[1]Botany Division, DSIR, Private Bag, Nelson, New Zealand.
[2]Botany Division, DSIR, Private Bag, Christchurch, New Zealand.

RESPONSE TO REDUCED IRRADIANCE OF 15 SPECIES OF NATIVE AND ADVENTIVE SHRUB AND TREE SEEDLINGS FROM EASTERN CANTERBURY

Summary: Seedlings of fifteen species of shrubs and small trees, commonly found in open sites and early stages of secondary succession, were grown in a glasshouse under light intensities of 16% and 66% full daylight, and their growth parameters (height, number of leaves, dry weight, mean relative growth rate) recorded. Three species from open habitats, *Coprosma robusta* and *Dodonaea viscosa,* and an adventive shrub, *Crataegus monogyna,* had the highest mean relative growth rates in 66% daylight and 16% daylight, but their ranking for other parameters (e.g. height) was variable. *Acer pseudoplatanus* and *Plagianthus regius* had particularly fast height growth. *Carpodetus serratus* was the fastest growing species of early successional vegetation on weakly to moderately leached soils, and it grew as well in 16% daylight as in 66% daylight. Many species had significantly faster height growth in 16% daylight, e.g., *Melicytus ramiflorus* and *Pittosporum tenuifolium,* and several species had faster height growth rates overall, in 16% daylight, e.g., *Myrsine australis, Melicytus ramiflorus,* and *Pittosporum eugenioides*. *Griselinia littoralis,* from moderately to strongly leached soils, had the slowest height growth rates in both light levels. All species had lower 'root:shoot ratios and a greater proportion of dry weight in leaves in 16% daylight. Such responses may contribute to the slow establishment of these species in secondary vegetation experiencing summer drought in the seedlings' rooting zone. Growth patterns are also likely to be adaptations to factors other than light, particularly soil fertility.

There is some evidence that seedlings of the earliest successional and less shade-tolerant species, especially those from weakly leached soils, grew more rapidly than those from later-successional vegetation and edaphically harsher sites. Some shade-tolerant species benefit from slight shade which concurs with their later entry into secondary vegetation.

Keywords: shade response; growth rates; woody seedlings; root:shoot ratio; weeds; succession; Canterbury.

Introduction

Large areas of lowland New Zealand are covered in small-scale mosaics of grassland, scrub, and forest (Blaschke *et al.,* 1981) which lack ecological stability (O'Connor, 1973). Consequently, secondary vegetation of indigenous and adventive shrubs and trees characterise many landscape (e.g. Esler and Astridge, 1974; Croker, 1953; Williams, 1983; Lee *et al.,* 1986). To understand the dynamics of lowland secondary vegetation, we need knowledge of growth patterns and response to environmental factors of the many shrub and tree species which are collectively important there. Intensive autecological studies have been conducted on *Leptospermum scoparium,* the main indigenous coloniser of open situations (e.g. Grant, 1967), *Nothofagus* species (Wardle, 1984), and other tall forest trees important at later stages of succession. The smaller hardwoods occupying early successional stages or subcanopy positions within tall forest have received less attention. Their mycorrhizal relationships were described by Baylis (1976) and Johnson (1976), and a comparative experiment, *sensu* Grime (1965), showed the rapid growth of *Myrsine australis* and *Pseudopanax arboreus* in comparison with native softwoods (Pook, 1979). Our study used a similar approach to investigate the mean relative growth rate and shade tolerance of 15 species of native and adventive shrubs and small trees found in a range of secondary vegetation in Eastern Canterbury, South Island.

Methods

The 15 species compared (Table 1) are all common in eastern Canterbury. Table 1 shows several of their environmental preferences. Most occur as adult trees on weakly to moderately leached soils *(sensu* Taylor and Pohlen, 1962), in the lowland or montane zone, but *Griselinia littoralis* has a wider range. Four species are common as seedlings on bare ground in open sites; *Acer pseudoplatanus, Coprosma robusta, Crataegus monogyna,* and *Dodonaea viscosa*. The others are found most commonly under shade, and of these *Elaeocarpus hookerianus, Melicytus ramiflorus, Myrsine australis,* and *Pittosporum eugenioides* are possibly less light-demanding. Some evidence for these subjective ran kings is shown in the tree or seedling data of Druce (1957), Lee *et al*. (1986), Williams (1983), and Williams and Buxton (1986).

Table 1: *Size and environmental preferences of the species studied. Nomenclature follows Allan* (196/) *for native species,* unless *indicated.*
[a] *Common maximum heights (m).*
[b] *L = lowland <500 m a.s.l. M = montane 500-1000 m a.s.l.*
S = subalpine 1000-/500 m a.s.l.
[c] *W = weakly leached; M = moderately leached;*
S = strongly leached, sensu Taylor and Pohlen (1962, p. 169).

Species	Height[a]	Altitude[b]	Soil[c]
Acer pseudoplatanus L.	15-20	L	W,M
Carpodetus serratus	8-12	L,M	W,M
Coprosma robusta	5-6	L	W,M
Crataegus monogyna Jacq.	5-8	L	W,M
Dodonaea viscosa	4-6	L	W
Elaeocarpus hookerianus	10-15	L,M	M
Griselinia littoralis	10-15	L-S	W-S
Melicytus ramiflorus	8-12	L,M	W,M
Myrsine *australis*	6-8	L	W,M
Pennantia corymbosa	8-12	L	W
Pittosporum eugenioides	8-12	L	W,M
Pittosporum tenuifolium	8-10	L,M	W,M
Plagianthus regius (Forst. et Forst. *f.)*	12-15	L	W
Pseudopanax arboreus	8-10	L	W,M
Pseudopanax crassifolius	12-15	L,M	W,M

For Experiment 1 (see below), all seedlings were gathered from a forest remnant on soils of moderate fertility, on the Canterbury Plains at 400 m a.s.l. (NZMS 1 S74 385856). They were grown for 14 weeks in an unheated glasshouse and were between 7-21 cm tall (Table 2) at the beginning of the experiment. In Experiment 2, *Acer pseudoplatanus, Crataegus monogyna, Elaeocarpus hookerianus,* and *Griselinia littoralis* were similarly gathered and grown for 24 weeks, but the others were grown for *c.* 25 weeks from seed collected from several lowland sites in Canterbury. All seedlings were between 3-11 cm tall at the beginning of Experiment 2 (Table 3).

Plants were grown at Lincoln in an unheated glasshouse in 1-litre plastic planter bags, containing a standard loamy potting mix that included organic fertiliser, superphosphate, potash, and lime, with nutrients equivalent to *c.:* N^- 57 mg kg^{-1}, P^- 87 mg kg^{-1}, S^- 105 mg kg^{-1}, K^+ 237 g kg^{-1}, $CaCO_3$, 670 g kg^{-1}. Small quantities of native soil were mixed in to ensure mycorrhizal infection of the plants grown from seed.

At the beginning of each experiment, 24 of the most similar-sized plants per species were randomly allocated between 8 shallow metal trays. The glasshouse gave a level of 66% daylight (light intensity relative to full daylight), measured with a 'Lambden' pyranometer with readings in watts m^{-1}. Alloy frames completely covered in black polypropylene shade cloth, that gave transmittance of 16% daylight, were placed over 4 randomly selected trays. This level of shade was used because it is within the range of transmittance, at midday during the height of summer, in the margins of open scrub similar to where seedlings used in this study were collected (unpublished data) and it approximates the 17% daylight used by Pook (1979) in a similar comparative study. All trays were watered regularly. Mean daily temperatures, and ranges were:

Experiment 1: 66% daylight mean 17.8ºC; 16% daylight mean 15.8ºC, range 14.5ºC.
Experiment 2: 66% daylight mean 18.6ºC; 16% daylight mean 16.7ºC, range 23.4ºC.

Table 2: *The initial and final numbers of shoots and leaves of 8 species grown in Experiment 1 in* 66% *daylight and* 16% *daylight for* an average *of* 82± 1 *days, arranged in order of decreasing initial shoot number in* 66% *daylight.*
[a]*Mean of plants placed in* 66% *daylight and* 16% *daylight.*

Species	Initial[a] height (cm)	Mean No. shoots $plant^{-1}$ Initial[a]	Final 66% daylight	Final 16% daylight	Mean No. leaves $plant^{-1}$ Initial[a]	Final 66% daylight	Final 16% daylight
Pennantia corymbosa	14.9	22.5	102.2	85.8	147.0	465.3	488.8
Carpodetus serratus	14.3	13.0	90.8	65.0	70.4	333.8	310.9
Melicytus ramiflorus	14.4	10.4	14.8	10.4	56.9	90.3	85.4
Myrsine australis	13.2	5.3	12.3	15.1	26.5	63.4	82.3
Pittosporum tenuifolium	15.2	3.7	4.8	6.6	35.4	71.1	86.8
Pseudopanax arboreus	14.1	1.5	3.5	2.2	18.8	16.6	16.1
Pseudopanax crassifolius	21.2	1.1	1.3	1.0	12.2	17.8	17.3
Griselinia littoralis	7.8	1.1	5.5	3.4	6.3	26.0	18.7
Mean	14.4	7.3	29.4	27.7	47.7	135.5	138.3

Table 3: *The initial and final number of shoots and leaves of* 9 *species grown in Experiment* 2 *in* 66% *daylight and* 16% *daylight for an average of 63* ± 1 *days, arranged in approximate order of decreasing initial shoot number in* 66% *daylight.*
[a] *Significant difference between pairs in* 66% *daylight and* 16% *daylight. *P=0.05, **P=0.0I*
[b] *Mean of plants placed in* 66% *daylight and* 16% *daylight.*

		Mean No. shoots plant^{-1}			Mean No. leaves plant^{-1}		
	Initial[b]	Initial[b]	Final		Initial[b]	Final	
Species	height (cm)		66% daylight	16% daylight		66% daylight	16% daylight
Plagianthus regius	9.6	2.7	37.4	25.5	10.8	153.0	115.0
Coprosma robusta	4.4	1.6	32.3	13.3*[a]	9.2	159.9	85.9**
Elaeocarpus hookerianus	5.4	1.1	7.7	5.9	8.2	48.7	41.8
Pittosporum tenuifolium	4.1	1.1	6.4	2.9*	9.3	75.7	39.3**
Dodonaea viscosa	3.6	1.0	7.7	5.9	4.8	52.4	34.2*
Griselinia littoralis	4.8	1.0	13.6	7.3	3.9	5.8	6.7
Pittosporum eugenioides	4.5	1.0	3.3	1.6*	5.4	28.0	20.7
Crataegus monogyna	4.3	1.0	2.8	1.0	4.9	34.9	18.9
Acer pseudo platanus	11.2	1.0	1.8	1.1	4.0	15.8	12.8
Mean	5.7	1.3	12.5	7.2	6.7	63.8	41.7

Experiment 1 commenced in February 1984, and measurements were made every 7-10 days for an average, over all species, of 63 ± 1 days of: terminal shoot height, the total number of leaf buds, and leaf number. All plants were harvested and the weight of stems, leaves, and roots determined, after drying overnight at *c*. 80ºC in a forced draught oven.

Experiment 2 commenced in September 1984, and ran for an average of 82 ± 1 days per species. Measurements were the same as for Experiment 1, and in addition 6 plants per species were partitioned at the beginning of the experiment to determine mean relative growth rates $\bar{R}$.

$$\bar{R} = \frac{\log_e W_2 - \log_e W_1}{T_2 - T_1} \text{ (Evans, 1972)}$$

where: W_2 and W_1 are the dry weights at the beginning and end of the harvesting period T_1 to T_2, and the units are day^{-1}.

Differences in response to 66% daylight and 16% daylight were tested by analysis of variance.

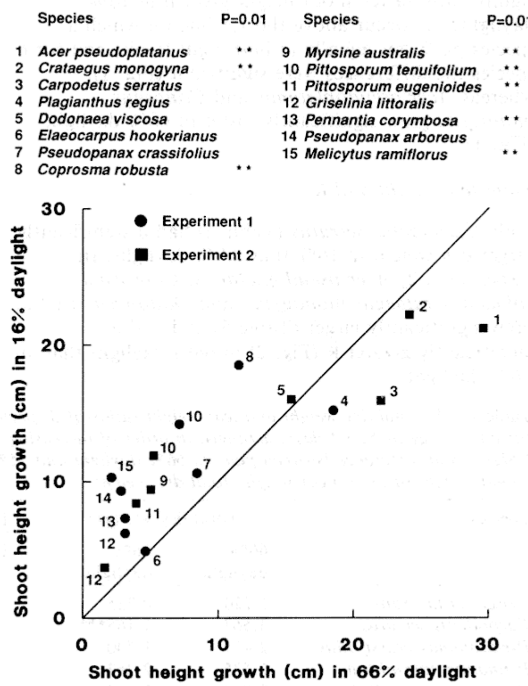

Figure 1: *Shoot height growth of seedlings of* 15 *species of shrubs and trees in Experiments* 1 *and* 2 *after 60 days, ranked in order of growth in* 66% *daylight: growth in* 16% *daylight.*

Results

The initial and final numbers of shoots and leaves of all species are shown in Tables 2 and 3, the shoot elongation rates in Fig.1, and the dry weights and root:shoot ratios in Tables 4 and 5, and Figs. 2 and 3.

Seedling shoot number and leaf number

Apart from *Pennantia corymbosa* and *Carpodetus serratus,* which shed a few small leaves in both 66% daylight and 16% daylight, the number of leaves in Tables 2 and 3 represent the total number of leaves produced.

Seedlings were mostly of a uniform height at the commencement of each experiment, but their initial number of shoots and leaves varied widely, especially in Experiment 1 (Table 2). In Experiment 1 under 16% daylight most species produced 60-70% of the number of shoots and 70-100% of the number of leaves produced under 66% daylight, except *Myrsine australis* and *Pittosporum tenuifolium* which produced 120-140% .

In Experiment 2 *Coprosma robusta, Pittosporum tenuifolium,* and *Pittosporum eugenioides* produced significantly fewer shoots and *Coprosma robusta, Pittosporum tenuifolium,* and *Dodonaea viscosa* produced significantly fewer leaves in 16% daylight.

Shoot height growth

The 15 species had a five-fold range in the rate of shoot height growth (Fig. 1). Most species had a significantly faster shoot height growth in 16% daylight, i.e. occur above the 1: 1 line on which a species performs equally in both light levels, and for 6 species the differences were significant (Fig. I), whereas *Acer pseudoplatanus* and *Crataegus monogyna* grew significantly faster in 66% daylight (Fig. 1).

Total dry weight and $\overline{R}$

Only *Carpodetus serratus* (Table 4) had a significantly larger dry weight in 16% than 66% daylight. In Experiment 2, *Acer pseudoplatanus, Coprosma robusta, Crataegus monogyna,* and *Dodonaea viscosa,* grew significantly larger (Table 5) and had a significantly greater $\overline{R}$ (Fig. 2) in 66% daylight than in 16% daylight.

Root:shoot ratios and leaf weight ratio

All species showed less root growth relative to shoot growth in 16% daylight compared with 66% daylight, and the difference was significant for 11 species (Fig. 3). In all species, a greater proportion of the plants consisted of leaves in 16% daylight compared with 66% daylight. The magnitude and pattern of the difference, however, as with the root:shoot ratios, appears unrelated to the responses of total dry weight or $\overline{R}$ (Tables 4, 5 and Fig. 2).

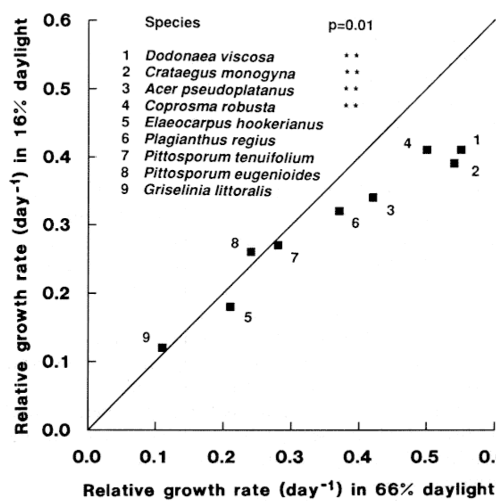

Figure 2: *Growth rate ($\overline{R}$) of seedlings of 9 species of shrubs and trees in Experiment 2, ranked in order of growth in 66% daylight : growth in 16% daylight.*

Table 4: *The total dry weight and leaf weight ratios of* 8 *species grown in Experiment 1 in* 66% *daylight and 16% daylight for an average of* 82±*1 days, arranged in order of increasing ratio of weight in 16% daylight: weight in* 66% *daylight.*
[a] *Significant difference between pairs in* 66% *daylight and 16% daylight. .P=0.05, ..P=0.01*
[b] *Leaf weight ratio = Leaf weight/total dry weight.*

Species	Total dry wt. (g)		Dry wt 16% daylight / Dry wt 66% daylight	LWR[b]	LWR	Diff.
	66% daylight	16% daylight		66% daylight	16% daylight	
Griselinia littoralis	1.220	0.725	0.59	39	45	+6
Carpodetus serratus	3.567	2.165**[a]	0.60	30	39	+9
Pseudopanax crassifolius	2.477	1.700	0.69	51	62	+11
Pennantia corymbosa	2.525	2.247	0.89	25	32	+7
Pittosporum tenuifolium	3.080	2.860	0.93	46	50	+4
Pseudopanax arboreus	3.085	2.925	0.95	51	56	+5
Myrsine australis	1.614	2.077	1.29	45	52	+7
Melicytus ramiflorus	2.225	3.138	1.41	26	33	+7
Mean	2.474	2.229	0.92	39	46	+7

Table 5: *The total dry weight and leaf weight ratios of* 8 *species grown* in *Experiment* 2 in 66% *daylight and* 16% *daylight for an average of 63 ± 1 days, arranged* in *order of increasing ratio of weight* in 16% *daylight: weight* in 66% *daylight.*
[a] ***Significant difference between pairs* in 66% *and* 16% *daylight (P<0.01).*
[b] *Leaf weight ratio = Leaf weight/total dry weight.*

Species	Total dry wt. (g) 66% daylight	16% daylight	Dry wt 16% daylight / Dry wt 66% daylight	LWR[b] 66% daylight	LWR 16% daylight	Diff.
Crataegus monogyna	2.170	0.657**[a]	0.30	55	57	+2
Dodonaea viscosa	2.230	0.723**	0.32	59	62	+3
Acer pseudoplatanus	4.237	2.140**	0.50	48	51	+3
Coprosma robusta	4.077	2.010**	0.49	50	60	+10**
Plagianthus regius	2.830	1.840**	0.65	23	36	+13**
Elaeocarpus hookerianus	0.250	0.177	0.71	36	44	+8**
Griselinia littoralis	0.173	0.153	0.88	50	53	+3
Pittosporum tenuifolium	0.767	0.697	0.91	63	64	+1
Pittosporum eugenioides	0.543	0.567	1.04	59	66	+7**
Mean	1.919	0.996	0.64	49	55	+6

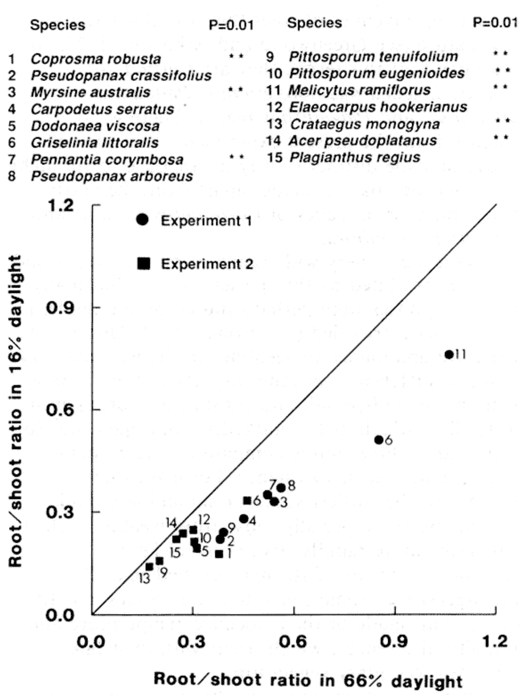

Figure 3: *Root:shoot ratios of seedlings of 15 species of shrubs and trees in Experiment 1 and 2 ranked in order of growth in 66% daylight: growth in 16% daylight.*

Discussion

The shade treatments resulted in lower temperatures and probably also higher humidities, both of which may have influenced plant growth. Similar differences, of varying magnitude, would occur in sheltered sub-canopy situations or in small gaps in the forest canopy compared with large gaps (Popma and Bongers, 1988). The shade cloth may also have slightly altered the spectral quality of the light, but the reduction in light in the 16% daylight treatment was of such a magnitude that it is likely to have been the main factor affecting plant growth. The irradiance provided by 16% daylight is likely to be well above compensation point for all species studied (Pook 1979), but they have, nevertheless, shown a wide range of responses.

The relative responses from all species studied, in the principal paramaters of total weight (Tables 4, 5), shoot heights (Fig. 1), and R (Experiment 2 only; Fig. 2), show that *Carpodetus serratus,* and five species whose seedlings are common in open sites, i.e., *Acer pseudo platanus, Coprosma robusta, Crataegus monogyna, Dodonaea viscosa,* and *Plagianthus regius,* are less shade-tolerant than the others. *Acer pseudoplatanus* and *Crataegus monogyna* are also more monopodial in their shoot numbers than other species, with the exception of the slow-growing *Griselinia littoralia* (Tables 3, 4 and Fig. 2). This shade-avoidance mechanism *(sensu* Grime 1979) has not been at the expense of fast seedling growth rate, and has the advantage of rapidly placing the shoots of *Acer pseudoplatanus* and *Crataegus monogyna* above the height of competing herbaceous plants and browsing animals. These growth characteristics contribute to the success of these two adventive species in invading marginal lands in eastern South Island (Williams, 1985; Williams and Buxton, 1986; Ledgard, 1988).

Apart from these open-habitat species, the most responsive was *Carpodetus serratus*. This produced more shoots and leaves in 66% daylight (Table 2) without loss of height growth. *Carpodetus serratus* is common in low-altitude forests where it rapidly occupies high-light sites created by wind-fall gaps and mass movement. Competition for light can be severe in these sites, particularly with *Coprosma robusta* at the lowest altitudes. These two species were unfortunately not grown in the same experiment.

A second group of seedlings appears to be more tolerant of shade. *Griselinia littoralis* and *Pittosporum tenuifolium* were used as 'markers' between experiments and although they responded slightly differently in both experiments, the latter has a rank below several species for response of total dry weight in both experiments. The results suggest that *Melicytus ramiflorus, Myrsine australis, Pittosporum eugenioides,* and *Pseudopanax arboreus* are likely to be more tolerant of shade than *Pittosporum tenuifolium*. Within this group, *Pseudopanax arboreus* would appear less shade-tolerant than *Myrsine australis* and similar to or slightly less shade-tolerant than *Melicytus ramiflorus*. Field observations and the ranking obtained by Pook (1979) tend to confirm this relative order.

Irrespective of the precise order within this group, however, they are all species found commonly as seedlings in quite deep shade associated with the highly competitive light environment of dense, early-successional vegetation, and for some species, also in tall forest (e.g., Lee *et al.,* 1986; Williams, 1983; Williams and Buxton, 1986). These results conform to the general pattern, that shade-tolerant or late-successional temperate trees generally grow more slowly than light-demanding species (Grime, 1979; Loach, 1970; Walker and Chapin, 1986). This pattern was not shown, however, by studies of numerous tropical seedlings (Augspurger, 1984; Pompa and Bongers, 1988).

Root growth was reduced in several species, such as *Pennantia corymbosa, Pittosporum tenuifolium,* and *Melicytus ramiflorus,* when grown in the moderate shade level of 16% daylight. The likely reduction in water and nutrient absorbing capacity could contribute to the slow establishment of these species in secondary vegetation experiencing summer drought in the seedlings' rooting zone, in eastern South Island (e.g., Lee *et al.,* 1986; Williams, 1983).

Some of the difference in growth patterns are likely to be adaptations to factors other than light. Rapid growth rates are characteristic of plants of high fertility sites, especially in combination with high irradiance (Grime, 1979). The rapid height growth of *Plagianthus regius* and *Acer pseudoplatanus* may be partially attributable to their preference for fertile soils (Greenwood and Atkinson, 1977; Clapham *et al.,* 1962, respectively). The slow growth rate of *Griselinia littoralis* probably reflects physiological characteristics that allow it to tolerate the relatively severe climatic and soil conditions found at altitudes higher than those encountered by most species studied, and to persist in quite dense understoreys, together with other relatively slow growing species, such as *Pittosporum eugenioides* and *Myrsine australis*.

Four microphyllous species studied are divaricating juveniles of trees that lose this habit as they mature (see Greenwood and Atkinson, 1977, for a discussion of this term); they are *Carpodetus serratus, Elaeocarpus hookerianus, Pennantia corymbosa,* and *Plagianthus regius*. There is no evidence from the present experiments that they all behave in some distinctive way in response to full light compared with partial shade, apart from the vastly greater number of leaves of *Carpodetus serratus* and *Pennantia corymbosa*.

There was a very wide range of morphologies and responses exhibited by the species studied, but many species responses were perhaps muted by the moderate level of shade provided (c.f Pook, 1979). Differences in relative abundance of seedlings in the wild may also be due to differences in other aspects of their biology, including seed dispersal, and resistance to drought and frost, all of which differ markedly from open sites to deep shade. These simple comparative experiments have provided further evidence, however, that seedlings of the earliest-successional and less shade-tolerant species, especially those from weakly-leached soils, grow more rapidly than those of later-successional sites or of strongly-leached soils. They also suggest that some shade-tolerant species benefit from partial shade or the associated temperature and humidity differences, which occur with their later entry into secondary vegetation.

There was concurrence in the shade tolerance ran kings of species examined here, with those of earlier New Zealand studies, and we agree with Pook (1979) that comparative experiments are a useful starting point in understanding the behaviour of forest seedlings. We also need clearer definitions of habitat requirements from field studies, with which the experimental studies can be compared.

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