MODELLING COMPETITIVE PASTURE EFFECTS ON NUTRIENT UPTAKE BY *PINUS RADIATA*

P. W. CLINTON
New Zealand Forest Research Institute, C/o University of Canterbury,
Private Bag 4800, Christchurch, New Zealand

C. M. FRAMPTON
Centre for Computing and Biometrics, Lincoln University,
Canterbury, New Zealand

and D. J. MEAD
Plant Sciences Department, Lincoln University,
Canterbury, New Zealand

(Received for publication 4 August 1994; revision 9 September 1995)

ABSTRACT

Nutrient uptake and growth of rapidly expanding needles in the upper crown of *Pinus radiata* D.Don were studied in a 3 × 2 factorial experiment in relation to competition with pasture for nitrogen and soil moisture. The monthly addition of 30 kg N/ha had little effect on needle growth or nutrient uptake and the effect of simulated grazing was intermediate to either the rank-pasture or the no-pasture treatment.

Pasture competition decreased maximum rates of needle growth and nitrogen, calcium, and magnesium uptake; needle mass; and needle nitrogen, potassium, calcium, and magnesium content. In the presence of pasture, needle growth and uptake of potassium and magnesium declined more rapidly. Maximum needle weight and potassium content were also achieved earlier when pasture was present.

Gompertz equations proved to be a useful technique for modelling nutrient uptake and making comparisons between treatments, particularly those that affected the dynamics of nutrient uptake, i.e., nutrient sources and addition rates, competition, species, and genotype.

Keywords: nutrient uptake; competition; modelling; *Pinus radiata*

INTRODUCTION

The outcome of competition between pasture and trees is often strikingly apparent (Balneaves 1987). But the mechanisms underlying competition are less obvious and are poorly understood. For example, how does competition affect nutrient uptake? Does it affect the quantity of nutrient taken up, the maximum rate and timing of nutrient uptake, or the time taken to achieve maximum needle nutrient content? Comparison of the time taken to achieve

New Zealand Journal of Forestry Science 24(2/3): 268–78 (1994)

maximum needle weight gain or nutrient uptake or the timing of maximum rate of nutrient uptake may improve understanding of the competitive interaction and the underlying mechanism operating.

Modelling of *P. radiata* foliage nutrient dynamics has been limited to time series analysis and the fitting of exponential decay curves to concentration data from long-term fertiliser response trials (Knight *et al.* 1983). Mead & Mansur (1993) used a modification of the vector analysis technique (Timmer & Stone 1978; Weetman & Fournier 1982) to describe the outcome of competition for nutrients and water between *P. radiata* and various pasture species. Vector analysis was developed to screen for fertiliser responses, but provides only a static analysis of the fertiliser response or competitive interaction (Mead & Mansur 1993).

For this study we used a growth analysis technique to describe nutrient uptake and accumulation during one growth season within needles of trees growing in a competitive silvopastoral system. Patterns of needle growth and nutrient uptake are related to changes in soil moisture deficit. A similar technique has been used by Whitehead *et al.* (1994) to describe canopy development in *P. radiata.*

METHODS

Site Description

The trial and site are described by Clinton & Mead (in prep.). Briefly, the trial was located in a stand of 4-year-old *P. radiata* planted at 400 stems/ha. The soil was a deep (>1.8 m) Templeton silt loam that was medium- to free-draining with a moderate capacity to retain moisture (Kear *et al.* 1967).

Rainfall for the duration of the trial was only 59% of the long-term (1965–80) average of 702 mm (range 372–988 mm), i.e., 415 mm fell between April 1988 and April 1989. There were 11 periods of 7 days' duration or longer when precipitation was 0.1 mm or less. Six of these periods occurred during the winter and spring.

Trial Design and Treatments

The trial was laid out as a 3 × 2 factorial in a completely randomised design with four replicates for each treatment (except for simulated-grazing-plus-nitrogen, which had six). Plots were 16 × 16 m, each containing nine trees, of which the central tree was used in this study.

A gradient of pasture competition was imposed by allowing the pasture to continue growing untreated (rank-pasture); mowing to a height of 3 cm at regular intervals and removing clippings, with return of some nutrients (80%) removed in the clippings as fertiliser additions (simulated-grazing); and kill-spraying to remove all competing vegetation (no-pasture).

Two levels of nitrogen (0 and 30 kg N/ha) were applied monthly from May 1988 until April 1989, except in December 1988 and January 1989 when drought caused the pasture to brown off. Ammonium nitrate was used in alternative months (15 kg/ha as NH_4^+ and 15 kg/ha as NO_3^-). In the other months, a mixture of calcium ammonium nitrate and potassium nitrate was used (10 kg/ha as NH_4^+ and 22 kg/ha as NO_3^-). Each nitrogen-treated plot also received a total of 128 kg K/ha and 69 kg Ca/ha.

Expanding needles were collected monthly (October 1988–May 1989) from tagged secondary branches in the upper crown from 26 trees after elongation had commenced (12 September 1988). Two to four fascicles per branch were collected and counted (approximately 30 fascicles per whorl) and oven-dried at 70°C prior to weighing. Duplicate 300-mg subsamples were digested in an H_2O_2/H_2SO_4 mixture (Nicholson 1984). Nitrogen was determined colorimetrically using an autoanalyser and cations were analysed using atomic absorption spectrophotometry.

The Gompertz equation (Causton 1977; Hunt 1982) was used to model needle growth (W) and nutrient uptake and accumulation (N) in terms of time since commencement of needle growth (T). The Gompertz equation was fitted to each individual tree using a non-linear least squares procedure.

$$\text{Gompertz equation} \qquad A = A_m e^{-ce^{-dT}}$$

Substituting W and N for A in the equation where A_m is either the maximum needle weight or maximum needle content of a specific nutrient and c and d are parameters, Whitehead *et al.* (1994) demonstrated that the utility of the Gompertz equation is in its ability to be differentiated, allowing the calculation of maximum rate of needle growth or nutrient uptake at the point of inflection in the relationship (s_m) and the value of T when this occurs (T_i) (Hunt 1982). The time taken to reach 95% of either maximum needle weight or specific needle nutrient content can also be calculated (T_{95}). Therefore, four parameters—maximum rate of nutrient uptake or needle growth (s_m), maximum needle nutrient content or needle weight (N and W, respectively), time when uptake or growth is maximum (T_i), and approximate elapsed time to achieve 95% of maximum needle nutrient content or needle weight (T_{95}) (Fig. 1)—that describe needle growth and nutrient uptake can be calculated from needle

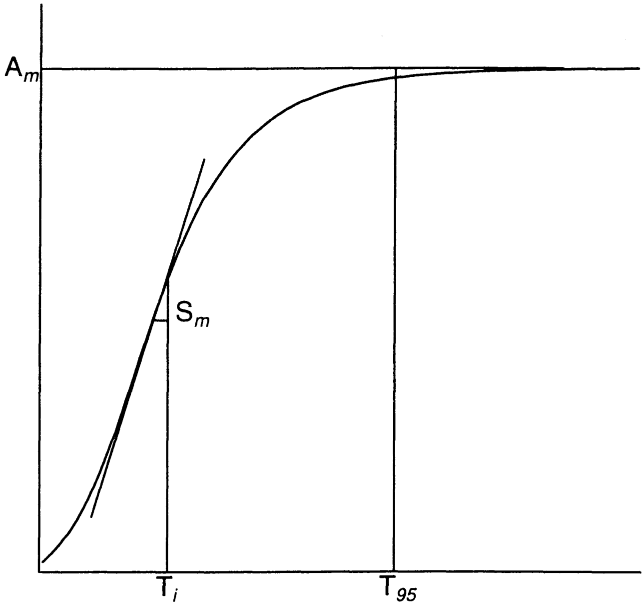

FIG. 1–Curve of Gompertz function showing maximum rate of nutrient uptake (s_m), maximum needle nutrient content (A_m), time when uptake is maximum (T_i), and approximate elapsed time to achieve 95% of maximum needle nutrient content (T_{95}).

weight and nutrient concentration data. These parameters as estimated for each individual tree were compared between nitrogen and pasture treatments using factorial ANOVA. The specific comparisons between the pasture treatments (no-pasture *v.* pasture, rank-pasture *v.* simulated grazing) were tested using orthogonal single degree of freedom contrasts.

Soil Moisture

Dynamics of soil moisture in the surface 10 cm of soil were monitored by assessing soil moisture content of two cores collected monthly from random locations within a 1-m radius of the stem and from between a 1- and 2.5-m radius. A Campbell Pacific Nuclear neutron probe moisture meter was used to follow soil moisture content between 10 and 100 cm soil depth weekly during the growing season at two locations relative to tree stems (radial distances of 1 m and 2.5 m). Fifteen tubes were monitored: four tubes at 1 m radial distance for the plus-pasture treatments, five tubes at 1 m radial distance for the no-pasture treatments, three tubes at 2.5 m radial distance for the plus-pasture treatments, and three tubes at 2.5 m radial distance for the no-pasture treatments. Data for both soil depths were analysed using analysis of repeated measures ANOVA. Orthogonal single degree of freedom contrasts were used to test differences between pasture treatments (no-pasture *v.* pasture, rank-pasture *v.* simulated grazing).

RESULTS

Soil Moisture

Surface soil (0–10 cm depth) was always wetter beyond the 1-m radius than soil closer to the stem ($p<0.01$) (Fig. 2a), except during January when soils were similarly very dry. The no-pasture treatment was always wetter than plots with pasture ($p<0.005$), and did not dry out as fast during early spring (September to October) (Fig. 2b) when there was little or no

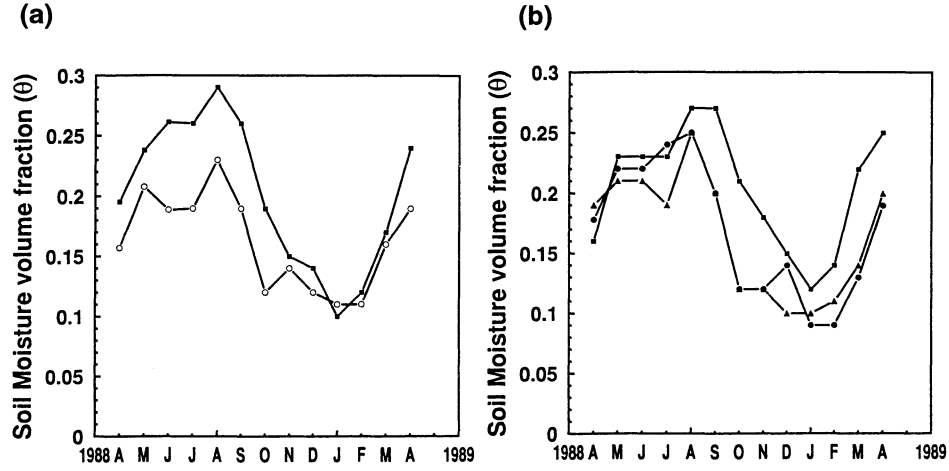

FIG. 2(a)–Surface soil (0–10 cm depth) moisture surface volume fraction (θ) within 1 m of stem (o) and between 1 and 2.5 m from the stem (■).

(b)–Surface soil (0–10 cm depth) moisture surface volume fraction (θ) as affected by pasture competition—control (■), rank-pasture (▲), and mowed pasture (●).

rainfall. The dynamics of soil moisture volume fraction (θ) were similar in the rank and mowed pasture treatments. On average, the no-pasture treatment was wetter at both distances from the stem than the plus-pasture treatments, although this difference was significant only at $p=0.0550$. There were no other significant ($p<0.05$) effects or interactions.

Below 10 cm depth, removing pasture competition reduced soil moisture deficit, at both 1 m and 2.5 m from the stem ($p<0.005$) (Fig. 3). Where pasture was present, water was lost rapidly at a distance of 2.5 m from the tree so that by Day 38 the soil moisture deficit (133 mm) was equal to that at the 1-m location. This equilibrium did not happen until Day 117 in the no-pasture treatment when the soil moisture deficit was 120 mm. Although rainfall influences soil moisture deficit as illustrated by short-term fluctuations (Fig. 3), its effect was pronounced only at 2.5 m from the stem and only where pasture had been removed.

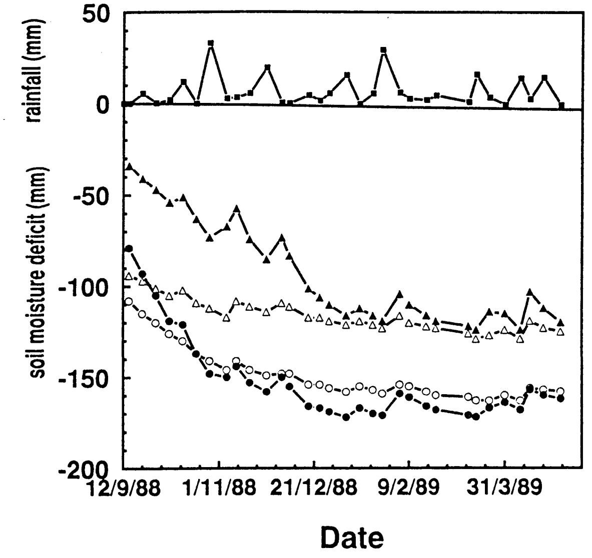

FIG. 3–Daily rainfall (■) and soil moisture deficit in the 10–90 cm soil depth in the presence of pasture within 1 m of stem (O) and between 1 and 2.5 m from the stem (●) and in the absence of pasture within 1 m of stem (Δ) and between 1 and 2.5 m from the stem (▲).

Foliage Growth and Nutrient Accumulation

The addition of nitrogen had no significant ($p<0.05$) effect on final needle nutrient concentrations. Neither was the final needle nitrogen concentration affected by level of pasture competition, although the mowed treatment was 11% higher than the rank-pasture treatment ($p=0.0866$) (Table 1). Removing pasture competition significantly ($p<0.05$) increased needle potassium concentration by 19% but reduced needle magnesium concentration significantly ($p<0.05$) by 25%. No nutrients were at levels regarded as deficient (Will 1985) and all nutrients were at satisfactory levels, except for magnesium in the no-pasture treatments which was marginal.

Addition of nitrogen did not affect the pattern of needle dry weight growth; however, the interaction between level of pasture competition and nitrogen addition was significant

TABLE 1–Nutrient concentration (%) at end of growing season (followed by s.d.).

	Rank-pasture	Simulated-grazing	No pasture	Single degree of freedom contrasts (p) Pasture *v.* no pasture	Rank-pasture *v.* simulated-grazing
N	1.57 (0.067)	1.74 (0.061)	1.68 (0.073)	0.8901	0.0886
K	0.69 (0.047)	0.77 (0.043)	0.87 (0.051)	0.0321	0.2403
Ca	0.23 (0.020)	0.24 (0.018)	0.22 (0.021)	0.5167	0.7881
Mg	0.12 (0.007)	0.12 (0.006)	0.09 (0.008)	0.0024	0.7533

($p=0.023$). Addition of nitrogen always increased the time taken to reach maximum needle weight when pasture was present (72 days, s.d.= 37.8) and greatly reduced the time taken to reach maximum needle weight when nitrogen was added to the no-pasture treatment (58 days, s.d.= 6.3). Addition of nitrogen did not affect the pattern of nutrient uptake ($p>0.05$), except for maximum needle magnesium content which was significantly increased by 77% in the plus-nitrogen treatments ($p=0.041$)—39.12 µg Mg/needle (s.d.=22.44) and 22.06 µg Mg/needle (s.d.=10.438) in plus-nitrogen and no-nitrogen treatments, respectively.

Pasture competition significantly reduced maximum rates of nitrogen and calcium uptake (48% and 52%, respectively) ($p<0.01$), and maximum rates of magnesium uptake and needle growth (32% and 22%, respectively) ($p<0.1$) (Table 2). There were no significant differences ($p>0.05$) between the mowed and rank-pasture treatments, and the effect of mowing (with nutrient return) was always intermediate to either the rank- or no-pasture treatments.

TABLE 2–Maximum rate of needle growth (mg/needle/day) and nutrient uptake (µg/nutrient/needle/day) (followed by s.d.) calculated using Gompertz equation.

	Rank-pasture	Simulated-grazing	No pasture	Single degree of freedom contrasts (p) Pasture *v.* no pasture	Rank-pasture *v.* simulated-grazing
Needle mass	0.44 (0.109)	0.52 (0.130)	0.62 (0.281)	0.087	0.368
N	3.12 (1.185)	5.22 (1.530)	8.00 (3.203)	0.004	0.160
K	6.22 (2.585)	6.57 (2.136)	7.16 (2.865)	0.515	0.794
Ca	0.53 (0.280)	0.82 (0.334)	1.41 (0.010)	0.0003	0.307
Mg	0.30 (0.139)	0.35 (0.118)	0.48 (0.240)	0.076	0.618

Maximum needle mass and needle nitrogen, potassium, and magnesium content were significantly increased (64, 65, 74, and 76% respectively) by removing competing pasture. The maximum needle calcium content was increased by 90% when pasture was removed; this increase was significant only at $p<0.1$ (Table 3). Mowing pasture and returning approximately 80% of nutrients increased maximum needle potassium content by 48% ($p<0.05$).

The time taken to achieve maximum rates of needle growth and potassium uptake was significantly shorter ($p<0.001$) in the presence of pasture than when pasture was removed (Table 4). However, the presence or absence of pasture did not affect the time taken to reach maximum rates of nitrogen and calcium uptake which occurred on average (with and without

TABLE 3–Maximum needle mass (mg/needle) and nutrient content (µg/nutrient/needle) (followed by s.d.) calculated using Gompertz equation.

	Rank-pasture	Simulated-grazing	No pasture	Single degree of freedom contrasts (p) Pasture *v.* no pasture	Rank-pasture *v.* simulated-grazing
Needle mass	17 (3.4)	22 (6.6)	32 (8.7)	0.0001	0.181
N	287 (50.6)	438 (210.5)	599 (201.9)	0.024	0.197
K	128 (34.1)	189 (42.1)	275 (62.9)	0.0001	0.023
Ca	51 (28.3)	75 (38.5)	120 (99.1)	0.072	0.524
Mg	22 (10.6)	27 (11.0)	43 (26.5)	0.031	0.666

TABLE 4–Elapsed time (days) since commencement of growth to reach maximum needle growth and nutrient uptake (followed by s.d.) calculated using Gompertz equation.

	Rank-pasture	Simulated-grazing	No pasture	Single degree of freedom contrasts (p) Pasture *v.* no pasture	Rank-pasture *v.* simulated-grazing
Needle mass	47 (8.1)	46 (3.9)	65 (11.5)	0.0001	0.562
N	43 (22.5)	61 (40.1)	71 (17.1)	0.285	0.416
K	28 (3.8)	30 (4.9)	49 (11.1)	0.0001	0.490
Ca	90 (49.5)	119 (75.4)	135 (128.5)	0.504	0.635
Mg	76 (31.7)	65 (21.5)	116 (75.1)	0.064	0.696

pasture) approximately 58 and 115 days after commencement of needle extension, respectively (Table 4). In the presence of pasture, the maximum rate of magnesium uptake occurred earlier than when pasture was removed (p=0.064).

Maximum needle weight and potassium content were reached significantly earlier (58 and 78 days earlier, respectively) when pasture was present ($p<0.001$ and $p<0.01$, respectively) than on the no-pasture plots where needle weight and needle potassium content continued to increase until 228 and 185 days after the commencement of needle extension, respectively (Table 5). In contrast, maximum needle nitrogen, calcium, and magnesium contents were not affected by pasture treatment.

TABLE 5–Elapsed time (days) since commencement of growth to reach 95% of maximum needle mass and nutrient content (followed by s.d.) calculated using Gompertz equation.

	Rank-pasture	Simulated-grazing	No pasture	Single degree of freedom contrasts (p) Pasture *v.* no pasture	Rank-pasture *v.* simulated-grazing
Needle mass	166 (9.5)	173 (20.5)	228 (51.7)	0.0001	0.607
N	361 (169.8)	315 (176.1)	307 (78.4)	0.699	0.650
K	95 (22.8)	119 (16.9)	185 (85.3)	0.003	0.371
Ca	359 (198.8)	452 (325.3)	423 (416.2)	0.913	0.661
Mg	345 (161.0)	298 (78.4)	440 (320.0)	0.248	0.714

DISCUSSION

Removing pasture competition had two effects on soil moisture. Firstly, soils were always wetter and also remained wetter for longer than in plus-pasture plots. Pasture competed directly for soil moisture but also indirectly as canopy processes also reduce soil re-wetting, thus reducing soil moisture storage. The period of rapid decline in θ corresponds to a period of low rainfall (22.3 mm 12 September to 30 October, Day 0 to Day 50), low humidity, and declining pasture production (Clinton & Mead unpubl. data).

Although there was no tree growth response to any treatment except removal of all pasture (Clinton & Mead unpubl. data), the analysis of nutrient uptake patterns using the Gompertz equation and its derivatives showed that competition from pasture affected the dynamics of needle growth and nutrient uptake. The effect of pasture competition is highlighted by the lack of tree growth or nutrient uptake response to returned nutrients in the plots mowed to simulate grazing. The results of this study also agree with those of Clinton & Mead (1994a) who found that ^{15}N uptake by *P. radiata* was reduced by pasture competition and patterns of ^{15}N uptake into needles were affected by pasture competition (Clinton & Mead 1994b).

Pasture decreased maximum rates of needle growth and nitrogen, calcium, and magnesium uptake, as well as needle mass and needle nitrogen, potassium, calcium, and magnesium content. In the presence of pasture, needle growth and uptake rates of potassium and magnesium declined more rapidly than in the no-pasture plots. Maximum needle weight and potassium content were also achieved earlier when pasture was present. The decrease in rates of needle growth and potassium uptake (47 and 29 days respectively) after commencement of needle expansion corresponded to a marked decrease in θ in the surface 10 cm of soil (Fig. 2) and a period of little rainfall. Maximum rate of potassium (Fig. 4) uptake occurred on average 17 days before maximum rate of needle weight growth, while nitrogen, magnesium,

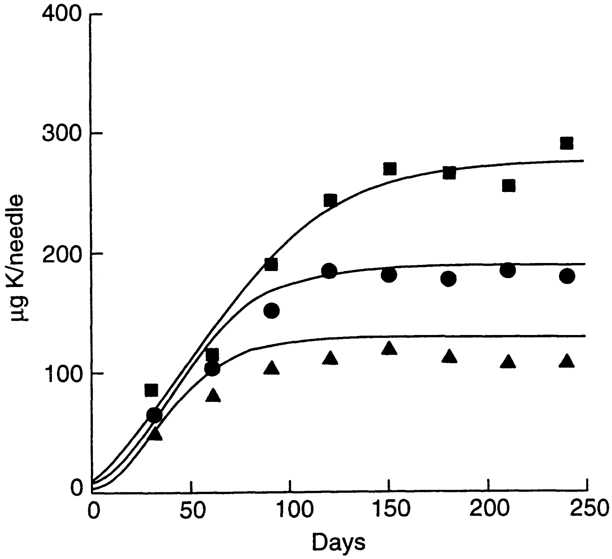

FIG. 4–Potassium uptake curves as affected by pasture competition—control (■), rank pasture (▲), and mowed pasture (●)—estimated using Gompertz equation.

and calcium uptake rates reached maxima 5, 33, and 62 days, respectively, after needle weight growth rate peaked. Therefore, the presence of pasture had different effects on the availability and uptake of specific nutrients by *P. radiata*.

Maximum rates of nutrient uptake and maximum nutrient contents were achieved considerably earlier for potassium than for magnesium, suggesting that there may be a temporal component to any imbalance in nutrient ratios that may affect plant nutrition status such as upper mid-crown yellowing (Beets *et al.* 1993). The factor responsible for determining temporal differences in nutrient uptake has not been identified, i.e., is it nutrient mineralisation or a nutrient-specific nutrient-cycling characteristic?

Plant uptake appears to be more limited for specific nutrients, i.e., calcium and magnesium, irrespective of competitive interactions because needles appear never to be saturated in terms of their potential calcium or magnesium content within a normal season, although older needles continue to take up calcium (Sheriff *et al.* 1986) but not magnesium.

Although nutrient data at the end of the season may show differences between treatments, conclusions as to when these differences come about are difficult to draw. Instead of describing the outcome of the competitive interaction, growth analysis improves our understanding of the interaction by providing a temporal component to the interaction—in this case, to the effects of pasture competition on nutrient uptake and needle growth. This temporal component may be explained in terms of growth of competitors or availability of resources such as water, as happened in this study.

The approach used in this study is compatible with that of Van Rees (1994) which described nutrient uptake in terms of movement of nutrients to roots and into roots. The modelling approach used in this study also supports the concept of relative rates of growth and nutrient supply (Ingestad 1987). In this study nutrient uptake rates varied for different nutrients and, in general, nutrient uptake rates lagged behind needle weight growth, except for potassium. This supports Ingestad's theory that, in order to maintain constant nutrient concentration, the relative uptake rate and therefore the relative addition rate must equal the relative growth rate (Ingestad 1987). In most situations, because growth rate varies during the season so too does the nutrient supply rate, especially in a stand without fertiliser. As the difference between maximum relative growth rate and maximum relative uptake rate for a particular nutrient increases, so a plant is more likely to be stressed for that nutrient. This nutrient stress can occur either through a reduction in supply due to direct or indirect competition, or because of low nutrient availability. In this study pasture competition indirectly affected nutrient supply by reducing soil moisture.

Currently the technique does not consider the effects of nutrient retranslocation into or out of foliage but, as indicated, maximum rates of increase in needle nutrient content occur soon after needle initiation and these rates are affected by competition. The model suggests that for some nutrients, maximum needle nutrient content is not attained and this may be a result of retranslocation of nutrients out of current year's foliage.

CONCLUSION

Declining patterns of needle growth and nutrient uptake mirrored patterns of soil moisture in the plus-pasture treatments, whereas in no-pasture treatments soils remained wetter longer, and needle growth and nutrient uptake continued at higher rates and for longer, resulting in larger needles that contained more nutrients. Further experimental approaches are required to investigate if the competitive effect of pasture acts directly on the size of the available nutrient pool or on processes that affect nutrient availability indirectly, i.e., mass movement of nutrients through soil drying or possibly allelopathy.

In future studies, the intensity of sampling times should reflect the rate of needle growth and nutrient uptake to give precise comparisons between parameters, although this may require different sampling strategies if treatment effects are large.

Gompertz equations offer a useful technique for modelling nutrient uptake and making comparisons between treatments, particularly those that affect the dynamics of nutrient uptake, i.e., nutrient sources and addition rates, competition, species, and genotype.

ACKNOWLEDGMENTS

We would like to thank Bill Clinton for his assistance with the collection of samples and Murray Lang for performing the many nutrient analyses required for this study. We would like to thank T.A.Williams for improving the quality of this manuscript.

REFERENCES

BALNEAVES, J.M. 1987: Growth response of radiata pine to area of herbaceous weed control. *Proceedings of the 40th Weed and Pest Conference*: 49–51.

BEETS, P.N.; PAYN, T.W.; JOKELA, E.J. 1993: Upper mid-crown yellowing (UMCY) in *Pinus radiata* forests. *New Zealand Forestry 38*: 24–8.

CAUSTON, D.R. 1977: "A Biologist's Mathematics". Edward Arnold, London. 326 p.

CLINTON, P.W.; MEAD, D.J. 1994a: Competition for nitrogen between *Pinus radiata* and pasture. 1. Recovery of ^{15}N after one growing season. *Canadian Journal of Forest Research 24*: 882–8.

———1994b: Competition for nitrogen between *Pinus radiata* and pasture. 2. Trends in plant and soil processes. *Canadian Journal of Forest Research 24*: 889–96.

———: Growth and performance of radiata pine as influenced by pasture competition in a dry season (in prep.)

HUNT, R. 1982: "Plant Growth Curves. The Functional Approach to Plant Growth Analysis". Edward Arnold, London. 248 p.

INGESTAD, T. 1987: New concepts of soil fertility and plant nutrition as illustrated by research on forest trees and stands. *Geoderma 40*: 237–52.

KEAR, B.S.; GIBBS, H.S.; MILLER, R.B. 1967: Soils of the downs and plains, Canterbury and North Otago, New Zealand. *New Zealand Soil Bureau Bulletin 14.*

KNIGHT, P.J.; JACKS, H.; FITZGERALD, R.E. 1983: Longevity of response in *Pinus radiata* foliar concentrations to nitrogen, phosphorus and boron fertilisers. *New Zealand Journal of Forestry Science 13*: 305–24.

MEAD, D.J.; MANSUR, I. 1993: Vector analysis of foliage data to study competition for nutrients and moisture: An agroforestry example. *New Zealand Journal of Forestry Science 23*: 27–38.

NICHOLSON, G. 1984: Methods of soil, plant, and water analysis. *New Zealand Forest Service, Forest Research Institute, FRI Bulletin No. 70.*

SHERIFF, D.W.; NAMBIAR, E.K.S.; FIFE, D.N. 1986: Relationships between nutrient status, carbon assimilation and water use efficiency in *Pinus radiata* (D. Don) needles. *Tree Physiology 2*: 73–88.

TIMMER, V.R.; STONE, E.L. 1978: Comparative foliar analysis of young balsam fir fertilised with N, P, K and lime. *Soil Science Society of America Journal 42*: 125–30.

VAN REES, K.C.J. 1994: Michaelis-Menten Kinetics: Calculation and use in nutrient uptake models. *New Zealand Journal of Forestry Science 24(2/3)*: 226–33.

WEETMAN, G.F.; FOURNIER, R. 1982: Graphical diagnoses of lodgepole pine response to fertilisation. *Soil Science Society of America Journal 46*: 1280–89.

WHITEHEAD, D.; KELLIHER, F.M.; FRAMPTON, C.M.; GODFREY, M.J.S. 1994: Seasonal development of leaf area in a young, widely spaced *Pinus radiata* D. Don stand. *Tree Physiology 14*: 1019–38.

WILL, G. 1985. Nutrient deficiencies and fertiliser use in New Zealand exotic forests. *New Zealand Forest Service, Forest Research Institute, FRI Bulletin No. 97.*