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ENVIRONMENTAL VARIABLES INFLUENCING THE INCREMENT OF RADIATA PINE

(1) PERIODIC VOLUME INCREMENT

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ABSTRACT

Earlier work expressing quantitative relationships between the growth of radiata pine (**Pinus radiata** D. Don) and environmental influences generally is reviewed. On the basis of a survey of 132 sites, selected to represent a maximum range of New Zealand climates, this paper then analyses the influence of over 50 site variables upon the periodic volume increment of individual dominant trees. After the effects of age had been removed, the following variables accounted for over 66% of the remaining variation: mean annual precipitation, seasonal rainfall distribution, effective soil depth, total nitrogen and available (Olsen) phosphorus in the topsoil, and the seasonal departures of ambient temperature from postulated optima of 5° C at night and 20° during the day.

INTRODUCTION

Radiata pine (*Pinus radiata* D. Don) is planted in New Zealand over a range of sites encompassing from 35 to at least 300 cm of annual rainfall, and with monthly mean temperatures extending from 2.8°C in June to 18.3°C in January. The ranges of these two parameters alone are respectively eight and two times greater than those in its

N.Z. Jl For. Sci. 4 (1): 3-26

natural habitat, and the species has been successfully planted over an even wider range of habitats throughout the Southern Hemisphere (Scott, 1960). Golfari (1963) attempted a synthesis of its climatic requirements, using survival as his criterion; but, despite the major differences of productivity of radiata pine that are apparent between different countries and regions within a country, no comprehensive analysis of the effects of climate on productivity has yet been published. Within any one climatic region of New Zealand, and elsewhere, there are also large differences in site productivity due to soil fertility and the deficiency of certain micronutrients. Quantitative investigations of many of these effects have been reviewed by Raupach (1967), but there remains the problem of interrelating many separate results that are overlaid by the influence of climatic differences.

This paper reports some of the results of a survey intended to assess the influence of some climatic variables upon the productivity of radiata pine. They are presented as a self-consistent set of relationships that may serve as provisional models for future investigations. Although a considerable number of variables was screened, it is in no sense an exhaustive examination, because the meteorological data were of necessity restricted to those available from a standard climate station. In two subsequent papers the influence of the same variables upon periodic height and basal area increment, and of seasonal rainfall variations upon current increment, will be examined.

METHODS

The Criterion of Productivity

The best measure of site productivity for a given species (cf. Jackson, 1965) is undoubtedly total stand volume or dry matter increment, expressed either as a mean over the rotation, or as a periodic increment related to stand age. Unfortunately such data are affected by changes of stocking, which may be particularly variable for radiata pine in New Zealand due both to the wide diversity of thinning intensities practised in different forests and the earlier epidemic of *Sirex noctilio*. The direct effect of stand density on increment per unit of area may, however, be much reduced by confining the measurement of increment to dominant trees. The range of stocking differences was further reduced by specifying that all stands included in the survey should be fully stocked. Finally, the residual variation due to stocking differences between trees may be accounted for by incorporating an estimate of the degree of competition as a covariate. Such a "Competition Index" was in fact measured for each sample tree in the survey. The index itself was the subject of an earlier report by Jackson and Gifford (1966).

Further sources of variability, irrelevant in a study of this nature, may be due to the many accidental factors that influence a stand during the early stages of establishment. By three years of age, however, such factors are usually becoming subordinate to the more permanent influences of site. A minimum stand age of ten years, with a retrospective increment period of seven years, was accordingly adopted to avoid these early vagaries.

With the trend towards shorter rotations of about 25 years for radiata pine, it was considered desirable to concentrate the survey on the period when maximum increment accrues, in order to ascertain what site-imposed limitations management might expect in

its quest for maximum productivity. Therefore, the survey was generally restricted to the age-class of trees between 10 and 20 years old.

Mensurational Technique

The number of sample trees in each stand to be measured was specified as the seven tallest dominant trees on a tenth-acre (0.0405 ha) plot. Such trees were selected after climbing one of the taller trees in the stand.

On each of the sample trees the following measurements were made in the course of climbing the tree:

- Height: at termination of previous season's growth $(H_{2,1})$ and exactly seven years earlier $(H_{1,1})$, time being represented by the first subscript.
- Diameter outside bark (d.o.b.), and bark thickness: at half and one-fifth of $H_{2,1}$ (represented by $d_{2,0.5}$ and $d_{2,0.2}$ respectively) and at half $H_{1,1}$ ($d_{1,0.5}$). D.o.b. and bark thickness were also measured at breast height (d_b), stump height (d_s), and at the point midway between $H_{1,1}$ and $H_{2,1}$ (d_m). (The second decimal subscript denotes fraction of tree height).
- Diameter increment: wherever diameters (except d_s and d_m) were measured, two radial increment cores were extracted at right-angles to one another, each including the seven outermost complete years of radial increment. At breast height, four cores were taken at equal arcs. Measurements were subsequently completed in the laboratory, according to the methods described by Jackson and Gifford (1970).

The interrelationships of these data are illustrated in Fig. 1. Volume increment over the preceding seven years, I in m³, may then be calculated from the formula:

$$I = 0.52416 d_{1,1}d_{m} (H_{2,1} - H_{1,1}) + 1.5708 [r_{1,1} {}^{2}(H_{1,1} - H_{2,0\cdot5}) + r_{2,0\cdot5} (d_{2,0\cdot5} - r_{2,0\cdot5}) (H_{1,1} - H_{1,0\cdot5}) + r_{1,0\cdot5} (d_{1,0\cdot5} - r_{1,0\cdot5}) (H_{2,0\cdot5} - H_{2,0\cdot2}) + r_{2,0\cdot2} (d_{2,0\cdot2} - r_{2,0\cdot2}) (H_{1,0\cdot5} - H_{2,0\cdot2}) + r_{b} (d_{b} - r_{b}) (H_{2,0\cdot2} - H_{s}) + r_{s} (d_{s} - r_{s}) (H_{b} - H_{s})] (1)$$

Linear dimensions in the above equation are all in metres.

The derivation of the equation is given in Jackson and Gifford (1970), where it is shown that this technique will generally provide estimates within 5% of the true volume increment, as well as increasing precision by a factor of eight to ten as compared with conventional volume table methods. Complete field and laboratory procedures are also given in detail in the same report.

Distribution of Stands Sampled

A primary source of information for the location of stands to be sampled was the records of the Exotic Forest Survey of New Zealand (Wardrop, 1966). The preliminary screening for stands of radiata pine in the 10- to 20-year age class was concentrated in regions that would provide a maximum range of mean annual precipitation (MAP)



STEM SECTION DRAWN TO LINEAR (Left) & QUADRATIC (Right) HORIZONTAL SCALES

FIG. 1—Diagram of tree measurements for calculation of periodic volume increment. Subscripts of $H_{i'0,i}$ refer to the decimal fraction, 0.j, of total height at which measurements were made for the two ages represented by i = 1, 2. Subscripts for d and r correspond with those for H.

and/or mean annual temperature (MAT). This was followed by field reconnaissance of all stands to ensure that they met certain criteria:

- (a) Proximity to an established climatological station or local rain-gauge;
- (b) Adequacy of stocking, and freedom from thinning within the preceding seven years;
- (c) Low incidence of malformation.

Vol. 4

Since the major objective of this survey was to determine climatic influences on productivity, stands from sites where unrelated factors were known to be limiting (e.g., soils with known boron or phosphorus deficiencies) were excluded. The only exceptions were several stands that had been top-dressed with superphosphate more than seven years previously (i.e., not during the increment period). These were included because the climatic pattern for the site would not otherwise have been represented in the survey. In general, level uniform sites were selected wherever possible. Valley-bottom, flood-plain, and ridge-top sites were normally excluded, to preclude the effects of rainfall being masked by excessive run-off interactions.

The final distribution of stands is represented in Table 1, as a two-way classification against MAP and MAT. The approximate location of all 132 plots is shown in Fig. 2.

°C				Me	ean ann	ual preci	pitation ·	– (cm)			
0	25	50		75	100	125	150	175	200	225	250
0			_	_	1			· _	_		
9		_	8	8	4	ì	_	_		_	
10			U		-						
11		5	4	7	2	1	3	4	_	1	
A.			1	9	10	_		5	_	1	
12			5	13	5	10	2	_	_		
13			Ū	10		10	-				
14		—		_		3		6	_	_	
		—	—	—	_	2					
15				_		4	2	_	_		
16						_					

TABLE 1-Distribution of sampled sites by mean annual temperature and precipitation

Field Observations

The meteorological data were derived from records of monthly rainfall and monthly mean temperature spanning the increment period for the plot concerned. They were provided by the New Zealand Meteorological Service. Since some plots were rather distant from a standard climate station, various adjustments to the basic data were required. In some cases data were available from an unofficial local rain-gauge, with which comparisons could be made and values adjusted proportionately. The main problem was with missing temperature data, for which values had to be interpolated in parallel with the nearest stations for which records were complete. Manipulation of these data is described in the appropriate section below.

In order to avoid the problems of interpreting subjective descriptions, field procedures were designed to provide quantitative estimates of the various site parameters. Sites that were not amenable to these procedures were avoided. The principal parameters that it was sought to assess were:



FIG. 2-Geographical location of stands sampled throughout New Zealand.

- (a) The factors affecting run-off and sub-surface movement of rainfall (i.e., slope and relief).
- (b) Effective soil volume, as affecting the available supply of water and the total supply of available nutrients.
- (c) Soil nutrient concentration, as determining the level of available supply.
- (d) Particle-size distribution in the soil, as affecting the soil-moisture holding capacity and nutrient exchange relationships.

The primary variables measured (as distinct from the secondary, or derived, variables) are listed in Appendix 1, together with their ranges and the units concerned.

ANALYSIS AND RESULTS

1. The Test Model

The data from this survey were intended to test various hypotheses regarding the influence of site variables upon productivity of radiata pine. The model used is entirely empirical, taking the form:

wherein I is the mean periodic volume increment, A represents age of stand, and X₁, X₂ . . . X_i are site variables, C is a constant, and e_i the error term. The limited range of stand ages avoids both major inflexions in the normal sigmoid curve of growth. Checks on plotted stem analyses over this age range indicate that there is a slight initial concavity at about 10 years, and that the increment is beginning to decrease again from 20 years onward. The term e^{-a/A} provides a simple expression for such a trend (cf. Stage, 1963). In the case of the environmental parameters, X_i, etc., it is assumed at this stage that the actual expression will depend upon previous work and hypotheses about the interactions involved. The exponential form of the expression has the advantage that, if negative, it provides for a diminishing effect as the value of X_i increases (i.e., e^{-biXi} approaches an asymptotic value), while, if positive, the reverse will obtain. In the former respect it is similar to the Mitscherlich yield equation, but does not require prior knowledge of the value of maximum yields. The chief advantage of the equation as a whole is that the logarithmic form is linear, *viz*.

 $Y = \ln (I) = a_0 \pm a/A \pm b_1 X_1 \pm b_2 X_2 \dots \pm b_i X_i + e_i \dots (3)$ thus permitting analysis by least squares regression procedures.

The actual independent variables, X_i , etc., to be used in the models are based upon current ideas regarding the site factors that influence productivity of radiata pine. Scott (1960) and Raupach (1967) provide comprehensive reviews of many of these influences. Other inferences may be based upon more recent experimental work (*see* Sec. 4 below). Such inferences are, however, restricted to the limited set of conditions within which most experiments are necessarily conducted. One of the most helpful contributions from a survey of this nature is that it provides the opportunity to relate such inferences one to another, by testing the validity of hypothetical relationships over a range of real situations.

It is convenient, initially, to consider the independent variables grouped separately under various categories, i.e., precipitation, temperature, physical soil factors, nutrient

New Zealand Journal of Forestry Science

factors. The reason for this is that there are in each group usually one or two variables which previous work has shown to be generally correlated with the dependent variable and which must be included in the model; but there are usually also many other expressions which may in fact improve upon the former. Although it is desirable to screen these out first, limited computer storage capacity precludes such screening for all groups simultaneously. The expedient of screening each group consecutively has, therefore, been adopted. The significant variables from each group are carried over into the succeeding groups. In the final regression, the screened variables are ranked solely according to the magnitude of their reduction of the residual sum of squares.

2. Precipitation Variables

General observation of radiata pine throughout its planted range in New Zealand and Australia had indicated that productivity would almost certainly be correlated with mean annual precipitation (MAP), although Hinds and Reid (1957) had indicated an optimum range of between 90 and 180 cm, while Golfari (1963) narrowed this to 110-170 cm. Poynton (1957) recommended that in South Africa radiata should be confined to silvicultural zones with over 63.5 cm per annum. It will actually form closed stands with rainfall as low as 50 cm (Western Flat, S. Australia; Anglesea, Victoria, from personal observation), but not at 36 cm (Alexandra, New Zealand, which was one of the sites sampled). There is further diversity of opinion regarding the best seasonal distribution of rainfall: Golfari (1963) recommends concentration in the colder half of the year, and Poynton's silvicultural zones agree with this. However, Raupach (1967) indicated that the relatively uniform distribution of rainfall over much of the planted area in New Zealand does not conform with the winter maximum that Prescott and Lane Poole (1947) regarded as most favourable. Scott (1960) similarly stated that in Australia radiata pine thrived only in areas with a pattern of adequate winter rainfall and a summer drought, and was not successful in the coastal belt of uniform precipitation; Poynton, however, indicated that the species will thrive in areas of uniformly distributed rainfall provided that the soils are deep and of sandy texture, with adequate drainage. Experience in New Zealand confirms this: the disagreements noted are almost certainly due to compensating interactions between the absolute amount of rainfall and critical deficits during the periods of most active growth. (Interactions with soil moisture storage will be considered later).

The most satisfactory way of securing an objective test would be to use a range of polynomial coefficients to provide differential weighting of the rainfall in each month (*see* Schumacher and Meyer, 1937) and to incorporate a series of such composite variables in the multivariate analysis. The actual coefficients used for this test are tabulated in Table 2, and it will be observed that they include sequences from linear (S2, S7) up to fifth order polynomials (S6, S11, S16). The sequences are not necessarily orthogonal one with another, as the phases have been shifted to test the various alternatives suggested by the writers quoted earlier.

For each series of coefficients the mean rainfall (r_j) for each month over the sevenyear increment period was multiplied by the corresponding coefficient (C_{ij}) , and then summated to provide the relevant series variable (S_i) , i.e., $S_i = \sum_{j=1}^{j=12} C_{ij} r_j$.

Conior	Month	ly coe	fficie	nt(C _i	j)used	to m	ultip	ly co	rresp	ondin	g mon	thly	rainfall
sum(S _i)	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	
S 1	1	1	1	1	1	1	1	1	1	1	1	1	
S 2	-11	-9	-7	-5	-3	-1	1	3	5	7	9	11	
S 3	55	25	1	-17	- 29	-35	-35	-29	-17	1	25	55	
S 4	-33	3	21	25	19	7	-7	-19	-25	-21	-3	33	
S 5	33	-27	-33	-13	12	28	28	12	-13	-33	- 27	33	
S 6	-33	57	21	-29	-44	-20	20	44	29	-21	-57	• 33	
S 7	11	-11	-9	-7	-5	-3	-1	1	3	5	7	9	
S 8	55	55	25	1	-17	- 29	-35	-35	-29	-17	1	25	
S 9	33	-33	3	21	25	19	7	-7	-19	-25	-21	-3	
S10	33	33	-27	-33	-13	12	28	28	12	-13	-33	-27	
S11	33	-33	57	21	-29	-44	-20	20	44	29	-21	-57	
S12	-33	-27	33	33	-27	-33	-13	12	28	28	12	-13	
S13	25	55	55	25	1	-17	- 29	-35	-35	- 29	-17	1	,
S14	-3	33	-33	3	21	25	19	7	-7	- 19	-25	-21	
S15	-27	33	33	-27	-33	-13	12	28	28	12	-13	-33	
S16	-57	33	-33	57	21	-29	-44	-20	20	44	29	-21	
S17	25	1	-17	- 29	-35	-35	-29	-17	1	25	55	55	
S18	, 3	21	25	19	7	-7	-19	- 25	-21	-3	33	-33	

TABLE 2-Polynomial coefficients used in differential weighting of monthly mean rainfall

Correlations of each of the eighteen series sums with Y were then determined, followed by partial correlations as the effect of each variable was removed. The first four variables, produced by a stepwise screening procedure, were as follows:

Series:	S 1	S 15	S18	S 4	
F ratio:	54.3	5.76	2.88	4.62	
Significance:	** **	*	NS	*	
Regression:	0.125	0.024	0.031	-0.021	(a = 3.534)

Given the monthly mean rainfall (\bar{r}_j) over all plots in the survey, the effect (E_j) on periodic increment (Y) of an additional unit of rainfall in any month (j) may be calculated by the following equation:

$E_j = ((0.125(C_{1j}) + 0.024(C_{15,j}) + 0.031(C_{18,j}) - 0.021(C_{4,j})) \times \bar{r}_j + 0.295/\bar{r}_j$ (4) The calculated effects for each month are represented as a histogram in Fig. 3,

3. General Site Variables

together with the mean values of monthly rainfall over all 132 plots.

The four weighted precipitation sums (S1, S18, S15, S4) were designated as the independent variables X_{33} , X_{34} , X_{35} , X_{36} respectively, and included with the reciprocal of age (X₄₈) and the general site variables X₁ to X₆ (Appendix 1) in a

11



FIG. 3—Relative effect of an additional cm of rainfall in any month on periodic volume increment.

determination of partial correlations. These are presented in Table 3, with the simple correlations between Y and each independent variable in the first column. Subsequent columns show the partial correlation between Y and the variable at the beginning of the row, after removing the effect of the variable at the head of the column.

The variable showing the greatest correlation with Y was X_6 , the competition index (Jackson and Gifford, 1966). However, the correlation was not negative, as one would expect, but positive—indicating that volume increment of the individual sample trees increased as the number and size of competing trees increased. This initial result

Variable	r	Part X1	ial co X2	rrelat X3	ions a X4	after X5	removin X6	g effe X48	ct of X33	column X34	varia X35	ble X36
X 1	.19	0	.19	.19	.19	.14	.14	.17	.15	.25	.21	.22
X 2	02	02	0	03	02	05	06	.02	18	11	02	04
X 3	05	03	05	0	05	06	05	03	02	05	05	05
X 4	.02	.02	01	.01	0	.05	.06	02	.20	.10	.02	.03
X 5	•44	•42	•44	•44	•4 4	0	10	•36	•44	•49	•45	•46
X 6	•47	•46	•48	•47	•48	.21	0	•38	•47	•50	•48	•49
X49	43	42	43	43	43	34	31	0	56	48	43	43
X33	.42	.41	•45	.42	.46	•41	•41	•55	0	•33	•43	•43
X34	.28	•32	•30	.28	.29	•35	•33	•36	03	0	.22	•37
X35	02	08	02	02	02	07	06	.01	.08	.16	0	0
X3 6	.03	.11	.04	.03	•04	•15	•13	.07	11	25	.03	0

TABLE 3 - Fartial correlations of Y with X1 to X6, X33 to X36 and reciprocal of age (X48)

Vol. 4

was disconcerting. On reflection, it became apparent that this must be due to the conditions imposed on the sampling process: viz the restriction to dominant trees, and the further condition that only fully stocked stands should be sampled. Both these conditions were intended to reduce as far as possible the anticipated effects of stand density differences on the dependent variable. However, because the survey was designed to sample the maximum range of environmental conditions within New Zealand, the most productive sites would have the highest densities and largest competitors for the sample dominant trees, and the poorest sites would have the least. In other words, the Competition Index, X₆ (which integrates the number and size of competing trees), was acting as a positive site index. Since a primary purpose of the analysis was to isolate the effective site parameters, further use of X₅ and X₆ would only confuse the issue. They were, therefore, excluded from all subsequent analyses.

The next most important variables were X_{33} , the mean annual precipitation, and the reciprocal of age. X_1 , the altitude of the plot above mean sea level, showed some correlation with Y and was accordingly carried forward with 10/A and the four precipitation variables (X_{33} to X_{36}) to the next stage of the analysis. X_2 to X_4 showed no correlation and were discarded, along with X_5 and X_6 .

4. Temperature and Day Length

Over most of New Zealand, radiata pine does not show any clear-cut dormant period: diameter growth is more or less continuous throughout the year or, if it does falter, such cessation is most frequently drought-induced. Moreover Barnett (1971) has shown that cambial division may be still quite active during midwinter. Height growth is continuous throughout the winter in the north of New Zealand, and in some districts (the drier East Coast particularly) may show a greater retardation during a dry midsummer than during the following winter.

Downs (1962) considered that radiata pine corresponds more closely with the seasonal behaviour of trees of the tropics than with the patterns of seasonal dormacy characteristic of most temperate zone perennials—i.e., those with a photoperiod-induced period of dormacy. Florence and Malajczuk (1970) showed, however, that radiata pine exhibited a large and positive growth response to increasing duration of photoperiod, under experimental conditions with a day/night temperature regime of $25^{\circ}/20^{\circ}$ C.

Hellmers and Rook (1973) have recently reviewed work on the effect of different artificial day/night temperature regimes on growth of radiata pine. They extended these studies in their own experiments and showed that, at least in its seedling stage, this species has a marked optimum night temperature at about 5°C. They also indicated that net assimilation rate attains a maximum at a photoperiod temperature of about 20° to 22°C.

For the purposes of this analysis, the problem of applying the experimental evidence to field conditions was resolved as follows. It was assumed that departures in either direction from the optimum night temperature (n) or the optimum day temperature (d) would be equally disadvantageous to growth. The interchange from one effective optimum to the other was assumed to take place at sunrise and sunset, for which the mean times in each month of the year may be readily calculated for any locality. Representing the departure of the ambient temperature (T_i) at any hour (i; i = 1-24) of the day by (T_i-d) and at any hour of the night by (T_i-n), the sum of the departures

for all daylight hours (D_m) and for all the hours of darkness (N_m) was calculated for each month of the year (m = 1-12) by the method shown in Appendix 2.

These vectors D_m and N_m were calculated for each of 38 representative stations for values of $d = 20^{\circ}C$ and of $n = 5^{\circ}C$. For each station, the vector of monthly sums was then multiplied by a vector of polynomials ($C_{\rm km}$) and summated to provide a weighted index of values over the whole year;

i.e., (Dk) =
$$\sum_{\substack{m=1\\m=1}}^{m \equiv 12} (C_{km} D_m) \dots \dots \dots \dots \dots \dots 5a$$

or (Nk) = $\sum_{\substack{m=1\\m=1}}^{m \equiv 12} (C_{km} N_m) \dots \dots \dots \dots \dots 5b$

where k is the particular polynomial used. Fuller details of the calculations are given in Appendix 2.

Partial correlations between Y and the 19 values of (Dk) and (Nk) were then calculated. The best ten of these are presented in Table 4.

Polynomial Index	r	Part	ial co	rrelat	ions_af	ter_rem	oving e	ffect	ofcolu	umn vari	able
Optimum night	temperature 5°C	(N1)	(N2)	(N3)	(N12)	(N11)	(N16)	(N7)	(N5)	(N18)	(N19)
(N1)	.045	-	32	05	23	07	06	18	04	.05	34
(N2)	.245	•40	-	.19	.16	.23	.17	.15	.21	.25	07
(N3)	.178	.18	03	-	.01	.17	01	.04	.09	.18	02
(N12)	.216	•31	08	.13	-	.18	.10	.07	.16	.21	11
(N11)	.122	.13	03	.12	02	-	.08	.02	.08	.12	07
(N16)	.190	.20	01	.07	0	.17	-	.06	.16	.20	01
(N7)	.214	.27	05	.13	.06	.18	.12	-	.15	.22	10
(N5)	156	16	.04	0	.06	13	.11	04	-	.18	.03
(N18)	.043	.05	.03	03	03	.05	08	.05	09	-	.04
(N19)	.265	•42	.10	.20	.19	•25	.19	.19	.22	.27	-
Optimum day t	emperature 20°C	(D1)	(D2)	(D3)	(D12)	(D11)	(D16)	(D7)	(D5)	(D18)	(D19)
(D1)	110	-	25	04	20	01	06	13	01	15	24
(D2)	106	25	-	21	02	07	11	.11	05	.07	.12
(D3)	.151	.11	.23	-	. 28	12	.01	.27	.03	.17	.24
(D12)	109	20	03	26	-	09	16	.16	09	.01	0
(D11)	319	30	31	31	31	-	32	26	18	26	31
(D16)	.173	.15	.18	.09	.21	17	-	.17	03	.11	.18
(D7)	244	25	25	32	27	16	24	-	12	14	24
(D5)	271	25	26	23	26	02	21	17	-	18	25
(D18)	.204	.23	.19	.22	.17	.06	.15	.03	0	-	.17
(D19)	118	25	13	23	05	08	13	.12	06	.05	-

TABLE	4	-	Parti	al	correlatio	ons b	etween	Y	and	the	weighted	monthly
			sums	of	departure	from	optimu	m	temp	perat	ture	

5. Soil Physical Factors

Hinds and Reid (1957) indicate tolerance by radiata pine of a wide range of soil textures, from sands to clays, but that optimum growth is attained on deep, well-drained sandy loams. Scott (1960) specifies that a soil depth of at least 0.9 to 1.2 m is

Vol. 4

necessary for it to attain a height of 30-35 m, and mentions that at Lota, Chile the height at a given age is clearly proportional to the effective depth of soil. He notes that clay soils are not suitable, and Poynton (1957) similarly states that stiff clayey soils, or those where drainage is impeded by clay near the surface, result in unthrifty development. These isolated pieces of evidence are neatly summarised in Raupach's Fig. 6 (1967), derived from data by J. Ruiter, showing the relationship between a site index (height at age 30 years) and effective soil depth (ESD). The latter may be defined, on appropriate soils, as the depth to a soil horizon that is markedly less penetrable by roots and/or less pervious to water (cf. the "least permeable horizon" (LPH) of Coile, 1952). It may be genetic in origin, as for a strongly alluvial or indurated zone, or it may be lithologically derived-as where aeolian sands or volcanic ash overlie rock or clay. The usefulness of ESD as a measureable parameter in site productivity studies is enhanced, within a plantation, by the competition from adjacent trees for soil-space within which to extend their root-systems. The ESD thus becomes a critical dimension for the overall volume of supply of both available nutrients and moisture.

These are, however, also affected by other physical characteristics of the soil, notably, the nature of the clay minerals, the particle size distribution and bulk density. The fraction of the soil with particles less than 0.02 mm diameter, i.e., the percentage of silt plus clay (Si + C), has repeatedly been shown to be closely correlated (negatively) with site productivity (cf. reviews by Coile, 1952; Jackson, 1962). Nevertheless, Raupach (1967) mentions instances of high productivity of radiata pine on soils for which the clay content was as much as 60 to 90%. Zahner and Hedrich (1966) have also shown that, on sandy soils particularly, an increasing proportion of very fine sand (VFS) (i.e., particles 0.02-0.10 mm diameter) markedly increased the amount of available soil water held in a profile. Higher proportions of VFS were associated in all cases with higher site indices. Pawluk and Arneman (1961) had similarly found that the percentage (VFS + Si + C) in the A and B horizons of glacial outwash sands was more highly correlated with the site index of jack pine than any other combination of particle size fractions.

Interactions between effective soil depth and soil texture are complex, particularly as they affect soil moisture storage, internal drainage and aeration. Pegg (1967), for example, showed that whereas on clay loam soils (S + C about 40%) the site index of slash pine in Queensland was positively correlated with increasing depth to LPH, on loamy soils the correlation was negative. On clay soils (Si + C, range 50 to 80%) the best correlations (negative) were with the reciprocal of depth to LPH. Jackson (1962) had earlier found that a weighted combination of both the direct and the reciprocal expressions, to provide a curvilinear relation, gave best fit to the data. Where the sites being compared occur in regions of different annual rainfall, the interactions with ESD may be expected to affect strongly the moisture storage and drainage properties, and to be reflected in some such index as (growing season rainfall)/LPH, found to be highly correlated with slash pine height increment (Jackson, 1962).

Bearing in mind that the primary objective of this survey was to explore the climatic interactions with site productivity, it was considered essential to reduce complicating factors wherever possible. To this end, sites were admitted to the survey only

15

when preliminary reconnaissance showed that the above soil variables could be measured successfully. This unfortunately resulted in exclusion of several forests that it would otherwise have been desirable to include in the survey: Balmoral and Eyrewell State Forests, situated on the gravel plains of Canterbury, were particular examples, together with areas of Golden Downs State Forest where the Moutere Gravels are still relatively unweathered. On the other hand, the strongly weathered sequences (Mapua Soils) provided acceptable sites for a number of plots. These were particularly valuable because of their close proximity to sites on the Tahunanui Sands, providing such a strong contrast of effective soil depth.

The six variables brought forward from Section (3) were now combined with X_7 to X_{11} (Appendix 1), and the derivations of some of these that are listed in Appendix 3 as X_{37} to X_{44} . A stepwise regression of Y was run against these variables, after the effects of X_{48} had been removed.

		Associate	ed Variation	
	Variable	(alone)	(after preceding variables)	F ratios
X ₄₈	10/age	10.033	10.033	62.98
X_{37}	ln (S1)	12.328	16.976	106.57
X_{41}	S15/(ESD)	0.201	4.776	29.98
X_{40}	Sl/(ESD)	0.021	2.301	14.45
	Residual Varia	ation	20.228	E.M.S. = 0.1593
	Total (on 131	d.f.)	54.314	

The following proved to be highly significant:

Highest correlation between the independent variables concerned was 0.455 (in the case of X_{37} and X_{40}).

The regression equation of Y on the above four variables was calculated to be:

Residuals from this equation, given by $(Y_i - \hat{Y})$, were calculated for each plot (i) and provided the independent variable for the next stage of correlation analyses.

6. Soil Nutrient Factors

The survey excluded soils where it was known that nutrient deficiencies were the principal limitation to productivity. Examples of such exclusion were sites on the Rosedale hill soils of Nelson Province where growth was known to have been affected by boron deficiency. Stands in Riverhead State Forest were similarly excluded because of phosphate deficiency, as were many compartments in Waitangi and Waipoua State Forests that had been fertilised during the preceding seven years. However, if such superphosphate top-dressing preceded the increment period, stands were regarded as acceptable for sampling.

The general dependence of radiata pine productivity on levels of soil nitrogen and phosphorus has been nicely summarised by Raupach (1967) for numerous investigations

in Australia, New Zealand, and South Africa. At levels below about 0.05% total N and 0.005% available P in the surface soil, growth is greatly restricted. Although anomalies exist, particularly on lateritic soils or those over limestone (of which two examples were encountered in this survey), it is clear that these are two major determinants of productivity that must be included in the site variables. Raupach also records responses to potassium and calcium. Although no stands known to be deficient in these elements were sampled, it was considered desirable to include them in the analyses. A further problem, particularly for phosphorus determinations, concerns the best measure of nutrient availability to the tree. Ballard (1971) has considered this in relation to the various extractants used for determining available phosphorus. In order to secure an impartial assessment of some of these alternatives, in addition to the determination of total P, three different techniques were used in the laboratory analyses of P for each sample (Ballard, 1971). They are referred to as citric acid extractant, Bray's procedure and Olsen's procedure. Separate determinations were made for both the surface soil and the bulk soil sample. Preliminary screening of the analytical values for each plot, for correlation with the periodic increment, showed that the Olsen P values were generally superior. These were accordingly used in subsequent steps of the calculations. The following analyses were also made on the composite topsoil sample: total N (Kjeldahl technique), pH, total carbon, cation exchange capacity (C.E.C.), and the content of individual cations: K, Na, Mg, Ca (see Appendix 1).

Since deficient sites had been deliberately avoided, it was considered that the major nutrients (N and P) would almost certainly not exhibit a simple linear relationship with site productivity. This might well occur, for example, at levels of HCl-soluble phosphorus below 65 ppm (Kessell and Stoate, 1938), but in the vicinity of 130 to 175 ppm (considered as optimal by Brockwell and Ludbrook, 1962) the response should become asymptotic. Similar reasoning can be applied to Waring's (1962) definition of critical levels of total N in the surface three inches of soil—with large responses expected below 0.05% but diminishing as the content approaches 0.1% total N. Accordingly, a logarithmic transformation of both the N and P values for each plot was eventually adopted for the ensuing calculations (subsequent tests confirmed that these were in fact more closely correlated with the dependent variable than the linear terms). Correlations were then calculated for each of these soil nutrient variables against residuals from the preceding Equation (6), and are presented in Table 5.

					Partial co	rrelatio	ns after	renoving	effect c	f column	variable	
Variab	ble	r	N X20	Olsen 1 X14	с К Х23	Mg X25	Ca X26	CEC X27	рН X21	ln(N) X49	ln(P) X50	ln(N*P) X51
X20	Topsoil N	.05	0	03	01	.03	.01	04	.05	23	04	18
X14	Olsen P	.24	.24	0	.17	.21	.20	.22	.25	.16	.09	.07
X23	к	.22	.21	.13	0	.12	.14	.20	.22	.12	.15	.10
X25	Mg	.22	.22	.19	.12	0	.12	.21	.22	.16	.17	.14
X 26	Ca	20	.19	.15	.11	.07	0	.18	.20	.12	.15	.11
X 27	C.E.C.	.09	.09	.04	02	.05	.04	0	.10	17	.04	09
X21	рH	0	16	11	12	.14	17	14	0	05	.10	04
X 49	ln(N)	.24	.32	.16	.15	.18	.17	•27	.28	0	.14	.01
X50	ln(P)	.23	.22	.04	.16	.18	.19	.21	.24	.13	0	01
X51	ln(N*P)	.27	.31	.14	.18	.21	.21	.27	.31	.13	.14	0

TABLE 5 - Partial correlations of residuals from Equation (4) with soil nutrient variables

Vol. 4

Although P and N were both positively correlated with residuals from Equation (6), a negative partial correlation became apparent when the effect of either one was removed first. It was thus not possible to incorporate them separately in the model and it was considered that a more rational analysis of the data might be provided by the product of N and P, as a single variable. This would have the major advantage of ensuring that, if either N or P approached a zero value, the effect of the other would be correspondingly reduced. Subsequent tests showed that the combined variable in fact accounted for a greater amount of the residual variation than did either N or P considered separately.

7. Final Analysis

The final stepwise regression was run for ln(I) against the reciprocal of age X_{48} , X_{37} , X_{40} , X_{41} , X_{51} and the best 10 temperature indices (Dk) and (Nk) brought forward from Section (4). In decreasing order of their contribution to the residual sum of squares, the following proved to be highly significant:

	Associ	ated Variation	
Variable	(alone)	(after preceding	F ratios
		variables)	
X ₄₈ : 10/Age	10.033	10.033	82.04**
X_{37} : ln(S1)	12.328	16.976	138.81**
X ₄₁ : (Polynomial S15)/ESD	0.201	4.776	38.96**
X_{40} : S1/ESD	0.021	2.301	18.77**
X_{51} : $\ln(N \times P)$	4.157	1.918	15.73**
X ₄₅ : (N1)	0.099	0.994	7.76**
X_{46} : (N7)	2.495	1.573	12.81**
X_{47} : (D3)	1.159	0.694	5.69*
Total due to regressi	on:	39.266	
Residual sum of squa	res:	15.048 on 123	3 D.F. (E.M.S. =
			0.1223)
Total sum of squares:		54.314	

The eight variables listed thus account for over 72% of the overall variation of Y about its mean value. The regression coefficients, together with their standard errors, are listed:

Variable	Coefficient	S.E.
X ₃₇	1.11582	0.1125
X_{48}		0.1927
X_{41}	0.00439	0.0078
X_{40}	0.11155	0.0188
X_{51}	0.09131	0.0230
X_{45}		0.3481
X_{46}	0.57197	0.1340
X_{47}	0.05932	0.0248
Constant term	—4.53257	

The corresponding equation, expressed in terms of the original units, may be written as follows:

The variables have the following meaning:

- I periodic volume increment, over an interval of seven years, in m³ per dominant tree
- MAP mean annual precipitation, for concurrent seven-year interval, in cm AGE in years, at end of the seven-year increment period
- S15 sum of mean rainfalls for each month, in cm, weighted by polynomial C15 (Table 2)
- ESD effective soil depth, in cm
- N total nitrogen in the top 7.5 cm of soil, expressed in % of soil o.d. wt
- P available P in the top 7.5 cm of soil, estimated by Olsen's technique, in ppm
- (N1) absolute sum of departures of night temperature from 5°C, over whole year, divided by 1000
- (N7) absolute sum of monthly departures, as above, weighted by polynomial (C7)
- (D3) absolute sum of monthly departures of day temperature from 20°C, weighted by polynomial (C3).

DISCUSSION

Interpretation of the equation expressing the influence of the most significant environmental variables upon periodic volume increment is necessarily subject to two major reservations: firstly, the fact that a great many other variables were not included in the tests, so that those found to be most significant are not necessarily the most important; and secondly, an appreciation that the forms of mathematical expression used for the variables actually tested are not necessarily the best that could be devised, given sufficient time and better experimental data.

With these reservations in mind, the model may be interpreted graphically by successively fixing all but one or two of the indepedent variables at their mean values, and calculating the value of Y over a range of values for the variables of immediate interest. The relationships depicted in Figs. 4 to 6 were calculated in this way. A mean age of 14.6 years was assumed unless stated otherwise.

Fig. 4 represents the influence of mean annual precipitation (X_{33}) upon periodic volume increment. On the deepest, freely-draining soils it is apparent that the increment increases almost linearly with rainfall; whereas on the shallowest soils (e.g., with an indurated horizon at 10 cm) the increase is minimal, and may even become negative when rainfall exceeds 150 cm per annum—presumably because of sustained water-logging and deficient aeration in the soil. It is also evident from this figure that there is a very rapid increase of productivity as effective soil depth increases from 10 cm to about 60 cm, but thereafter the influence of soil depth *per se* becomes progressively less,





FIG. 4—Interacting effects of mean annual precipitation and effective soil depth on periodic volume increment at age 15.

Fig. 5 (calculated from Equation (4)) illustrates the result of a seasonal redistribution of precipitation, compared with a hypothetical climate in which the rainfall is distributed uniformly throughout the year. For this condition, the response of periodic volume increment to increasing soil depth would be represented by the solid lines in the figure: following the lower curve for a MAP of 100 cm, and the upper curve for a MAP of 250 cm. However, if one postulates a 10% shift in the seasonal distribution of rainfallsay 10% more in the months of June, July, November, December, January, February (cf. Fig. 3), and a compensating reduction in the remaining spring and autumn monthsthe response curve follows the upper dot-dashed line. If the redistribution is reversed (i.e., 10% more rain in spring and autumn), the response follows the lower dashed curves. It is particularly notable that the model indicates relatively less effect from such seasonal differences on the deepest soils, whereas on soils less than 100 cm deep the seasonal distribution of rainfall becomes progressively more critical-presumably because of the decreasing volume of soil available for storage of water. Over all the 132 New Zealand sites, the mean seasonal distribution corresponded with a 49:51% ratio (cf. Fig. 5).



FIG. 5—Effects on periodic volume increment, of a ten percent difference in the seasonal rainfall distribution, compared with a climate having uniform distribution throughout the year.

In Fig. 6, the interacting effects on site productivity of both the total amount of nitrogen and the "available" P in the surface 7.5 cm of soil are represented as a response surface in a three-dimensional diagram. The curve of response to nitrogen corresponds well with expectations of field behaviour published by both Waring (1962) and Kessell and Stoate (1938): the latter authors stating that growth of radiata pine is generally unsatisfactory when topsoil N is less than 0.1%, but normal above 0.2%, while Waring (1962) indicated positive response to nitrogen applications below the former level. For the other parameter, P, Ballard (1971) similarly states that for mature stands of radiata pine the region of 3.1 to 8 ppm separates levels at which responses to superphosphate application do, or do not, occur. For seedling growth after transplanting, responses occur anywhere below 9 ppm. The relatively small range of response by the dependent variable to either soil nutrient parameter must be largely due to an unsatisfactory correspondence between overall nutrient supply available to the tree and the nutrient concentration in the topsoil only. It has frequently been stated that foliar nutrient concentrations should provide a more direct, and therefore better, measure of this availability to the plant. Although provision was made for such a contingency by standard analysis of foliar nutrient percentages on all sample trees in this survey, correlations with either the periodic annual increment (I) or with the residuals after adjustment for major site variables (see last two columns of Table 6) did not lend themselves to constructive interpretation.



FIG. 6—Interacting effects of topsoil total nitrogen and available phosphorus (Olsen technique) on periodic volume increment, at age 15.

	:	Soil Nutr	ients	and C	orresp	onding	Varia	ble	Residual
Foli V	ar Nutrient: ariables	N X20	P X14	K X23	Mg X25	Ca X26	NP X45	Y	(Y-Ŷ4)
N	X2 8	.25	•32	.21	.18	•04	•42	14	.17
Р	X29	10	.22	•21	.04	.08		29	•04
K	X30	.10	.03	•25	.01	10	.11	02	.07
Mg	X31	18	•02	21	03	23	17	37	23
Ca	X32	05	.03	0	03	14	04	14	05
Resi	dual (Y - $\hat{Y}4$) .05	•24	.22	.22	.20	.27	-	-

TABLE 6 - Correlations between foliar nutrient concentrations, Y, residuals from Equation (4) and relevant soil analyses

Vol. 4

Finally, while our earlier (unreported) attempts at relating productivity of radiata pine to polynomially-weighted temperatures had all proved fruitless, it is particularly notable that no less than three of the experimentally-based temperature variables proved to be significant in these tests. However, for interpreting these results, there would seem to be no *a priori* reason why the same optimal temperature, during either day or night, should hold throughout the growing season-as seems to have been assumed in all experimental work hitherto. This analysis indicates the contrary, in fact. Thus, departures from the optimum night temperature of 5°C appear to have a depressing effect on volume increment during the spring months, September through to December; whereas the opposite holds for January through to May. Since the departures from a 5°C night temperature were generally positive throughout the range tested by this survey, except in the south of South Island during the winter, one could interpret this as implying that night temperatures in New Zealand are generally too warm during the spring for maximum production by radiata pine, and not warm enough during the summer and autumn. As far as the daytime temperatures are concerned, the analysis again indicates that productivity would be increased if temperatures were lower during August through to November, and rather higher during April-May.

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APPENDIX 1

Variable	Parameter Concerned	Units	Range
X ₁	Altitude	m.a.m.s.l.	5 to 1150
X,	Slope	degrees	0 to 35
X ₃	Run-off index		-113 to 100
X4	Aspect index		-219 to 24
\mathbf{X}_{5}	Number of competing trees		1.29 to 10.0
X ₆	Competition index		0.38 to 4.64
X_7	Effective soil depth	cm	6 to 200
$\dot{X_8}$	% fine sand in LPH	%	0 to 33.4
X	% silt plus clay in LPH ⁺	%	14.6 to 91.5
\mathbf{X}_{10}	% fine sand in bulk sample	%	0 to 41
X11	% silt plus clay in bulk sample	%	9 to 96
X_{12}^{11}	total P in top 7.5 cm of soil	ppm*	54 to 1940
X13	Bray P in top 7.5 cm of soil	ppm*	2 to 166
X_{14}^{13}	Olsen P in top 7.5 cm of soil	ppm*	0.2 to 74.3
X_{15}^{11}	Citric acid-soluble P in top 7.5 cm of soil	ppm*	4 to 472

LIST OF INDEPENDENT VARIABLES

Variable	Parameter Concerned	Units	Range
X ₁₆	total P in bulk soil sample	ppm*	8 to 1990
X_{17}^{10}	Bray P in bulk soil sample	pp m *	1.2 to 98.3
X_{18}^{-1}	Olsen P in bulk soil sample	ppm*	0.5 to 55.1
X_{19}^{10}	Citric acid-soluble P in bulk soil sample	ppm*	2 to 400
X_{20}^{10}	total N in top 7.5 cm of soil	%*	0.01 to 1.10
X_{21}^{20}	pH in top 7.5 cm of soil		4.0 to 7.3
X_{22}^{-1}	total C in top 7.5 cm of soil	%*	0.1 to 14.8
X_{23}^{22}	K in top 7.5 cm of soil	m.eq./100 g	0.04 to 0.82
$\tilde{X_{24}^{5}}$	Na in top 7.5 cm of soil	m.eq./100 g	0 to 0.79
$\tilde{X_{25}^{1}}$	Mg in top 7.5 cm of soil	m.eq./100 g	0.2 to 4.6
$\tilde{\mathbf{X}_{26}}$	Ca in top 7.5 cm of soil	m.eq./100 g	0.2 to 7.3
X_{27}^{20}	C.E.C. in top 7.5 cm of soil	m.eq./100 g	1.5 to 46.2
X_{28}^{-1}	Foliar content—N	%*	0.8 to 2.3
X_{20}^{20}	Foliar content—P	%*	0.06 to 0.24
X.30	Foliar content—K	%*	0.4 to 1.1
X ₃₁	Foliar content Mg	%*	0.04 to 0.24
X3.9	Foliar content—Ca	%*	0.03 to 0.56
02	Age at end of 7-year increment period	yr	9 to 26
	Mean annual precipitation	cm	33 to 269

LIST OF INDEPENDENT VARIABLES (Contd.)

* expressed as ppm or % of soil o.d. weight or foliage weight, as pertinent. † least permeable horizon.

APPENDIX 2

(i) CALCULATION OF TEMPERATURE/DAYLENGTH PARAMETERS

The following procedure was used for each of the 38 representative stations for which appropriate data were available.

(1) **Determination of hourly temperature values** (T). These were calculated from the sevenyear means of monthly mean daily maximum (max.) and minimum (min.) temperatures, according to the equation for a two-phase cycle such as that for diurnal temperatures:

$$\mathbf{T}_{mi} = \mathbf{a}_{m} - \mathbf{A}_{m} \cos (\mathbf{K}\mathbf{i})$$

wherein, a_m is the mean temperature, derived from (max. + min.)/2 for the month m; A_m is the semi-amplitude, derived from (max.-min.)/2; $K = 2\pi/k = 0.2618$, where k (= 24) hourly values of T are required, at sequential intervals given by the integer i = 0 to 23.

The above simplified equation provides that T is at a minimum when i = 0

(2) Calculation of monthly sums of departure from optimum. Given the optimal temperatures for the hours of darkness (n) and daylight (d), together with the mean time of sunrise (\mathbf{r}_{m}) and sunset (\mathbf{s}_{m}) during the month (m) the monthly sums were calculated by the following algorithms:

if
$$i > r_m$$
 and $i < s_m$ then D_m : $= \sum \sqrt{(T_{mi}-d)^2}$

if
$$i < r_{m}$$
 or $i > s_{m}$ then N_{m} : $\sum \sqrt{(T_{m} - n)^{2}}$

This produced vectors, D and N, each comprising twelve monthly sums of absolute departures from optimum; i.e., disregarding whether departure was in a positive or negative direction.

(3) Differential weighting of monthly D or N values. The polynomial coefficients (C_k) used for weighting each vector of D or N, to produce a corresponding index (Dk) or (Nk), are tabulated below:

APPENDIX 2 (ii)													
	MONTHLY COEFFICIENTS OF POLYNOMIAL Ck												
k	Month :	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1		1	1	1	1	1	1	1	1	1	1	1	1
2		11	9	7	5	3	1	1	-3	-5	7	-9	-11
3		55	25	1	-17	-29	-35	-35	-29	-17	1	25	55
4		33	-3	21	- 25	-1 9	-7	7	19	25	21	3	-33
5		33	-27	-33	-1 3	12	28	28	12	-13	-33	-27	33
6		33	-57	-21	29	44	20	-20	-44	-29	21	57	-33
7		7	19	25	21	3	-33	33	-3	-21	-25	-19	-7
8		28	12	-13	-33	-27	33	33	-27	-33	-13	12	28
9		-20	-44	- 29	21	57	-33	33	- 57	-21	29	44	20
10		0	30	23	15	7	0	0	-7	-15	-23	-30	0
11		-17	1	25	55	55	25	1	-17	-29	-35	-35	-29
12		1	25	55	55	25	1	-17	-29	-35	-35	-29	-17
13		-5	-7	-9	-11	11	9	7	5	3	1	-1	-3
14		-7	-9	-11	11	9	7	5	3	1	-1	-3	-5
15		25	21	3	-33	33	-3	21	- 25	-19	-7	7	19
16		21	3	-33	33	-3	-21	-25	-19	-7	7	19	25
17		-13	-33	-27	33	33	-27	-33	-13	12	28	28	12
18		-33	-27	33	33	-27	-33	-13	12	28	28	12	-13
19		7	15	12	8	4	0	0	-4	-7	-12	-15	-10

APPENDIX 3 LIST OF COMPOSITE VARIABLES

Variable	Derivation	Interactions Concerned			
X ₃₃	S1)	Weighted Range: 33 to 269		
X_{34}^{00}	S18)	Precipitation " —137 to 719		
X_{35}^{01}	S15)	variables " —391 to 338		
$\mathbf{X_{36}}$	S4)	(See Table 2) '' -452 to 376		
X_{37}	$\ln (X_{33})$		ln (Mean annual precipitation/10)		
X_{38}^{0}	$(\mathbf{X}_8 + \mathbf{X}_9)$		% fine sand, silt and clay in LPH		
X_{39}^{30}	$1/X_7$	Reciprocal of effective soil depth (ESD)			
\mathbf{X}_{40}^{*}	X_{33}/X_{7}	Mean annual precipitation/ESD			
X_{41}^{10}	X_{35}/X_{7}	(Polynomial S15)/ESD			
$X_{42}^{}$	X_9/X_7	(% silt plus clay)/ESD			
$X_{43}^{}$	X_{38}^{-}/X_{7}^{-}		(% fine sand, silt and clay)/ESD		
X_{44}^{-3}	$exp (-1/X_7)$		exp ($-1/ESD$)		
$X_{45}^{}$	(N 1))	Weighted departures		
X_{46}^{10}	(N7)) from temperature optima			
X47	(D3))	(See Table 4)		
X_{48}^{-1}	10/Age		Reciprocal of age		
X_{49}^{10}	$\ln (\mathbf{X}_{20})$		ln (topsoil N)		
X_{50}^{10}	$\ln (\mathbf{X}_{18})$		ln (Olsen P)		
X_{51}^{50}	$\ln (X_{20} \times X_{18})$	$_{8}$) ln (topsoil N \times Olsen P)			