PINUS RADIATA STEM VOLUME INCREMENT AND ITS RELATIONSHIP TO NEEDLE MASS, FOLIAR AND SOIL NUTRIENTS, AND FERTILISER INPUTS

I. R. HUNTER, J. A. C. HUNTER, and J. D. GRAHAM
Ministry of Forestry, Forest Research Institute,
Private Bag, Rotorua, New Zealand

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ABSTRACT

The hypothesis was tested that the stem volume increment in the first year after fertiliser application in a series of **Pinus radiata** D. Don fertiliser trials would be proportional to the needle mass, and the amount of nitrogen and phosphorus in foliage, soil, and applied fertiliser. Soil nitrogen and phosphorus contributed little to the relationship and the model could be simplified to:

$$\Delta \text{ Volume } (m^3/ha/yr) = -0.115 + 0.269 \text{ kg N in the needle mass.}$$

This simple relationship was then tested on a range of independent data and found to predict accurately. It can be used in simple physiological growth models and when reversed may be used to estimate the efficiency of fertiliser uptake.

Keywords: nitrogen; foliage mass; volume increment; **Pinus radiata**.

INTRODUCTION

The volume growth of a tree results from the partitioning of photosynthate generated by its green crown. The quantity of photosynthate is affected by the size of the crown, amount of radiation, and availability of nutrients and water.

The establishment of five central composite fertiliser trials in nitrogen and phosphorus in young *Pinus radiata* trees in 1983 provided an opportunity to test a simplified hypothesis based on these relationships – namely, that volume growth is a function of canopy volume and available nutrients (nitrogen and phosphorus). A series of biomass determinations in a variety of trials enabled validation of the hypothesis.

Nutrient availability has three main components: reallocation of nutrients already in the tree, uptake from the soil, and input from fertiliser. In a mature stand "soil uptake" is itself complex, being composed of both nutrient release from fallen litter and uptake from the soil solution. In young stands such as those used in the fertiliser trials, however, the litter component is absent and the system correspondingly simplified.

Our hypothesis, therefore, was that:

Δ volume = f (needle mass, needle N%, needle P%, soil N%, soil P, fertiliser N, fertiliser P)

where Δ volume = stem volume increment (m^3/ha/yr) in the year immediately following trial establishment.

needle mass = dry weight (kg/ha) of all ages of needles
needle N% = concentration of nitrogen in the needles as a percentage of dry weight
needle P% = concentration of phosphorus in the needles as a percentage of dry weight
soil N% = topsoil total nitrogen (%)
soil P = topsoil Bray-extractable phosphorus (ppm)
fertiliser N = kilograms of nitrogen applied as fertiliser
fertiliser P = kilograms of phosphorus applied as fertiliser

METHODS

Fertiliser Trial Design

Five trials were established in 4- or 5-year-old *P. radiata* in winter 1983 (Table 1).

TABLE 1—Location and climatic characteristics of the five trial sites

Location	Latitude (°S)	Average annual temp. (°C)	Yearly rainfall (mm)	Yearly sunshine (hours)	Tree age (years)
Parengarenga	34.6	15.5	1448	2091	4
Maromaku	35.6	13.1	1905	1902	4
Kaingaroa 1	38.7	9.3	1704	1896	5
Motueka	41.2	11.8	1372	2341	5
Nemona	42.6	11.0	2488	1769	4

At each site two replications of a modified central composite design were established. The central composite design is similar to a factorial, except that not all treatment combinations are present. It is an efficient design for sampling a wide range of treatments with equal precision across the sampled range. Nitrogen fertiliser (as urea) and phosphorus fertiliser (as food-grade mono-calcium phosphate) were applied at the rates given in Table 2.

The treatment rates were designed to be linear on a logarithmic scale around the central rate of 150 kg N and 75 kg P/ha. A plot size of approximately 0.0256 ha was used to ensure that, despite the slightly varying stocking levels between sites, 24 trees were included in each plot. The plot size was constant throughout any one site.

Calculation of Volume Increment

All trees in the measurement plot were measured in both winter 1983 and winter 1984 for diameter at breast height and for total height (using height poles). Tree volume was calculated using standard logarithmic volume tables. Volume increment was calculated by the difference between the 2 years.

TABLE 2—Fertiliser rates used

Treatment No.	N (kg/ha)	P (kg/ha)	Number of replications per site
0 (control)	0	0	4
1	80	40	2
2	150	0	2
3	240	40	2
4	240	120	2
5	400	75	2
6	0	75	2
7	80	120	2
8	150	200	2
9	150	75	8

Determination of Total Needle Weight

At each site 10 trees, spanning the diameter range encountered on that site, were felled in winter 1983. The diameter at breast height and height of each sample tree were recorded. For most of the trees all the branches were cut off and the foliage was stripped, dried, and weighed. For a few of the largest trees sample branches only were taken after weighing of the total canopy.

Needle Nutrient Concentrations

All the foliage of the sample trees was required for weight estimation. A separate, composite sample of all ages of foliage and all crown positions was collected from a large sample of the remaining trees on the site (prior to fertiliser application). Concentrations of nitrogen and phosphorus for the bulk sample were determined using the methods given by Nicholson (1984).

Soil Nutrient Concentrations

Composite soil samples of the top 10 cm were taken from each trial site prior to fertiliser application and analysed by the methods given by Nicholson (1984) for total nitrogen and Bray phosphorus. Available-nitrogen was determined after incubating soil (Waring & Bremner 1964).

Statistical Analysis

(a) Significance of volume response to fertiliser within each trial was determined by analysis of variance using the structure given in Table 3.

(b) Calculation of needle weight per hectare: Multiple regression of needle weight per sample trees for each site, against the natural log (Ln) of tree diameter and Ln height showed that regression of weight on diameter alone yielded a very satisfactory high correlation and inclusion of height was unneccessary. The five separate regressions were tested for significant differences in slope and intercept by analysis of variance.

TABLE 3—Analysis of variance structure used for trial response

Term	Degrees of freedom	Tested against term
1. Covariate (Vol. 83) and replicate	2	
2. Linear effect of N and P	2	3
3. Residual A	23	
4. Lack of fit	7	8
5. Quadratic effect of N and P	3	6
6. Residual B	20	
7. Lack of fit	4	8
8. Pure error	16	

Pooled regressions were then applied to plot tree diameters to calculate needle weight per hectare for each plot.

(c) Model fitting: The multiple regression utility of the GENSTAT package (GENSTAT MANUAL 1983) was used to fit the model that tested the stated hypothesis.

Validation

The regressions developed from the initial study were tested on results from a variety of other trials (Table 4).

Needle weight and nutrient content were determined as above. In order to calculate needle weight in pruned and unpruned plots the sample trees' canopies were divided at pruning height and weighed separately.

TABLE 4—Characteristics of the trials used in verification

Location	Tree age (years)	Treatments	Stems/ha	Pruning height (m)
Kaingaroa 2	5	Thinning	600 and 3000	
		Pruning		0 and 2.4
Woodhill	5	Thinning	750 and 1500	
		Pruning		0 and 2.4
Kaingaroa 3	15	Thinning	400 and 220	
Tauhara	9		200	6

RESULTS

This paper presents only a limited report of the individual trials in so far as they have a bearing on interpretation of the model surface (Table 5).

Three trials had a strong linear response to nitrogen; two had a complex nitrogen and phosphorus response. Cumulative response to both elements was either positive or neutral.

TABLE 5—Statistical significance of the volume increment response to applied fertiliser in the first year after trial establishment

Trial	Significance of linear effect	Significance of quadratic effect	Comment
Parengarenga	**	NS	N linear
Maromaku	**	NS	N linear
Kaingaroa 1	**	NS	N linear
Motueka	**	*	Complex positive N + P
Nemona	**	*	Complex positive N + P

NS = not significant
* = significant at $p \leq 0.05$
** = significant at $p \leq 0.01$

The five regressions of Ln needle mass against Ln tree diameter did not differ in slope, but they did differ in intercept (Table 6).

TABLE 6—Relationship of Ln needle mass to Ln diameter

Trial	Intercept	Slope
Parengarenga, Maromaku	3.9	1.96
Kaingaroa 1, Nemona	4.3	1.96
Motueka	3.6	1.96

Average needle mass by trials, and soil and foliar nutrients are reported in Table 7.

Volume increment averaged 11.3 m^3/ha/yr and ranged from 2.7 m^3/ha/yr in a plot without fertiliser at Parengarenga to 41.4 m^3/ha/yr in a plot with fertiliser at Maromaku.

TABLE 7—Average needle weight, foliar, and soil nutrients prior to fertiliser application

Trial	Average needle weight per trial site (kg/ha)	Foliar nutrients		Soil nutrients	
		N (% d.wt)	P (% d.wt)	Total-N (%)	Bray P (ppm)
Parengarenga	840	1.296	0.105	0.163	1.97
Maromaku	5420	1.652	0.091	0.190	2.69
Kaingaroa 1	3800	1.186	0.117	0.178	22.93
Motueka	2150	1.338	0.065	0.211	16.20
Nemona	3760	0.966	0.110	0.121	3.12

The result of fitting the full model is shown in Table 8. This relationship explained 96.2% of the variation in volume increment. Foliar nitrogen and needle weight apparently contributed strongly to the structure. The non-significant contribution of soil nitrogen and the strong negative effect of soil phosphorus were unexpected. Available-nitrogen was substituted for total-nitrogen, with the same result. After inspection of the data it was found that volume increment in Kaingaroa 1 was low but soil phosphorus was higher in Kaingaroa than elsewhere (Table 7). Soil phosphorus was therefore selected as a probable surrogate for this reduced volume increment. The Kaingaroa 1 site is the coldest of the set, with the shortest growing season, so lower volume increment per unit of canopy weight and nutrition is probable. This theory was tested in two ways – by including the environmental data from Table 1 (unsuccessfully) and by deleting the Kaingaroa 1 observations from the data set. After this latter step the significance of the soil phosphorus term was greatly reduced (t of 2.0), thus confirming our view.

TABLE 8—Relationship between volume increment (Y), needle weight, foliar and soil nutrients, and fertiliser input: Stage 1

Term	Coefficient	t-value
Intercept	–22.23	
Canopy weight (kg/ha)	+0.0033	19.8
Foliar N (%)	+18.0	23.1
Foliar P (%)	–8.2	0.3
Soil total-N (%)	+5.1	0.3
Soil P (ppm)	–0.15	6.3
Fertiliser N (kg/ha)	+0.005	3.6
Fertiliser P (kg/ha)	+0.006	2.0

Percentage variation accounted for 96.2%

Because some of the variables were non-significant the model could be simplified (Table 9).

TABLE 9—Relationship between volume increment (Y), needle weight, foliar nutrients, and fertiliser input: Stage 2

Term	Coefficient	t-value
Intercept	–27.0	
Needle weight	+0.003	27.0
Needle N (%)	+21.26	22.9
Fertiliser N (kg/ha)	+0.005	2.6
Fertiliser P (kg/ha)	+0.005	1.2

Percentage variation accounted for 92.2%.

The magnitude and direction of the fertiliser responses are entirely consistent with the reported trial results (Table 5). Since the fertiliser effect was small the surface can be still further simplified (Tables 10 and 11).

TABLE 10—Relationship between volume increment, needle weight, and foliar nitrogen: Stage 3

Term	Coefficient	t-value
Intercept	–26.00	
Needle weight	+0.003	26.2
Needle N (%)	+21.29	22.2

Percentage variation accounted for 91.7%.

TABLE 11—Relationship between volume increment and nitrogen in the needle mass: Stage 4

Term	Coefficient	t-value
Intercept	–0.155	
N content of the needles (kg N/ha)	+0.269	30.5

Percentage variation accounted for 87.2%.
Standard error 3 m^3/ha/yr.

The simple correlation coefficient between volume increment and nitrogen in the needle mass is 0.94. Between volume increment and needle mass it is 0.78.

The finding from Table 11, that 87% of stem volume increment could be explained by the amount of nitrogen in the needle mass alone, was surprising. The validity of the equation was tested on another set of results (Table 12 and Fig. 1). The correlation between actual and predicted values is 0.94 – equivalent to an r^2 of 0.88 – very similar to the original test data.

TABLE 12—Biomass data selected for validation

Trial	Treatment	Needle weight (kg/ha)	Needle nitrogen (kg/ha)
Kaingaroa 2	Unpruned, unthinned	8650	117.6
	Unthinned, part-pruned	7710	105.0
	Thinned, unpruned	2250	30.6
	Thinned, pruned	1070	14.7
Woodhill	Unpruned, unthinned	5950	96.7
	Unthinned, part-pruned	3030	69.2
	Thinned, unpruned	3480	48.1
	Thinned, pruned	700	12.5
Kaingaroa 3	Unthinned	9110	125.7
	Thinned	6480	90.5
Tauhara		3250	64.7

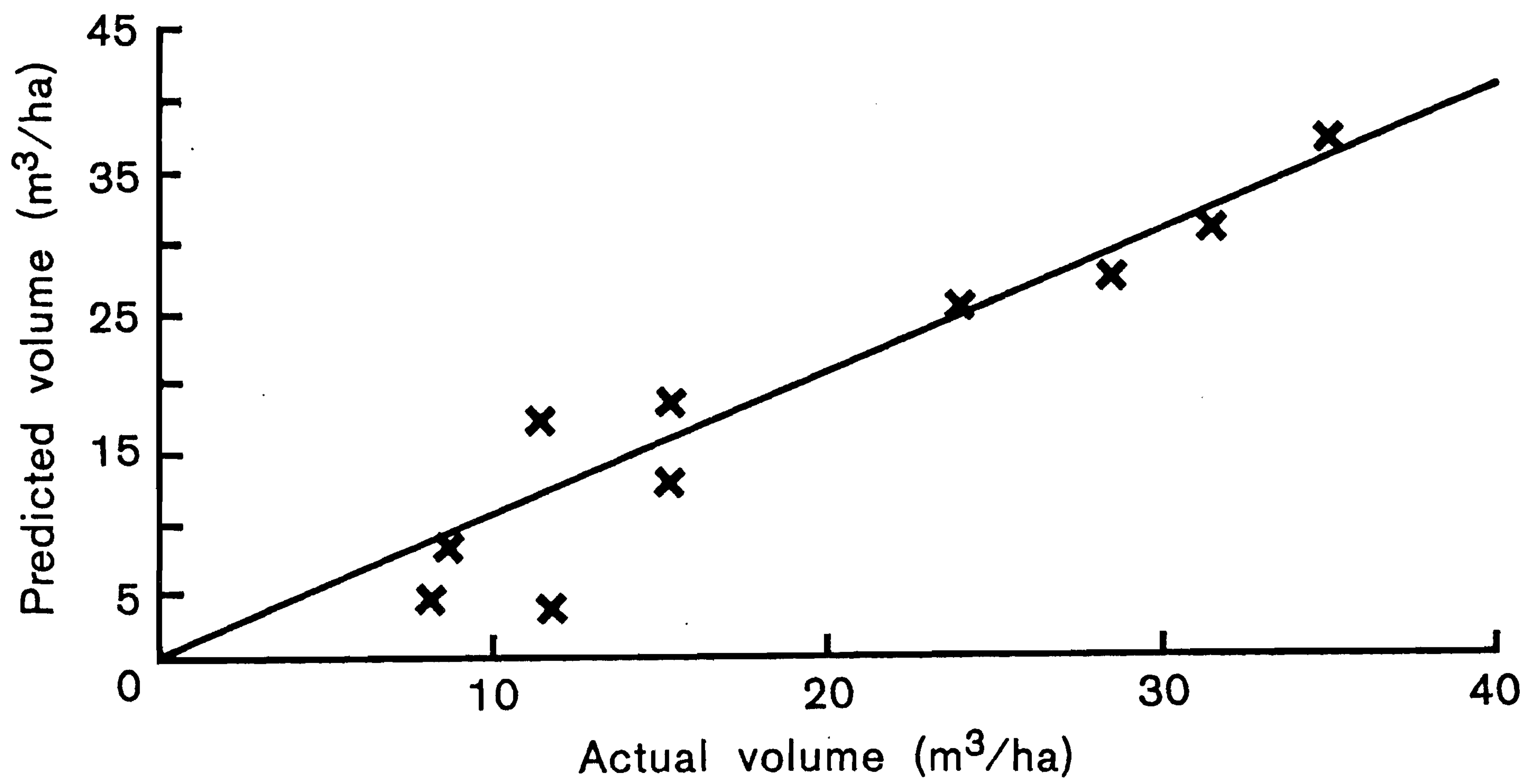

FIG. 1—Verification of model data - predicted **v.** actual volume increment.

DISCUSSION

We began by proposing the hypothesis that the volume increment of *P. radiata* would be proportional to its existing needle mass, its initial nutrient status, and nutrients available from soil and applied in fertiliser. However, neither soil nitrogen nor soil phosphorus contributed significantly to the relationship. The problem seems to be in the fact that the canopy nitrogen not only indicates the amount of nitrogen available for retranslocation, but it also indicates the historical ease with which the stand has acquired nitrogen.

As a result the model could be greatly simplified to the point where it was similar to the nitrogen productivity concept outlined in a series of papers by Agren (1983, 1985). Agren developed his concept from a theoretical base and tested it on empirical data. We started with empirical data but, by the process of reduction, arrived at a similar point and in so doing may have helped to explain why the nitrogen productivity concept is such a useful generalisation.

When tested on trial data which ranged well outside the set of silvicultural conditions and tree ages contained in the original data set, the equation predicted volume increment reliably and had a similar degree of accuracy. Models of this type make an exciting contribution to physiological modelling, enabling working hypothesis models to be constructed quickly and robustly.

There is a minor reservation about the tendency of the equation to underpredict growth in harshly treated stands where, as a result of thinning and pruning, needle weight is reduced to below 1000 kg/ha. This characteristic is probably due to the fact that the canopy in the growth period is, as a result of bud extension, substantially greater than that determined in the winter biomass. At higher canopy weights the increment added by bud burst would be proportionately less. This problem would probably be corrected by using a shorter time frame for the growth period (G. I. Agren, pers. comm.).

It may be possible to calculate the uptake of nitrogen fertiliser and its efficiency of use by reversing the equation given in Table 11. For example, the first-year volume increment gain in the nitrogen rates trial reported by Hunter & Hoy (1983) was 5 m^3/ha to 100 kg N-fertiliser applied/ha, 7.9 m^3/ha to 200 kg N/ha, and 8.4 m^3/ha to 300 kg N/ha. These volume gains equate respectively to 18.1 kg, 29 kg, and 30.9 kg more nitrogen in the canopy.

The canopy uptake percentages are therefore 18%, 14.5%, and 10.3% of the amounts applied. These figures must understate total uptake since they ignore stem-wood and tree root uptake and they make no allowance for subsequent uptake from the soil. However, if it proves possible to find experience factors to take account of these factors, we have a potentially useful tool for studying nitrogen fertiliser efficiency.

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