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Site and Climatic Factors and their Effect
on the Growth of *Eucalyptus regnans*.

B. D. Murphy and T.W. Payn

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Executive Summary

Combining site and BIOCLIM climate data to describe the growth of Eucalyptus regnans (F. Muell.) in the central North Island, it was found that success of the species has been limited by unsuitable climatic conditions. In particular, the distribution of rainfall delimits where the species can be successfully grown, as it is intolerant of summer maxima precipitation. Rainfall in the Bay of Plenty region has in recent years varied from evenly distributed to summer maxima on several occasions, and may be associated with various root pathogens. Temperatures throughout the year appear to be too mild to attain maximum growth, and the species might benefit from reduced temperatures differences between the hottest and coldest periods. Negative correlations of solar radiation indices with growth may indicate that the growth habit of E. regnans allows a thick vegetative understorey that provides substantial competition for soil-bound resources. Best sites combine moderate slope and topex, positive correlations of growth with increasing pH also exist.

ABSTRACT

Combining site and BIOCLIM climate data to describe the growth of Eucalyptus regnans (F. Muell.) in the central North Island, it was found that success of the species has been limited by unsuitable climatic conditions. In particular, the distribution of rainfall delimits where the species can be successfully grown, as it is intolerant of summer maxima precipitation. Rainfall in the Bay of Plenty region has in recent years varied from evenly distributed to summer maxima on several occasions, and may be associated with various root pathogens. Temperatures throughout the year appear to be too mild to attain maximum growth, and the species might benefit from reduced temperatures differences between the hottest and coldest periods. Negative correlations of solar radiation indices with growth may indicate that the growth habit of E. regnans allows a thick vegetative understorey that provides substantial competition for soil-bound resources. Best sites combine moderate slope and topex, positive correlations of growth with increasing pH also exist.

INTRODUCTION

Eucalyptus regnans (F. Muell.) is a species highly suitable for short-fibre pulp plantations due to its fibre qualities and rapid growth rates. Interest in the species by forestry interests led to current plantings of over 8,000 ha, 80% of which occur in the Bay of Plenty and Waikato region. In New Zealand the species is temperamental, requiring sites that give protection from frosts and high winds. The literature suggests it prefers cool, temperate conditions (mean annual temperature of 7.5-12° C) with an annual rainfall of 750-2000 mm (Hay *et al* 1984). Site conditions should include sloping ground, adequate moisture all year round, good soil drainage and shelter from salt winds (Payn & Oliver 1994). Despite attempts to plant the species in suitable areas, most sites have been characterised by inexplicable variability of growth and health, particularly at a microsite level (Bathgate *et al* 1993).

Multiple regression models were amongst the first tools used to attempt to explain this variation in growth experienced by *E. regnans* stands in the Bay of Plenty region. After collection and analysis of data from stands in the Kinleith Forest, Payn and Oliver (1994) concluded that environmental factors were the most significant causes for this inconsistency in growth patterns, with nutritional factors contributing to a lesser degree. Growth models were developed that used easily measured site parameters as predictors of the suitability of each site, to predict values for *E. regnans* stands at age 11 years for the variables of volume, basal area, mean top height and mean top diameter.

The subsequent validation found that all the models under-predicted when used in the Kinleith region, and all but the mean top diameter models over-predicted in the wider Bay of Plenty region (Murphy 1995). Statistical analysis showed that all four models were significantly accurate for their use as management tools in the Kinleith region, but at the larger scale only the mean top diameter model was accurate enough for use at that time.

It is strongly believed that the results of the model validation were extensively influenced by the distribution of stocking levels beyond those used in the model generation procedure; this would have a significant effect on the accuracy of the volume and basal area models, which are influenced by stocking levels. Model development was also hindered by the lack of available suitably aged sites. In order to improve the accuracy of the models, and attempt to explain more of the variation in stand growth, it was decided to repeat the modelling process using a greatly expanded dataset (112 plots) for the initial generation of the regression functions, and incorporate 27 climatic parameters generated from the BIOCLIM computer programme.

BIOCLIM has been previously used to map the distribution and climatic ranges for plant and animal species (Busby 1991; Mitchell 1991); it and similar climatic assessment programmes have also been used to create multiple regression models for eucalypt species (Austin *et al* 1990). It was hoped that the inclusion of climatic parameters would explain more of the variation based on solar radiation, precipitation and temperature variables for each site.

The use of BIOCLIM to determine the potential distribution range of *E. regnans* in New Zealand has already been achieved, using combined climatic profiles from New Zealand, Australia and South Africa (Ashby 1995). Although previously described as a stenovalent species (Cochrane 1969), this description may be inaccurate in view of knowledge of environmental conditions in which it has successfully grown as an exotic species around the world.

METHODS

Site Dataset Collection

Data for the 112 sites was previously gathered in the model building process (Payn & Oliver 1994) and subsequent model validation (Murphy 1995), from the information stored on the FRI Permanent Sample Plot (PSP) database. This included the original 46 plots from the model development, 53 plots from the subsequent model validation, plus additional plots that have since become available. A break-down of the plot locations and ownership is shown in Table 1.

Table 1. Location and ownership of the plots used in the model building/validation for *E. regnans*.

Forest	Number of plots	Owner
Kinleith	62	Carter Holt Harvey Forests Ltd
Kaingaroa	29	Forestry Corp. of New Zealand Ltd
Pouturu	15	Caxton Forests Ltd
Herepuru	3	Fletcher Challenge Forests Ltd
Pinnacles	3	Fletcher Challenge Forests Ltd
Total	112	

Field and Growth Data

Field data for each plot had been previously collected that described stocking, altitude, aspect, slope, topex and class of landform (crest, top-slope, mid-slope, toe-slope, terrace, basin) occurring in each 0.04 ha sample plot.

The 15 Pouturu sites ranged in age from 8 to 10 years, and required 'growing' to age 11 years using *E. regnans* growth functions (Maclean & Lawrence 1995). It must be noted that this function predicted mean top diameter scores for 11 years that were below the calculated site values before the plots were grown. The Pouturu plots' MTD scores did seem inflated, consistently in the 30-40 cm range despite their relatively young age.

The other available *E. regnans* growth model, that of Hayward (1991) was also tested, but the later model was chosen in preference. Although the Maclean and Lawrence model produced volume values significantly larger than those of the Hayward model, analysis of the results concluded that they were statistically better fitting (C. Maclean *pers comm*). Due to the clumping habits of good and poor growing *E. regnans* (Bathgate *et al* 1993), sample plots may not be truly indicative of the total stand performance. This may help explain, to an extent, the range of basal areas and volumes found in Table 3.

Soil Variables

Topsoil (A horizon) depth was measured for each plot, and sampled for bulk density using 4 random undisturbed ring cores per plot. These were then analysed for pH according to the methods of Nicholson (1984).

Growth Variables

Data from each 0.04 ha plot were collected and entered into the PSP data system. This included DBH at 1.4 m above ground level for all trees, and a sample of height measurements to enable calculation of Petterson regression coefficients for estimates of heights based on tree diameters. The variables of Basal Area (BA), Volume (VOL), Mean Top Height (MTH) and Mean Top Diameter (MTD) were calculated for each plot.

BIOCLIM Variables

Site data incorporating map coordinates, altitude, aspect and slope for each plot were sent to the Department of Environmental Sciences at the University of Auckland, where they were processed using the Bioclimatic Prediction System, which will be referred to as BIOCLIM in this report. BIOCLIM uses mathematical algorithms and data from climate stations, then generates Laplacian smoothing splines to model climate trend surfaces (Mitchell 1991). From these are derived the climatic parameters for each *target point* or *geocode*, which were defined by the geographical data (ie. site data for each plot).

BIOCLIM software generates two subsets of data, *monthly data* and *summary data*. The first subset consists of monthly values generated for each geocode for the parameters of solar radiation (flat slope and corrected slope), minimum temperature, maximum temperature and rainfall (giving 60 data values per geocode). The second subset is created by an analysis program that uses the monthly data to generate the summary data, adding (currently 27) data values to each of the 112 geocodes (Ashby 1995). There are 9 summary values for each of temperature, rainfall and solar radiation, and are the climatic variables used in this project. The condensed codes for each climatic variable used in this report are shown in Appendix 1.

Climatic Range of *E. regnans*

The climatic requirements of *E. regnans* have been determined by several authors and are given in Table 2.

Table 2. Climatic requirements for *E. regnans*.

Mean annual rainfall	Rainfall regime	Dry seasons	Mean maximum temp (hottest month)	Mean minimum temp (coldest month)	Mean annual temperature	Absolute minimum temperature
(mm)		(months)	(° C)	(° C)	(° C)	(° C)
700-2000 ^a	w, u/b	0-5	18-29	0-10	10-20	> -7
750-1650 ^b	w	-	23	0-2	-	-
1000-2000 ^c	w	-	17	5	-	-

Note: w = winter, u/b = uniform/bimodal

a = Booth and Pryor (1991) b = FAO (1976) c = Turnbull and Pryor (1984)

Ashby's (1995) climatic assessment of *E. regnans* range in New Zealand suggests that some of these parameters need to be modified, at least for New Zealand conditions, and that the potential growth range of the species may be larger than previously assumed. He suggests that the mean annual temperature of around 20° C underestimates the actual limit, and is in fact below the optimum temperature for the species, which could now be around 34-35° C. The mean annual rainfall range has also been underestimated, as sites in Ashby's study had annual mean rainfall levels of 565 - 2975 mm.

Statistical Methods

Site and growth variables for the dataset and the BIOCLIM variables were described statistically to determine their distribution and variation. Pearson correlation coefficients were determined for the dependant growth variables with each of the site and climatic variables, general linear models were used where class variables were tested. The SAS (SAS Institute 1985) statistical program was used for the correlation and GLM procedures.

RESULTS

Growth Data

Growth data for plots is summarised in Table 3.

Table 3. Summary of stocking and growth data from the 112 plots in the *E. regnans* study.

Statistic	Stocking (stems ha ⁻¹)	BA (m ² ha ⁻¹)	VOL (m ³ ha ⁻¹)	MTH (m)	MTD (cm)
Mean	570	23.9	218.0	25.4	31.5
Min	87	4.3	32.7	18.9	23.0
Max	2144	51.7	518.0	33.4	46.3
S. Dev	371.4	10.2	107.3	2.7	4.5
C.V. (%)	65.2	43.0	49.2	10.7	14.3

The range in stocking in the model building plots was exceptionally large, with a difference of over 2,000 stems ha⁻¹ between the lowest and highest stocked stands. This was also reflected in the large ranges between the minimum and maximum values for the growth variables of basal area (4.3 - 51.7 m² ha⁻¹) and volume (32.7 - 518 m³ ha⁻¹). Stocking displayed a high coefficient of variation, which is reflected in the CVs of between 40-50% for basal area and volume. The CV values for MTH and MTD are somewhat smaller at around 10-14%, suggesting they may be independent of stockings (although see Table 5).

Table 4 contains a summary of the environmental data for the 112 model building plots. Slope, topex and depth of A horizon all exhibit large coefficients of variation, with scores between 42 and 84%, with altitude showing a more moderate score of around 26%. As would be expected, pH had a low CV.

Table 4. Summary of environmental data from the 112 plots in the *E. regnans* study.

Statistic	Altitude (m)	Slope (%)	Topex (°)	Depth A Soil (cm)	pH
Mean	256.4	10.9	109.5	8.2	5.1
Min	110	1.5	7.0	0.9	4.3
Max	408	33.5	372.0	20.6	6.2
S. Dev	70.6	9.2	60.2	4.1	0.4
C.V. (%)	27.5	84.2	55.0	50.2	6.9

Correlations with Stocking

The growth variables were tested against the stocking levels to detect what effect the high variance in stocking has against the growth measures. These values are shown in Table 5.

Table 5. Correlations of Stocking with Growth Variables.

Growth Measure	Correlation
MTD	-0.3955
MTH	0.0106
VOL	0.1949
BA	0.2887

The strongest correlation was that of the mean top diameter, suggesting that MTD was not independent of stocking; as stocking increased the MTD decreased. The effect of stocking on MTH is not significant, with volume and basal area showing weak positive correlations. This suggests that the MTH variable is the most accurate parameter to test the site and climatic factors against, as it has not been affected by stocking levels in the history of the stands.

Summary of the BIOCLIM variables

A descriptive summary of the 27 derived BIOCLIM climatic parameters is given in Table 6. Important conclusions from this summary are that the annual mean temperature across all the plots is only 12.5° C; at the lower end of temperatures recommended as optimum for this parameter (see Table 2). The mean maximum temperature for the hottest month falls in the range of Booth and Pryor (1991) and is exactly the same as suggested by FAO (1976), while above that of Turnbull and Pryor (1984). The coldest month's mean temperature of 2° C fits the description set by those authors.

Seasonality scores are a measure of the variability of a parameter over the year. Large scores (>1) indicate large changes within a year, and scores less than that show a more uniform distribution. In the *E. regnans* dataset, the temperature seasonality range of 1.4 - 1.7 (summer maximum) is within the combined climatic profile of Ashby (1995) of 1 - 2.43. The total annual rainfall ranges from 1367 to 2062 mm, with a mean of 1547 mm and a seasonality of 0.4 (suggesting a very uniform distribution), fitting with the distribution suggested by Booth and Pryor (1991). Solar radiation exhibits a mean seasonality score of 1.1, suggesting a distribution with a slight

increase in levels over the summer period. The range of solar radiation seasonality from 0.9 to 1.4 suggests that some areas are receiving a uniform distribution throughout the year, while other areas receive a distinct summer peak.

Table 6. Summary of BIOCLIM climatic parameters for 112 *E. regnans* plots.

Parameter	Code ²	Unit measure	Mean	Minimum	Maximum
annual mean temperature	TAM	°C	12.5	12	13.3
hottest month mean max. temperature	TMAXM	°C	23.7	22.5	24.7
coldest month mean min. temperature	TMINM	°C	2	0.7	4.1
annual temperature range	TRAN	°C	21.7	18.5	23.6
temperature seasonality ¹	TSEAS		1.7	1.4	1.9
wettest quarter mean temperature	TWETQ	°C	7.8	7.3	8.6
driest quarter mean temperature	TDRIQ	°C	15.7	11.9	17.2
coldest quarter temperature	TCOLQ	°C	7.7	7.1	8.6
warmest quarter temperature	TWARQ	°C	17.2	16.5	17.9
annual total rainfall	RAT	mm	1546.5	1367	2062
wettest month mean rainfall	RMAXM	mm	153.1	123.4	201.7
driest month mean rainfall	RMINM	mm	98.3	83.0	124.5
annual rainfall range	RRAN	mm	54.8	30.5	78
seasonality rainfall ¹	RSEAS		0.4	0.3	0.6
wettest quarter mean rainfall	RWETQ	mm	441.4	346.7	594.8
driest quarter mean rainfall	RDRIQ	mm	334.2	280	424.4
coldest quarter mean rainfall	RCOLQ	mm	440.2	341	594.8
warmest quarter mean rainfall	RWARQ	mm	361.1	294.6	454.9
mean annual daily solar radiation	SRAM	MJ m ² day ⁻¹	12.8	9.5	14.3
sunniest month max daily solar radiation	SRMAXM	MJ m ² day ⁻¹	20.2	15.2	22.5
darkest month min daily solar radiation	SRMINM	MJ m ² day ⁻¹	5.8	3.7	7.1
annual daily solar radiation range	SRRAN	MJ m ² day ⁻¹	14.4	10.7	16.6
seasonality solar radiation ¹	SRSEAS		1.1	0.9	1.4
wettest quarter solar radiation	SRWETQ	MJ m ² day ⁻¹	6.8	4.5	8.4
driest quarter solar radiation	SRDRIQ	MJ m ² day ⁻¹	16.5	12.5	20.1
coldest quarter solar radiation	SRCOLQ	MJ m ² day ⁻¹	6.9	4.5	8.4
warmest quarter solar radiation	SRWARQ	MJ m ² day ⁻¹	19.9	14.1	19.3

¹ seasonality = range/annual mean.

² see appendix 1

Correlation Analysis

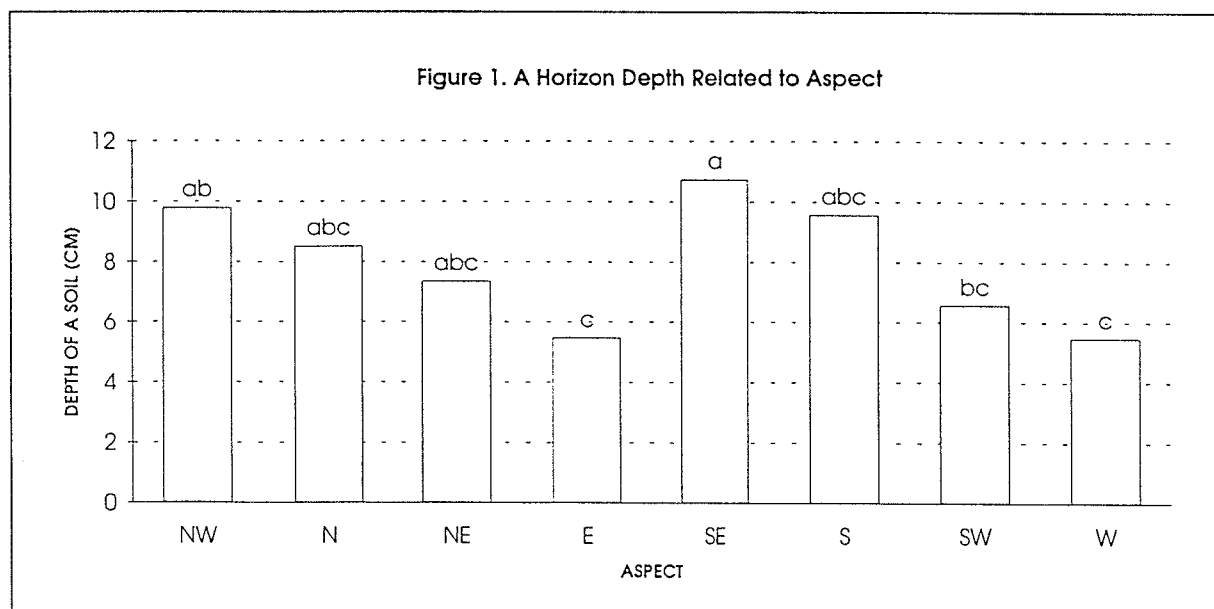
The Pearson correlation analysis of site variables on the dependent growth variables were positively correlated with the exception of A soil horizon depth, which was a negative relationship (Table 7).

Table 7. Significant correlations between site and growth variables.

Variable	BA	VOL	MTD	MTH
Slope	0.2365 0.0120	0.2478 0.0084	0.2131 0.0024	0.2500 0.0078
Topex	0.2755 0.0033	0.2761 0.0032	0.2293 0.0150	0.2293 0.0150
A soil depth	-0.2970 0.0015	-0.2931 0.0017		-0.2452 0.0092
pH	0.2182 0.0208	0.2518 0.0074	0.5390 0.0001	0.3071 0.0010

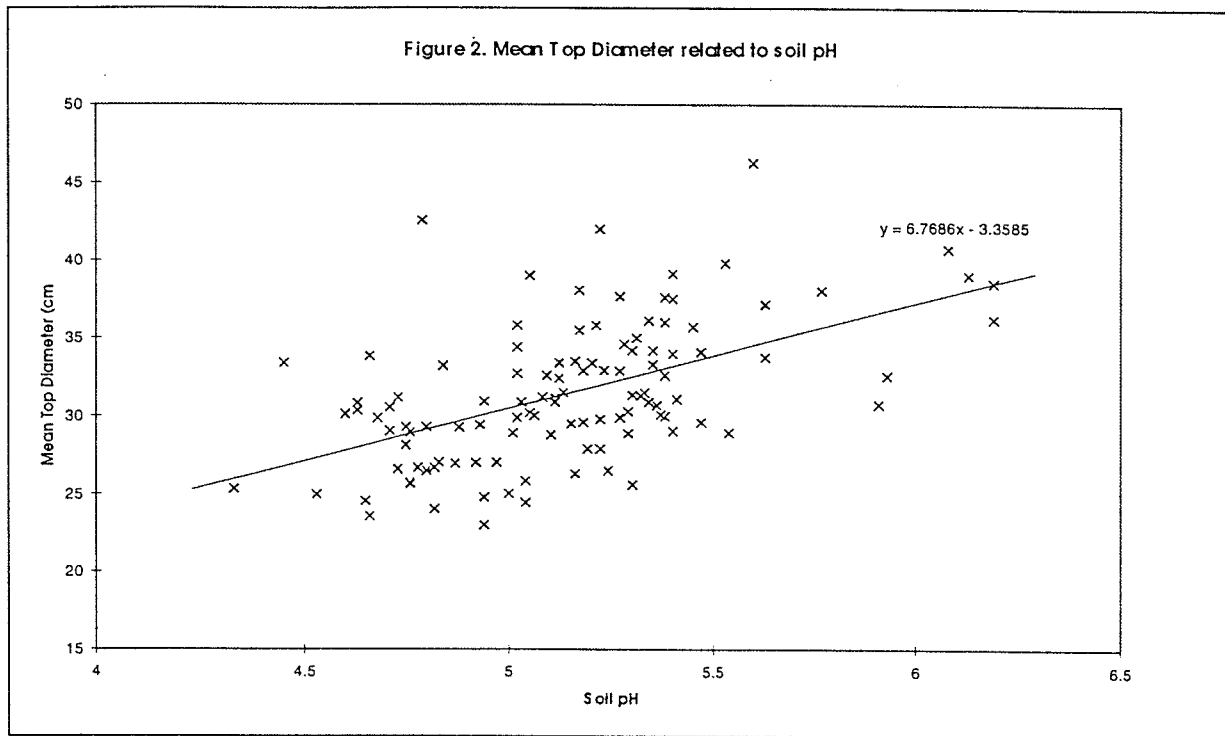
The variable of slope has a positive correlation with all the growth measures, and this could be the benefit of soil drainage or frost protection that steeper slopes can provide. In the study of topex on growth variables in the Kinleith region, Payn and Oliver (1994) found topex negatively correlated with growth; this correlation has been reversed by expanding the geographical range of the dataset. It is now suggested that as topex scores increase, exhibiting less exposure, site productivity is increased. Less exposure leading to better growth suggests that protection from wind or some other agent benefits the trees on the site.

Increase in depth of the A soil horizon has previously been linked to poorer growth of *E. regnans*, and investigations into factors contributing to this are under way (Murphy *et al* 1996). The A horizon depth was influenced by aspect, with a distinct pattern appearing as shown in Figure 1.



Note: Bars with common letters are not significantly different at $p < 0.05$

A strong correlation exists between soil pH and MTD (Figure 2). Except for this value (0.5390), the other site correlations were weak.



That altitude failed to show any effect on growth at all was surprising, considering the negative correlations found by Payn and Oliver (1994) in less than a 100 m altitude range between sites studied. In this project the range in altitude was nearly 300 m.

Aspect and landform were tested with Analysis of variance to determine their effect on growth, but no significant relationships were found.

All of these variables are also likely to be interrelated with slope. As slope increases it would affect topex due to less exposure. Depletion of the A soil horizon would be expected on steep slopes due to gravity and/or erosion (ie colluvial processes) with the material amassing in gullies or on lower slopes. Soil pH may be affected by this accumulation of organic and decomposing matter, as this material has been shown to be a source of soil acidity (Thomas & Hargrove 1984).

Correlations between the temperature and growth variables were generally significant, with the variables of temperature maximum, temperature range, temperature seasonality and temperature of the warmest quarter showing negative correlations with growth. These correlations are summarised in Table 8.

Table 8. Significant correlations of temperature variables with growth variables.

Variable	BA	VOL	MTD	MTH
TAM	0.2458	0.2632		0.2231
	0.0090	0.0050		0.0180
TMAXM	-0.2603	-0.2777	-0.4567	-0.3321
	0.0056	0.0030	0.0001	0.0003
TMINM	0.4764	0.5048	0.5410	0.5510
	0.0001	0.0001	0.0001	0.0001
TRAN	-0.3962	-0.4208	-0.5280	-0.4733
	0.0001	0.0001	0.0001	0.0001
TSEAS	-0.4953	-0.5264	-0.5458	-0.5575
	0.0001	0.0001	0.0001	0.0001
TWETQ	0.2095	0.2326		0.2275
	0.0266	0.0136		0.0159
TDRIQ	0.5439	0.5592	0.3828	0.5259
	0.0001	0.0001	0.0001	0.0001
TCOLQ	0.4569	0.4848	0.3575	0.4697
	0.0001	0.0001	0.0001	0.0001
TWARQ			-0.2317	
			0.0140	

That the temperature of the hottest month shows a negative correlation with growth suggests that for biological reasons, high temperatures may be detrimental or inhibiting to growth. Other important points to note are that both temperature range and temperature seasonality are strongly negatively correlated with growth. This suggests that an increasing range of temperatures between the hottest and coldest months of the year, and increasing seasonality (in this case the same thing) are bad for the growth of the species, ergo it prefers similar temperatures throughout the year without distinct seasonal peaks.

Temperature of the coldest month has a strong positive correlation with growth; the warmer the coldest month the better, whereas the cooler the hottest month the better (slight negative correlation). These two parameters support the negative relationships of the temperature range and seasonality, and from this it could be concluded that *E. regnans*, in the geographical regions studied in this project, fares better in a temperature regime that is moderately warm throughout the year with little seasonal difference.

Temperatures of the driest (generally summer) and coldest quarters also show strong positive relationships with growth, supporting the idea that *E. regnans* enjoys warmer temperatures over summer when it relies on soil moisture for water, and that it also prefers moderately warm temperatures in the winter period.

The correlations of temperature of the wettest quarter (positive) and temperature annual range (negative) contrast with the results found by Ashby (1995). His hypothesis that *E. regnans* growth was improved as a result of acclimation may be challenged; possibly *E. regnans* growth is inhibited due to inability to acclimatise when temperature seasonality increases.

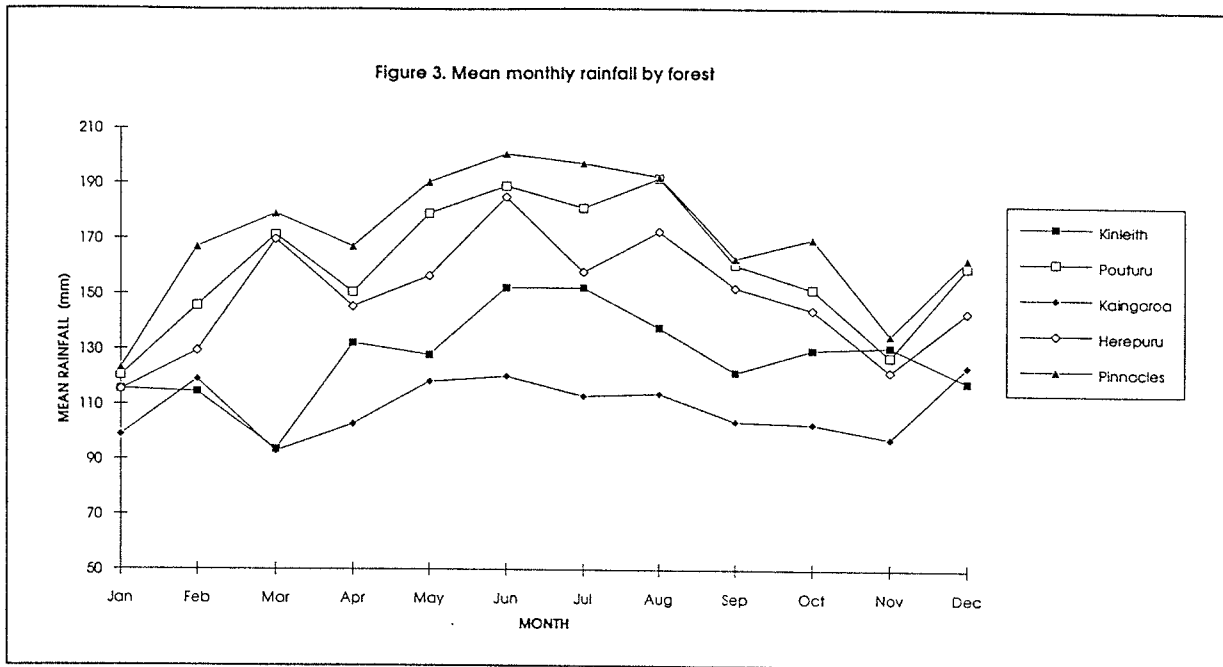
Rainfall parameters were all significant and positively correlated with the growth variables (Table 9).

Table 9. Significant correlations of rainfall parameters with the growth variables.

Variable	BA	VOL	MTD	MTH
RAT	0.5454	0.5691	0.3256	0.5200
	0.0001	0.0001	0.0005	0.0001
RMAXM	0.5690	0.5924	0.3669	0.5462
	0.0001	0.0001	0.0001	0.0001
RMINM	0.3850	0.4102	0.2130	0.3632
	0.0001	0.0001	0.0241	0.0001
RRAN	0.5934	0.6110	0.4083	0.5743
	0.0001	0.0001	0.0001	0.0001
RSEAS	0.5212	0.5292	0.3868	0.5064
	0.0001	0.0001	0.0001	0.0001
RWETQ	0.5846	0.6088	0.3585	0.5619
	0.0001	0.0001	0.0001	0.0001
RDRIQ	0.4677	0.4884	0.2251	0.4272
	0.0001	0.0001	0.0170	0.0001
RCOLQ	0.5883	0.6124	0.3629	0.5663
	0.0001	0.0001	0.0001	0.0001
RWARQ	0.3921	0.4109		0.3581
	0.0001	0.0001		0.0001

Overall increasing rainfall is good for growth, and these parameters show stronger correlations than the others examined. Correlations for wettest quarter and coldest quarter were stronger than those of the driest and warmest quarters, suggesting that rainfall in the winter period is more beneficial to growth than if it occurs in the warmer summer period.

Strong correlations with the range and seasonality of rainfall both suggest that the greater the bimodal distribution in rainfall over the year, the more suitable it is for *E. regnans*. This is assuming that the rainfall is distributed with a winter maximum. The correlation with total rainfall over the year also suggests that increasing available moisture benefits the species, and as Figure 3 shows, considerable differences also exist as to total amounts of rainfall that different forests receive. RAT was also implicated strongly with soil pH (correlation of 0.5415).



Ashby (1995) found that annual mean rainfall (annual total rainfall in this document) was negatively correlated with site index, in contrast to the positive response noted above.

Solar radiation parameters displayed negative correlations, and three of the parameters, solar radiation seasonality, solar radiation wettest quarter and solar radiation driest quarter were not significantly correlated with any of the growth variables (Table 10). That increases in solar radiation, or irradiance, is detrimental to growth seems highly unusual. This phenomenon may require further investigation.

Table 10. Significant correlations of solar radiation and growth variables.

Variable	BA	VOL	MTD	MTH
SRAM	-0.3251	-0.3493	-0.2810	-0.3591
	<i>0.0005</i>	<i>0.0002</i>	<i>0.0027</i>	<i>0.0001</i>
SRMAXM	-0.3629	-0.3938	-0.2531	-0.3574
	<i>0.0001</i>	<i>0.0001</i>	<i>0.0071</i>	<i>0.0001</i>
SRMINM				-0.2136
				<i>0.0237</i>
SRRAN	-0.3330			-0.2907
	<i>0.0003</i>			<i>0.0019</i>
SRCOLQ				-0.2248
				<i>0.0172</i>
SRWARQ	-0.3646	-0.3927	-0.2610	-0.3609
	<i>0.0001</i>	<i>0.0001</i>	<i>0.0054</i>	<i>0.0001</i>

Increasing light intensity itself has no negative effect on the leaves, as once they have attained photosynthetic saturation point, they are unable to fix carbon any faster, and excess light is reflected away (Boardman 1977).

Solar radiation should not be a limiting factor in the region under study; this supports the theory that the apparent negative effects of solar radiation are not the result of direct damage to the trees, but are caused by an indirect influence.

The strongest correlations are those of solar radiation maximum and solar radiation of the warmest quarter, suggesting that the apparent negative effects of solar radiation are more evident during the active growing season. Solar radiation annual mean also shows consistent negative correlations, so as the total level of solar radiation received in a year increases, so does the detrimental effect on the plants, affecting the growth of the trees. Solar radiation minimum and solar radiation of the coldest quarter correlate weakly with one growth variable, that of mean top height, whereas the solar radiation range correlates with basal area and mean top height.

Ashby (1995) noted that in his analysis of solar radiation effects on *E. regnans* plots throughout New Zealand, solar radiation of the darkest month (SRMINM) was the most restricting parameter; in this case it is only significant for the measure of MTH and is negatively correlated. For the North Island model, solar radiation of the wettest quarter was the most significant radiation factor, but in this analysis it has not appeared as a significant variable.

DISCUSSION

The extreme variation in stocking levels was the result of using PSP plots that were established to permit growth modelling for *E. regnans*, and as such were installed in sites and trials that were selected or treated to give a wide stocking range (H. McKenzie *pers comm*). For species such as *E. nitens*, where homogenous stocking regimes have been accepted by the majority of forestry interests (1100-1200 spha, Author *pers obs*), describing the effects of climate or site on growth would be less subject to 'noise' associated with stocking. Because of the distribution of the sites used in this project, with some PSP plots located within the same compartment or stand in relatively close proximity to each other, often the climatic values ascribed to each site were similar. This resulted in graphs of climatic data related to growth variables exhibiting clumping, an example of which is shown in Appendix 2.

It must be assumed that many of these climatic parameters interact strongly with each other with regards to growth. Margules *et al* (1987) found that species diversity of eucalypts was related to the environmental variables of mean annual rainfall, mean annual temperature and a measure of solar radiation. Effects of rainfall and temperature were significant and large, whereas the effect of solar radiation as a descriptive tool was significant but small. As was suggested above, the influence of rainfall and temperatures were not independent but were interacting in a complex manner. If that was found with only simple measures of climatic data, then it should be expected that some of the correlations of climate with growth in this project will be difficult to interpret and explain.

Growth responses to a climatic parameter are unlikely to exhibit a straight linear correlation; Austin *et al* (1990) described the responses of several eucalypt species to climatic gradients, and found that responses were

asymmetric and complex. This suggests that the use of correlation analysis, where large values of one set are tested to see if they are associated with the large or small values of another set, may not be the ideal method to describe the relationships between climate and growth. Correlations do not explain how an effect is occurring or its biological significance.

Some of the variability in growth experienced in New Zealand conditions may be attributable to the genetic stock used in initial plantings. These plantings were of seeds from 'phenotypically superior' provenances but of unimproved seed quality, so variability of growth rates and tolerance of climatic conditions should have been expected. Recent breeding programmes have been undertaken to improve this (H. McKenzie *pers comm*). In naturally regenerating *E. regnans* plantations, the initial stocking levels are extremely high, and self thinning becomes evident early on in growth (Polglase & Attiwill 1992). This allows the rapidly growing, successful trees to dominate and suppress poorer trees, leading to the selection of superior genotypes for the conditions. Another variable that was not considered in this project is that of provenance, and may be of importance in particular for frost resistance (Wilcox 1979) and growth rates (Pederick 1976), with Pederick also finding a strong provenance * location interaction in plantings.

Examination of site characteristics showed that soil pH was moderately correlated with BA, VOL and MTH, but showed a strong correlation with MTD. Therefore soils that are approaching a neutral pH may provide the best substrate. It was unfortunate that no scores approaching pH 7 were recorded for the sites under study, as it would have been interesting to see if the beneficial effects on growth of increasing pH continued up to or past this level. This data lends support to any pre or post-planting program that would tend to increase the alkalinity of soils under *E. regnans* sites. Applications of lime or similar products may benefit sites with acidic soils as it has been shown to improve the carbon exchange complex (CEC) and hence the availability of nutrients (Thomas & Hargrove 1984) as well as increasing microbial activity and nutrient cycling, which can suffer as a result of soil acidity (Robson & Abbott 1989).

Because annual total rainfall was also strongly correlated with pH, it may be that total rainfall is mostly responsible for the better growth, and the apparent correlation of pH with better growth is an artefact of the rainfall effect on both growth and the soil pH.

Increasing slope and topex scores were also corresponded with improved growth, suggesting that sites benefit by protection from harsh winds and frosts, plus improved soil drainage. Obviously at extremes of slope and topex measures there would be some decline in site suitability, as the steepness of slope affects soil stability and moisture content (due to drainage), and increasing topex reduces the solar radiation available to the trees.

The relationship of A soil depth and reduction in growth may be a complex problem. One Hypothesis being tested in a parallel study is that the horizon thickness builds up as organic matter accumulates on certain aspects, because temperatures and moisture contents are unsuitable for microbial decomposition. These temperatures may

likewise be unsuitable for *E. regnans* root mass expansion and mycorrhizal development when the Spring growth flush is about to begin (J. Bathgate *pers comm*). The pattern of A horizon depth related to aspect in Figure 1 lends support to this theory, as there are obvious differences between the warmer and colder aspects.

Evaluation of the climatic parameters has posed considerable problems. Interpretation of how these climatic effects are influencing growth leads to hypotheses that are generally not testable. The BIOCLIM procedure gives a historical average climate record, therefore masks the effects of short term climate changes (ie El Niño cf. La Niña)

The temperature variables provided a mixture of positive and negative correlations with growth. The sites studied have a distinct seasonal distribution of temperature (seasonality scores of 1.4--1.7, summer maxima) that is negatively correlated with growth. This raises questions about the effects that a large temperature range or distribution has on growth.

Young *E. regnans* has shown a frost tolerance of about -3.5° C in summer, which can increase to about -9° C in winter (Menzies *et al* 1981). Hardening for frost resistance generally requires exposure to moderately low temperatures ie. ~5° C, and the process is metabolic, requiring an energy source. Factors that promote rapid growth, such as high nitrogen, irrigation, etc, can inhibit the process of acclimation to an extent, so that slower growing plants are more resistant to environmental extremes (Salisbury & Ross 1992). With a large seasonal temperature range, the average monthly decline in temperatures from summer to winter would be more rapid than would occur in a site with a less seasonable distribution. Possibly this could lead to trees still displaying rapid growth as the frost season approaches, and therefore are more susceptible, or that the trees have not experienced temperatures suitable for hardening for a sufficient period to acclimatise properly.

Overall annual mean temperatures may play an important part in the growth of *E. regnans*. Cremer (1975) found that the dormancy of shoot development of *E. regnans* during winter is a quiescence imposed by low temperatures, and that the pattern of growth development of the vegetative shoots of the species is related to the air temperatures that exist throughout the year. Therefore if winter mean temperatures are not below a certain threshold, growth can still continue, albeit at a reduced rate *cf.* warmer temperatures. This might explain the strong positive correlation with temperatures of the coldest quarter, because as temperatures in this period show an increase, all other growth conditions being acceptable, growth rates will increase. Laboratory work by Cremer showed that growth was slight or nil below 10° C, and increased as temperatures rose from 10 - 25° C. The fastest growth rates occurred with day/night temperatures of 24/19 - 30/25° C. Growth of *E. regnans* is therefore indeterminate and essentially continuous if climatic conditions are suitable.

Examination of the site temperatures in this study showed that in the coldest quarter a range of 7.1 - 8.6° C existed (Table 8) which suggests that in these three months, under the conditions described by Cremer (1975) growth would cease. Several authors have suggested an optimum annual mean of 19° C; when compared to the

12.5° C found here, it is simple to conclude that overall growth will be far from optimum. Even the warmest quarter only reaches a 17.2° C average, below the 24° C suggested as nearing the optimum for that period. However the temperature of the hottest month averages 23.7° C which indicates trees may attain good growth rates for at least a small period of the year. From this evidence it may be suggested that *E. regnans* has failed to fulfil its potential in New Zealand simply because the average annual air temperatures have not been high enough to allow the growth potential to be expressed.

Ashby (1995) concludes that this should lead to considerations of planting *E. regnans* further north. There is a perception that *E. regnans* does not grow well in the Northland region, possibly based on the very limited extent of plantings in the region. However some sites of *E. regnans* in areas close to Whangarei have displayed acceptable growth rates and don't seem to be adversely affected by site or climatic conditions (H. McKenzie & E. Hay *pers comm*).

The negative correlation of growth with temperature of the hottest month suggests that the temperatures experienced may be too hot for growth. This may be misleading, as the species should be capable of excellent growth at higher temperatures *providing* that soil moisture is sufficient to allow for its capture and use in evapotranspiration. Similarly, if available moisture is limiting, nutrient uptake is reduced.

The weak negative correlations of temperature maximum and temperature of the warmest quarter with MTD, could possibly be related to the incidence of leaf spot pathogens such as *Mycosphaerella* spp. that can occur in warm moist conditions, and are detrimental to the growth of *E. regnans*. If this was the case however, we might have expected to see some similar correlations with rainfall of the warmest quarter, etc.

The inability of species from the sub-genus *Monocalyptus* to adapt to rainfall conditions that differ from the naturally occurring distribution has already been well documented, being intolerant of sites that experience summer maxima precipitation (Turnbull & Pryor 1984). Soils must be well drained to avoid waterlogging yet still able to store considerable moisture in winter which is then made available for the summer months. Although the species can survive periods of dry conditions, recharging of water tables over summer is probably beneficial (J. Bathgate *pers comm*; Nicolls *et al* 1982). This is supported by higher correlations for the cold/winter period rainfall parameters than those of the hotter/summer conditions. Along with the air temperature problems mentioned above, rainfall (or moisture availability) may provide the greatest limiting factor to the success of *E. regnans* in New Zealand.

Rawcliff (1987) examined the seasonality of rainfall in the Kinleith forest region with regards to *E. regnans*' growth, assessing median rainfalls from November to April (summer) and May to October (winter). It was suggested that a seasonal rainfall ratio (greater:lesser) of 1.3:1 is the level where a non-uniform distribution has occurred, ie. a distinct seasonal peak appears. Overall, from metrological data recorded from 1971 to 1986, Kinleith Forest was considered to have a uniform rainfall distribution. Study of individual years showed that from

1971 to 1979 consistent winter maxima occurred, but that between 1979 and 1985, summer maximum rainfalls occurred on four occasions. This suggests conditions were sporadically unsuitable for *E. regnans* growth, and that a shift of climatic rainfall patterns may be occurring in the Kinleith region.

Although this does not necessarily imply the same pattern for all the sites in this study, Table 6 showed that in many areas the rainfall seasonality is uniformly distributed (0.3 to 0.6), leading to a greater chance that a fluctuation towards a slight summer maximum may occur in any given year. Using the climatic data supplied for this project, summer and winter rainfall ratios were created for each site. The results (not shown) suggested that the ratios were all below the 1.3:1 ratio that delimits a unimodal distribution, and so were all relatively uniform in rainfall distribution (range of 1.05:1 to 1.22:1). All sites had winter maxima rainfall, but not by large amounts in some cases.

Rawcliff summarised that "the lack of adaptability may have been disguised in the 1970's when the Kinleith area consistently had winter rainfall peaks. Now in the 1980's when the rainfall pattern is truly uniform, with fluctuating seasonal peaks, the poor adaptability of the species may be becoming evident."

One disease that may be associated with this summer maxima rainfall is that of the Barron Road Syndrome (BRS), an unidentified pathogenic agent that affects the trees' growth by causing leaf fall and reduction of the crown area. Evidently some sites have recently recovered from this disease and are returning to a healthy status (J. Bathgate *pers comm*). The possibility exists that the disease is triggered or spread to the roots by summer rainfall maximum conditions. A subsequent return to winter maxima or uniform distributions could alleviate or remove the problem, as soil conditions become unsuitable to the pathogen.

Research on effluent treatment on eucalypts in Australia showed that 30 out of 31 eucalypt species that suffered from root associated pathogen problems were from the sub-genus *Monocalyptus* (CSIRO 1994). It was suggested that species in this sub-genus are more susceptible to root pathogens than those in other sub-genera, and the constantly moist soils create very suitable conditions for the growth and spread of these pathogens. Water deficit eventually kills the trees, despite available moisture. In this trial *E. regnans* actually performed with distinction, but the noted susceptibility of the species to moist sites where pathogens are likely to occur, ie *Phytophthora* spp. could suggest why gullies and similar sites are unsuitable sites for growth of the species. The suitability of *E. regnans* to sites that are dry in summer compared to other species is evidenced by its success in the species trials for seasonally dry hill country in the Wairarapa district (Bulloch 1991). *Eucalyptus regnans* rated overall as the best of 60 species trialed at the site, although heights and DBHs were approximately half those of trees from site in Rotorua.

The most difficult interpretations of the climate data involve those of the solar radiation correlations. As the direct effects of solar radiation on *E. regnans* cannot be considered detrimental to the physiology of the trees, this suggests that an indirect effect is occurring, and may be more related to the ecology of the species than the

physiology. It would have been expected that increasing levels of solar radiation would be correlated positively with growth, not as it appears, negatively.

Ashton (1958) suggested that 30-40% of sunlight is not intercepted by the vertically hanging, pendulous leaves of the canopy of *E. regnans* during the growing season, allowing for the development of a rank and complex understorey. As well as light penetrating the *E. regnans* canopy, its crown-shy habit means that the canopies of adjacent trees avoid contact each other, as this leads to abrasion of the naked buds (Ashton 1975), allowing more light through the substantial gaps amongst canopies of trees.

As the amount of solar radiation made available to the understorey increases, this increases the competition for moisture and nutrients by the understorey crop, and may go some way to explaining this negative correlation. If solar radiation reaches the forest floor in sufficient quantity to encourage ample establishment of biomass, the plant coverage will prevent light reaching the litter and soil layers, compounding the effects of competition for resources by not allowing the soils to heat up, preventing attainment of the optimum soil temperature for the growth of *E. regnans*. There may in fact be a positive correlation of solar radiation indices and understorey growth rates.

This begs the question, if *E. regnans*' growth habit encourages the growth of the understorey, what is the advantage to the species, an advantage that outweighs the negative effects of competition for resources? *Eucalyptus regnans* is notable for its sensitivity to fire, as it does not possess lignotubers and the thin bark allows for its destruction by even moderate fires (Turnbull & Pryor 1984), yet seems to encourage the development of a substantial fireload under the canopy by the shedding of fibrous bark and development of dense understorey populations. This increases the risk of episodic fires, especially when the wet sclerophyll forests periodically dry out.

The rapid growth habit of *E. regnans* and fast attainment of height rather than girth (Ashton (1975) states *E. regnans* has a lower ratio of trunk diameter to tree height than other trees of similar stature) suggests that by the time fire is likely to occur, the canopies of the trees are above the reach of burning. The trees are killed by ensuing fires, but the seeds escape damage by virtue of their height off the ground. Seed capsules do not actually confer fire protection to the seeds, so seed survival is limited to seconds in the heats experienced, and little or no seed storage in the soil occurs (Judd 1994). *Eucalyptus regnans* stands are thus regenerated only in the case of fires of intensity sufficient to wipe out the stand, and these fires result in the *ash-bed* effect, notable for the rapid increase in available nutrients such as N and P. Seed subsequently fall to the ground *en masse*, rapid germination and growth of the seedlings follows. This results in even-aged pure stands of *E. regnans* (Chambers & Attiwill 1994). Therefore, encouragement of a substantial fireload under *E. regnans* stands ensures the eventual regeneration of the species.

Ecological studies of *E. regnans* also suggest that maintenance of an understorey dominated by species such as the nitrogen-fixers *Acacia melanoxylon* and *A. dealbata* is an important part of the nutrient cycling system. After fires *Acacia* spp. rapidly germinate in substantial numbers, up to 750 000 ha⁻¹. Swift uptake of nutrients in biomass thus conserves them until a time when the *E. regnans* canopy is sufficiently developed to reduce the *Acacia* spp. population down to one third of its original density. This releases some nutrients back into the system, as well as N that is fixed by the *Acacia* species (Adams & Attiwill 1984). Therefore by encouraging the *Acacia* spp. to develop underneath *E. regnans* by allowing substantial light through the canopy, the nutritional status of the stands may be considerably improved, particularly on impoverished soils where N and P are deficient.

This may prove to be an ecological advantage in its natural environment, where the subsequent fire and *Acacia* spp crop provide beneficial conditions to the dispersal and success of the species, but is a practical hindrance to its success as a plantation crop in New Zealand, where the understorey provides competition for resources rather than improving soil nutrition by N fixation. However the growth habit of *E. regnans* does lend itself to agroforestry regimes with sawlogs as final products. James (1986) concluded that *E. regnans* intercepts less light than radiata pine at the same stocking, so grass growth should be better under that species.

The strongest correlations are those of solar radiation maximum and solar radiation of the warmest quarter. Both measures would be of increasing benefit to the growth of the understorey as they increased in intensity, as they describe the solar radiation made available in the period of maximal understorey growth. The solar radiation annual mean also shows consistent negative correlations with growth, so as the total level of solar radiation received in a year increases, so does the amount that the competing plants receive.

There are no correlations for solar radiation levels in the wettest quarters, and only one weak negative correlation for the coldest quarter, suggesting that solar radiation is less damaging to growth in periods where moisture is more abundant.

If research was to continue into understanding the nature of *E. regnans*' growth responses to environmental conditions, monitoring of the effects of soil moisture might provide valuable information. Combined with measurements of soil moisture deficit and soil temperatures, monitoring of the growth of *E. regnans* at stages of different field capacities might elucidate whether or not high rainfall levels in summer are detrimental to growth. Possibly BIOCLIM generated maps of the potential growing range of *E. regnans* should be modified to exclude areas where rainfall is summer maxima or uniformly distributed, and where temperature limitations may be apparent.

Ashby (1995) argued that *E. regnans* should no longer be described as a stenovalent species on the basis of the climatic range of *E. regnans* as an exotic plantation species in countries such as South Africa, and successful plantings outside its normal distribution range in Australian sites. This study suggests *E. regnans* may be at the

border of its climatic tolerance in the BOP region, and a stenovalent model may still be possible. Although the species will still grow under less than optimum conditions, whether or not this growth equates to satisfactory rates for plantation management purposes remains open to discussion.

CONCLUSIONS

The analysis of combined site and climatic data suggests that the growth of *Eucalyptus regnans* is influenced strongly by certain variables of temperature and rainfall, which has prevented the species achieving its full potential. Siting should concentrate on locating regions where a large range between the wettest and driest months occurs, with the seasonal maxima occurring in winter. Temperature range and seasonality scores suggest best locations have mild winters and are warmer in the summer period. Air temperatures above 10° C are required before vegetative shoots can grow, so despite indeterminate growth potential, growth is stalled through winter. Best sites receive sufficient rainfall in winter to act as storage for the summer months, combined with soils that are free draining yet contain excellent water storage for summer supply. Sites should contain moderate slopes with soil pH approaching neutral. Ecological adaptations of the species appear to hamper its success as a plantation species due to its facilitating a dense understorey, but its suitability for agroforestry regimes may allow for future plantings with improved genetic stock.

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APPENDIX

Appendix 1. Codes for Bioclimatic Parameters.

Code		Bioclimatic Parameter
TAM	=	TEMP ANNUAL MEAN
TMAXM	=	TEMP HOTTEST MONTH MEAN
TMINM	=	TEMP COLDEST MONTH MEAN
TRAN	=	TEMP RANGE
TSEAS	=	TEMP SEASONALITY
TWETQ	=	TEMP WET QUARTER MEAN
TDRIQ	=	TEMP DRIEST QUARTER MEAN
TCOLQ	=	TEMP COLDEST QUARTER MEAN
TWARQ	=	TEMP WARMEST QUARTER MEAN
RAT	=	RAIN ANNUAL TOTAL
RMAXM	=	RAIN WETTEST MONTH MEAN
RMINM	=	RAIN DRIEST MONTH MEAN
RRAN	=	RAIN RANGE
RSEAS	=	RAIN SEASONALITY
RWETQ	=	RAIN WETTEST QUARTER MEAN
RDRIQ	=	RAIN DRIEST QUARTER MEAN
RCOLQ	=	RAIN COLDEST QUARTER MEAN
RWARQ	=	RAIN WARMEST QUARTER MEAN
SRAM	=	SOLAR RADIATION ANNUAL DAILY MEAN
SRMAXM	=	SOLAR RADIATION SUNNIEST MONTH DAILY MEAN
SRMINM	=	SOLAR RADIATION DARKEST MONTH DAILY MEAN
SRRAN	=	SOLAR RADIATION ANNUAL DAILY RANGE
SRSEAS	=	SOLAR RADIATION SEASONALITY
SRWETQ	=	SOLAR RADIATION WETTEST QUARTER
SRDRIQ	=	SOLAR RADIATION DRIEST QUARTER
SRCOLQ	=	SOLAR RADIATION COLDEST QUARTER
SRWARQ	=	SOLAR RADIATION DRIEST QUARTER

Appendix 2. Example of Climatic Clumping of Sites.

