CONIFER ESTABLISHMENT IN SOUTH ISLAND HIGH COUNTRY: INFLUENCE OF MYCORRHIZAL INOCULATION, COMPETITION REMOVAL, FERTILISER APPLICATION, AND ANIMAL EXCLUSION DURING SEEDLING ESTABLISHMENT

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ABSTRACT

Seeding trials with *Pinus* species and *Pseudotsuga menziesii* (Mirb.) Franco were undertaken to investigate known constraints to low-cost afforestation of depleted short grasslands of the South Island high country.

In field trials mycorrhizal development of *Ps. menziesii* seedlings was enhanced by drilling seed with soil collected under an existing stand. Seed inoculation with mycorrhizal fungal spores appeared to be more successful than soil inoculation in promoting pine mycotrophy. Seed inoculation was less effective for *Pinus nigra* Arn. than for *P. radiata* D.Don, possibly because the method used resulted in attachment of more spores to the larger *P. radiata* seed. Inoculation of pine seed with spores of *Rhizopogon rubescens* Tul. was more effective than inoculation with *R. luteolus* Fr. or *Suillus luteus* (L. ex Fr.) S.F.Gray.

Exclosure trials at two Mackenzie Basin sites showed that browsing of seedlings was due to rabbits. Mechanical removal of residual herbaceous species resulted in reduced tree seedling numbers as rabbits were attracted to the bare soil or to seedlings exposed by turf removal. Control of rabbits for several years may be necessary to allow successful establishment by seeding. In the absence of rabbits, turf removal may improve seedling establishment in drier areas. Fertiliser application decreased tree seedling numbers through increased competition from the herbaceous sward.

Establishment of pines by seeding on the drought-prone outwash gravel soils of the Mackenzie Basin is not reliable. On less drought-prone soils forest establishment by seeding is possible if rabbits are controlled. Further experimentation with mycorrhizal inoculation is required.

Keywords: browsing; competition; establishment; inoculation; mycorrhizas; seeding; *Pinus nigra*; *Pinus radiata*; *Pseudotsuga menziesii*.

INTRODUCTION

Exotic conifer species occupy less than 1% of the area of the South Island high country (Ledgard & Belton 1985a), but forestry provides a potentially more productive, profitable, and sustainable land-use than extensive pastoral farming as currently practised in the region, and has been promoted on a number of occasions (Nordmeyer 1979; Ledgard & Belton 1985a, b; O'Connor 1986; Belton 1991). Because of such factors as rotation length and distance to ports, which make forestry in the high country less attractive to investors, afforestation is proceeding only slowly. Much of the land suitable for conifers is of gentle topography and would be suitable for establishment by direct seeding. Costs of establishment by this method are potentially much lower than for planting, and may encourage development of a forest resource in the region.

Trials at Broken River (Waimakiriri catchment) and Ribbonwood (Ahuriri catchment) in the early 1980s showed that it was possible to establish pines by drilling seed in undeveloped grassland, but not in grassland modified by oversowing and topdressing where competition from the herbaceous sward was more vigorous (Davis 1989). Seeding of *Pseudotsuga menziesii* was unsuccessful, probably because of a lack of appropriate mycorrhizal fungi in the vicinity. With the development of increased interest in forestry as a land use in the high country during recent years, further trials were established in 1992 at Balmoral Station (Mackenzie Basin) to compare the performance of direct-seeded pine species on contrasting soil types in a dry, sub-humid environment. Results from these trials indicated that mycorrhizal development of the pine seedlings was sporadic, despite the fact that pine plantations existed a short distance upwind from the site and wilding pines were present in the immediate vicinity. Observations also indicated that browsing of young seedlings might be a major constraint. This paper presents results of trials established in 1993 and 1994 to examine the feasibility of introducing mycorrhizas by inoculation of seed or soil, and to determine the agents of browsing. The effects of mechanical removal of plant competition and of fertiliser application on the establishment of conifer seedlings were also examined.

CHARACTERISTICS OF THE TRIAL SITES

The trials were carried out at five locations: the upper and the lower terrace at Balmoral, Mt John, The Tui Homestead, and Mt Barker (Table 1). The Upper Balmoral and Lower Balmoral sites are old- and intermediate-aged terraces respectively in the moist sub-humid zone of the Mackenzie Basin (Webb 1992). The soil at the Lower Balmoral site is formed from outwash gravels, is an excessively drained stony sandy loam of the Fork series, and is highly drought-prone. Topsoils at the other sites are of moderate depth and are stone-free. The vegetation at the Lower Balmoral and Mt John sites consists almost entirely of hawkweeds (*Hieracium pilosella* L. and *H. praealtum* Vill.) and there is a high proportion (approximately 50%) of bare ground at the Lower Balmoral site. Vegetation at the other sites is short grassland, in which hawkweeds, hard tussock (*Festuca novae-zelandiae* (Hack.) Ckn.), and browntop (*Agrostis capillaris* L.) are prominent species. All sites are flat.

Precipitation data for the 1993–94 and 1994–95 growing seasons at stations near the trial sites are given in Fig. 1. The Balmoral and Mt John sites are within 3 km of the Tekapo Station

TABLE 1–Characteristics of the trial sites

Site	Location	Altitude (m)	Precipitation (mm)	Soil series	Dominant vegetation	Grid reference¶
Upper Balmoral	Mackenzie Basin	730	580	Pukaki	Hawkweed* Browntop† Hard tussock‡	I37 035825
Lower Balmoral	Mackenzie Basin	700	580	Fork	Hawkweed	I37 039825
Mt. John	Mackenzie Basin	760	650	Tekapo	Hawkweed	I37 056887
The Tui	Rangitata Valley	700	720	Cass	Hard tussock Browntop Hawkweed	J36 395221
Mt. Barker	Rakaia Valley	620	900	Acheron	Hard tussock Moss§	K35 976604

* Mainly *Hieracium pilosella*, some *H. praealtum*
† *Agrostis capillaris*
‡ *Festuca novae-zelandiae*
§ *Racomitrium* sp.
¶ New Zealand Department of Survey and Land Information Infomap 260

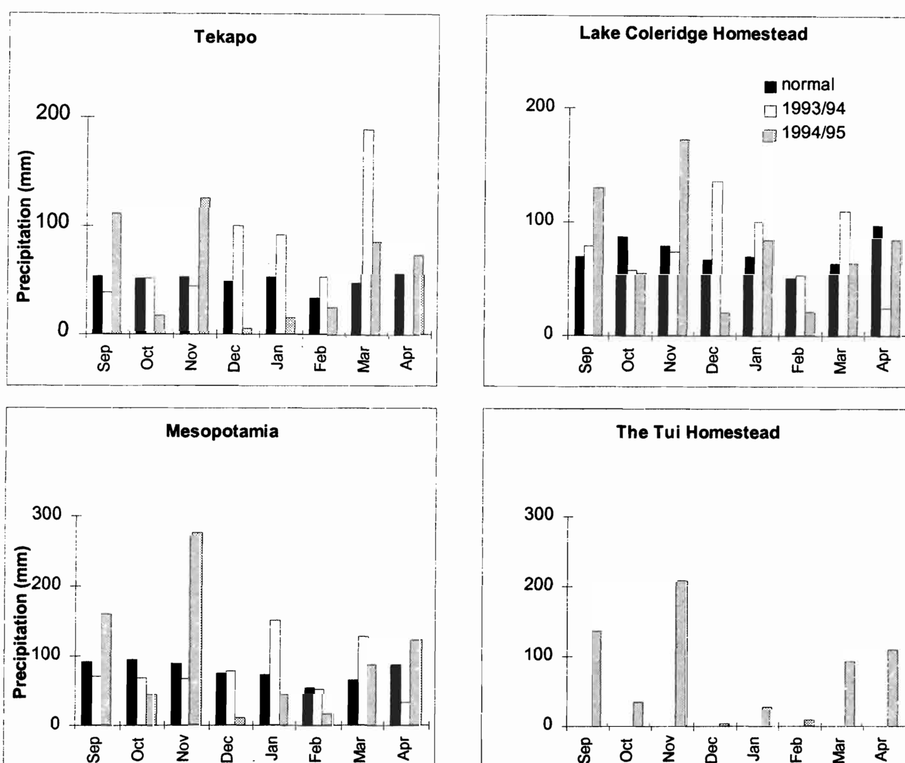

FIG. 1–Growing season precipitation at stations near the trial sites. Normals are from Meteorological Service (1983). The 1993–95 data for all sites except The Tui are from the National Institute of Water and Atmospheric Research, and for The Tui are from D.Prouting.

and are of similar elevation. The Mt Barker site is within 1 km of the Lake Coleridge Homestead, and is about 100 m higher in elevation. Records for The Tui Homestead (472 m) are not available for 1993–94 and so data for the Mesopotamia Station (552 m), approximately 5 km west of the trial site (610 m), are presented. Rainfall at The Tui Homestead for the months August 1994 to June 1995 was 76% of that at Mesopotamia. For the three summer months of December, January, and February, rainfall in 1994–95 was substantially lower than the annual average at both Tekapo and Mesopotamia, and for two of those months at Lake Coleridge. Rainfall was particularly low at The Tui Homestead over the same period.

Wilding pines were present in the immediate vicinity of the Upper Balmoral site, and a large area of mature pines was located near the Mt Barker site. No pines existed within 3 km of the Tui site. There were no *Ps. menziesii* trees within 2 km of the Upper Balmoral site, but isolated trees were present within the area of mature pines at Mt Barker.

METHODS

Four groups of trials were conducted, each at two or more sites. All trials were laid out in a randomised complete block design. Each treatment combination was replicated at least four times. Unless stated otherwise, conifer seed was sown at a nominal spacing of 100 mm, and a depth of 15–20 mm, in 20-m-long rows spaced approximately 1 m apart. The New Zealand Agricultural Engineering Institute (NZAEI) experimental drill rig "J. Tull" described by Horrell (1993) was used for seed sowing. In all except the animal exclusion trials, the basic experimental unit (plot) consisted of a single row.

Trial Details

Effect of inoculation with mycorrhizal fungi on conifer seedling establishment and mycorrhizal status (Mt Barker and Upper Balmoral sites)

These trials were carried out with three conifer species: *P. radiata*, *P. nigra*, and *Ps. menziesii*. Two methods of inoculation were investigated. The first was soil inoculation, using mycorrhizal material contained in mineral soil (0–50 mm depth) collected from young (approximately 10-year-old) stands of trees of the same species as the seed, growing in Craigieburn Forest, central South Island. Forest soil was collected in mid-September, dried to 20% moisture content, passed through a 5-mm sieve, and stored in a refrigerator. The soil was drilled below the seed at a rate determined by the capacity of the cone seeder (33 g/m or 165 kg/ha at 2-m row spacing). The second method was seed inoculation, using a modification of the procedure described by Theodorou & Benson (1983). Only the two pine species were treated by this method. Partially air-dried (4 days at 22–29°C) sporophores of *Rhizopogon rubescens* (100 g) collected from Owhata Nursery, near Rotorua, in mid-September, were macerated in a blender with 200 ml water and 100 ml 30% gum arabic solution. The macerate was passed through an 853-μm sieve, and used to coat the pine seeds. Coating was achieved by adding the macerate dropwise to the pine seeds in a plastic bag, followed by shaking, until the seed was fully moistened. The seed was then placed in the shade to dry. The number of *R. rubescens* spores attached to each seed, estimated from haemocytometer counts of spores contained in water-washings from each of 10 coated seeds, was 1.28×10^5 for *P. nigra* and 1.14×10^6 for the larger *P. radiata* seed.

The trial at each site consisted of eight treatment combinations: 2 pine species × 3 inoculation treatments (soil; seed; nil) + *Ps. menziesii* × 2 inoculation treatments (soil; nil). Each combination was replicated five times. Seed was sown in September 1993. A "strip" coulter was set to cut and remove a ribbon of turf 20 mm deep × 100 mm wide for the drill row.

At the end of the first and the second growing seasons (8 months and 20 months after sowing), seedling height was measured and mycorrhizal status was assessed from seedling colour. Dark-green seedlings were considered to be mycorrhizal, while pale-green, yellow, and yellow-brown seedlings were classed as non-mycorrhizal. Shoot colour had been found to provide an accurate assessment of the relative proportion of dichotomised short roots in drill-sown 2-year-old plants at the Upper Balmoral site.

At the end of the first growing season, five yellow and five dark-green seedlings were excavated from the uninoculated *P. radiata* plots at Mt Barker. Five or six dark-green seedlings were also excavated from each of the *P. radiata* inoculation treatments and the two *Ps. menziesii* treatments. Seedling roots were washed free of soil and the proportion of dichotomised short roots was estimated visually. Morphological characteristics were used to identify the fungal species involved from descriptions given by Chu-Chou & Grace (1983a, b). In January 1996 (2.25 years after sowing), root systems of *P. radiata* and *P. nigra* (the first five seedlings in each of four replicate plots; uninoculated and seed inoculation treatments only) were examined in the same way.

Effect of inoculation of P. muricata *D.Don seed with different species and provenances of mycorrhizal fungi on seedling establishment and mycorrhizal status (The Tui and Upper Balmoral sites).*

Sporophores of four species of fungi known to form ectomycorrhizas with *Pinus* spp. were collected, processed, and stored according to methods outlined in Table 2. Dried material was ground to pass a 1-mm sieve and dusted on to seed of *P. muricata* that had been moistened with gum arabic (30%). The number of spores per seed was estimated as described in the previous section, and it was found that inoculation with all species except *Amanita muscaria* (L. ex Fr.) S.F.Gray material had been successful. Treated seed was air-dried and stored in a refrigerator overnight before sowing.

TABLE 2–Collection and processing of sporophore material and effectiveness of inoculation of *Pinus muricata* seed.

Species	Collection site	Collection date	Sporophore processing	Number of spores/seed
Suillus luteus	Balmoral Station, Tekapo	6/4/93	Dried at 22–29°C for 7 days then over-winter in refrigerator	3.57×10^6
Amanita muscaria	Woodend, Canterbury	4/3/93	As above	0
Rhizopogon luteolus	Woodend, Canterbury	30/3/93	As above	4.80×10^6
Rhizopogon rubescens	Owhata nursery, Rotorua	13/9/93	Dried at 22–29°C for 7 days then stored 3 weeks in refrigerator	2.53×10^6
Rhizopogon rubescens	Eyrewell Forest, Canterbury	4/10/93	Stored 4 days in refrigerator	6.65×10^5

In early October 1993 seed was hand-sown in rows placed 1 m apart, each row containing 50 seeds. The experimental unit was one row of seed inoculated with one species of mycorrhizal fungus per provenance.

At the end of the first growing season seedling height was measured and mycorrhizal status was assessed from seedling colour as before. Seedling mortality during the second year precluded further assessment. This was associated with browsing at the Upper Balmoral site, but was caused by some other factor at The Tui.

Effect of plant competition removal and fertiliser treatment on pine seedling establishment (Mt Barker, Upper Balmoral, and Lower Balmoral sites)

The NZAEI drill rig was used to sow seed and to remove vegetation. A "strip" coulter cut and laid to one side a ribbon of turf 150 mm wide and 25 mm deep before seed was sown at the centre of the cut strip. A "slot-wing" coulter, built for these trials, cut and removed a ribbon of turf 50 mm wide and 40 mm deep, and also undercut but left in place a strip of vegetation 75 mm wide on either side of the drilled seed row. The conventional "Baker Boot" coulter placed seed in a cut row, but did not remove vegetation. The effect of all three coulters was tested with and without added diammonium phosphate applied at a rate of 12.25 g/m row (500 kg/ha at conventional drill coulter spacings).

Species tested were *P. nigra* at Mt Barker and *P. radiata* at the Upper Balmoral and Lower Balmoral sites. Six treatment combinations (3 levels of competition removal × 2 fertiliser levels) were investigated at each site.

At the end of the first and second growing seasons, surviving seedlings were counted and their height was measured.

Effect of animal exclusion on establishment of P. radiata *seedlings (Upper Balmoral and Mt John sites)*

Rabbit exclosures (plot sides fenced with 50-mm-mesh netting anchored at the base with turves) and control plots (unfenced) were used at both sites. The Upper Balmoral trial tested the effect of two additional treatments: rabbit/bird exclusion (plots fenced and covered with 15-mm-mesh netting), and rabbit/bird/small animal exclusion (plots fenced and covered with 2-mm-mesh horticultural shade cloth). The latter was designed to exclude large flying insects, lizards, mice, etc.

A "strip" coulter was set to cut and remove ribbons of turf 100 mm wide for centred seed rows which were placed 200 mm apart. Plot size was 5 × 1 m and each plot spanned four seed rows.

Seedlings were counted twice during the first growing season at the Upper Balmoral site and three times at Mt John. Plots were checked for evidence of browsing during the assessments.

Statistical Analysis

Data for individual sites were analysed separately. Analysis of variance was used to determine whether there were significant differences between treatment means. Individual means were compared using the Least Significant Difference (LSD) test. Data expressed as percentages were arcsine transformed prior to carrying out analysis of variance and the LSD test and back-transformed for presentation.

RESULTS

Inoculation with Mycorrhizal Fungi

At Mt Barker, the overall seedling survival rate at the end of the first season ranged between 30% and 51%. In uninoculated control plots, 48% of *P. radiata*, 73% of *P. nigra*, and 4% of *Ps. menziesii* seedlings were mycorrhizal (Table 3). Soil inoculation increased the proportion of *Ps. menziesii* mycorrhizal seedlings and the height growth of *P. radiata*. Seed inoculation increased both the height growth and the proportion of *P. radiata* mycorrhizal seedlings. Neither method had a significant effect on *P. nigra*. After the second season at least 95% of seedlings of both pine species were mycorrhizal and no influence of inoculation treatment on their survival or height growth could be detected. Soil inoculation increased the number of mycorrhizal *Ps. menziesii* seedlings by 77% and their height by 50%.

TABLE 3–Effect of soil inoculation and seed inoculation on seedling height growth and mycorrhizal development at Mt Barker. Mycorrhizal development was assessed from seedling colour.

Species	Inoculation treatment	8 months after sowing		20 months after sowing		
		Mycorrhizal seedlings (%)	Seedling height (cm)	Survival (%)	Mycorrhizal seedlings (%)	Seedling height (cm)
P. radiata	Control	48 cd*	3.9 c	64 bcd	98 a	11.6 a
	Soil	65 bc	4.6 b	48 d	100 a	13.1 a
	Seed	72 ab	5.3 a	60 cd	100 a	11.6 a
P. nigra	Control	73 ab	1.5 e	83 abc	98 a	2.8 b
	Soil	82 a	1.3 e	90 a	95 a	2.3 b
	Seed	87 a	1.4 e	87 ab	97 a	3.1 b
Ps.menziesii	Control	4 e	2.5 d	70 bcd	8 c	1.7 b†
	Soil	33 d	2.5 d	83 ab	85 b	3.0 b
	S.E. mean	8.3	0.22	10.8	3.7	1.48

* Within columns, values followed by the same letter are not significantly different (LSD test $p = 0.05$).
† The height difference between control and forest soil inoculated *Ps. menziesii* seedlings was highly significant ($p<0.001$) when the data were subjected to the T-test.

At the end of the first season, 60% of the Mt Barker uninoculated *P. radiata* seedlings that had been classified as non-mycorrhizal had a small proportion (4%) of mycorrhizal roots (Table 4). Those classified as mycorrhizal had an estimated 51% of the root system infected. A *Suillus* sp. (presumably *S. luteus,* which was known to be common in the area) was identified on roots of both groups, and on the soil-inoculated seedlings. All six seedlings taken from the seed inoculation treatment had a high proportion of roots (71%) infected by *R. rubescens* (Table 4). A high proportion of the roots of *Ps. menziesii* seedlings from the soil inoculation treatment which were classified as mycorrhizal were infected with unidentified mycorrhizal fungi (Table 4).

After 2.25 years 95% of seed-inoculated *P. radiata* seedlings but only 32% of seed-inoculated *P. nigra* seedlings were infected with *R. rubescens* (Table 5). All other seedlings were infected with *S. luteus*. *Suillus* spp. were not found on 8-month-old seed-inoculated *P. radiata* seedlings, which all carried *R. rubescens*. Among the 2.25-year-old seed-inoculated seedlings, 18% of *P. radiata* and 14% of *P. nigra* roots were carrying *Suillus* spp. as well as *R. rubescens*.

TABLE 4–Mycorrhizal status of roots of 8-month-old uninoculated and inoculated seedlings of *Pinus radiata* and *Pseudotsuga menziesii* at Mt Barker.

Species	Inoculation treatment	Seedlings with mycorrhizal roots (%)	Short roots mycorrhizal (%)	Species forming association
P. radiata (6)*	Uninoculated (yellow seedlings)	60	4	*Suillus* sp.
P. radiata (5)	Uninoculated (green seedlings)	100	51	*Suillus* sp.
P. radiata (6)	Soil	100	46	*Suillus* sp.
P. radiata (6)	Seed (with *R. rubescens*)	100	71	*Rhizopogon rubescens*
Ps. menziesii (5)	Uninoculated	0	–	–
Ps. menziesii (5)	Soil	100	70	Uncertain†

* The value in parentheses indicates the number of seedlings examined

† Two forms of mycorrhizal fungus were present on roots of *Ps. menziesii* inoculated with soil. One form was either *R. parksii* or *S. lakei*, while the other form was thought to be either *Laccaria laccata* or *Thelephora* sp. Both forms were present together on three of the five seedlings examined, and present alone on one of each of the other seedlings.

TABLE 5–Mycorrhizal development on roots of 2.25-year-old seedlings of *Pinus radiata* and *P. nigra* at Mt Barker. Seedlings were grown from either uninoculated seed or from seed inoculated with spores of *Rhizopogon rubescens*. n = 20.

	Pinus radiata		*Pinus nigra*	
	Control	Seed inoculated	Control	Seed inoculated
Percentage of short roots mycorrhizal	27	51	40	39
Percentage of seedlings infected with *Suillus* sp.	100	18	100	77
Percentage of seedlings infected with *Rhizopogon* sp.	0	95	0	32
Percentage of seedlings infected with both *Suillus* and *Rhizopogon* spp.	0	18	0	14

Seedling establishment at Balmoral was poor (<5%) due mainly to browsing, and to the low seed viability of *P. nigra*. Available data indicated that, by the end of the first growing season, seed inoculation had increased the proportion of mycorrhizal *P. radiata* seedlings (Table 6). By the end of the second season some improvement in the mycorrhizal status of *P. radiata* and *Ps. menziesii* was noted in the soil inoculation plots.

Inoculation of *P. muricata* with Different Mycorrhizal Fungi

At The Tui, the proportion of seedlings found to be mycorrhizal at the end of the first season was significantly greater where seed had been treated with *S. luteus*, *R. luteolus*, or *R. rubescens* material than where uninoculated seed or that treated with *A. muscaria* had been sown (Table 7).

Low seedling survival rates at the Upper Balmoral site (Table 7) were associated with evidence of browsing. The proportion of seedlings that had developed mycorrhizas was lower than at The Tui. Seed inoculation with the Owhata provenance of *R. rubescens* was the only treatment that significantly increased the proportion of mycorrhizal seedlings.

TABLE 6–Effect of soil inoculation and seed inoculation on mycorrhizal development and height growth of 1- and 2-year-old seedlings of conifer species, Upper Balmoral Trial.

Species	Inoculation treatment	8 months after sowing			20 months after sowing		
		No. of seedlings	Mycorrhizal seedlings (%)	Seedling height (mm)	No. of seedlings	Mycorrhizal seedlings (%)	Seedling height (mm)
P. radiata	Control	29	7	33 (1.8)*	15	53	48 (5.8)*
	Soil	21	9	27 (2.1)	7	86	53 (10.6)
	Seed	15	47	37 (2.5)	9	89	85 (9.9)
Ps.menziesii	Control	31	10	24 (0.9)	11	1	21 (1.8)
	Soil	46	15	24 (0.6)	17	35	24 (1.7)

* SEM in parentheses

TABLE 7–Effect of mycorrhizal species on mycorrhizal status and height of *Pinus muricata* seedlings after one growing season.

	No. of seedlings/m	Percentage mycorrhizal	Height (mm)
The Tui Homestead site			
Control	3.0	4 c*	31 b
Amanita muscaria	3.2	0 c	29 b
Suillus luteus	2.6	29 b	30 b
Rhizopogon luteolus	3.8	34 ab	30 b
Rhizopogon rubescens (Owhata)	3.0	55 a	35 a
S.E. mean	0.70	7.7	1.6
Upper Balmoral site			
Control	0.9	0 b	24 bc
Amanita muscaria	1.4	5 b	29 a
Suillus luteus	1.6	0 b	25 bc
Rhizopogon luteolus	1.7	5 b	23 c
Rhizopogon rubescens (Owhata)	1.5	28 a	27 ab
Rhizopogon rubescens (Eyrewell)	1.1	6 b	24 bc
S.E. mean	0.48	7.3	1.8

* Within columns, values followed by the same letter are not significantly different (LSD test, $p = 0.05$).

Fertiliser Treatment and Removal of Competition

Where fertiliser had been used in combination with the "slot-wing" and "Baker Boot" coulters at Mt Barker, *P. nigra* seedlings were inundated by the resident vegetation during the first growing season. No measurements could be made for these treatments. Seedling survival rate in plots without fertiliser was not significantly affected by competition removal (Fig. 2a). Seedling height was decreased slightly but significantly by competition removal in the first season; however, this difference was reduced over the following year because of slightly greater growth where competition was removed (Fig 2b). Within the "strip" coulter treatment, fertiliser application clearly depressed survival rate (Fig 3a), but had no effect on seedling height (Fig 3b).

The response of resident vegetation to fertiliser treatment was less vigorous at Balmoral than at Mt Barker. In the Upper Balmoral trial, seedling survival and height were both

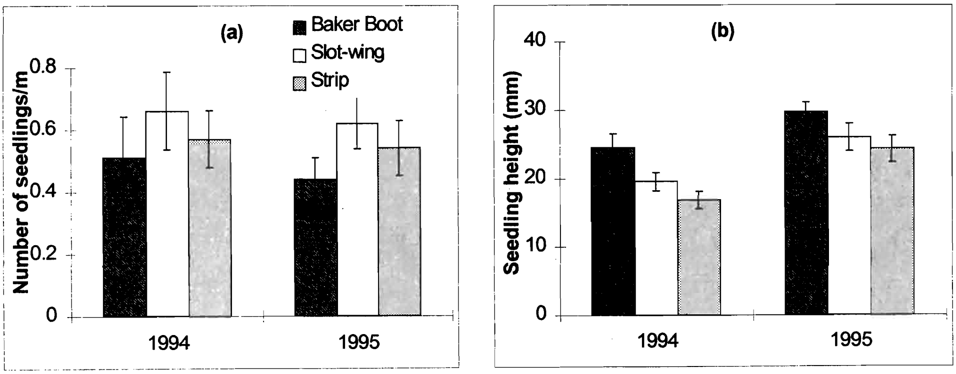

FIG. 2–Effect of coulter type on *P. nigra* seedling survival (a) and growth (b) in the absence of fertiliser, Mt Barker. Vertical bars ± 1 s.e.

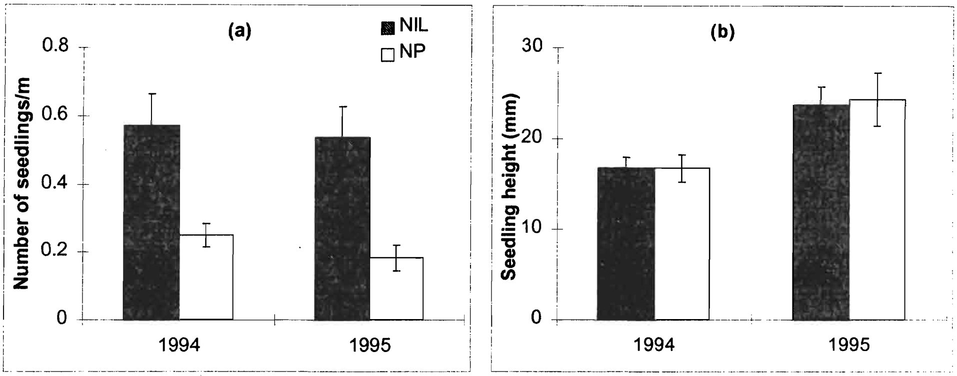

FIG. 3–Effect of fertiliser on *P. nigra* seedling survival (a) and growth (b) from seed sown using the strip coulter, Mt Barker. Vertical bars ± 1 s.e.

reduced where competition had been removed (Fig. 4a, b), and it was clear that the effect was due to browsing. The reduction was greater where the "strip" coulter had been used. Fertiliser treatment had a negative effect on survival, but did not influence seedling height (Fig. 5a, b).

At the Lower Balmoral site, none of the seedlings survived to the end of the second season. During the first year, competition removal had no significant effect on survival, but was associated with a slight reduction in seedling height (Fig. 4c, d). Few seedlings survived in plots treated with fertiliser (Fig. 5c). Those that remained showed a height response to fertiliser treatment where there was no competition removal (Fig. 5d).

Animal Exclusion

Exclusion of rabbits had a significantly positive effect on seedling survival at both sites (Fig. 6a, b). Evidence of browsing was confined to the unfenced plots and took the form of shoot decapitation. At Balmoral survival was similar for all exclosure types, and there was no evidence of damage by agents other than rabbits. Seedling numbers in control plots in January and in May were higher at Balmoral than at Mt John.

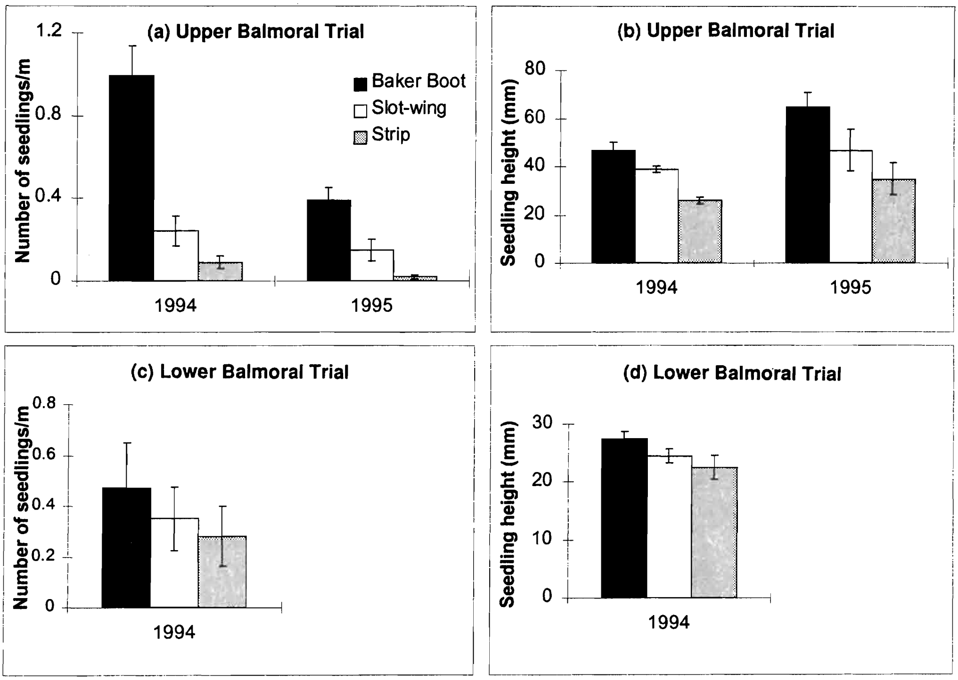

FIG. 4—Effect of coulter type on *P. radiata* seedling establishment at Balmoral. Values are means of two fertiliser treatments. Vertical bars ± 1 s.e.

DISCUSSION

Mycorrhizal Inoculation

From the inoculation trials it seems that appropriate mycorrhizal species can be successfully introduced by drilling forest soil with the seed, or by inoculation of seed with fungal spores. Soil inoculation was highly effective in promoting mycorrhizal development in *Ps. menziesii* at Mt Barker. It appeared to be less effective at the Upper Balmoral site, but here results were available from only a small number of seedlings. Seed inoculation was apparently more successful than soil inoculation in promoting pine mycotrophy, but there is some uncertainty about results at both sites due to the possible confounding effect of resident inoculum. Further trials on a range of sites are needed to confirm the observations. The rate of soil drilled (165 kg/ha) seems quite modest, being equivalent to a relatively low rate of fertiliser application. Further studies are needed to determine whether age and location of the tree stand from which soil is collected, or depth in the profile, will influence its effectiveness. Tree age may be important since the dominance of mycorrhizal species may change during the life of the stand (Bowen 1994).

Seed inoculation of *P. radiata* was associated with greater early seedling height growth than soil inoculation. At Mt Barker 72% of seed-inoculated *P. radiata* seedlings were mycorrhizal by the end of the first growing season. Six seedlings examined at that stage all had a high proportion of fine roots infected with *R. rubescens*, in contrast to seedlings from other treatments in which no *R. rubescens* was found. This indicated that seed inoculation had been highly effective. Seed inoculation of *P. nigra* was less effective, with *R. rubescens*

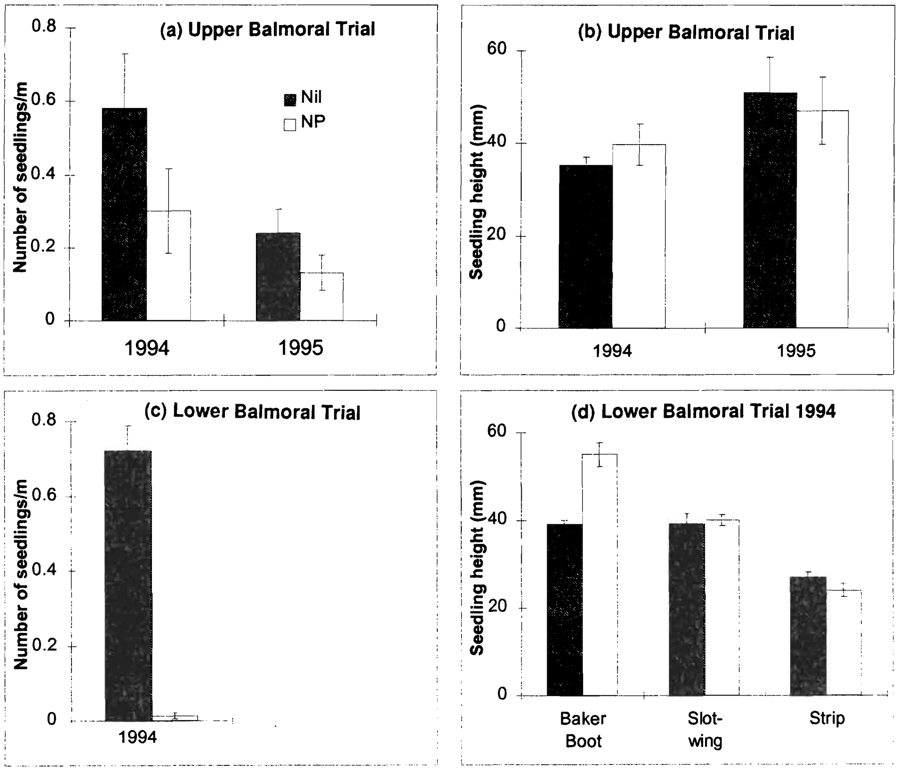

FIG. 5–Effect of fertiliser on *P. radiata* seedling establishment at Balmoral. Values are means of three coulter types. Vertical bars ± 1 s.e.

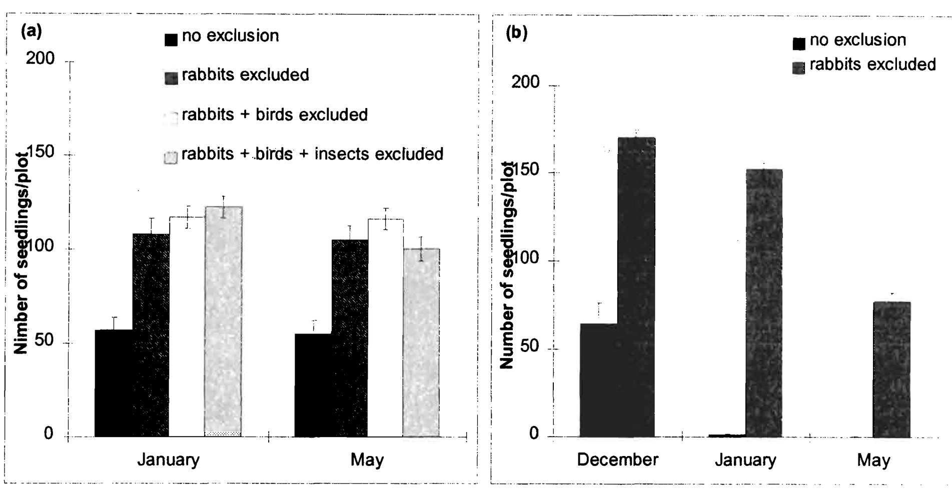

FIG. 6–Effect of excluding possible browsing agents on seedling establishment at Upper Balmoral (a) and Mt John (b). Vertical bars ± 1 s.e.

found on a maximum of 32% of seedlings. The smaller *P. nigra* seed was known to retain fewer spores (10% of the number found on *P. radiata* seed), and this may have contributed to poorer mycorrhizal development in *P. nigra*. Experience with *P. muricata*, which has a similar seed size to *P. nigra*, suggests that greater spore numbers would adhere to the seed if dry sporophore material was dusted on to seed moistened with gum arabic (Table 2).

Pinus muricata seedlings inoculated with *R. rubescens* showed greater mycorrhizal development at both the Upper Balmoral and The Tui sites than seedlings treated with other fungal species. At the Upper Balmoral site, the poor performance of Eyrewell Forest *R. rubescens* material when compared with inoculum from Owhata may have been due to lower spore numbers per seed associated with different storage techniques or with different stages of sporophore development. Differences in spore numbers do not account for the inferior performance of *R. luteolus* or *S. luteus*. Spore viability, speed of mycelial growth, or site compatibility could have been involved. *Rhizopogon luteolus* is commonly found in sandy soils (Lange & Hora 1963), and may not be well-adapted to high country soil conditions, but *S. luteus* is common in pine stands throughout the high country and could be expected to be suitable for the sites used in this study. Further work on a range of sites is required to confirm the suggestion that *R. rubescens* is the most suitable species for seed inoculation.

The high mortality of seedlings in the inoculation trial at The Tui during the second (1994–95) season was probably due to the low summer rainfall (Fig. 1) and to competition from the grass/hawkweed sward.

Removal of Competition and Fertiliser Application

Use of the strip and slot-wing coulters resulted in a marked increase in browsing damage at the Balmoral sites. It became evident during the second year of the trial that rabbits were responsible for the browsing. They may have been attracted to the bare soil or to seedlings exposed by turf removal. Browsing masked any positive effects of competition removal at Balmoral. At Mt Barker, no benefit from removal of competition was observed during the first growing season, when summer rainfall was high, but there was evidence of a small positive effect on seedling height growth during the second season when summer rainfall was particularly low. Further testing of the effects of competition removal in rabbit-free areas is required before definite conclusions can be drawn.

Herbaceous plants responded strongly to fertiliser application and reduced the rate of establishment of pine seedlings, confirming results from a previous trial (Davis 1989). Increased seedling mortality occurred even where the strip and slot-wing coulters were used to remove competition, since weeds, particularly mouse-ear hawkweed, rapidly invaded bare soil in plots where fertiliser was applied. In stimulating the quantity and quality of herbage, fertiliser treatment may have attracted rabbits, leading to greater seedling losses at the Balmoral sites. Where rabbits are not a major problem, any positive effect of fertiliser on pine seedling growth is likely to be outweighed by the increased competition of herbaceous plants for water and light.

Browsing

The results show that browsing may be a major constraint to the successful establishment of conifers by direct seeding in the undeveloped short grasslands of the high country. Total shoot decapitation was most common although chewing of needles and stems was occasionally observed. At the Balmoral and Mt John exclosure trials rabbits were clearly a major cause of seedling failure. As noted above, rabbits may have been attracted to the bare soil or to exposed seedlings where strip or slot-wing coulters were used. The close within-row spacing (100 mm) of seedlings in the trials could have resulted in greater damage (the "oasis" effect) than would occur in larger-scale sowings where seedlings would be more widely spaced over a greater area. Even so it is clear that near-total control of rabbits over several years would be necessary to allow tree establishment from seed, since seedlings would need 2–4 years to reach the size of nursery planting stock.

Seedling Survival on Mackenzie Basin Outwash Gravel Soils

No seedlings survived to the end of the second growing season at the Lower Balmoral site. Some were killed by frost-lift during the first winter (particularly in the strip and slot-wing coulter treatments). Mortality during the second growing season was probably caused by drought, although a severe (–6.3°C) summer frost was recorded at the site on 23 December. On the adjoining upper terrace, needle-frosting was observed on new growth of *P. nigra* as a result of this event, but no other damage to pines was noted on either the upper or the lower terrace. In an adjacent trial on the lower terrace, sown in 1992, seedlings of *P. radiata, P. muricata, P. nigra,* and *P. ponderosa* P.Lawson et Lawson all died during the 1994–95 growing season (Davis unpubl. data). In an earlier (1991) trial at the same site, none of the sown *P. nigra* survived to the end of the first growing season (Davis unpubl. data). These trials have demonstrated the unreliability of pine establishment from seed on the Mackenzie Basin drought-prone outwash gravel soils. It can be inferred that the spread of wilding pine populations on these soils is likely to be a very slow process.

CONCLUSIONS

Successful establishment of conifers by sowing seed in the short grasslands of the South Island high country will require control of the rabbit population over a period of several years, and also the introduction of mycorrhizal inoculum. Appropriate mycorrhizal fungi can be introduced either by drilling forest soil with the seed or by inoculation of seed with spores. Removal of herbaceous plant competition may improve seedling establishment in drier areas. Establishment of pines by seeding on the drought-prone outwash gravel soils of the Mackenzie Basin is not reliable. The technique has potential for soils less likely to be affected by drought and should be considered for forest establishment. Further field testing of the effects of competition removal and of mycorrhizal inoculation would be advisable.

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