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MODELLING THE GROWTH AND INTERACTIONS OF YOUNG *PINUS RADIATA* WITH SOME IMPORTANT WEED SPECIES

MARK O. KIMBERLEY and BRIAN RICHARDSON

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

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ABSTRACT

Results from a trial at Rotorua, on a moist, moderately fertile site, suggested that tall fast-growing weed species reduced growth of *Pinus radiata* D. Don by restricting availability of light to tree crowns. Data from this experiment were used to model the height growth of the trees relative to neighbouring weeds to create a simple shade index. The model demonstrated that reductions in tree growth could be expressed as a function of this simple index of shading. However, the index was not independent of weed species or age, possibly because of the lack of a term in the model to describe weed abundance, and future studies will test this. The data showed that tree diameter growth was reduced by less than 10% when weeds were 50% tree height, and by about 30% when the weeds were 75% tree height. Thus, an appropriate time for management intervention to minimise tree growth losses would be when weeds exceed 50–75% tree height.

Keywords: plant competition; weeds; competition index; light interception; early growth; irrigation; fertiliser; *Pinus radiata*.

INTRODUCTION

Weed control in newly established *Pinus radiata* plantations usually results in increased tree growth (Richardson 1993). This positive response can often be explained in terms of increased availability of water, nutrients, or light, or improved environmental conditions (e.g., temperature). With the high cost of weed control, the greatest priority should be given to operations that maximise tree productivity gains. Also, the most competitive species should be targeted. Thus, optimisation of weed control strategies can be achieved only through a thorough understanding of the nature of tree/weed interactions and the way they vary over different sites, climates, and time.

A trial to investigate the mechanism of *P. radiata* growth suppression by some common forest weed species was reported by Richardson *et al.* (1993, 1996). Results from this trial at Rotorua, on a moist moderately fertile site, suggested that tall fast-growing weed species reduced *P. radiata* growth by restricting availability of light to tree crowns. Many overseas studies have also concluded that light is often the key growth-limiting resource when weeds and trees interact (Brand 1986; Morris & Forslund 1991; Jobidon 1994), although this is clearly not always so, especially on dry or infertile sites (e.g., Sands & Nambiar 1984; Smethurst & Nambiar 1989).

Regression analyses from the Rotorua trial indicated that the effect of a range of weed species on crop growth could be related to a simple shading index, i.e., relative height or weed height *vs* tree height. There appeared to be a relative weed/tree height ratio, below which there was a much reduced effect on tree growth. The purpose of the study reported here was to model the relative height growth of *P. radiata* and four weed species to enable a clearer identification of the effect of relative weed height on tree diameter or height growth. Specific objectives were to:

(1) Obtain estimates of *P. radiata* and weed height growth at regular time intervals so that an integrated shade index could be calculated over time;

(2) Define the threshold of competition (relative height) below which crop growth losses are insignificant;

(3) Test the hypothesis that reductions in tree growth could be explained by a simple index of shading that is independent of specific weed type.

METHODS

Experimental Design and Measurements

The experimental design and measurements from which the data set used in this study was derived have been described in detail elsewhere (Richardson *et al.* 1993). Briefly, *P. radiata* seedlings (GF17, 1/0) were grown weed-free (control) and with either *Cytisus scoparius* L. (broom), *Ulex europaeus* L. (gorse), *Buddleja davidii* Franchet (buddleia), or *Cortaderia selloana* (Schult) Asch. et Graeb. (pampas). Water and nutrient levels were varied by factorial irrigation and fertiliser treatment. The three replicates (randomised complete blocks) of each set of treatment combinations were installed at intervals of 1 year between 1990 and 1992. Plots were 5 × 5 m, containing 25 tree seedlings at 1 × 1 m spacing. Gorse, broom, buddleia, and pampas seedlings, germinated during or shortly after the winter of tree planting, were planted at 0.5 × 0.5 m spacing in the October following tree planting.

Only the nine trees in the centre of each plot were measured. Root collar diameter and height were measured at time of planting—monthly for the first 18 months, and at 3-monthly intervals thereafter. At approximately 3- to 4-monthly intervals, the heights of eight sample plants per subplot of broom, buddleia, pampas, and gorse were recorded.

Obtaining 3-monthly Height and Diameter Values

Because assessments were not always obtained at regular intervals, and because weed and tree data were not always obtained simultaneously, it was decided to firstly predict plot means of the tree and weed growth variables at regular 3-monthly intervals. These were obtained using cubic interpolation for heights of both *P. radiata* and weeds; *P. radiata* diameters were obtained using a twelfth-order spline function. The spline function smoothed out slight imperfections in the diameter data that were most likely the result of measurement errors, and a twelfth-order function was found to be necessary to account for seasonal growth fluctuations. Derivatives of these interpolation and spline functions were also readily obtained at each 3-monthly interval. This process was carried out using interpolation and spline fitting functions implemented in the GENSTAT statistical analysis programme (Genstat 5 Committee 1997). The following variables were obtained for subsequent modelling:

D = *P. radiata* diameter (mm)
H = *P. radiata* height (cm)
D' = derivative of diameter (mm/year)
H' = derivative of height (cm/year)
W = weed height (cm).

Values were obtained at 3-monthly intervals, starting 6 months after planting (weed height was minimal at 3 months) and terminating at 33 months. This gave a total of 10 values for each of the 60 plots, or 600 observations in total.

The effects of the treatment factors (weed species, fertiliser, and irrigation) at the completion of the trial were tested using analysis of variance and least significant difference tests. This was performed on the 33-month values of seedling diameter and height, and weed height.

Competition Models

A variety of non-linear regression models were tested for predicting the effects of the weeds on *P. radiata* diameter and height growth using the SAS procedure PROC NLIN (SAS Institute Inc. 1989). The dependent variables used were relative *P. radiata* diameter and height growth, obtained by dividing growth rate in each weed plot by the rate in the corresponding control plot:

$RD = D' / D'_{control}$ – relative diameter growth
$RH = H' / H'_{control}$ – relative height growth

The control plot used for each weed competition plot was the weed-free plot from the same replication, and with the same irrigation and fertiliser treatment as the weed competition plot. Note that under this definition, the "controls" varied according to the treatments applied to the weed competition plots.

The main independent variable used was relative weed height, obtained by dividing the weed height in each plot by the tree height:

$RWH = W / H$ – relative weed height

Other independent variables considered were age, weed species, and the fertiliser and irrigation treatment factors.

The relationship between relative diameter and relative weed height was examined graphically. This indicated that for low values of relative weed height there was no reduction in growth, but for high values the growth tended towards zero. A flexible equation reflecting these properties was required, and the following was chosen:

$$y = 1 - (1 - e^{z})^{b}$$

where y is either RD or RH,
Z is a function of the independent variables as described below, and
b is a regression coefficient.

This equation is essentially the Chapman-Richards growth equation with an intercept of one and an asymptote of zero.

The simplest model considered included only relative weed height as an independent variable:

$$Z = a\text{RWH} \qquad (1)$$

where a is a regression coefficient.

To test whether relative weed height had the same influence on growth regardless of age, the following model was used:

$$Z = a\text{RWH}(1 + \text{age}_i) \qquad (2)$$

with a different coefficient, age_i, for each 3-monthly age, except for the final age (33 months) where the coefficient was set to zero to avoid over-paramaterisation.

Examination of the data suggested that at young ages, weed height had less influence on relative growth than at older ages. A third model incorporating this effect was therefore also tested:

$$\begin{aligned} Z &= a\text{RWH}(1 - c^{\text{age}-d}), & \text{age} > d \\ &= a\text{RWH}, & \text{age} \leq d \end{aligned} \qquad (3)$$

In this equation, the influence of age is described by the coefficients c and d. The coefficient d can be thought of as a threshold parameter. It is the age, in months, at which measurable competition begins. The coefficient c determines how quickly the competition effect stabilises over time.

To test whether the effect of relative weed height was the same for all weed species, the following model was used:

$$Z = \text{weed}_j\text{RWH} \qquad (4)$$

with a different coefficient, weed_j, for each of the four weed species.

Fertiliser and irrigation treatments were modelled using:

$$Z = a\text{RWH}(1 + \mathit{fert}) \qquad (5)$$

and, $$Z = a\text{RWH}(1 + \mathit{irr}) \qquad (6)$$

with coefficients for plots with fertiliser (*fert*) and plots with irrigation (*irr*), respectively.

A combined model was also fitted:

$$\begin{aligned} Z &= \mathit{weed}_i\text{RWH}(1 - c^{\text{age}-d})\,(1 + \mathit{fert})\,(1 + \mathit{irr}), & \text{age} > d \\ &= \mathit{weed}_i\text{RWH}(1 + \mathit{fert})\,(1 + \mathit{irr}), & \text{age} \leq d \end{aligned} \qquad (7)$$

The variances of both RH and RD were not homogeneous, but tended to be higher in winter (when growth rates were lower), and lower in summer, particularly for RH. The inverse of the variance within each 3-monthly measurement was therefore used as a weighting variable when all the above models were being fitted.

The analysis used nonlinear regression models to help understand the nature of the interaction between weeds and *P. radiata* for this site. Although standard errors and tests of significance were calculated for the terms in each model, the validity of these was highly questionable for several reasons. Firstly, the 3-monthly increments could not be regarded as statistically independent over time. Secondly, when relative growth values were calculated for each weed species, a common weed-free control was used — again compromising the assumption of independence.

To confirm that the terms included in the models represented genuine effects, a repeated measures linear model was fitted using the SAS procedure PROC MIXED. This model was much less useful for prediction purposes, but provided statistically valid tests. The dependent variables in this analysis were the 3-monthly values of D' and H'. The experimental factors used in this model were: trial block, weed species, age, irrigation, and fertiliser. Relative weed height was fitted as a covariate (using linear and quadratic terms), and the interactions between RWH and the experimental factors were also fitted.

RESULTS

Three-monthly Heights and Diameters

The means of the 3-monthly interpolated values for weed and *P. radiata* height (Fig. 1) showed that all the weeds, with exception of gorse which did not grow well on this site, matched the height growth of the weed-free *P. radiata* for the first 2 years. The effects of weeds on *P. radiata* diameter (Fig. 2) and height (Fig. 3) were readily apparent. A marked seasonal pattern of growth for both weeds and *P. radiata* was also clearly apparent.

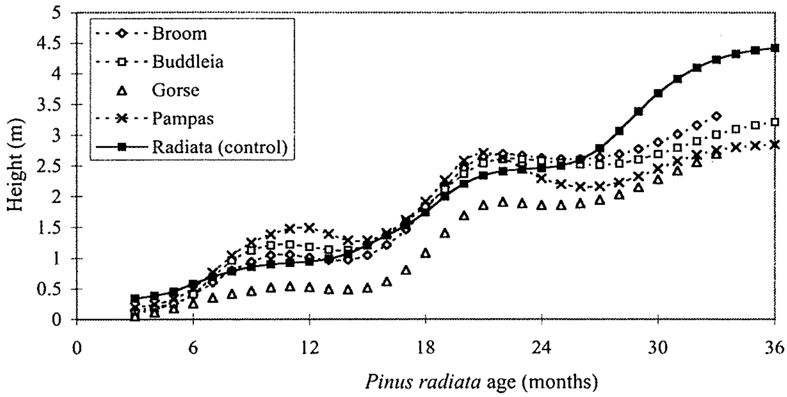

FIG. 1–Height of weeds and *P. radiata*. Values obtained by interpolating the measurement data. *Pinus radiata* controls are from weed-free plots. Results are meaned across replications, and across fertiliser and irrigation treatments.

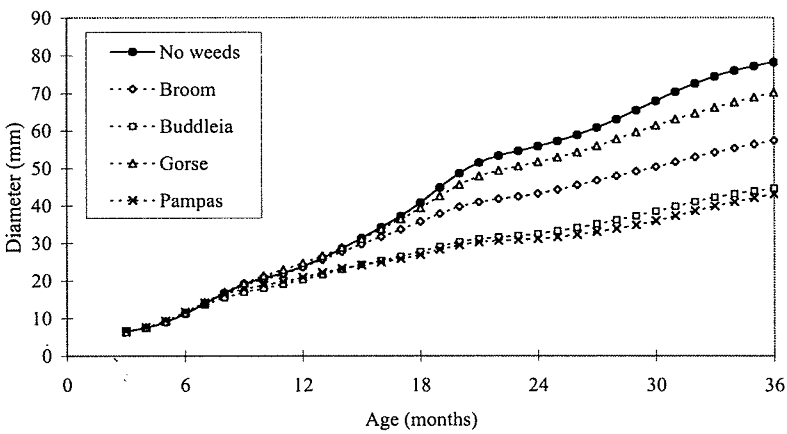

FIG. 2–Root collar diameter of *P. radiata* growing alone or with various weed species. Values obtained by interpolating the measurement data. Values are meaned across replications, and across fertiliser and irrigation treaments.

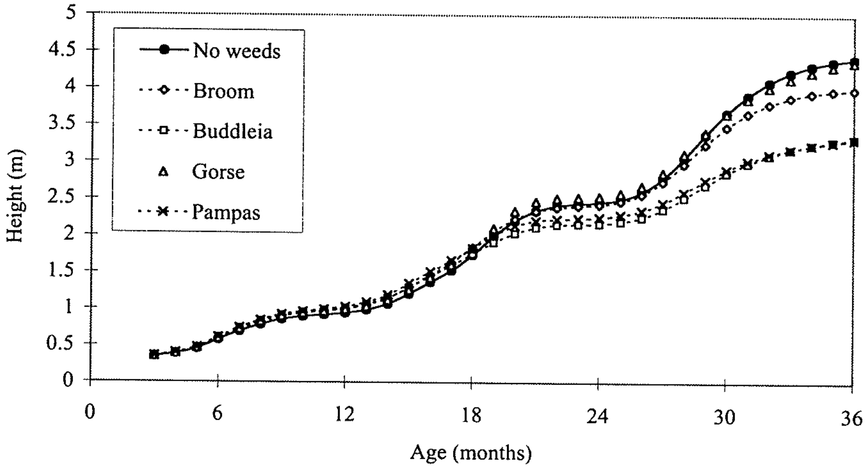

FIG. 3–Height of *P. radiata* growing alone or with various weed species. Values obtained by interpolating the measurement data. Values are meaned across replications, and across fertiliser and irrigation treaments.

An analysis of variance of the final (33-month) values showed that weed species effects were highly significant for seedling height ($F_{4,40} = 20.3, p < 0.0001$) and diameter ($F_{4,40} = 40.4, p < 0.0001$). There were significant interactions between fertiliser and weed species for both height ($F_{4,40} = 4.48, p = 0.004$) and diameter ($F_{4,40} = 30.19, p = 0.023$). There was a small but significant positive height response to fertiliser in weed-free plots, but a significant negative height response to fertiliser in the buddleia and pampas plots which also showed the greatest weed competition (Table 1). Diameter showed similar but less significant trends. Irrigation had no significant effect on either height or diameter, and there were no significant interactions between irrigation and other experimental factors. Neither fertiliser nor irrigation had any significant effect on height of any of the weed species.

TABLE 1–Summary of the 33-month *Pinus radiata* diameter and height values.

Weed species	Height (cm)		Diameter (mm)	
	No fertiliser	With fertiliser	No fertiliser	With fertiliser
Weed-free	398	449 *	70.3	78.6
Pampas	352	287 **	45.1	34.6 *
Broom	395	384	54.6	53.9
Buddleia	343	295 *	45.7	38.7
Gorse	404	426	62.4	69.9

* significant fertiliser effect (p=0.05)
** significant fertiliser effect (p=0.01)

Competition Model Predictions

The percentage variance explained by each of the nonlinear regression models (Equations 1 to 7) is given in Table 2. Relative weed height (Equation 1) explained 37.1% of the variation in relative diameter growth, but only 12.8% of the variation in relative height growth. When

TABLE 2–Percentage R^2 values for the seven nonlinear regression models.

Model	Independent variables	Relative diameter growth	Relative height growth
1	RWH	37.1	12.8
2	RWH, age	57.7	47.9
3	RWH, age	52.1	45.9
4	RWH, species	40.0	16.2
5	RWH, fert	38.5	20.7
6	RWH, irr	37.1	12.8
7	RWH, age, species, fert, irr	56.4	56.3

age was included in the model (Equation 2), the variation explained increased to 57.7% for RD, and 47.9% for RH. When Equation 1 was fitted separately to selected 3-monthly growth periods, the interaction between age and RWH on RD was clearly demonstrated (Fig. 4). It was clear that the influence of relative weed height on diameter growth increased with age. For diameter growth, this increase occurred over the first few 3-monthly periods, but stabilised after the period 15–18 months. Equation 3, which attempts to model this, explained nearly as much variation as Equation 2, but with fewer parameters (four rather than 10). The value of the threshold parameter, d, in this model, indicates that competition begins early for diameter (0.3 years after establishment), but much later for height (1 year after establishment). Other factors (weed species, fertiliser, and irrigation) had much less effect than age. For example, Equation 3, which includes only RWH and age, had an R^2 of 52.1% for RD and 45.9% for RH, while the full model (Equation 7) increased the R^2 only slightly to 56.4% and 56.3% respectively. Weed species appeared to be the most important additional factor (Fig. 5). A reduced model containing RWH, age, and weed species was therefore fitted. This model had an R^2 of 55.6% for RD and 52.0% for RH, only slightly less than the full model (Equation 7).

These models are best understood by examining predictions of relative diameter and height growth. Predictions using Equation 7 are tabulated for relative weed heights of 0.5 and

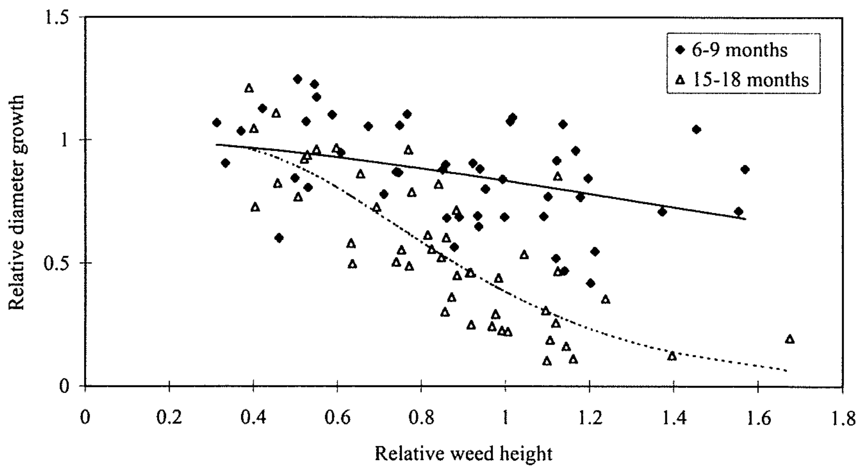

FIG. 4–Relative diameter growth *vs* relative weed height for two selected 3-monthly periods. Each point represents the relative diameter growth in one plot. Predictions from Equation 7 are overlaid.

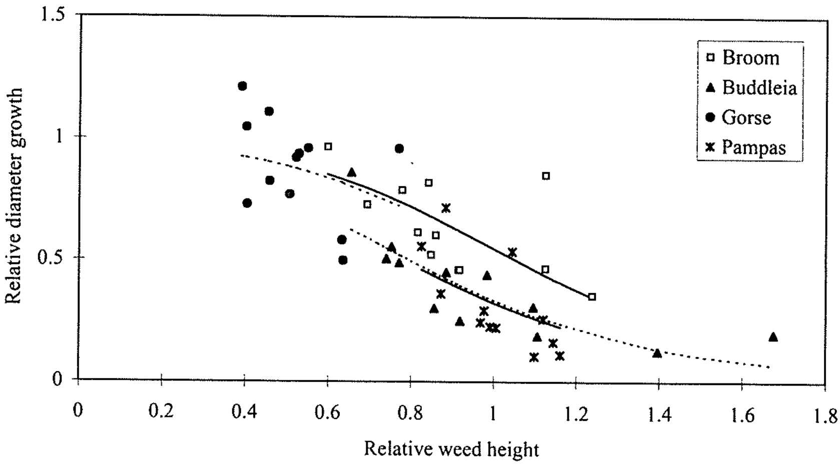

FIG. 5–Relative diameter growth *vs* relative weed height and species during the 15- to 18-month period. Each point represents the relative diameter growth in one plot. Predictions for each species from Equation 7 are over-laid.

1.0 (i.e., 50% and 100% *P. radiata* height) in Table 3. Note that, for example, a prediction of 0.8 implies a growth rate equal to 80% of the competition-free level. The reduction in relative diameter growth with age stabilises after about 18 months, but continues much longer for relative height growth.

A noticeable reduction in tree growth occurs when weeds are about half the height of the *P. radiata* (when there is a 9% reduction in diameter growth) and the effect increases rapidly in severity at weed heights greater than this (Table 4). There are some species differences,

TABLE 3–Regression predictions showing the influence of age on relative growth.

Age (months)	Relative diameter growth		Relative height growth	
	Relative weed height = 0.5	Relative weed height = 1	Relative weed height = 0.5	Relative weed height = 1
6	1.00	1.00	1.00	1.00
12	0.97	0.69	1.00	1.00
18	0.92	0.48	0.99	0.89
24	0.91	0.47	0.97	0.71
30	0.91	0.47	0.95	0.63
36	0.91	0.47	0.94	0.60

TABLE 4–Regression predictions showing the influence of weed height on *P. radiata* diameter and height growth at age 2 years.

Relative weed height	Relative diameter growth	Relative height growth
0	1	1
0.25	1.00	1.00
0.5	0.91	0.97
0.75	0.71	0.87
1	0.47	0.71
1.25	0.29	0.54
1.5	0.17	0.39

with pampas and buddleia having greater competitive effects than gorse or broom (Table 5). Application of fertiliser results in slightly reduced diameter and height growth predictions but irrigation has little effect (Table 6).

TABLE 5–Regression predictions showing the influence of weed species on relative growth of *P. radiata*.

Weed species	Relative diameter growth		Relative height growth	
	Relative weed height = 0.5	Relative weed height = 1	Relative weed height = 0.5	Relative weed height = 1
Pampas	0.88	0.39	0.93	0.55
Broom	0.94	0.56	0.99	0.84
Buddleia	0.90	0.43	0.95	0.63
Gorse	0.93	0.53	0.98	0.80

TABLE 6–Regression predictions showing the influences of irrigation and fertiliser on relative growth.

Treatment	Relative diameter growth		Relative height growth	
	Relative weed height = 0.5	Relative weed height = 1	Relative weed height = 0.5	Relative weed height = 1
No fertiliser	0.93	0.53	0.98	0.80
Fertiliser	0.89	0.42	0.95	0.61
Unirrigated	0.91	0.48	0.97	0.73
Irrigated	0.91	0.47	0.96	0.69

Statistical Significance of Effects

A repeated measures linear model analysis of D' and H' indicated that age and RWH were highly significant ($p < 0.0001$). The interactions between RWH and age, and RWH and species, were also significant ($p < 0.0001$) for both D' and H'. This indicates that the effect of RWH varies with age, and between species, as suggested by the nonlinear regression model. The interaction between RWH and fertiliser was not significant for diameter increment, but marginally significant for height increment ($p = 0.039$). The interaction between RWH and irrigation was not significant for either D' or H'. There were significant block effects, but these are catered for in the competition model by using relative growth increments (i.e., each growth increment is divided by the corresponding weed-free plot increment). Therefore, of the treatment effects shown in Table 6, only the lower RH in the plots with fertiliser compared with those without fertiliser for a given RWH is likely to be statistically significant.

DISCUSSION

The models described here give a detailed insight into how weeds influence growth rates of young *P. radiata* on moist, moderately fertile, forest sites in the central North Island. They support the idea that for such sites, shading is the main competition factor. Irrigation had no effect, indicating that water was not a growth-limiting resource. Fertiliser had a slight but negative effect on growth, the most likely explanation for this being that increased weed foliage resulted in greater shading (Richardson *et al.* 1996).

The use of relative weed height as a simple index of shading competition was not entirely successful. The influence of weeds on tree growth was found to increase with age (Table 3, Fig. 4), probably because the weeds did not initially achieve complete site cover. Because of this, an index based purely on weed height could not adequately represent their shading characteristics. However, once complete weed cover was achieved (about 12–18 months), relative height was a good index for diameter growth. The influence of weed competition on height growth appears to be more complex. At a given relative weed height, the growth reduction became more severe with age for at least the first 3 years, long after full weed cover was achieved, suggesting that the effect of weeds is cumulative. However, overall, height growth was much less reduced than diameter growth for a given relative height (weed height/ tree height).

There were also some significant differences between species. The most likely reason for this is that a simple relative height index does not totally account for foliage density effects. For example, many broom plants died because of infection with pathogens (Richardson *et al.* 1996) but surviving tolerant plants grew well. So, although broom performed well in terms of relative height growth, the plots were not fully occupied by broom foliage and light attenuation was less than it might otherwise have been. It is also possible that there are some inherent differences between species in terms of their effects on light attenuation.

In a subsequent trial, more detailed weed measurements were collected, although at less frequent intervals than in the current study (Richardson *et al.* 1999). This allowed a range of competition indices to be evaluated. The best index combined measures of weed height relative to tree height, proximity of the weed to the tree, and weed abundance. For a given value of this index, the effect on tree growth was independent of weed species, and for diameter growth, the effect was independent of tree age. However, for height growth the negative effect of a given index value remained much higher in Year 3 than in Years 1 and 2, suggesting that competition has an immediate effect on diameter but a delayed effect on height growth.

Although it would be preferable to use an index reflecting the shading properties of the weeds more directly, by incorporating age, species, and fertiliser into the model described in this paper, it was possible to obtain good predictions using relative weed height as the basic competition index. As an example of how the model could be used in practice to demonstrate the results of weed control, the effect on diameter and height growth of controlling pampas for 1 year was modelled (Fig. 6 and 7). This was achieved by offsetting the pampas height curve by 1 year, with zero weed height for the first 12 months after planting. The predictions suggest that with this level of control, pampas would have minimal influence on growth of *P. radiata*.

The model helps define the relative weed height threshold at which weed competition begins to significantly reduce growth (Table 4). This appears to be somewhere between 50% and 75% *P. radiata* height. At 50%, diameter growth is predicted to be reduced by less than 10% and height growth is unaffected. However, when the weeds are 75% *P. radiata* height, diameter growth is seriously reduced by about 30%, and there is a greater than 10% reduction in height growth. Wagner & Radosevich (1991) concluded that the critical relative height

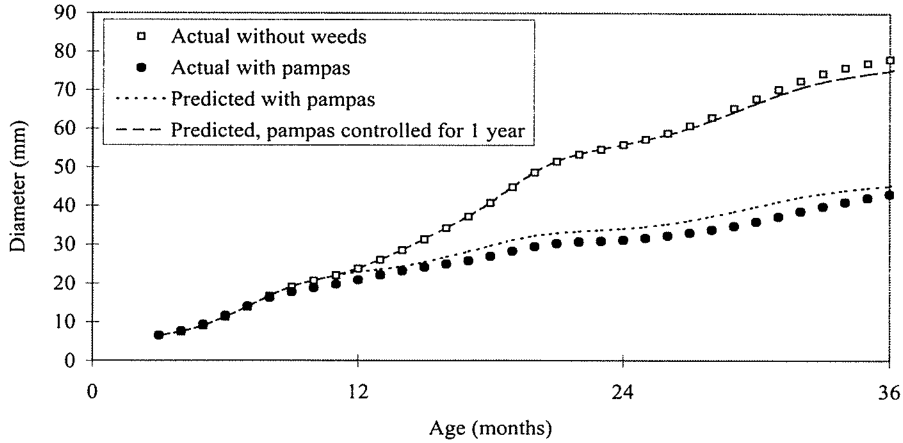

FIG. 6–Actual and predicted *P. radiata* diameter in weed-free control and pampas competition plots.

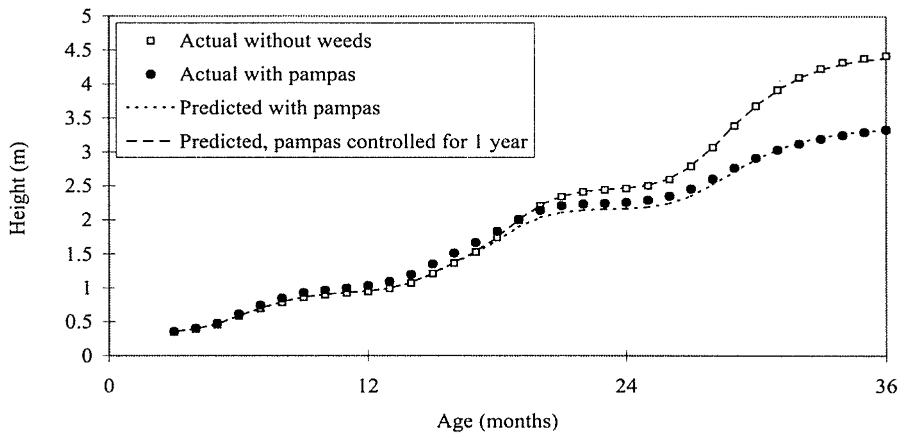

FIG. 7–Actual and predicted *P. radiata* height in weed-free control and pampas competition plots.

thresholds for young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were 0.5 for tree diameter and 1.0 for tree height.

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