# MECHANISMS OF *PINUS RADIATA* GROWTH SUPPRESSION BY SOME COMMON FOREST WEED SPECIES

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## ABSTRACT

In a trial designed to quantify the reduction of *Pinus radiata* D.Don growth caused by a range of weed species, tree seedlings were grown weed-free or with herbaceous broadleaves (a volunteer mixture of species from which grasses were excluded), *Cytisus scoparius* L. (broom), *Ulex europaeus* L. (gorse), *Buddleja davidii* Franchet (buddleia), *Holcus lanatus* L. (Yorkshire fog) plus *Lolium multiflorum* L. (Italian ryegrass), *Lotus uliginosus* Schk. (lotus), or *Cortaderia selloana* (Schult) Asch. et Graeb. (pampas). Water and nutrient levels were varied by factorial irrigation and fertiliser treatment. After 3 years tree stem volume was greatest in weed-free, lotus, gorse, and grass treatments and least with buddleia and pampas. The effect of herbaceous broadleaves and broom was intermediate. It was concluded that tall, fast-growing, weed species reduced *P. radiata* growth by restricting light availability to tree crowns. No convincing evidence was found to link the large growth losses with interference in water or nutrient supply.

**Keywords**: weeds; water; nutrients; light; resources; *Pinus radiata*.

## INTRODUCTION

In *Pinus radiata* plantation forests of New Zealand, plants are categorised as "weeds" for a number of reasons (Richardson 1993), the most common of which is that they are known or are thought to have a negative effect on tree growth. In practice, most common plants that rapidly colonise *P. radiata* forests at the time of establishment have high growth rates and are regarded as weeds. Large growth benefits after removal of weeds are apparent over a wide range of site types and with many different species (Baker *et al*. 1988; Balneaves 1982,1987; Balneaves & Christie 1988; Balneaves & Henley 1992; Balneaves & McCord 1990; Brunsden 1980; Cellier & Stephens 1980; Mason 1992; Nambiar & Zed 1980; Ray *et al*. 1989; Sands & Nambiar 1984; Schonau 1984; Smethurst & Nambiar 1989; Squire 1977; Turvey *et al*. 1983; Turvey & Cameron 1986; West 1984). Because of this, intensive vegetation management, with heavy emphasis on herbicide use, is recommended during the establishment of *P. radiata* plantations in New Zealand (Richardson 1993).

Although growth gains after weed control are well documented, little information exists about the mechanisms of interaction between the tree and associated plants (Richardson *et al*. 1993). This type of information is needed for the development of tree growth models that

can be applied to different sites with a range of resident plant species. Increased tree growth resulting from plant removal can usually be explained in terms of improved moisture, nutritional, or light conditions. These factors enhance physiological processes such as leaf area development, carbon assimilation, diffusive conductance, and water-use-efficiency (Boomsma & Hunter 1990). With the increasing cost of weed control and mounting pressure against herbicide use, it is essential that weed control operations are limited to situations giving optimal tree productivity gains. They should be targeted against the most-damaging species. These objectives can be achieved only through a thorough understanding of the nature of tree/weed interactions and the way they vary over different sites and climates.

A study was designed to analyse the growth response of young *P. radiata* trees to some well-known forest weed species. Year 1 data have already been reported (Richardson *et al.* 1993). This paper presents results from data collected in Year 3.

## METHODS
### Sites

The trial site was adjacent to the New Zealand Forest Research Institute nursery at Rotorua (38° S 176° E), where a mean annual rainfall of 1491 mm is evenly distributed throughout the year, mean annual temperature is 12.7°C, and the annual average raised pan evaporation is 1186 mm (NZMS 1981). The deep, moderately fertile, pumice soil (yellow-brown Ngakuru loam), is well drained and has a high water-holding capacity.

### Experimental Design

A complete factorial set of treatments was laid out in a split-plot design. There were three treatment factors—weed type, fertiliser, and irrigation—with eight weed types and two levels of fertiliser (nil; fertiliser applied) and irrigation (nil; water applied). Weed type treatments were weed-free, herbaceous broadleaves (all volunteer species except grasses), broom, gorse, buddleia, a mixture of Yorkshire fog and Italian ryegrass, lotus, and pampas. Three experimental blocks were divided into two, one half of each being irrigated. Within each of the six main plots, fertiliser and weed type treatment combinations were completely randomised in 5 × 5-m subplots. The three replicates (randomised complete blocks) of each set of treatment combinations were installed at intervals of 1 year between 1990 and 1992. The advantages of replication through time are that effects of different climatic conditions on species interactions can be observed, that there is some protection against atypical conditions in any one year, and that limited manpower and financial resources can be deployed more effectively. The disadvantage is that the results accumulate over a longer time period. In this trial, Year 3 growth data were not complete until the fifth year. Sites of the first two replicates were previously under grass. The third replicate site had been occupied by mature *P. radiata* until the year prior to commencement of the experiment.

### Soil Characterisation

Soil core samples (0–85 cm), taken from a transect across each experimental block, were analysed by standard methods (Soils laboratory, FRI, Rotorua) to characterise the nutritional status of the site.

## Installation

A combination of mechanical cultivation and herbicide application was used to eliminate existing vegetation, predominantly a mixture of herbaceous broadleaves and grasses. *Pinus radiata* seedlings (GF17, 1/0) were lifted from the nursery adjacent to the trial site and planted in July 1990, August 1991, and August 1992 using conventional techniques. To ensure uniform planting stock, seedlings were graded according to root collar diameter and height. Twenty-five seedlings per subplot were planted at 1 × 1-m spacing. Gorse, broom, buddleia, and pampas seedlings up to 15 cm high (germinated during or shortly after the winter of tree planting) were planted at 0.5 × 0.5-m spacing in October after tree planting. At the same time, Yorkshire fog (6 kg/ha), Italian ryegrass (18 kg/ha), and lotus (5 kg/ha) seeds were scattered by hand, and herbaceous broadleaves were allowed to emerge and grow on the appropriate plots.

Unwanted plants were periodically killed using a combination of hoeing, hand weeding, and spot applications of glyphosate. Haloxyfop was used to remove grasses from the herbaceous broadleaf plots and clopyralid to remove broadleaves from the grass plots.

## Irrigation and Fertiliser

The goal of irrigation and fertiliser application was to ensure that moisture and/or nutrients would not limit plant growth in treated plots. The trial was irrigated from an automatic overhead irrigation system every night using a volume of water that was greater than the calculated amount of maximum evaporation. This exceeded annual rainfall by approximately 1000–1100 mm/year. The fertiliser regime (P. Knight, pers. comm.) is summarised in Table 1. All fertilisers were broadcast evenly. Total weights of nutrient elements applied over 3 years were 291 kg N/ha, 117 kg P/ha, 176 kg K/ha, 57 kg S/ha, 150 kg Ca/ha, and 53.3 kg Mg/ha.

TABLE 1–Fertiliser treatment regime.

| Timing | Treatment | Rate (kg/ha) |
|---|---|---|
| Before tree planting | 15% potassic Magphos (0-8-8-6(S)-20(Ca)-5(Mg)) | 750 |
| Before tree planting | IBDU (Isobutylidenediurea) (32%N) | 500 |
| Before tree planting | FTE 36 (trace elements) | 20 |
| At tree planting | Nitrophoska yellow (15-7-5-4(S)-2.4(Mg)) | 100 |
| Summer (annually) | Nitrophoska blue (12-5-14-1.2(Mg)+TE) | 120 |
| Autumn (annually) | Nitrophoska blue (12-5-14-1.2(Mg)+TE) | 120 |
| Spring (Year 2 on) | Nitrophoska yellow (15-7-5-4(S)-2.4(Mg)) | 100 |

## Measurements

Only the nine trees in the centre of each subplot were measured. Root collar diameter and height were measured at time of planting and then at 3-monthly intervals. At intervals of approximately 3–4 months, the height of eight sample plants per subplot of broom, buddleia, pampas, and gorse was recorded. Above-ground biomass production was determined at the same intervals for each grass, lotus, and herbaceous broadleaf subplot. Biomass sample areas (two 900-cm$^2$ squares) were selected from random positions in the subplot borders that had not been harvested previously. The oven-dry weight of each sample was recorded.

*Pinus radiata* fascicles from current-year foliage were sampled in each subplot in February of the first and third years. Nitrogen, phosphorus, potassium, calcium, magnesium, boron, manganese, zinc, and copper concentrations were analysed (Soils laboratory, FRI, Rotorua) using standard methods.

Using a pressure bomb, *P. radiata* fascicle water potential was measured on several days during dry periods in mid to late summer of Year 2 (all replicates). Sampling was restricted to plots with fertiliser, because of the large number of treatments. Measurements were taken continuously from pre-dawn to mid-afternoon. All weed type × irrigation treatments were sampled once in a random order before another cycle was commenced, using a new randomisation of treatment order. At each sampling, two fascicles from the current-year foliage were randomly selected from each of two trees in the subplot. One pair of samples was given to each of two independent pressure bomb operators who recorded fascicle water potential and time of measurement.

Profiles of photosynthetically active radiation (PAR) through the canopies of weed-free, buddleia, gorse, broom, and pampas subplots were constructed from PAR readings obtained with a Sunfleck Ceptometer (Decagon). Measurements were made at 3-month intervals in Replicate 3 only. Readings were taken above the vegetation canopy; at tree top level if trees were overtopped by the weeds; at 75, 50, 25% of canopy height; and at ground level.

## Data Analysis

Third-year tree and weed growth, foliar nutrient concentrations and contents, and physiological data were all analysed using analysis of variance. A natural logarithm transformation was used to stabilise the variance where appropriate. Initial tree size (height and diameter) was used as a covariate in the analysis of tree growth. Time of measurement and time squared were used as covariates in the analysis of fascicle water potential.

The seasonal patterns of tree and weed height growth were fitted to a regression model. The regression lines were graphed to illustrate the point in time at which trees were overtopped by the weeds. The model consisted of two components: (1) an underlying trend using a quadratic polynomial on age; (2) a seasonal growth pattern consisting of a polynomial on time within each season, constrained to ensure a smooth transition from one year to the next.

For tall weeds which clearly had shading potential (gorse, broom, buddleia, pampas), analyses were undertaken to test two hypotheses:

(1) That reductions in tree growth could be explained by a simple index of shading;

(2) That this index is independent of specific weed type.

A sample of five growth periods of duration from 2 to 10 months were selected (8–10, 10–18, 17–20, 20–27, and 27–37 months). These periods were selected to represent a range of ages. The lengths of the periods varied because of the practical requirement for age data from six datasets (weed and tree height growth from each replicate) to be exact matches. For each period, mean tree diameter increment was calculated for the following treatments: no weeds, broom, buddleia, gorse, pampas. Relative height (defined as weed height/tree height) was calculated at the beginning and the end of each growth period. The average of these two values, defined as mean relative height (MRH), was used as a simple index of shading. Non-

linear regression analysis was used to derive the following logistic function from MRH and tree diameter increment data:

$$\text{Tree diameter increment} = b/(1 + \exp(c + d(\text{relative mean height})))$$

where b, c, and d are determined by the regression analysis.

Dummy variables were added to the exponential term to represent individual species. An F-value was calculated to determine whether the inclusion of individual species improved the overall model.

## RESULTS

Unless stated otherwise, all results refer to Year 3 data.

### Meteorological Conditions

Average annual rainfall (August–July) over the 5 years of the trial was 170 mm lower than the long-term average, and ranged between 1274 mm (Replicate 2) and 1372 mm (Replicate 3). Mean annual temperatures were 0.8°C lower than the long-term average (0.6°C/year lower in Replicate 3 and 1°C/year lower in Replicate 2). Average "summer" (December–March) rainfall and temperature over the 3-year growth period for each replicate were 138–144 mm and 0.7–1.2°C lower than the long-term average respectively.

### Tree Growth and Mortality

Mean tree height, root collar diameter, and tree stem volume (calculated as root collar diameter$^2 \times$ height $\times \pi/4$) were all significantly influenced by weed type (p = 0.0001 for all) (Fig. 1a, b, c), replication (p = 0.0008), and the interaction between weed type and fertiliser (p = 0.0223) (Fig. 2). No other experimental factors or interactions had a significant effect. Root collar diameter was a more sensitive indicator of interference than height. The greatest stem volume reductions occurred when *P. radiata* was grown with buddleia or pampas (up to 76% reduction). Herbaceous broadleaves and broom had an intermediate effect (38–51% reduction). Although mean values for grass, gorse, and lotus treatments indicated possible reductions in stem volume (19–24%), no significant difference could be demonstrated (Fig. 1c). By age 3, trees growing with the most competitive species (buddleia (Fig. 3) or pampas) had a stem volume equivalent to that achieved 14 months earlier by weed-free trees.

Weed type was the only factor that affected tree mortality (p = 0.0054) (Fig. 4). Mortality was greatest with buddleia (14%) and pampas (9%), but did not exceed 2% with any other weed types. Due to low mortality levels, the effects of weed type on total tree basal area were similar to those described for volume.

Tree growth varied considerably across the three replicates. Mean root collar diameter after the third year was greatest in Replicate 2 and was approximately 10% and 25% lower in Replicates 1 and 3 respectively. Growth trends in the various treatments were consistent across all replicates.

### Weed Growth

The three herbaceous weed types in this experiment were volunteer broadleaves, grasses (Yorkshire fog plus Italian ryegrass), and lotus. A wide variety of species was noted in the

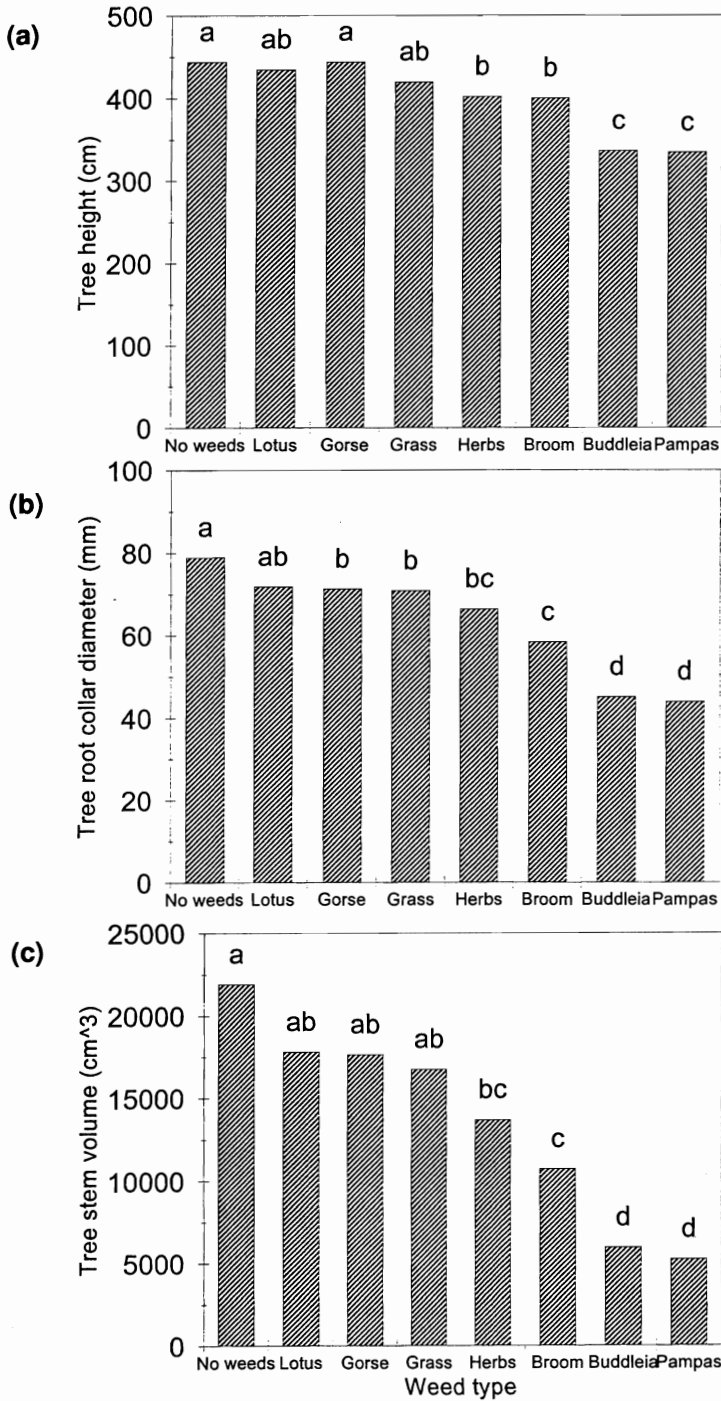**(a)**



**(b)**



**(c)**



FIG. 1—Effect of weed type on *P. radiata* (a) height, (b) diameter, and (c) stem volume, 3 years after planting, and averaged for all irrigation and fertiliser treatments. Bars topped by the same letter are not significantly different at the 5% level according to Fisher's Protected LSD test.
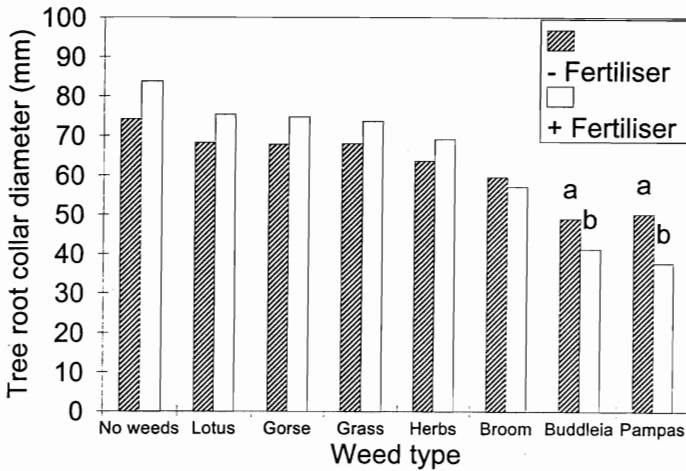
FIG. 2–Effect on *P. radiata* diameter of weed type with or without fertiliser application. For each weed type treatment, bars topped by the same letter are not significantly different at the 5% level according to Fisher's Protected LSD test.
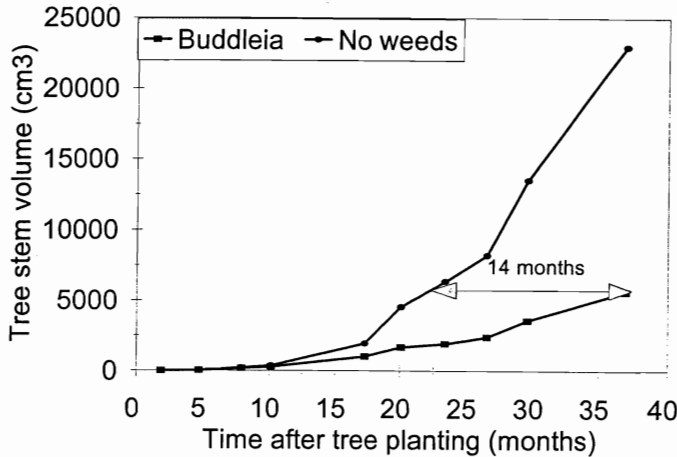


FIG. 3–Stem volume growth trends over time for *P. radiata* growing in weed-free plots or with buddleia.

herbaceous broadleaf subplots, the most frequent being *Rumex* spp. especially sorrel (*Rumex acetosella* L.), plantains (*Plantago* spp.), catsear (*Hypochaeris radicata* L.), willow weed (*Polygonum persicaria* L.), yarrow (*Achillea millefolium* L.), and lotus. During the third year, lotus productivity reached the same level as the other two weed types, which by this time had passed their peak growth period (Fig. 5). All three weed types declined after month 28 (December), presumably due at least in part to shading by the tree canopy.

Height of herbaceous weeds was not recorded, but grasses and herbaceous broadleaves overtopped the trees for periods in the first year and early in the second year. The fastest-growing weed types in terms of height growth were pampas and buddleia. These species had similar height growth curves. Seasonal patterns of buddleia and tree height growth derived
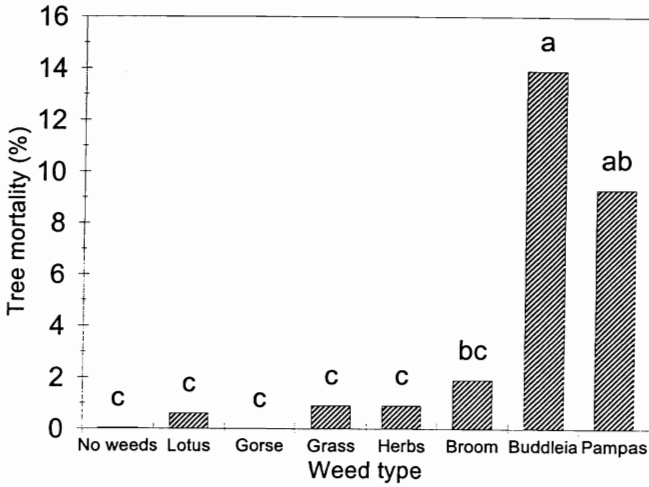
FIG. 4–*Pinus radiata* percentage mortality after 3 years, according to weed type treatment. Bars topped by the same letter are not significantly different at the 5% level according to Fisher's Protected LSD test.
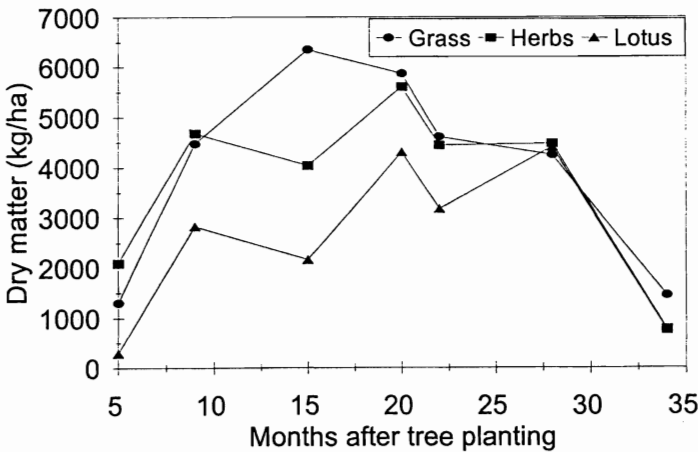


FIG. 5–Mean above-ground dry weight of grass, herbaceous broadleaf, and lotus weed types, over time.

by non-linear regression are given in Fig. 6. Although not shown here, trees growing with pampas had a similar response. Buddleia began to overtop the trees within 4 months of weed planting (7 months after tree planting) and subsequent tree diameter growth in these treatments was substantially reduced. Buddleia and pampas both grew more rapidly than the trees in spring and summer but actually showed a greater decline in growth rate during winter months. Stem breakage and shoot curvature in buddleia and leaf curvature in pampas contributed to this effect. After year 2, trees in weed-free subplots were taller than those associated with buddleia or pampas, both of which clearly suppressed tree growth. Broom growth was slower than that of pampas and buddleia, due at least in part to pathogens *Pleiochaeta setosa* (Kirchn.) Hughes and *Phytophthora* spp., which caused significant
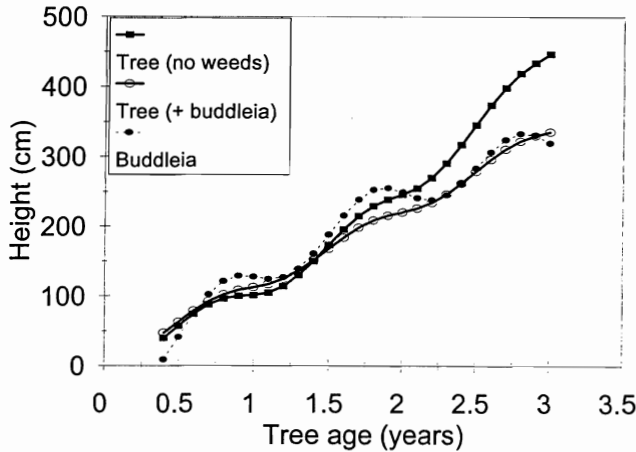
FIG. 6–Predicted height growth trends over time for *P.radiata* growing alone or with buddleia, and for buddleia.

mortality in Replicates 2 and 3. Although broom in all replicates was sprayed with fungicide (chlorothalonil plus benomyl), the intensity of any broom effect was probably reduced.

## Water Effect

Irrigation increased the rate of establishment of herbaceous broadleaves but had no other significant effect on either tree or weed growth. The absence of significant interactions between irrigation and weed type implies that water did not limit plant growth at this site. Measurements of fascicle water potential supported this hypothesis. In the second year there was a small but significant response to weed type, the fascicle water potential for trees growing with buddleia being greater than for those in weed-free controls (–0.823 MPa $v.$ – 0.912 MPa, respectively, averaged across all times; $p = 0.035$).

## Nutrient Effect

Data presented here are mean values for core samples taken to a depth of 20 cm. The soil was moderately acid (mean pH = 4.86 ranging from 5.09 in Replicate 1 to 4.64 in Replicate 3). Although total nitrogen levels were 0.21, 0.22, and 0.11% in Replicates 1, 2, and 3 respectively, low C/N ratios (16–20) indicated that net mineralisation was likely to occur and that tree growth would not be limited by nitrogen availability (M. Skinner pers. comm.). Phosphorus levels were rated as very good, potassium as average, and magnesium as very low.

While there was no overall effect of fertiliser application on tree growth, interactions between weed type and fertiliser affected tree height ($p = 0.006$), diameter ($p = 0.022$) (*see also* Fig. 2), and stem volume ($p = 0.011$). No significant fertiliser effect was noted in the absence of weeds, or in the presence of lotus, grasses, herbaceous broadleaves, gorse, or broom. In pampas and buddleia subplots, on the other hand, a small but significant decrease in tree growth was found to be associated with fertiliser treatment.

Nutrient element concentrations in tree foliage (Table 2) showed no consistent relationship with fertiliser or other treatments. Most values were above the levels considered to be

TABLE 2—*Pinus radiata* foliar nutrient concentrations in the third growing season†.

| Weed type | Nutrient concentration -------%------- | | | | | Nutrient concentration -------ppm------- | | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | P | K | Ca | Mg | B | Mn | Zn | Cu |
| No weeds | 1.15 | 0.112 | 0.94 | 0.43 | 0.061 | 22.1 | 330 | 58.8 | 8.47 |
| Broom | 1.29 | 0.119 | 1.02 | 0.41 | 0.065 | 18.9* | 337 | 46.5 | 7.65 |
| Buddleia | 1.27 | 0.140* | 1.18* | 0.42 | 0.068 | 22.4 | 354 | 59.0 | 8.61 |
| Gorse | 1.20 | 0.106 | 0.96 | 0.44 | 0.058 | 19.9 | 426* | 52.2 | 6.57 |
| Grass | 1.18 | 0.153* | 1.08* | 0.48 | 0.056 | 23.8 | 402 | 74.0* | 10.46 |
| Herbaceous broadleaves | 1.25 | 0.136* | 1.06* | 0.42 | 0.058 | 22.8 | 384 | 59.0 | 11.43* |
| Lotus | 1.24 | 0.116 | 1.02 | 0.37 | 0.058 | 21.5 | 355 | 62.0 | 9.32 |
| Pampas | 1.19 | 0.127 | 0.92 | 0.38 | 0.065 | 17.1* | 241 | 55.3 | 7.41 |
| Critical level‡ | 1.20 | 0.110 | 0.30 | 0.10 | 0.060 | 8.0 | 10 | 10.0 | 2.00 |

† Values followed by * are significantly different to values for no weeds (p = 0.05).
‡ Critical values from Will (1985) except those for phosphorus (M.Skinner pers. comm.) and magnesium (T.Payn pers. comm.).

associated with tree growth reduction. The only significant second-order interactions between weed type, irrigation, and fertiliser treatment occurred where all foliar nutrient concentrations were well above the critical levels.

Height growth of the tallest weeds (broom, buddleia, pampas, gorse) in Years 2 and 3 was not influenced by fertiliser treatment.

## Light Effect

There was a noticeable attenuation of PAR through the weed-free and buddleia treatments at age 20 months (Fig. 7). At the top and half-height levels, trees in the buddleia canopy
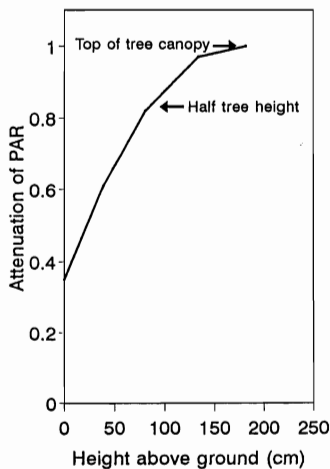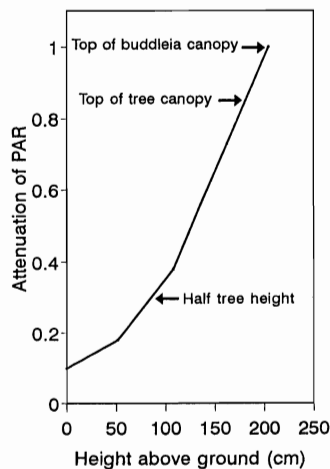
### (a) Weed-free              (b) Buddleia



FIG. 7—Light attenuation with height through (a) a canopy of *P. radiata* growing alone and (b) a mixed buddleia/*P. radiata* canopy, both at age 20 months.

received about 80% and 30% full sunlight, respectively. Trees in weed-free subplots received about 80% full sunlight at half tree height. Similar effects on PAR availability were observed with pampas and broom, although broom mortality reduced the rate of PAR attenuation.

A strong relationship was found between MRH (the average of weed height/tree height at the beginning and end of a specified interval) and diameter increment for each of the periods tested (*see* Fig. 8 for a typical example). Approximately 63% of the variation in diameter increment was accounted for using the logistic model with MRH as the independent variable.
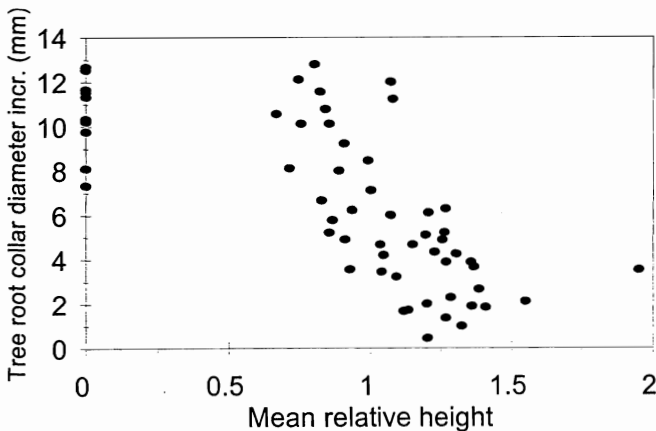


FIG. 8—*Pinus radiata* mean diameter increment between the ages of 20 and 27 months as a function of mean relative height, the mean ratio of weed height/tree height at the beginning and end of this period.

Mean relative height did not account for the effects of all individual weed species on tree growth. Addition of dummy variables to represent broom ($F_{1,55} = 15.79$; $p < 0.0001$) and gorse ($F_{1,55} = 9.18$; $p < 0.0001$) as individual species improved the overall model (Fig. 9). For the same value of MRH, *P. radiata* diameter increment was greater when it was associated with either broom or gorse, i.e., broom and gorse were less competitive than buddleia or pampas. Approximately 76% of the variation in diameter increment was accounted for when MRH was the independent variable and broom and gorse were identified as individual species.

## DISCUSSION

Although herbaceous broadleaves had the greatest effect on *P. radiata* stem volume after 1 year (Richardson *et al.* 1993), tree growth in Year 3 was limited to the greatest extent in the presence of the fast-growing tall species (pampas, buddleia, and broom). Gorse was the slowest-growing of the shrub weed types and had the least effect on tree growth. Broom growth and survival were variable because of disease problems. The lack of consistent volume response to the grass, gorse, and lotus weed types may be attributable to variable rates of establishment.
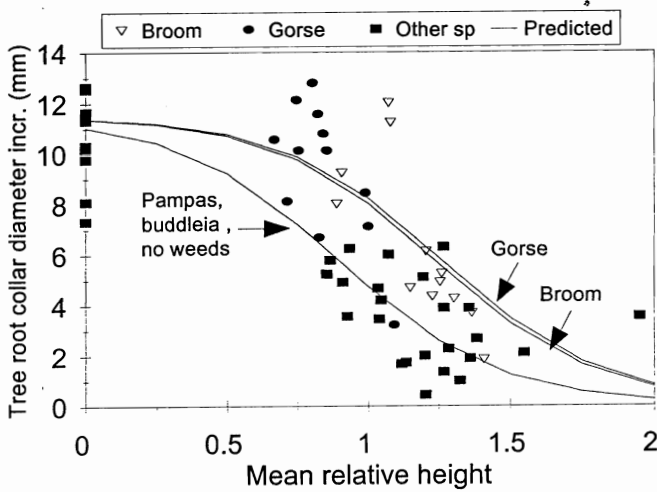
FIG. 9–Predicted and measured *P. radiata* mean diameter increment between the ages of 20 and
27 months by weed type treatment, plotted as a function of mean relative height, the
mean ratio of weed height:tree height at the beginning and end of this period.

The effectiveness of herbaceous broadleaves as competition in the early months after tree
planting probably reflected the rapid vegetation growth in this treatment compared with the
grass mixture or lotus. After 5 months, there were significant differences among these
species in terms of above-ground dry matter (p = 0.0001) with 2095 kg/ha on the herbaceous
broadleaf subplots compared to 1303 and 290 kg/ha on the grass and lotus treatments
respectively. By the end of the first year there was little difference between the herbaceous
broadleaf and grass treatments but lotus dry matter production continued to lag behind.
Towards the end of the experiment, production of all species gradually declined, presumably
because of shading as the *P. radiata* canopy closed. During the establishment phase, biomass
production was higher with irrigation and fertiliser (Richardson *et al.* 1993). While the
irrigation effect was short-lived, the benefit from added fertiliser was apparent throughout
the first half of the experiment.

After 3 years, branches of adjacent tree crowns became intermingled in all except the
buddleia, pampas, and broom subplots. This was a consequence of close tree spacing. With
one possible exception, graphs of growth trends over time did not indicate any associated
reduction in tree growth rate. Only with gorse was there any suggestion that wider tree
spacing would have influenced the conclusions drawn from this study. Due to the relatively
slow height growth of gorse, it is possible that the trees exerted a negative influence on the
weed. This situation is unlikely to occur under operational conditions where tree spacing is
wider, and there are many examples of the severe impact gorse can have on *P. radiata* growth
(Balneaves & McCord 1990).

Richardson *et al.* (1993) observed that growth rate of trees and weeds was lower in
Replicate 3 than in Replicates 1 and 2. Inadequate nitrogen nutrition was unlikely to be
involved, since growth in the fertiliser subplots was also lower in Replicate 3 in spite of
additions of 290 kg N/ha over the 3-year period. Low temperature is also unlikely to have

been involved. Mean temperature was marginally below average during the 3-year period in Replicate 3, but was even lower during growth in the other two replicates.

Diameter growth of *P. radiata* seedlings is very sensitive to competitor-induced water stress (Nambiar 1984; Sands & Nambiar 1984). In the central North Island of New Zealand, where annual rainfall is high and evenly distributed and the pumice soil has a high water storage capacity, soil water deficits should not limit *P. radiata* growth in a typical year (Whitehead & Kelliher 1991). However, Richardson (1993) suggested that, even in this situation, soil water deficits may develop near the soil surface causing stress to newly planted *P. radiata* seedlings with roots restricted to upper soil layers. Evidence from the current experiment does not support this hypothesis. No severe moisture stress was observed in Year 1 (Richardson 1993) or Year 2, even though recorded summer and annual rainfall levels were lower than the long-term averages.

Tree volume growth was lower in the herbaceous broadleaf treatment than in either the grass or lotus treatments. In the dry environments of South Australia, variability of water stress in *P. radiata* is thought to reflect water-usage patterns related to the growth habit and physiological characteristics of associated herbaceous species (Flinn *et al.* 1979; Jackson *et al.* 1983; Nambiar & Zed 1980; Sands & Nambiar 1984). In the moist Rotorua environment there is no evidence that moisture was implicated. The greater effect of herbaceous broadleaves may have been related to their faster rate of establishment but the precise mechanism is not clear.

Interspecific competition can limit the ability of a crop to respond to treatments such as fertiliser application (Flinn *et al.* 1979; Flinn & Aeberli 1982; Squire *et al.* 1979; Waring 1972; West 1984; Woods 1976). In our study, the relatively small tree growth response to fertiliser in weed-free subplots indicated that the site was reasonably fertile. While there was a trend for improved tree growth on addition of nutrients in the presence of the less-competitive weed types, this does not necessarily imply that competition for nutrients was occurring. It may simply reflect an increase in site quality. From the small responses to the addition of large quantities of nutrients, it can be concluded that the large growth reductions associated with some weed types are unlikely to have resulted from a limited nutrient supply. This conclusion is also supported from analysis of *P. radiata* foliar nutrient concentrations which showed no consistent pattern of treatment effects in Year 3 (Table 2) or Year 1 (data not shown). Only a few foliar nutrient concentrations were significantly different from the weed-free controls, and most were above critical levels (Table 2). Trees from the no-weeds treatment had the lowest nitrogen concentration and this was below the nominal critical value. However, it was largely a dilution effect as these trees had the largest leaf area and total nutrient contents (data not shown). Significant interaction between weed type and fertiliser caused reduction in tree growth when fertiliser was added in the presence of either buddleia or pampas. These weed types grew more rapidly in response to fertiliser, and suppressed tree growth.

Assuming that the large weed effect on tree growth was not due to restriction of water or nutrient supply, the most probable explanation was restriction of light, although other mechanisms such as competition for carbon dioxide or allelopathy cannot be ruled out. Sensitivity of *P. radiata* growth rate to light intensity was first demonstrated by Fielding (1967) in unreplicated shading experiments. Overseas studies on other conifer species have

led to the conclusion that light availability can control growth, particularly on moist sites (Brand 1986; DeLong 1991; Howard & Newton 1984; Jobidon 1994; Morris & Forslund 1991).

When the degree of shading was expressed as MRH (a crude index of shading), it was clear that tree growth rates declined rapidly as soon as the weeds reached the approximate height of the trees. The threshold MRH below which weeds have little effect on tree growth will be defined in further modelling studies using growth data from this and other experiments. A similar effect has been recorded for *Pseudotsuga menziesii* (Mirb.) Franco on moist sites in the Oregon Coast Range, United States. Here, tree growth was reduced only when the associated vegetation overtopped the trees (Howard & Newton 1984) or exceeded a threshold tree height (Wagner & Radosevich 1991). Indices based on vegetation abundance, proximity, and degree of overtopping relative to crop trees have been suggested (Brand 1986; Howard & Newton 1984; Morris & Forslund 1991; Wagner & Radosevich 1991). Sometimes these have been related to direct measures of available light (Comeau *et al*. 1993; DeLong 1991; Jobidon 1994). Proximity was not considered in the present study since all weed types were planted at a single density and, except for broom, appeared to fully occupy the subplots.

The effects of buddleia and pampas on tree growth were equivalent for a given value of MRH. Gorse and broom produced slightly different responses which may have been related to slower growth of gorse and high broom mortality in some subplots. However, the data in their present form do not provide a good test of the hypothesis that the index is independent of specific weed type. This is because:

(1) The current analysis assumes linear tree and weed height growth for the duration of each period and does not account for seasonal variation.

(2) Height growth on its own is unlikely to account for all shading effects as it ignores other canopy characteristics that will affect the degree of shading, such as canopy architecture and leaf area density. For example, in many of the broom subplots, plant density and leaf area were lower than for other weed types because of poor growth and mortality. On the other hand, height growth of some of the unaffected plants was still greater than some of the other weed types.

(3) Mean relative height was not distributed in the same way among all of the weed species. For example, MRH for gorse was nearly always lower than for the other weed types (Fig. 9) and appeared to be associated with slight stimulation of tree diameter increment. With the current data it is not possible to conclude whether this is due to chance, to a real effect of gorse, or to a real effect of low MRH independent of weed type.

Future studies have been designed to resolve these issues.

It is less likely that tree growth reduction associated with herbaceous weed types can be explained entirely in terms of light availability, since overtopping occurred for only brief periods during the time of peak growth (summer months). Future work is designed to determine the degree of growth reduction that can be explained in this way. It is possible that the development of tree roots was directly inhibited by interactions with roots of the various weed types, such as by the production of allelochemicals (Putnam & Tang 1986).

The mechanism of interference has important management implications. On moist, moderately fertile, central North Island sites the effect of weeds on tree growth appears likely

to be mediated mainly through light availability, and the identity of individual species may not be critical. If this is so, management of shrub and herbaceous weed types must ensure that weeds do not overtop *P. radiata*. Further data analysis will identify a threshold level of mean relative height below which weed control is likely to have little or no effect on tree growth. Where light is the primary growth-limiting factor, it is a relatively simple matter to develop indices of competition from which effects of weed abundance and distribution on tree growth can be predicted. Model development will help to improve the definition of economic intervention levels. On sites where competition for water and/or nutrients is also an important factor influencing tree growth (Richardson *et al.* 1993), vegetation management would also have to take below-ground interactions into account. From a manager's perspective, further research is required on the identification of sites where competition for moisture or nutrients is not important.

## ACKNOWLEDGMENTS

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