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Predicting the spatial distribution of *Sequoia sempervirens* productivity in New Zealand

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Abstract

Data from a nationwide set of permanent sample plots and interpolated climate and nutrition surfaces were used to develop multiple regression models describing *Sequoia sempervirens* (D.Don) mean top height at age forty (referred to as Site Index) and volume mean annual increment at age forty for a stocking of 400 stems ha^{-1} (referred to as 400 Index). The final Site Index model explained 82% of the variance in the data using mean annual daily air temperature and mean summer vapour pressure deficit, with the variables accounting for 71 and 11% of the variance, respectively. The final 400 Index model accounted for 76% of the variance in the data. Independent model variables for the 400 Index include mean spring air temperature, subsoil acid soluble phosphorus, and mean summer vapour pressure deficit, with these variables respectively accounting for 55, 16 and 5% of the variance in the data. A one-at-a-time validation procedure indicated both final models were relatively unbiased and accurate.

For Site Index, partial response curves show a positive linear relationship with mean annual daily air temperature and a downward facing parabolic relationship with summer vapour pressure deficit that reached an optimum Site Index at 0.53 kPa. Partial response curves show a positive relationship between 400 Index and mean spring air temperature, and acid soluble phosphorus, and a negative linear relationship with summer vapour pressure deficit. Maps illustrating the spatial variation in 400 Index and Site Index for *S. sempervirens* across New Zealand are provided.

Keywords: national scale modelling; New Zealand plantation forestry; productivity model; redwood; *Sequoia sempervirens*; spatial modelling.

Introduction

Sequoia sempervirens D.Don (coast redwood) naturally occurs within a narrow coastal belt from southernmost Oregon to Monterey County, California, USA. Frequent summer fogs are a feature of this coastal belt and provide a humid atmosphere, which is considered a governing factor in its natural distribution (Knowles & Miller, 1993). The species is a hexaploid (Ahuja & Neale, 2002), and has been shown to have more diversity within than between natural populations (Rogers, 2000).

In New Zealand, *Sequoia sempervirens* was initially planted between 1860 and 1870 and first planted in state forests around 1900. The species was planted on a larger scale by state and private foresters (at least 4000 ha) between 1920 and 1945 (Knowles & Miller,

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1993). While the growth of some stands has been very impressive, many have suffered from poor productivity and survival. Siting, establishment and seed source are three reasons identified for poor performance (Knowles & Miller, 1993). Recently there has been renewed interest in this species (Cown & McKinley, 2008) because more than 95% of old-growth coast redwood has now been set aside in public holdings in California (Stuart, 2007; Cown, 2008). This situation provides an opportunity for New-Zealand-grown timber to compete with the second-growth coast redwood resource from the USA. The emergence of an emissions trading scheme (New Zealand Government, 2009) and the likelihood of attaining carbon credits for forests has also spurred interest in establishing *S. sempervirens* over the longer term (Turner et al., 2008).

Research on *Sequoia sempervirens* in New Zealand has a long history, but has not always been well supported (e.g. Colbert & McConchie, 1983; Vincent, 2001) and much remains unpublished. With renewed interest over recent years in establishment of *S. sempervirens* within New Zealand there is an increased need to clarify variation in productivity of the species throughout New Zealand. Development of models that can predict spatial variation in productivity of *S. sempervirens* are a critical element to understanding where to best to grow this species. The recent development of spatial surfaces describing a diverse range of environmental (Leathwick et al., 2002a, b; 2003) and climatic data (Tait et al., 2006), has meant that the development of spatial models covering large areas is now possible. From a management perspective, these spatial models represent a major advance, as the maps that can be produced provide very detailed information of how productivity varies at a fine resolution across the landscape.

Using values of *Sequoia sempervirens* productivity obtained from the New Zealand permanent sample plot database, the objectives of this study were to: (i) develop a multiple regression model of *S. sempervirens* Site Index and 400 Index using independent variables obtained from national extent ancillary maps and interpolated surfaces; and (ii) using this model develop 400 Index and Site Index surfaces for New Zealand.

Materials and methods

Dataset used

Stand level data for planted *Sequoia sempervirens* stands were extracted from the New Zealand Forest Research Institute Permanent Sample Plot system (Pilaar & Dunlop, 1990). A total of 23 plots were available for modelling. Although the final dataset covered a wide environmental range across New Zealand sub-tropical areas in northern regions of the North Island were not represented (Figure 1).

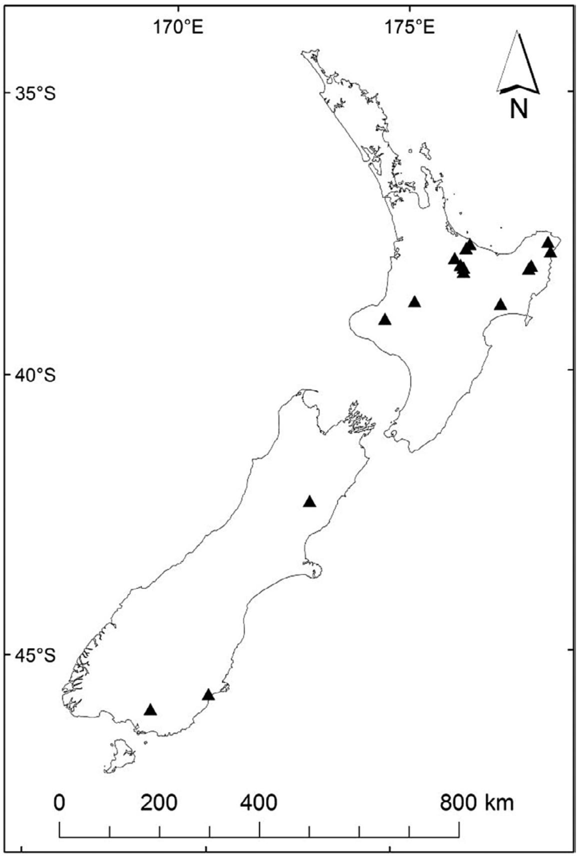

FIGURE 1: Map showing the location of the permanent sample plots used in this study.

Standardised measurements of productivity for the plot data

A redwood growth model was used to derive site productivity estimates, at age forty, for each permanent sample plot measurement. Site Index (SI) was derived from measurements of age and mean top height (mean height of the 100 largest diameter trees per hectare). Site Index, an index of height growth, is defined for this species as mean top height (MTH) at breast height, BH, (1.4 m) age 40 years (i.e. 40 years after attaining a MTH of 1.4 m, which, under current establishment practices, typically occurs at about age 3 years). An index of basal area growth, $BA_{40/400}$ was derived from measurements of age, stocking and BA using the BA model. $BA_{40/400}$ is defined as the BA at BH age 40 years for a stand growing at 400 stems ha^{-1}.

The 400 Index, an index of stem volume productivity, and defined as the under-bark stem volume mean annual increment (m^3 ha^{-1} yr^{-1}) at BH age 40 years, was then derived from SI and $BA_{40/400}$ for each plot. As the typical redwood stand at BH age 40 years and 400 stems ha^{-1} stocking has an under-bark stem volume of BA×MTH×0.259 m^3 ha^{-1}, the 400 Index was calculated as $BA_{40/400}$×SI×0.259/43. These derivations of 400 Index and Site Index were used as the dependent variable in the multiple regression models described in the next section.

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Independent variables for regression modelling

Spatial datasets used to model the 400 Index and Site Index included a wide range of environmental, biophysical, and climatic data. The final 400 Index model used the climate variables mean spring air temperature, mean summer vapour pressure deficit (Mitchell, 1991; Leathwick et al., 2002a; Tait et al., 2006), and subsoil acid-soluble phosphorus (Leathwick et al., 2002b; 2003). Subsoil acid-soluble phosphorus was included in the model as a categorical variable. For this variable, the categories included in the surface were: very low; low; moderate; high; and very high, defined as: 0 – 7; 7 – 15; 15 – 30; 30 – 60; and 60 – 100 mg phosphorus 100 g^{-1} respectively (Blakemore et al., 1987). The Site Index model used mean annual daily air temperature and mean summer vapour pressure deficit. Mean annual daily air temperature was calculated from (2 T_{max} + T_{min})/3, where T_{max} and T_{min} are mean monthly estimates of daily maximum and minimum air temperature, respectively. Independent data for these models were extracted from existing datasets for each of the permanent sample plot locations.

Model construction

Multiple regression models for 300 Index and Site Index were constructed using the general linear model procedure in SAS (SAS Institute, 2000). Variables were introduced sequentially into the model starting with the variable that exhibited the strongest correlation, until further additions were not significant or did not improve the overall model R^2. Variable significance was determined manually using an *F*-test, with the significance tested for each variable addition against the residual sum of squares from the previous model. Variable selection was undertaken manually one variable at a time, to ensure that non-linear relationships and relationships with categorical variables were identified, from residual plots, and correctly incorporated into the model.

For the final models, residuals were plotted against independent variables and predicted values to determine model bias. A “one-at-a-time” cross validation was undertaken to determine model stability. The cross-validation process excluded the first plot as a single-element test set and fitted the model over the remaining sites. This process was iterated for each site, generating validation data. Predicted values for the 400 Index and Site Index were then plotted against their respective actual values to assess bias (Figure 2). Model accuracy was examined using the coefficient of determination (R^2) between predicted values and actual 400 Index and Site Index.

Preparation of digital surfaces

Digital surfaces were developed for 400 Index and Site Index using the final SAS regression models and the GIS platform ArcInfo™. Arc macro language (AML) was used in association with the ArcInfo™ Grid module to calculate spatial surfaces using the

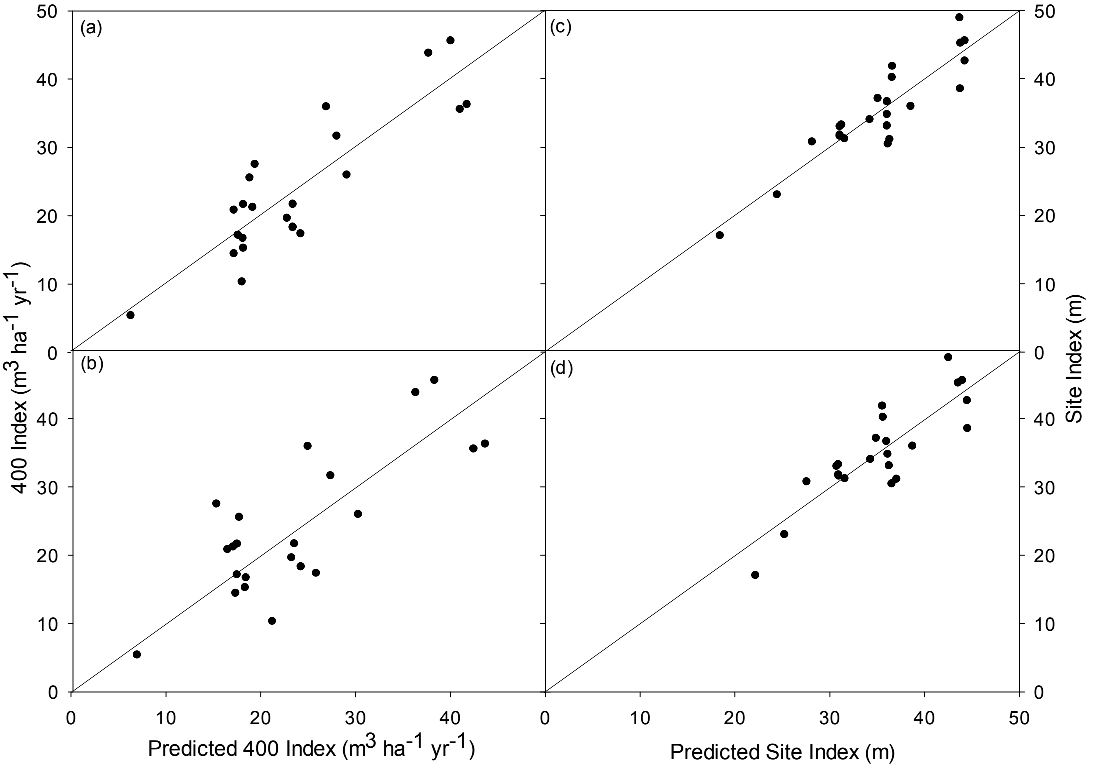

FIGURE 2: Relationship between predicted and actual 400 Index for: (a) the fitting; and (b) validation datasets. Also shown is the relationship between predicted and actual Site Index for: (c) the fitting; and (d) validation datasets. The 1 : 1 line is shown on each figure as a solid line.

SAS modelled intercept, regression coefficients, and their independent variables. Independent data within the spatial models were also constrained with the 400 Index surface and limited to a lower mean spring temperature of 9 °C to ensure that projections were not made too far beyond the bounds of the data. As there were no high, or very high values of acid-soluble phosphorus represented in the dataset, extrapolated spatial values of 400 Index for these categories were conservatively set to values estimated for the moderate category. For Site Index, the mean annual daily air temperature was limited to a lower value of 10.6 °C and mean summer vapour pressure deficit constrained between 0.42 and 0.77 kPa. Sites beyond the range of these bounds were displayed as undefined.

Results

Rainfall ranged four-fold across sites from 684 to 2988 mm yr^{-1}. Mean annual air temperature and mean daily solar radiation varied substantially across sites ranging, respectively, from 9.9 to 14 °C and 12.4 to 15.3 MJ m^{-2} day^{-1}.

The 400 Index model included mean spring air temperature (T_s), sub-soil acid-soluble phosphorus (P), and mean summer vapour pressure deficit during summer (D) (Table 1). The final model formulated using these variables accounted for 76% of the variance in 400 Index (Table 1). The terms T_s and P were both highly significant ($p < 0.001$) with partial R^2 values of 0.55 and 0.16, respectively. Although D was marginally insignificant ($p = 0.07$) this variable was included in the model as it was considered physiologically sound, reduced model bias and substantially increased model precision (partial $R^2 = 0.05$).

The final model for Site Index included mean annual daily air temperature (T_a) and mean summer vapour pressure deficit (D) (Table 1). The variable D was also fitted as a downward facing parabola that reached an asymptote at a D of 0.53 kPa. The final model formulated using these variables accounted for 82% of the variance in Site Index. Both T_a and D were highly significant ($p < 0.01$), with partial R^2 values of 0.71 and 0.11, respectively (Table 1).

Residuals for the final models of 400 Index and Site Index were normally distributed and exhibited little apparent bias with predicted values (Figures 3a & 4a, respectively. Residuals also exhibited little apparent bias with independent variables used in the 400 Index and Site Index models (Figures 3 & 4). The results from one-at-a-time validation indicated that the final models were relatively unbiased, and accurate, with the predicted values accounting for 61% and 74% of the variance in the actual 400 Index and Site Index, respectively (Figure 2).

To assess the functional forms of the independent variables, partial response curves were generated for models of 400 Index (Figure 5) and Site Index (Figure 6). The 400 Index was positively and linearly related to mean spring air temperature (Figure 5a), and exhibited a negative linear relationship with summer

TABLE 1: Summary of statistics for the final predictive models of the 400 Index and Site Index for *Sequoia sempervirens*. For acid-soluble sub-soil phosphorus, the values of the coefficient (c) used for each of the three categories of the variable are shown. Parameter values and variable partial R^2 and cumulative R^2 values (in brackets) are shown. For the significance category, the F values and P categories from an F-test are shown, with asterisks *** and ** respectively representing significance at $p < 0.001$, 0.01; ns is not significant at $p = 0.05$.

Equation: 400 Index = $a + bT_s + cP + dD$

Parameter	Coefficient Value	Variable	Units	R^2	Significance
a	-68.7				
b	9.9	Mean spring air temperature (T_s)	°C	0.55 (0.55)	25.7***
		Acid-soluble phosphorus (P)	-	0.16 (0.71)	5.1***
c	-13.7	*very low*			
c	-3.8	*low*			
c	0	*moderate*			
d	-30.9	Mean summer vapour pressure deficit (D)	kPa	0.05 (0.76)	3.8^{ns}

Equation: Site Index = $e + fT_a + gD + hD^2$

Parameter	Coefficient Value	Variable	Units	R^2	Significance
e	-84.1				
f	4.9	Mean annual daily air temperature (T_a)	°C	0.71 (0.71)	51.3***
g	204.5	Mean summer vapour pressure deficit (D)	kPa	0.11 (0.82)	6.0**
h	-192.2				

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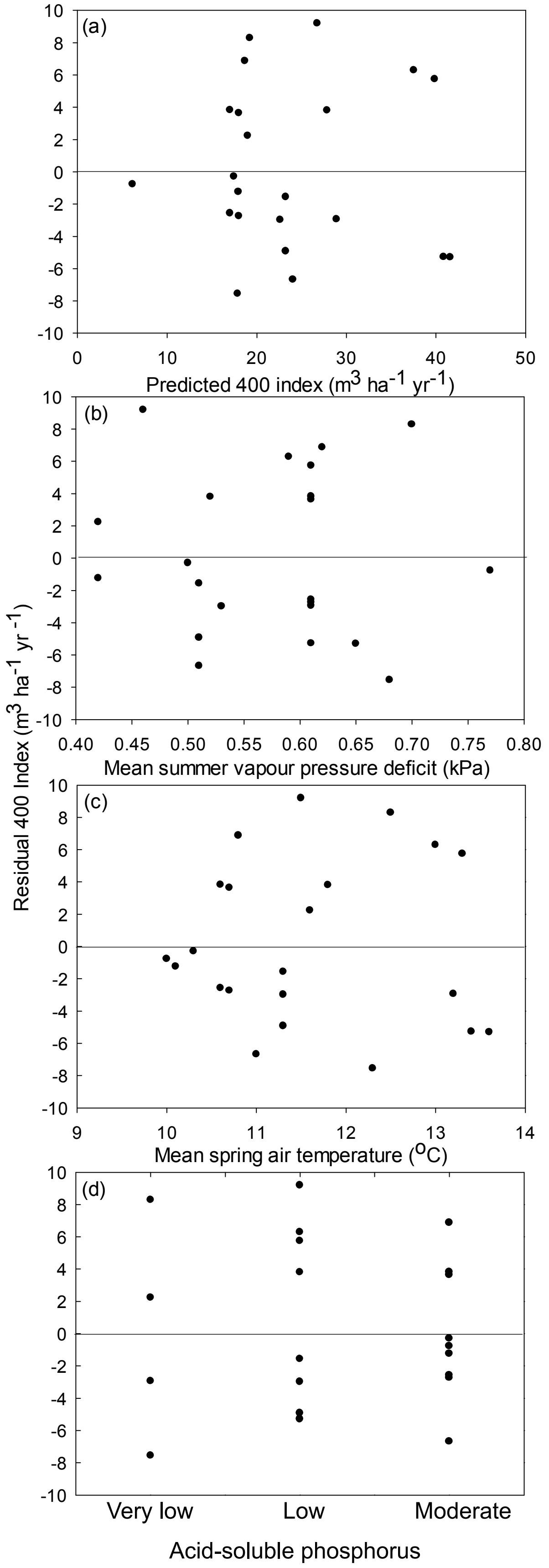

FIGURE 3: Plot of residual 400 Index values against: (a) predicted 400 Index; (b) mean summer vapour pressure deficit; (c) mean spring air temperature; and (d) acid-soluble phosphorus.

vapour pressure deficit (Figure 5b). The categorical independent variable acid-soluble phosphorus was positively related to 400 Index with the partial response function showing values of 14, 24, and 28 m^3 ha^{-1} yr^{-1}, respectively, for the very low, low and moderate classes (Figure 5c). The strong influence of air temperature was clearly shown in the productivity map (Figure 7a) with 400 Index values diminishing, with increasing latitude and at elevated inland regions in the main axial ranges, and the central North Island.

Partial response curves for Site Index show a positive, linear relationship with mean annual daily

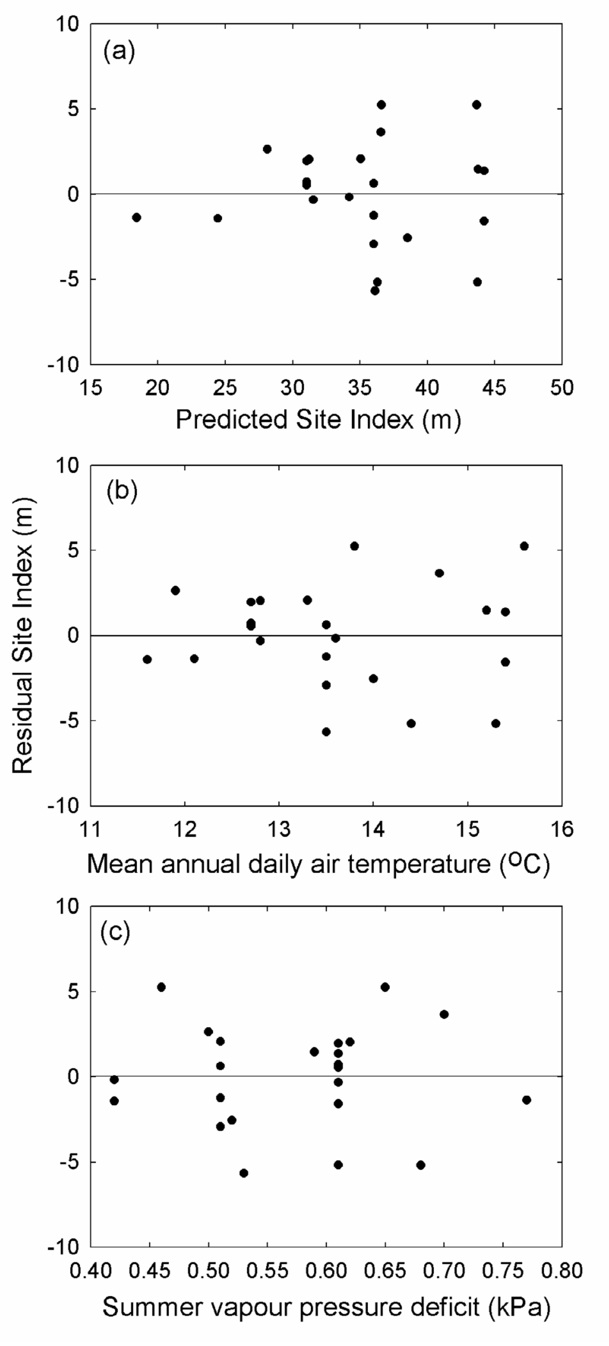

FIGURE 4: Plot of residual Site Index values against: (a) predicted Site Index; (b) mean annual daily air temperature; and (c) mean summer vapour pressure deficit.

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air temperature (Figure 6a). The relationship between Site Index and mean summer vapour pressure deficit, was modelled as a downward facing parabola, with an optima reached at 0.53 kPa (Figure 6b). The Site Index surface clearly demonstrates the strong influence of air temperature with values showing a general increase from south to north, and declining from warmer coastal sites inland towards frost prone, higher elevation sites (Figure 7b).

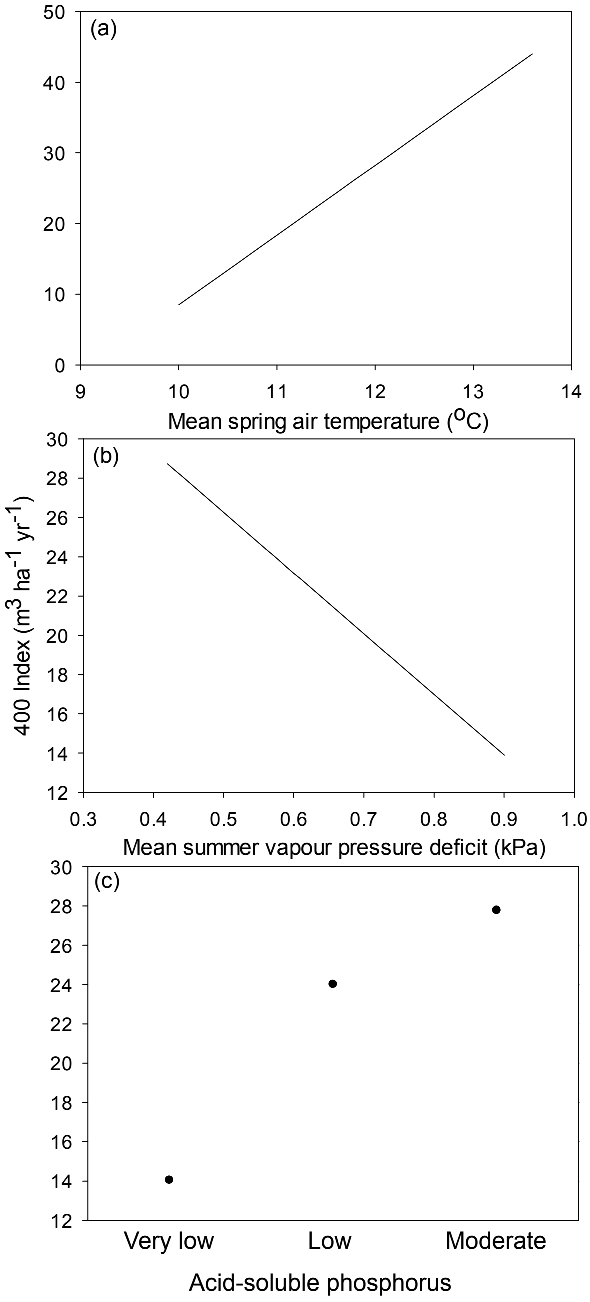

FIGURE 5: Partial response curves of 400 Index for: (a) mean spring air temperature; (b) mean summer vapour pressure deficit; and (c) acid-soluble phosphorus. When each partial response curve was generated all other variables in the model were held constant at mean values.

Discussion

The productivity models and maps developed here considerably advance our understanding of how environment regulates productivity of *Sequoia sempervirens*. This study clearly highlights the importance of air temperature as a determinant of productivity for the species, with this variable accounting for 55 and 71% of the respective variance in 400 Index and Site Index. The accuracy and lack of bias of the developed models provides confidence in the spatial projections and highlights the utility of thematic spatial layers as driving variables in the development of productivity models.

The dominance of air temperature as a driving variable is consistent with productivity models developed for other plantation species within New Zealand (Palmer 2008; Watt et al., 2009; Kirschbaum & Watt, 2011). Although the quantity of radiation intercepted controls the maximum growth attainable, air temperature is a primary determinant of the amount of intercepted radiation that can be utilised by the plant (Monteith,

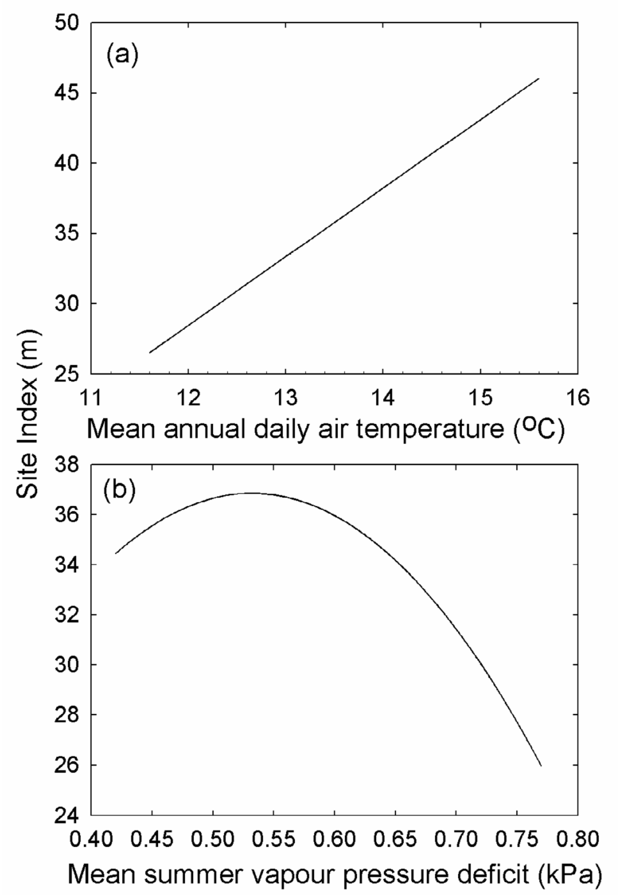

FIGURE 6: Partial response curves of Site Index for: (a) mean annual daily air temperature; and (b) mean summer vapour pressure deficit. When each partial response curve was generated all other variables in the model were held constant at mean values.

1977). The positive relationship often found between tree growth and air temperature in other species (Watt et al., 2005, 2008, 2009) is thought to be principally driven by the lengthening of the growing season (Lieth, 1973). The importance of such lengthening of the growing season was demonstrated recently by Kerkhoff et al. (2005), who showed that net primary production (NPP) expressed as NPP per month of growing season was virtually invariant with air temperature.

The negative relationship between vapour pressure deficit and productivity has a physiological basis. Considerable process-based research has shown increases in vapour pressure deficit induce reductions in both stomatal conductance (Watt et al., 2003) and growth (Landsberg & Hingston, 1996). This relationship is embodied in the widely used and generally applicable process-based model 3PG (Landsberg & Waring, 1997) which uses an exponential decay relationship to model the decline in utilisable radiation and growth with increasing vapour pressure deficit.

Mean annual increment was found to be significantly related to the class level variable subsoil acid-soluble phosphorus. One limitation of this categorical variable is that it does not account for subtle variations in soil fertility within New Zealand (see Watt et al., 2008) that can be accommodated using continuous variables. Further research should therefore focus on the development of spatial layers for soil chemical properties such as soil C : N ratio and total phosphorus that have previously been found to be significantly correlated to productivity for a range of plantation species (Watt et al., 2008). Use of layers for continuous variables describing soil fertility is likely to improve predictions of productivity for this species.

The maps show very high productivity for Northland regions. These high values should be interpreted with some caution as the models were not developed using data from these regions. Although it is reasonable to expect productivity will be enhanced similarly by higher air temperature at different locations, it should be noted that Northland soils may be of lower fertility compared with other New Zealand soils. It is likely that subsoil acid-soluble phosphorus does not fully capture the influence of this low fertility on the 400 Index. It is also worth noting there is no fertility-related variable for Site Index. Further research should therefore focus on validating the model described here against plot data from Northland.

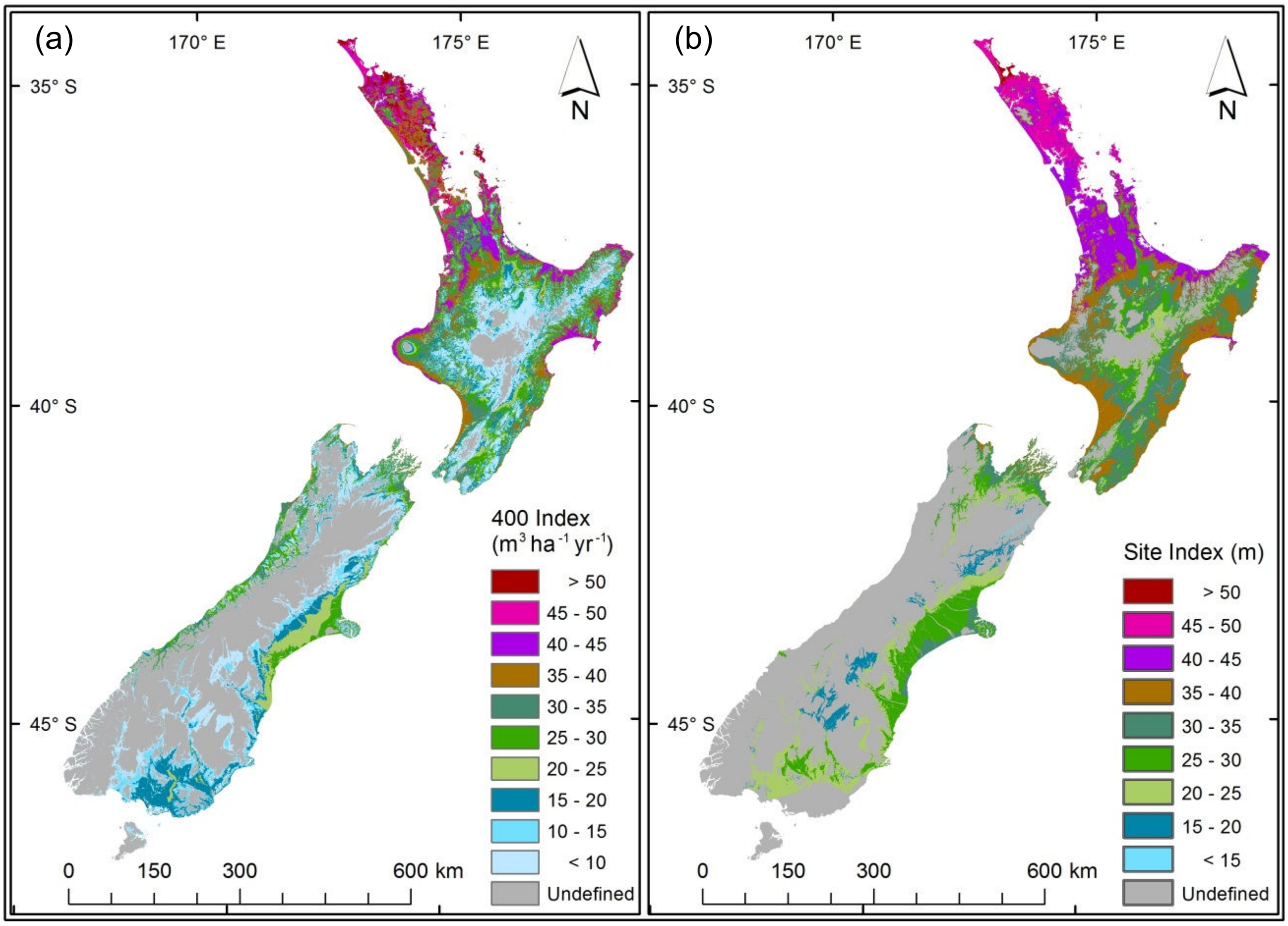

FIGURE 7: Productivity surfaces for *Sequoia sempervirens* describing: (a) 400 Index; and (b) Site Index across New Zealand.

Although the final models had high precision, they were developed from a relatively small dataset and are essentially empirical. While empirical models are often accurate, these types of models are limited to site conditions under which they were originally developed (Landsberg et al., 2003). Such models cannot simulate tree growth and yield under changing environmental conditions (Battaglia & Sands, 1997, 1998). This is a particular issue for simulating the impact of climate change on forests as climate change may modify ecosystem processes in a number of direct and indirect ways. An alternative modelling approach is process-based modelling, which is based on a species physiological response to the environment. Process-based modelling is dynamic and is able to incorporate climate changes multitude of direct, indirect, gradual, and abrupt impacts on the forest ecosystem to robustly predict future growth under a range of scenarios. Further research should therefore focus on collecting sufficient data, covering a wide enough environmental range, so that a process-based model can be developed to project redwood growth under current and future climate.

In conclusion, these results highlight the utility of thematic spatial layers as driving variables in the development of productivity models. Models developed from these layers are likely to improve in the future as more variables, such as soil chemical properties, become available. This approach greatly reduces model development cost. The development of detailed maps from these models will provide invaluable decision support for determining optimal sites for plantation species such as *Sequoia sempervirens*.

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