-tolerance, based on the means from the four frost levels, was Te Teko (4.6_a), Bulls (4.5_a), Owhata (3.8_a), Edendale (2.9_b), Athol (2.6_b), Rangiora (2.5_b), and Kaingaroa (2.3_b).

The percentage of seedlings critically damaged for each nursery is given in Fig. 3b. From all nurseries except Te Teko and Bulls less than 20% of the seedlings were critically damaged by a –10°C frost. The –12.5°C frost critically damaged more than 20% of the seedlings from all the nurseries, but less than 50% of the seedlings from Athol and Kaingaroa were critically damaged in this frost.

Thus the frost levels set in winter provided a clear separation of frost-tolerance differences between nurseries. Even the mildest frost (–10°C) almost killed the Bulls stock which had a mean frost damage rating of 3.7, and the Te Teko stock too was severely damaged with a rating of 2.5 (Fig. 2b). Stock from Kaingaroa, Rangiora, Athol, and Edendale consistently showed greater frost-tolerance at each frost level than stock from Te Teko, Bulls, and Owhata nurseries (Figs 2b and 3b).

Spring Frost: The results for the seven nurseries are shown in Figs 2c and 3c. As in the autumn and winter frosts, there was a significant interaction (0.1% level) between nurseries and frosting level, and significant differences between nurseries

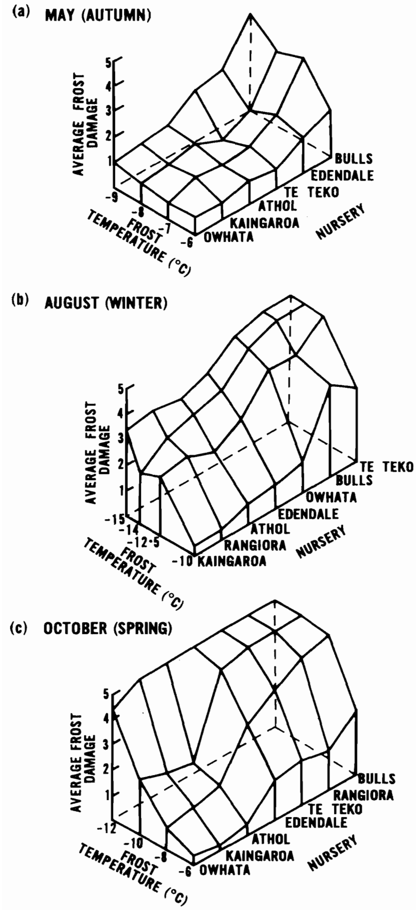

FIG. 2 (left)—Average frost damage at each frosting level (nurseries in order of increasing overall mean damage).

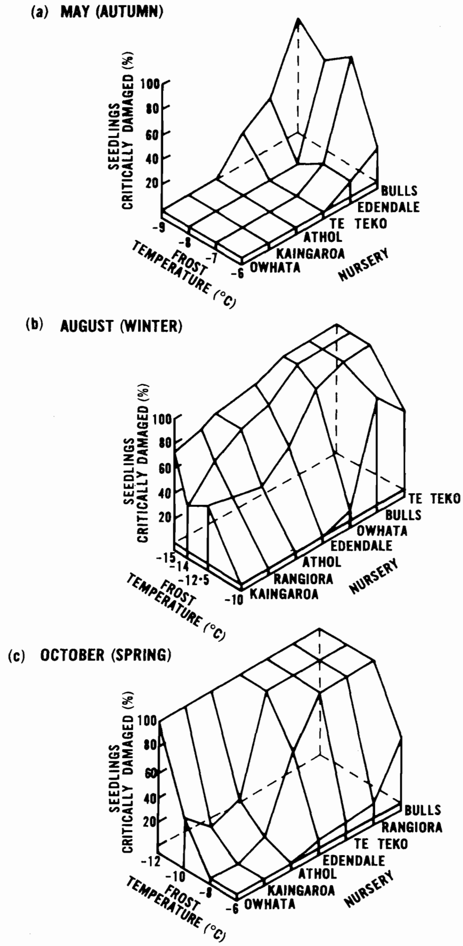

FIG. 3 (right)—Percentage of seedlings rated with frost damage greater than 2 (critically damaged); nurseries in order of increasing overall mean damage.

and between frosting level (0.1% level). The order of increasing frost-tolerance, based on the means from the four frost levels, was Bulls (4.4_a), Rangiora (4.0_a), Te Teko (4.0_a), Edendale (3.7_a), Athol (2.1_b), Kaingaroa (2.1_b), and Owhata (2.0_b).

The percentage of seedlings critically damaged for each nursery is given in Fig. 3c. From all nurseries except Bulls less than 20% of the seedlings were critically damaged by a –6°C frost, and more than 20% of the seedlings from Bulls, Rangiora, and Te Teko were critically damaged by a –8°C frost. Only Kaingaroa stock had less than

20% critically damaged by a –10°C frost, and all stock from all nurseries was critically damaged by a –12°C frost. The Owhata stock together with that from Kaingaroa and Athol nurseries consistently through the spring series of frosts showed superior frost-tolerance, while the Bulls stock showed the poorest frost-tolerance, closely followed by the stock from Rangiora, Te Teko, and Edendale.

Foliage Nutrient Levels

The results from the analyses are given in Table 1. Based on foliar nutrient levels (Knight 1978a), the following nursery stock was deficient in nitrogen – Athol in May; Athol, Bulls, Kaingaroa, and Rangiora in August; and Athol, Bulls, Kaingaroa, Owhata, Rangiora, and Te Teko in October. The levels of nitrogen declined over the winter period except at Edendale. In addition, the Athol seedlings were deficient in potassium in August, and the seedlings from Athol, Kaingaroa, and Rangiora were deficient in potassium in October. Levels of phosphorus and calcium were adequate in all stock throughout the experiment, and only the Athol nursery seedlings were low in magnesium (in October).

TABLE 1—Foliage nutrient levels for seedlings from the seven nurseries at time of frosting (nurseries in alphabetical order)

Nursery	Sampling time	Nutrient level (% of dry weight)				
		N	P	K	Ca	Mg
Athol	Autumn	1.29	0.11	0.73	0.24	0.06
	Winter	1.02	0.11	0.13	0.34	0.11
	Spring	1.07	0.12	0.33	0.24	0.05
Bulls	Autumn	1.73	0.14	1.16	0.43	0.11
	Winter	1.38	0.16	0.93	0.55	0.12
	Spring	1.29	0.20	1.03	0.33	0.13
Edendale	Autumn	1.47	0.16	0.63	0.33	0.10
	Winter	1.83	0.17	0.75	0.43	0.09
	Spring	2.32	0.28	0.96	0.37	0.15
Kaingaroa	Autumn	1.85	0.16	1.07	0.27	0.10
	Winter	1.29	0.13	0.63	0.36	0.11
	Spring	1.01	0.12	0.08	0.30	0.07
Owhata	Autumn	1.74	0.14	0.69	0.29	0.06
	Winter	1.44	0.13	0.80	0.38	0.08
	Spring	1.27	0.13	0.72	0.34	0.11
Rangiora	Autumn	—	—	—	—	—
	Winter	1.11	0.13	0.67	0.28	0.06
	Spring	1.00	0.12	0.33	0.25	0.10
Te Teko	Autumn	1.48	0.15	0.79	0.29	0.10
	Winter	1.46	0.17	0.81	0.29	0.11
	Spring	1.23	0.20	0.81	0.36	0.14
Critical minimum nutrient level*		1.4–1.6	0.12–0.14	c. 0.35	c. 0.10	0.06–0.08

* Knight 1978a

Multiple Regression Analyses

The significant regression equations (5% level) with the average frost damage as the dependent variable, and the foliage nutrient levels and nursery environmental conditions (Table 2) as independent variables, were:

Autumn: average damage = 2.24 + 11.70 Ca (%)

$R^2 = 0.67$

Winter: average damage = 3.59 − 0.12 No. days frost + 1.27 K

$R^2 = 0.95$

Spring: average damage = 4.03 − 0.0042 altitude

$R^2 = 0.84$

Overall (autumn, winter, and spring): average damage = 14.43 − 0.0053 altitude − 0.32 mean temp. − 0.19 latitude

$R^2 = 0.67$

In autumn none of the environmental factors was significant, although grass minimum temperature was the first environmental variable to enter the equation. In winter the number of days with frost was significant, and in spring altitude was significant.

DISCUSSION

Menzies & Holden (1981) exposed seedlings of radiata pine to a range of frosts at 4-weekly intervals throughout the year. Frost damage of the seedlings was assessed 1 month after frosting using the same rating system as in this study. In Fig. 4 Menzies' & Holden's (1981) data are replotted to show the levels of frost tolerance throughout the year, i.e., the maximum level of frost the seedlings will tolerate with a damage rating of 2 or less. The $1\frac{1}{2}/0$ seedlings used in that study were raised at the Forest Research Institute Nursery, Rotorua, and then transported to Palmerston North and potted up 1 month before frosting (the month was allowed for the seedlings to acclimatise to the Palmerston North climate).

In Fig. 4 the frost tolerances of the stock from each nursery have been estimated from the May, August, and October frosting periods. These estimates are based on the data presented in Figs 2 and 3. For example, in the autumn frost the Te Teko stock could tolerate −9°C, the Edendale stock slightly milder than −9°C, and Bulls stock −6°C. In several trials the frosts were too mild or too severe so the frost tolerances had to be estimated.

The results clearly show that the stock from some nurseries, e.g., Bulls, are consistently less frost-tolerant than stock from other nurseries, e.g., Kaingaroa. In autumn there is about 5°C difference in frost-tolerance levels between stock from these two locations, in winter about 3°C difference, and in spring about 4°C difference. When the seasonal patterns of frost tolerance for the individual nurseries are compared with the general pattern several major differences are apparent (Fig. 4). The Bulls stock show seasonal changes in frost tolerance similar to the general pattern, except that Bulls

TABLE 2—Meteorological conditions and daylengths at the contributing nurseries and at Palmerston North during the month preceding frosting of seedlings

Nursery	Nearest met. station*	Lat.	Alt. (m)	Daily mean temp. (°C)	Grass min. (°C)	No. frost days	Rainfall (mm)	Photoperiod (h : min)
				April				
Athol	Kinleith	38°17′	383	12.1	-5.4	7	73	10 : 05
Bulls	Ohakea	40°12′	48	13.9	-1.2	2	72	9 : 56
Edendale	Woodlands	46°22′	47	10.9	-1.2	2	194	9 : 24
Kaingaroa	Kaingaroa	38°24′	544	11.2	-7.0	9	68	10 : 04
Owhata	Rotorua Airport	38°07′	287	13.0	-3.2	5	55	10 : 06
Rangiora	Rangiora	43°19′	46	11.3	-3.2	6	28	9 : 40
Te Teko	Te Teko	38°02′	8	14.6	-2.3	2	60	10 : 06
Palmerston North	DSIR	40°23′	34	13.8	-1.1	1	67	9 : 55
				July				
Athol	Kinleith	38°17′	383	7.7	-5.9	12	222	10 : 10
Bulls	Ohakea	40°12′	48	8.5	-4.1	5	80	10 : 02
Edendale	Woodlands	46°22′	47	5.5	-7.0	14	40	9 : 32
Kaingaroa	Kaingaroa	38°24′	544	6.0	-7.6	19	176	10 : 09
Owhata	Rotorua Airport	38°07′	287	8.1	-4.6	10	244	10 : 11
Rangiora	Rangiora	43°19′	46	5.6	-6.1	15	171	9 : 48
Te Teko	Te Teko	38°02′	8	9.5	-1.5	1	243	10 : 11
Palmerston North	DSIR	40°23′	34	8.8	-3.1	7	80	10 : 02
				September				
Athol	Kinleith	38°17′	383	7.5	-6.8	11	120	13 : 01
Bulls	Ohakea	40°12′	48	8.8	-5.4	8	109	13 : 05
Edendale	Woodlands	46°22′	47	6.8	-5.7	17	124	13 : 20
Kaingaroa	Kaingaroa	38°24′	544	6.7	-10.2	22	94	13 : 02
Owhata	Rotorua Airport	38°07′	287	8.2	-6.0	16	75	13 : 01
Rangiora	Rangiora	43°19′	46	7.1	-5.3	8	103	13 : 12
Te Teko	Te Teko	38°02′	8	10.1	-3.0	6	50	13 : 01
Palmerston North	DSIR	40°23′	34	8.8	-4.5	8	107	13 : 06

* No nursery was more than 20 km from the nearest meteorological station

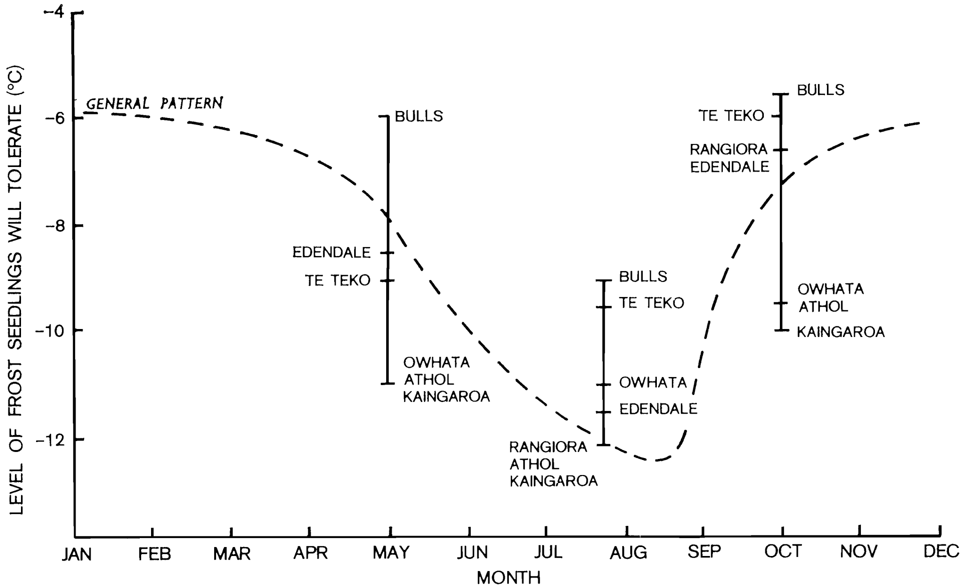

FIG. 4—General pattern of frost tolerance of **Pinus radiata** seedlings from the nurseries sampled.

stock is about 1.5°C less frost-tolerant in autumn and spring and 3°C less frost-tolerant in winter. The Athol and Kaingaroa stock were approximately 3°C more frost-tolerant than the general pattern in autumn and spring but the levels in winter were similar. This would suggest, therefore, that –12°C was close to the maximum frost-tolerance of radiata pine. It should be noted, however, that some individual Kaingaroa seedlings were not critically damaged at –14°C, their damage rating being above 2 but less than 3. The data from Edendale and Rangiora show similar seasonal frost-tolerance values to those obtained by Menzies & Holden (1981). The Te Teko and Owhata seedlings, in contrast, showed relatively greater autumn frost-tolerance than the general pattern, but inferior winter frost-tolerance, and in spring the Owhata stock was more hardy and the Te Teko seedlings were of similar frost-tolerance to the general pattern.

It is generally agreed that frost tolerance in conifers develops largely in response to short days and cool temperatures (Glerum 1976; Christersson 1978). Generally, Kaingaroa was the coldest site with the greatest number of days of frost and produced the most frost-tolerant stock. In contrast, Te Teko was the warmest site but stock from that nursery was generally more hardy than that from Bulls nursery which did not have such warm daily mean temperature and had lower grass minimum temperatures. The difference in mean temperature between Kaingaroa and Bulls was about 2°C, with the grass minimum temperatures being between 3° and 6°C different (Table 2). It is recognised in the literature that cold temperatures and a greater number of frosts induce greater frost-tolerance and the data from this study are in broad agreement. However, in addition to temperature, day length has a strong effect on frost tolerance and during April/May the day lengths were approximately 10 hours and decreasing, while during July/August and September/October the day lengths were approximately 10 and 13 hours respectively and increasing; differences in daylengths between the more northerly and southerly sites were approximately 40 min. Photoperiod did not show any strong effect on hardening in autumn, but the seedlings from Rangiora and Edendale nurseries dehardened more rapidly in the spring during a time of increasing photoperiod, despite the lower temperatures and greater frequency of frost in spring than in winter (Table 2). The stock from the other five nurseries had very similar photoperiods in the spring and dehardened at the same rate. Thus photoperiod apparently affected the dehardening phase more than temperature.

It has been suggested that nutrient deficiencies or imbalances can prevent full development of frost tolerance, and stock from New Zealand nurseries are often low in some elements, especially nitrogen (Knight 1978b). The only elements significant in the regression equations were calcium in May and potassium in August, when higher levels of calcium and potassium increased the frost damage. Both calcium and potassium have been implicated in frost tolerance but normally higher levels of these elements are considered to provide greater frost tolerance (Palta & Li 1978; Weiser 1978). Further research would be required to confirm whether differences in the levels of calcium and potassium affect frost tolerance.

It may be argued that part, at least, of the differences between stock from different nurseries could be due primarily to differences in cultural and conditioning treatment of the stock at different nurseries, although evidence indicates that these would account for differences of only some 0.5°C (Rook *et al.* 1974), and they would not be sufficiently great to account for the 3° to 5°C differences observed in stock from the different nurseries in this study. Stock height/basal-diameter ratios have been used to characterise stock quality as these reflect satisfactorily the effects of previous cultural and conditioning treatments. However, previous work by Menzies (unpublished data) on radiata pine of different genotypes found no significant differences in frost tolerance of stock based on height, basal diameter, or height/basal-diameter ratios.

It was not possible in this study to identify the environmental factors or nutrient levels responsible for increased levels of frost tolerance in radiata pine seedlings, only to provide vague agreement with other published work that cool temperatures and decreasing daylengths are associated with increased frost tolerance during hardening, and that increasing photoperiods are more important than temperature during de-hardening. Generally, however, the nurseries at higher altitudes produced stock which could tolerate frost at least 3°C more severe than stock grown at low altitudes.

ACKNOWLEDGMENTS

This study was made possible by the assistance and co-operation of the officers in charge of the nurseries that supplied plants. We are also grateful to Mr Ian Warrington and DSIR technical staff for help and advice in providing the frost conditions requested, and to Mr R. M. H. C. Scott for carrying out the statistical analyses.

REFERENCES

ALDEN, J.; HERMANN, R. K. 1971: Aspects of the cold-hardiness mechanisms in plants. **Botanical Review 37(1):** 37–142.

BAULE, H.; FRICKER, C. 1970: "The Fertiliser Treatment of Forest Trees." [Translation by Whittles, C. L.] BLV, Verlagsgesellschaft mbH, Munich. 259 p.

CHRISTERSSON, L. 1978: The influence of photoperiod and temperature on the development of frost hardiness in seedlings of **Pinus sylvestris** and **Picea abies**. **Physiologia Plantarum 44:** 288–94.

GLERUM, C. 1976: Frost hardiness of forest trees. Pp. 403–20 **in** Cannell, M. G. R.; Last, F. T. (Eds.) "Tree Physiology and Yield Improvement." Academic Press, London, New York, San Francisco.

GREEN, L. M.; WARRINGTON, I. J. 1978: Assessment of frost damage in radiata pine seedlings using the diffusate electroconductivity technique. **New Zealand Journal of Forestry Science 8:** 344–50.

KNIGHT, P. J. 1978a: Fertiliser practice in New Zealand forest nurseries. **New Zealand Journal of Forestry Science 8:** 27–53.

——— 1978b: The nutrient content of **Pinus radiata** seedlings: a survey of planting stock from 17 New Zealand forest nurseries. **New Zealand Journal of Forestry Science 8:** 54–69.

MENZIES, M. I.; HOLDEN, D. G. 1981: Seasonal frost-tolerance of **Pinus radiata**, **Pinus muricata**, and **Pseudotsuga menziesii**. **New Zealand Journal of Forestry Science 11(2):** 92–9.

PALTA, J. P.; LI, P. H. 1978: Cell membrane properties in relation to freezing injury. Pp. 93–115 **in** Li, P. H.; Sakai, A. (Eds.) "Plant Cold Hardiness and Freezing Stress: Mechanisms and Crop Implications." Academic Press, New York, San Francisco, London.

ROBOTHAM, R. W.; LLOYD, J. B.; WARRINGTON, I. J. 1978: A controlled environment room for producing advective white or black frost conditions. **Journal of Agricultural Engineering Research 23:** 301–11.

ROOK, D. A.; MENZIES, M. I.; ROBOTHAM, R. W. 1974: Artificial frosting studies of radiata pine planting stock. **New Zealand Journal of Forestry 19(2):** 295–300.

TIMMIS, R. 1974: Effect of nutrient stress on growth, bud set and hardiness in Douglas fir seedlings. Pp. 187–93 **in** Proc. North American Containerised Forest Tree Seedling Symposium, Denver, Colorado, 26–29 August 1974. **Great Plains Agricultural Council Publication No. 68.**

WARRINGTON, I. J.; ROOK, D. A. 1980: Evaluation of techniques used in determining frost tolerance of forest planting stock: a review. **New Zealand Journal of Forestry Science 10(1):** 116–32.

WASHBOURN, R. W. 1978: Establishment practice on frost-prone sites at Kaingaroa Forest. **New Zealand Journal of Forestry 23(1):** 107–20.

WEISER, C. J. 1978: Plant cold hardiness seminar, summary and general remarks. Pp. 391–4 **in** Li, P. H.; Sakai, A. (Eds.) "Plant Cold Hardiness and Freezing Stress: Mechanisms and Crop Implications." Academic Press, New York, San Francisco, London.