

Leaf Area Index in Closed Canopies: An indicator of site quality

A thesis submitted in partial fulfilment of the requirements
for the degree of Master of Forestry Science

By

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STATEMENT OF ORIGINALITY

I certify that this thesis and all work relating to leaf area index, and the research to which it refers, are the product of my work, except for the minor exceptions which are described here;

This thesis incorporates data from research undertaken in collaboration with Ensis and Landcare Research as part of a project called “Soil Based Indicators of Site Quality” under the supervision of a number staff; Dr Brian Richardson, Dr Tim Payn, Dr Roger Parfitt and Dr Robyn Simcock. All the initial soil characteristics and profile descriptions were completed by Landcare Research, with the exception of the microbial biomass analyses.

Pinus radiata specific leaf area samples were determined by Dr Michael Watt and Horacio Bown, a PhD candidate at the School of Forestry, University of Canterbury.

Rod Brownly a technical officer at Ensis carried out a pilot study to determine the best Plant Canopy Analyser sampling technique.

I declare that any ideas or quotations from the work of other people, published or otherwise, are fully acknowledged in accordance with standard referencing practices of the biological and forestry sciences.

I acknowledge the helpful guidance and suggestions of my supervisors.

Signed:

Date:

ABSTRACT

This study examined leaf area index (LAI) and relationships with corresponding tree growth, climate and soil characteristics across New Zealand forest plantations. The aim of this study was to determine if quick measures of projected leaf area across environmental gradients of New Zealand were an accurate indicator of site quality. Projected leaf areas of *Pinus radiata* D Don and *Cupressus lusitanica* Mills seedlings were measured using a Li-Cor LAI-2000 plant canopy analyser at 22 locations representing the soil and climatic diversity across New Zealand plantation forests. Seedlings planted at 40 000 stems per hectare were used to test treatment effects of fertiliser, site disturbance and species over a 4 year period. It was hypothesised that collected climate and soil information would explain differences in LAI development patterns across sites as the canopies approached site and seasonal maxima.

Averaged across sites *Cupressus lusitanica* 7.28 (\pm 2.59 Std.) $\text{m}^2 \text{m}^{-2}$ had significantly ($p = 0.0094$) greater projected LAI's than *Pinus radiata* 6.47 (\pm 2.29) $\text{m}^2 \text{m}^{-2}$. Maximum site LAI (LAI_{max}) varied from 2.9 to 11.8 $\text{m}^2 \text{m}^{-2}$ for *Pinus radiata* and from 3.1 to 12.6 $\text{m}^2 \text{m}^{-2}$ for *Cupressus lusitanica*. LAI_{max} of both species was significantly and positively correlated with vapour pressure deficit, soil carbon, nitrogen, phosphorous and CEC, but negatively with solar radiation, temperature and soil bulk density. A seasonal model of LAI across sites illustrated an 8.5% fluctuation in LAI of established canopies over the course of a year. Despite considerable variation in climate and soil characteristics across sites the combined effects of LAI at harvest and temperature were significantly correlated with site productivity ($r^2 = 0.84$ and 0.76 for *Pinus radiata* and *Cupressus lusitanica* respectively). A national model of LAI_{max} ($r^2 = 0.96$) was proposed for *Pinus radiata* across climate and soil environments and the significance of LAI_{max} as a component of site quality monitoring tools is discussed.

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ABBREVIATIONS and SYMBOLS

% = percent
°C = degrees celsius
Adj Rsqr = adjusted R squared
Base saturation = total exchangeable bases divided by CEC = %
BD = bulk density (g cm^{-3})
CEC = cation exchange capacity (cmol g^{-1})
Dia. = diameter (mm)
 ε = light use efficiency (g d^{-1})
Evap = average monthly evaporation
Exch. = exchangeable
Field = Field available water (mm)
GF19 = growth and form factor for improved *Pinus radiata* seedlings in NZ
H = height (m)
J = joules of energy
 J = intercepted light energy ($\text{J m}^{-2} \text{d}^{-1}$)
LAI = leaf area index ($\text{m}^2 \text{m}^{-2}$)
 LAI_{max} = predicted maximum leaf area index ($\text{m}^2 \text{m}^{-2}$)
Lat = Latitude, degrees north or south of the equator
Long = Longitude, degrees east or west of the prime meridian
Macro = Macroporosity -5 kPa Matric potential. (% v/v)
Maxtemp = average maximum monthly temperature
Meantemp = average mean monthly temperature
Mintemp = average minimum monthly temperature
MSE = mean square error
MTA = mean tilt angle (0-90 degrees)
 η = the daily proportion of growth partitioned to wood
 p = probability
PAR = photosynthetic active radiation 400-700 μm ($\text{MJm}^{-2} \text{yr}^{-1}$)
Pen = Penetration resistance in kPa.
pg. = page
pH = acidity
PinOrg = inorganic phosphorous (mg g^{-1})
POrg = organic phosphorous (mg g^{-1})
Porosity = Porosity (% v/v)
Pretention = phosphorous retention (mg g^{-1})
 r = Pearson correlation coefficient
 R^2 = model mean square divided by the error mean square
rain = annual rainfall (mm yr^{-1})
RAW = readily available water (% v/v)
RH = relative humidity (%)
SLAI = silhouette leaf area index
SMB = soil microbial biomass
SOM = soil organic matter
SQI = site quality index
Std. = standard deviation

TAW = total available water (% v/v)
V = rate of dry matter loss (g m⁻² d⁻¹)
VPD = vapour pressure deficit (kPa)
v/v = volume per volume
WHC = Water holding capacity (% by mass)
 $\pi = 3.142$
PCA = principal component analysis

Chemical elements

Al = aluminium
B = boron
C = carbon
Ca = calcium
Cu = copper
Fe = iron
K = potassium
Mg = magnesium
Mn = manganese
Na = sodium
P = phosphorous
S = sulphur
Zn = zinc

Site codes - names of trial sites

ATLANG = Kinleith forest
ASHYMA = Ashley forest
BALSH8 = Tekapo farm
BALSSP = Golden Downs forest
CATLRI = Catlins forest
GLNGSM = Glengarry forest
HOCHSI = Hochstetter forest
HOCKPA = Bulls agro-forestry farm
KARI49 = Karioi forest
KINRTU = Kaniere forest
KANGPY = Kaingaroa forest
LONGMA = Longwoods forest
MAHUMA = Mahurangi forest
MANTMI = Mangatu forest
NGAUBU = Ngaumu forest
OKUKQU = Okuku forest
RAISH8 = Rai Valley forest
RVHDSH = Riverhead forest
TIRUGU = Tairua forest
TIKITE = Tikitere forest
WMARAR = Waimarino forest
WOODMU = Woodhill forest.

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CHAPTER 1

Introduction and Rationale

Studies and predictions of dramatic climate change over the next century are raising environmental concerns across the globe. Such concerns are based on a premise that changes in climate will occur at a rate which normal biological adaptations of fauna and flora may not be able to keep pace with. Global climate change is speculated to increase the occurrence of destructive weather patterns and raise global average temperatures between 2-9°C over the next century (Flannery 2005). Rising temperatures are predicted to melt substantial polar ice, increase the sea level and inundate highly productive land. These consequences combined with increasing global population and demands for consumer products, such as wood, are expected to multiply pressures on intensively managed plantations and it is feared that over time this may lead to a degradation of site quality and a loss of productivity which is irreversible.

Public and political concerns (Kilvert 1996) for the effects of the environment on forestry and the effects of forestry on the environment (Fox 2000; Hock and Hay 2003; Kelting et al. 1999) have encouraged some researchers to monitor site quality. Accurate monitoring of site quality over time will enable guidelines and regulations to be developed in the near future so that forecasts of adverse growing conditions can be identified before costs of rehabilitation are prohibitive or irreversible consequences occur.

A standard indicator or set of site quality indicators has not yet been employed across environments because of the complex interacting processes that influence site quality. The problem with current measures of site quality are: 1) They are time consuming, 2) costly and, 3) there appears to be little consistency or agreement on appropriate indices across varying environments. In the future a site quality index (SQI) may be more widely accepted if it is: 1) sensitive to changes induced over time and across environments, 2) inexpensive and 3) easy to measure (Schoenholtz et al. 2000).

This thesis evaluates the use of maximum site leaf area index (LAI_{max}) which may be used to ground truth remotely sensed measures of site quality. LAI_{max} measures across New Zealand plantations forests will be of value because of the strong physiological links between climate and soil characteristics with leaf area, and because LAI may be efficiently monitored over large scale areas in the near future. These links between LAI_{max} and soil chemistry or climate will be demonstrated in the following chapters and the perceived benefits and challenges of leaf area measurement will be discussed.

OBJECTIVES

This aim of this study was to investigate the use of leaf area index as an efficient and robust measure of site quality across the diverse forest environments in which New Zealand plantations are grown. The specific goals were to determine:

- 1) The variation in maximum leaf area index across New Zealand plantation forests? As simulated using highly stocked plots with a constant planting density.
- 2) What are the likely causes of variation in leaf area index?
- 3) How do calculations of LAI compare with productivity measurements, which are the currently favoured index of site quality?

CHAPTER 2

Literature Review - Monitoring Site Quality -

What is site quality?

Site quality is a concept that aims to quantitatively assess a site's ability to maintain productivity, diversity and resilience of flora and fauna while also providing social, aesthetic and recreational benefits to the local population. The site quality concept is an attempt to simplify numerous complex functions and processes that occur at a site, until a time that process-based models can accurately predict the complex soil processes and interactions of induced management and climatic changes on site quality (Burger and Kelting 1999). It is also important to note that maintenance of site quality should be considered over a relevant time scale, such as those dictated by natural weathering processes and ecological succession (Wardle et al. 2004).

Why monitor forest site quality?

History has provided many examples that link a society's prosperity and health with the presence of productive forests (Diamond 2005; Fox 2000; Rolett and Diamond 2004). Given increasing global population, demanding higher standards of living and greater requirements for sustainable wood products with climate change pressures, intensively managed plantations will probably be degraded over time without a greater understanding and guidance from further research. Public and political concerns (Kilvert 1996) of the effects of the environment on forestry and also the effects of forestry on the environment (Fox 2000; Hock and Hay 2003; Kelting et al. 1999) have focused research objectives which aim both to monitor site quality and certify practices that promote sustainable forestry¹.

¹ (www.qualifor.com Jun 06), (www.certifiedwood.org ,Jan 07), (www.scs-certified.com, Jan 07), (www.smartwood.org, Jan 07)

Maintenance of site quality is a key component of sustainable forest management philosophies. Certification schemes and sustainable management practices utilise site quality indices (SQI's) to monitor a range of complex functions such as soil processes, health and crop growth over time. A number of principles and criteria are being applied to significant areas of plantation forestry in New Zealand (610 000 ha)² in order to demonstrate good management practices (FSC 2000).

Accurate monitoring of site quality over time will facilitate sustainable plantation practices and develop improved guidelines for forest managers. Monitoring changing conditions should provide forecasts of either improved or adverse effects on site quality. Then it may be possible to target specific properties which will benefit from rehabilitation or improvement operations. Various indicators of site and soil properties that are linked to site quality have been monitored ever since measurements of tree growth were first compared with site characteristics (Karlen et al. 2001; Storie 1933). Today there are a large number of methods for measuring site quality; to date the chosen indicator has depended on a specific function which is of interest (Burger and Kelting 1999; Schlöter et al. 2003).

Site quality indicators

Many of the papers critically reviewed during this study suggest that there a number of key components which are required to build a holistic measure of site quality, and because site and soil quality are intrinsically linked (see later) many of the measures can be quantified through soil assessments. For example key site quality functions that have been suggested are the ability of soil to; 1) store and supply water, 2) promote root growth, 3) provide nutrient storage, turnover and exchange, 4) support biological activity and 5) enhance gas exchange (Kelting et al. 1999). Several of these key components that provide important site quality functions are briefly described below.

Soil organic matter (SOM)

Soil organic matter has been shown to have many beneficial properties that contribute to improved plant growth (Lutzow et al. 2002; Scott et al. 2002). SOM has chemical,

² as at Jan 2003

physical and biological properties that can be affected by management practices over time, enabling changes to be monitored. SOM provides essential chemical properties required for plant growth. SOM provides a physical substrate and sustenance for the growth of microbial organisms which cycle nutrients and manipulate the nutrient flow to plants (Sparling 1992). In addition, the physical properties of SOM provide important sites of ion and nutrient exchange, while pore spaces provide sites for gas exchange and influence the water holding capacity of soils.

However, the use of SOM as an indicator of site quality is probably most applicable to agricultural crops, but because of high background levels of carbon (from crop residues) even then short term changes are not easily measured. Despite the main benefits of SOM which are, that the carbon content of the SOM component is easily measured, from loss on ignition assessments and that soil carbon can be incorporated into a soil profile by tillage, over seasonal periods it can be rapidly broken down into its basic elements. Because of this, turnover rates of SOM are reported to be more useful indicators of site quality (Sparling 1992) and this is examined further in the following example.

Soil biological criteria

Site quality is strongly linked to the biological properties of soil (Elliott et al. 1996) and soil microbial biomass (SMB) is important for sustained crop growth because of the contributions microbial organisms provide to the decomposition and nutrient turnover processes which aid soil fertility and site quality. Seasonal variations occur in SMB and these are related to changes in rates of gas exchange, soil temperature and moisture (Haney et al. 2001; Zak et al. 1999). Greater microbial biomass and activity is associated with greater carbon contents, warmer temperatures in moist and aerated environments (Ross and Tate 1984; West and Sparling 1986) and the soil physical characteristics that enhance these conditions.

There are three levels at which studies of soil microbiology can be conducted to assess site quality; 1) ecosystem - focuses on nutrient retention and cycling, 2) community - focuses on the importance of diversity of species and 3) population - focuses on the importance of individual species (Visser and Parkinson 1992). One proposed soil biological indicator is the ratio of soil microbial respiration to total

microbial biomass over a defined period of time, this is referred to as the metabolic quotient ($qCO_2 = \mu gCO_2 : Cg^{-1} C_{micro} h^{-1}$) (Blagodatskaya and Anderson 1998; Mamilov and Dilly 2002).

However, changes in microbial activity in the field are affected by climate extremes such as drought, which substantially masks the effects of many management practices on SMB (Visser and Parkinson 1992). Despite this, other concerns have also been reported, such as fertiliser applications which have increased productivity but reduced microbial activity over time (Thirukkumaran and Parkinson 2000). The metabolic quotient is also reported to be insensitive to site disturbance, and there is evidence of unpredictable associations with ecosystem development (Wardle and Ghani 1995). Despite the potential of SMB and SOM there are a number of challenges to overcome before this indicator would be widely applicable.

Invertebrates

Fauna play a crucial role in soil systems and amelioration of site disturbance (Stork and Eggleton 1992). They can rapidly alter chemical and physical attributes of the soil (Edwards and Bajer 1992) and similar to soil biological criteria, measurements of species density, richness and activity indicate functions of site quality at a number of scales ranging from micro to macro fauna, e.g. nematodes to beetles.

However, the inconsistent distribution of keystone species across environments is one stumbling block to the use of invertebrates as site quality indicators. Another is large seasonal changes that prevent snap shot measures being captured. Despite these challenges functional redundancy is a concept that may provide future assessment criteria. This concept needs further research efforts, but could potentially indicate how far a community can be reduced before it loses trophic cohesion which harms soil or site quality (Stork and Eggleton 1992).

Productivity index of stem volume

The forest industry employs productivity based SQI's for resource and logistic planning at present. One example is a pre harvest assessment that estimates the proportion of a particular log grade and harvestable stand volume. Another is "Site Index" which is the currently favoured site assessment tool which aids silvicultural

planning. Site index is defined for *Pinus radiata*³, as the mean top height at age twenty years (Eyles 1986)⁴. Typically in New Zealand site index ranges from 13 to 39 metres (Garcia 1999). Trees at locations with high site indices are generally straighter with less unfavourable branching characteristics and have low stem taper (Maclaren 1993). Site indices are also used in Ethiopia to compare the productivity of *C. lusitanica* (Teshome and Petty 2000).

However, the effectiveness of productivity to define levels of sustainability has been debated because management options continually improve production, perhaps at the expense of long term site quality (Richardson et al. 1999). For example improved seedling selection (Carson 1986; Carson et al. 1999; Libby and Rauter 1984), and both mechanical pre-plant and broadcast fertilising operations (Zwolinski et al. 2002) are possibly compensating for underlying changes to soil properties. Another example of productivity increases that mask site quality changes is shown by some herbicide applications that have negative affects on other measures of soil quality, specifically microbial biomass (Perie and Munson 2000).

Relative stocking index (RSI)

Bergusson and colleagues proposed that deviations from a self thinning line could be used as an indicator of site quality (Bergusson et al. 1994). They developed very strong relationships between tree size and stand density for 5 native cover types of the Lake States (USA) with R^2 ranging from 0.96 - 0.98. Relationships were developed using extensive USDA forest inventories. Deviations from mean values by 10% were considered outside the norm and classified accordingly. However, this type of site quality index is unlikely to be suitable for New Zealand plantation forests because stands are planted at a specific stocking, generally maintained at densities well below the self thinning line and harvested before canopies reach this development stage.

³ From this point on *Pinus radiata* and *Cupressus lusitanica* shall be referred to as *P. radiata* and *C.lusitanica*.

⁴ Site index may be superseded by the new 300 Index. Kimberley, M.O., G. West, M. Dean and L. Knowles 2005. The 300 Index - a volume productivity index for radiata pine. New Zealand Journal of Forestry. 50:13-18.

Environmental factors influencing physiological processes and growth

Climate

Climate has a fundamental influence on plant physiological processes and hence production across New Zealand plantation forests. Solar radiation, temperature, rainfall, evaporation and vapour pressure deficit are key determinants of growth and hence site quality (Landsberg 1986). For example, warmer temperatures generally enhance chemical reactions and metabolic processes such as photosynthesis. An increase in temperature leads to a state with higher kinetic energy where more frequent collisions of molecules give rise to an increased reaction rate. At excessive temperatures denaturing of plant enzymes occur, so an optimum temperature exists for differently aged plants, elements of a plant, with different water and nutrient status (Landsberg 1986).

Research on climatic factors influencing tree growth in New Zealand have reported effects of temperature and rainfall on tree growth (Hunter and Gibson 1984; Jackson and Gifford 1974; Snowdon et al. 1998; Woollons et al. 2002). Mean annual temperatures vary along a north to south gradient, ranging from 15.5 to 5.0°C. In comparison rainfall exhibits a west to east gradient, mean annual values for plantations ranging from 3700 in the west to 610 mm yr⁻¹. A seasonal relationship between soil moisture and evaporation also contributes significantly to productivity (Watt et al. 2003) and a steady supply of moisture, or the availability at crucial times, is important for consistent growth. Across New Zealand this relationship influences the distribution of indigenous tree species (Leathwick and Whitehead 2001), which have adapted to specific rainfall zones and temperature environments.

Over time, climate also significantly influences soil development (Molloy 1988). Rainfall causes nutrient leaching, temperature and rainfall affects weathering rates (Zabowski 1990), and wind exacerbates soil erosion. These influences demonstrate the intrinsic links between soil, climate and site quality.

Correlations exist between some climatic variables and site characteristics such as topography. For example, solar radiation and temperature are positively correlated; generally high mean annual temperatures are observed where high solar radiation

intensities are recorded. Across New Zealand, temperature and rainfall are negatively related, and temperature and evaporation are positively related. These relationships cause problems when the independent effects of each variable are being calculated, but these types of correlations also mean that predictions of critical variables such as solar radiation from mean monthly temperatures are possible. Studies have shown that recorded values of temperature can provide estimates of solar radiation to within 7% of actual values (Coops et al. 2000).

Despite these challenges the combined influences of climate contributes significantly to variations in site productivity and site quality.

Soil characteristics influencing productivity

Chemical

Soil chemical properties are also key determinants of crop growth. Extensive work predominantly using hydroponics in controlled conditions have determined both optimum and critical nutrient levels for a broad range of species (Ingestad 1991; Ingestad and Agren 1988; Ingestad and Agren 1991; Ingestad and Agren 1992; Ingestad and Agren 1995). The concentration and availability of elements such as nitrogen, phosphorous, exchangeable cations, carbon and several others contribute significantly to measures of site quality (Schoenholtz et al. 2000), because these elements are fundamental to plant growth. They are needed to build plant structures or power photosynthetic processes (Chapin III et al. 1987). For example, plant energy is stored in phosphorous compounds such as adenosine triphosphate (ATP).

Long term site quality depends on a sustained nutrient supply. However, nutrient pools are subject to environmental characteristics such as temperature, rainfall, rate of parent material weathering, microbial breakdown and mineralisation, amongst others, which influence availability (Payn and Clinton 2005; Zabowski 1990; Zabowski et al. 1994). Accurately predicting stand nutrient changes over time will provide tremendously important tools, so that silvicultural operations can manipulate nutrient inputs and outputs in order to sustain site quality (Payn and Clinton 2005).

A soil based property which has been shown to influence site quality is mineralised-N. Significant correlations between productivity of intensively grown loblolly pine (*Pinus taeda* L.) and mineralised-N in South Carolina (USA) soils have been reported (Kelting et al. 1999), sufficiency curves for sites were developed and the mineralised-N needed for maximum production was calculated to be $140 \text{ kg ha}^{-1} \text{ yr}^{-1}$.

Additional work with indices of potentially mineralisable-N and phosphorous sorption capacity has also provided a basis for comparing site quality (Smethurst 2000). Phosphorous sorption capacity tested with sequential extraction procedures has been suggested as an independent predictor of growth response. Ion exchange resins can be used to absorb this and many other cations and anions from the soil solution and test availability. This later technique is better because it simulates uptake by plant roots, as it incorporates the effects of temperature and rainfall on nutrient availability over specific time periods (Smethurst 2000). However, it requires ongoing frequent time consuming measurement, and because nutrients end up at a root surface from three mechanisms; interception by growing roots through the soil, in the mass flow of soil water and diffusion (see review by Smethurst, 2000) these all need to be quantified before comparisons can be made across sites.

However, while this ion exchange technique is widely applicable like many other techniques it requires calibration. There are still many factors such as sampling regime that affects results and which need careful consideration.

Physical

Soil physical properties provide the storage capacity of a site, and the environment for plant growth promoting components like water, nutrients, and gas exchange. Physical characteristics such as soil texture, the distribution of pore sizes and the amount of charge dependent surfaces (McLaren and Cameron 1990; Molloy 1988; Zou 1999) are important characteristics which influence root and plant growth and hence site quality (Schoenholtz et al. 2000).

Site disturbance from forest harvest operations often cause damage to the physical characteristics of the soil, especially across highly trafficked areas of the stand (Balneaves 1990; Firth and Murphy 1989; Mason et al. 1988). These characteristics

often manifest themselves as a combination of compaction, organic matter displacement and/or removal, soil deformation with reduced porosity (Zabowski et al. 1994). Different soil textures have different tolerances to compaction and frequently responses vary with different moisture conditions at the time of exposure. As a consequence of compaction, water infiltration and gas exchange are normally reduced, this in turn affects root growth.

However, because of the complex interactions between climate and soil type not all compaction reduces site quality. For example, compaction of coarse textured soils at relatively dry sites may improve their water holding capacity and this may improve tree growth and hence site quality.

A review of forest soil compaction showed that the average loss of productivity due to tractor logging was 15% of volume across reported studies (Greacen and Sands 1980). Greater losses calculated in terms of value have been predicted from a New Zealand study analysing older trees (Murphy et al. 2004). The study took into account both tree volume which decreased by 8% due to the effects of compaction and also the change in wood quality. These changes meant there was a potential decrease in the crop value of up to 60% at harvest. However, different species also respond differently to various levels of soil compaction and this may give rise to competitive advantages for some plants (Nugroho 1999).

The least limiting water range (LLWR) has been proposed as a combination of crucial soil physical characteristics that contribute to measures of site quality. LLWR combines soil water holding capacity, soil strength and aeration into one factor that influences plant growth (Benjamin et al. 2003; Letey 1985; Zou et al. 2000). The graphical area which encompasses these functions is calculated and significant relationships ($R^2 = 0.76$) were shown between this measure and wheat growth (Benjamin et al. 2003). Management practices that maximise LLWR are believed to encourage optimum soil physical conditions but this concept is still not widely utilised.

Schoenholtz *et al.* (2000) presents a comprehensive review of forestry soil chemical and physical properties used to study and quantify changes in site quality.

Perspectives in Australian agriculture indicate similar issues are being addressed with catchments studies and models that integrate multiple factors (Schwenke et al. 2003).

This thesis evaluates the use of maximum site leaf area index (LAI_{max}) as a key component of site quality measures across New Zealand plantations forests. LAI_{max} is a potential measure because of the strong physiological links between leaf area, climate and soil characteristics and the ease at which it can be assessed.

What is leaf area index?

Leaf area index (LAI) is a measure of canopy density. It is defined as the projected leaf area per unit of ground area ($m^2 m^{-2}$) (Pierce and Running 1988). Projected LAI measures typically range from 3-10 $m^2 m^{-2}$ in temperate forests. Plant or canopy leaf area index at a certain time is influenced by the accumulated effects of climate and nutrients over the preceding period (Frazer et al. 2000; Grier and Running 1977; White and Scott 2006). Leaf area is sensitive to changes from year to year (Jonckheere et al. 2004) and strong relationships have been shown between leaf area and climate or soil characteristics, especially in conifer and mixed conifer-hardwood forests (Fassnacht and Gower 1997; Gholz 1982; Hoff and Rambal 2003; Nemani and Running 1989). As an example Gholz (1982) showed that leaf area explained 96% of the variation in net primary production in parts of the Pacific Northwest (USA).

Strong relationships between leaf area and growth are evident because leaves provide sites for photosynthesis, where carbon dioxide and water are converted to carbohydrates and oxygen using solar radiation to provide energy requirements. Leaf area provides sites where energy, gas and moisture exchange are necessary for growth (Atwell et al. 1999; Tuzet et al. 2003). So a plants total leaf area helps determine its productivity (Warren and Adams 2000). Plant growth is regulated by stomata⁵, amongst other things, and by the actions of leaves under site constraints of temperature, moisture and nutrient availability (Chapin III et al. 1987; Osmond et al. 1987). Therefore a site's carrying capacity is illustrated by the amount of foliage present, once the canopy has matured and an equilibrium point has been reached between the above and below ground available resources.

⁵ A flow chart of the properties influencing stomatal control is given in appendix 2.

As an example, during dry conditions stomata close to reduce moisture loss and therefore CO₂ uptake is reduced and cellular growth is restricted. If moisture stress is prolonged, cells and hence leaves are reduced in size (Linder et al. 1987; Otieno et al. 2005). Reliable links between LAI and physiological responses of plants to changing microclimate and soil conditions are the basis for LAI use in several common process-based stand models (Dewar 2001; Gower et al. 1999; Landsberg and Waring 1997). The widespread use of LAI in these process-based models and the years of research invested on this topic illustrate the importance of LAI in predicting growth to the scientific community.

Therefore, LAI is a potential means for assessing site quality across New Zealand forest plantations because it is a recognised function of canopy development and stand growth. LAI provides an assessment of the current site resources, because of the intrinsic links with climate and soil conditions which affect leaf area growth (see later chapters).

Leaf area measurement

Other practical benefits of site quality measures from leaf area are the ease and speed with which measurements are possible using new and developing technology. An array of available tools provides major advantages through high speed data collection (Coops et al. 2004) at relatively low cost. Several reviews of handheld devices and techniques have been published and instruments such as the Sunfleck Ceptometer or hemispherical camera (Coops et al. 2004; Frazer et al. 2001; Hyer and Goetz 2004), DEMON (CSIRO, Canberra, Australia) and TRAC (Tracing Radiation and Architecture of Canopies) have been compared (Jonckheere et al. 2004). One popular device, used in this study, is the LAI-2000 Plant Canopy Analyser (Cutini et al. 1998; LI-COR 1990; Welles and Norman 1991).

Use of different tools and techniques has led to a number of leaf area definitions, and comparisons between studies need to appreciate these. The most common definition of leaf area is based on the horizontal area, as cast by a shadow perpendicular to the light source, and this is referred to as the silhouette leaf area index (SLAI) (Barclay

and Goodman 2000). Measurements from the LAI-2000 Plant Canopy Analyser used in this study are based on this SLAI definition and are a combined stem, branch, and foliage index.

History of leaf area measurements

Initially in the 1970s, leaf area measures were based on time consuming biomass studies. Trees were harvested, dry weights were determined and then relationships between foliage weight and foliage area were calculated. The allometric relationships were then extrapolated to larger scales. Following this, close correlations between sapwood basal area and leaf area were extensively used in the early 1980's (McLeod and Running 1988; Waring 1983; Whitehead 1978; Whitehead et al. 1984). Subsequently many leaf area measures have been based on canopy transmittance (Lang 1987) and reflectance (Buermann et al. 2001; Lee et al. 2004; Stenberg et al. 2004).

Now multispectral satellites and airborne platforms can rapidly collect canopy measures at various scales. Aerial photography, laser radar (Nelson 1984) and video imagery (Crowther and Neale 1991; Everitt et al. 1989; King 1991) are all possible techniques that can be used, although developments in the technology are still essential (Buermann et al. 2001; Coops and Waring 2001; Luo et al. 2002; Spanner et al. 1994; Wang et al. 2003; Zhang et al. 2004). A comprehensive synopsis of remote sensing concepts and image processing techniques is outside the scope of this study but a very good overview is given by the following web site (<http://www.gisdevelopment.net/tutorials/tuman008.htm>, Jan 07).

Unfortunately remotely sensed data is only available from a limited number of satellites and current measures are subject to interference from characteristics, such as soil optical properties, canopy geometry and cloudiness (Baret and Guyot 1991; McDonald et al. 1998). To account for these interferences a number of indices have been developed.

Baret and Guyot (1991) compared several vegetation indices using a sensitivity analysis and observed that most vegetation indices at that time reached a saturation

point which limited its wider application, although now multispectral data provides superior estimates (see later). Baret and Guyot (1991) also showed that the transformed soil adjusted vegetation index (TSAVI) seemed to provide a more reliable estimate of vegetation cover when leaf inclination is known, as in plantation monocultures (Baret and Guyot 1991). They noted that the normalised difference vegetation index (NDVI) (Rouse et al. 1973) and the perpendicular vegetation index (PVI) (Richardson and Wiegand 1977) were particularly sensitive to soil optical properties, especially at low canopy covers. Baret and Guyot concluded that there is little doubt that vegetation indices based solely on the reflectance range of red and near infra-red spectral bands can not possibly account for all measurement ambiguities in canopy covers and that more spectral bands are necessary.

The promise of cheap and accurate remotely sensed data has been anticipated for a considerable time (Soudani et al. 2006) but unfortunately the promise seems unfulfilled to the wider research community at the present. Here in New Zealand remotely sensed data of local sites is only distributed sparsely across a number of government organisations (pers. com. Peter Stephens MfE). This may be partially because of a high cost of collection and this is in spite of a desire to collate this data for a number of wider research applications (pers com. Kimberly Cullen, Official Statistics Research and Data Archive Centre NZ (OSRDAC)).

Patterns of leaf area development

There is general agreement concerning the patterns of leaf area development (Ryan et al. 2004; Vose et al. 1994; Waring and Schlesinger 1985). From the point of establishment, LAI of the crop and/or other vegetation progresses at a rate proportional to the demand and supply of available resources. Initially this growth is exponential while resources such as water, light and nutrients are plentiful. As the competition for resources increases the effects of aging and self shading diminish the rate of LAI development, which reaches a peak at around $3 \text{ m}^2 \text{ m}^{-2}$. The rate of development then slows as LAI approaches a site maximum around $6.5 - 7.5 \text{ m}^2 \text{ m}^{-2}$ (see later). Over time LAI may decline by approximately 10-20%, particularly if resources such as water are inconsistent over the long term (Waring and Schlesinger 1985).

At maximum site LAI the crop is in balance with the above and below ground resources, because plants respond to an environment so that optimal use of site resources are made (Agren and Franklin 2003). This concept is based on Brouwer's 1963 theory called Functional Equilibrium advocates that an equilibrium is maintained between root and shoot allocations and this allocation is controlled by the availability of site resources (Brouwer 1983; Poorter and Nagel 2000).

The development of LAI in this study is represented by a sigmoid with a non symmetrical (logistic) shape (Fig. 2.1). The Chapman-Richards (a variation of the von Bertalanffy) function (Equation 2.1) is a flexible growth curve which was shown during early analysis to give the best representation of the data provided, as more sites and plots obtained statistical convergence than either of the Gompertz or the Weibull functions. The 3 parameter Chapman-Richards function was also well suited to the LAI analysis because it provides 2 asymptotes and an inflection point.

One asymptote is based at a LAI of 0. This means initial measurements are not overly weighted and the other at maximum LAI, which shall be shown to be of value in later chapters. The non symmetrical inflection point represents unique site characteristics and development patterns where LAI growth is at a maximum or the point where site resources become limiting to growth.

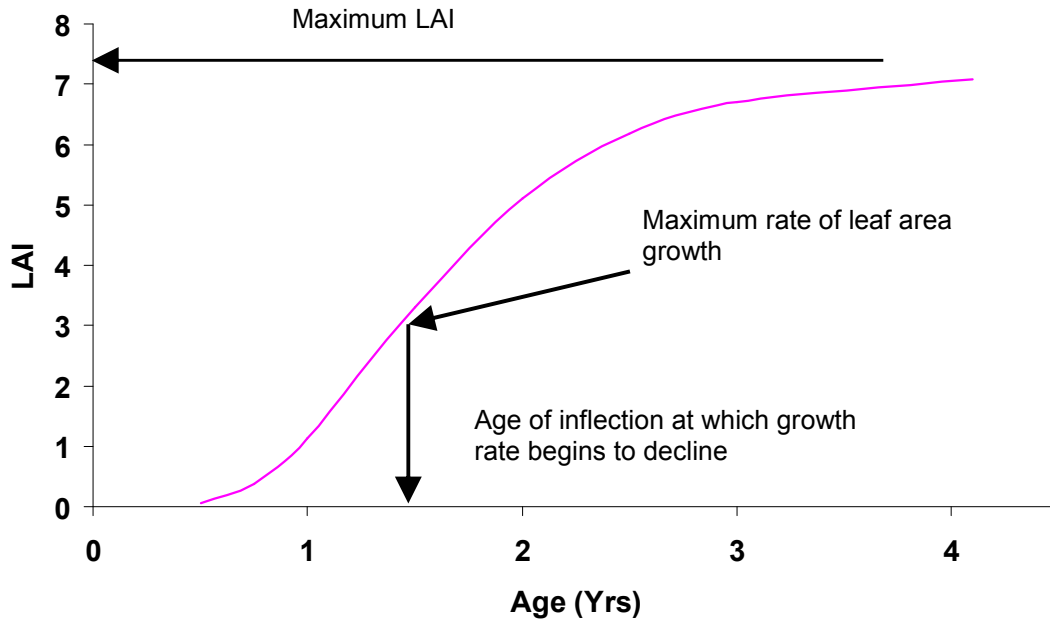


Figure 2.1 Representation of a Chapman-Richard's sigmoidal function, illustrating maximum LAI, slope and the age of inflection for the highly stocked trials utilised for this experiment. Multiply the age by 10 to simulate conventional stocking development trends without silvicultural intervention.

Unique development patterns of leaf area have been reported for different plant species and environments (Frazer et al. 2000; Gholz 1982; Hoff and Rambal 2003; Linder et al. 1987; Vose et al. 1994; Waring 1983). Models of LAI and plant growth which are based on the Chapman-Richards function have been widely reported in the literature over a number of years (Colbert et al. 2004; Fekedulegn et al. 1999; Lee 2000; Pienaar and Turnbull 1973; Zeide 1999) and these studies provide support to the belief that the Chapman-Richards function is also an appropriate model for this study.

$$\text{LAI} = c (1 - \exp^{-a \cdot \text{yrs}})^b \quad (2.1)$$

Parameters a and b are scale and shape descriptors of the curve respectively, and c is the maximum asymptote (Hunt 1982; Richards 1959). In Chapter 3 mathematical descriptions of the slope and age at inflection are given. Seasonal effects are also incorporated into the Chapman-Richards function in the following chapters.

CHAPTER 3

Methods and Materials

Approach

There are 3 methods for determining patterns of leaf area development in stands:

1) repeated measures of the same stand over time, 2) measurement of stands across a range of sites and ages, or 3) use well tested models with data collected from situations from 1 and 2 in which treatments are applied or gradients across natural environments are compared to determine factors that limit leaf area development (Vose et al. 1994).

This study incorporates measurements from both repeated measurements of the same trial, and measurements of trials across a range of sites and ages. With this type of data it will be possible to build a model representing maximum site leaf area index across New Zealand plantation forests.

In the case of this study the general development patterns of a forest canopy approaching a site maximum is simulated by small experimental areas with seedlings planted at high density. The main reasons for this are that it becomes possible to target and measure more uniform soil conditions within smaller areas and create a more rapid development of treatment effects within a reasonable time frame for study purposes.

Scope of this study

Leaf area index measurements were collected from a national Site Quality trial series (Watt et al. 2005). Establishment of 35 trial sites occurred over a three year period and repeated leaf area index measurements were made on average approximately four times a year as plants (averaging 4 - 5m in height at age 4) approached a maximum site LAI. The data presented in this study relates to the first 22 sites which have been harvested. A map in appendix 1 indicates the general geographic locations of the individual trial sites across New Zealand and broadly illustrates the diverse environmental and soil conditions these 22 sites represent.

Key assumptions made at the beginning of the study were:

- Other than the effects of site disturbance, treatment plots received the same light, nutrients and water at each individual location.
- The use of the Plant Canopy Analyser to estimate leaf area index for both species makes direct comparisons possible.
- The effects of dead foliage, branches and stem material on measured leaf area index would be dependent on tree size and species.
- The trials were established for sufficient time to monitor possible treatment changes and measure maximum site leaf area index.
- Effects of high density plantings on canopy development in very young stands are similar to those found in typical forestry regimes over much longer periods.

Trial design and layout

Plantation forests in New Zealand exist on 9 of the 15 different soil orders (Hewitt 1993) and trial sites representing soils from 99.2% of the New Zealand forest estate by area were established over a three year period. The 35 sites cover a broad range of climate and soil conditions across New Zealand (Table 3.1). At each site eight plots were planted in the winter after crop harvest (approximately 27 year old *Pinus radiata* D Don). Plots consisted of nine central measurement trees surrounded by two buffer rows, all at a spacing of 0.5 x 0.5 m (40,000 stems per hectare). Small plots (3 * 3 m) and high density plantings were used because soils vary considerably across a forest compartment. Using this technique it was possible to target more uniform soil conditions and create rapid development of treatment effects. The experimental design incorporated 2 species under 2 contrasting disturbance conditions, given 2 alternative fertiliser regimes (or 2³) factorial, replicated across 35 random locations.

Two tree species either *Pinus radiata* D Don (GF19) or *Cupressus lusitanica* Mills were planted in four separate plots at each trial site. Growth and form (GF) selection is explained by Burdon (1992). Consistency among seedling material was obtained by raising the same seedlot at the same nursery in Rotorua.

To study the effects of soil physical characteristics on LAI four plots at each site were located on both compacted and un-compacted (or undisturbed) soil. Field observations were used to determine areas of high harvest compaction prior to establishment. Seedlings were then planted in these areas or in undisturbed areas adjacent to these. Later soil bulk density was sampled to characterise site disturbance from each soil horizon to a depth of 1m using 100mm diameter intact cores, each 75mm deep (see later).

A fertiliser treatment was broadcast over half the plots. Nutrients were supplied in excess of plant requirements and various quantities were applied three times a year during the first year then at annual intervals. The elemental quantity in kg ha^{-1} applied at each site over the 4 year period was 690 N; 200 P; 558 K; 160 S; 40 Mg and 160 Ca.

The layout was arranged as a split plot with disturbance comprising the whole plots and fertiliser and species the subplots. Significant interactions were expected between site and treatments because of huge variations in characteristics across sites (see later).

Table 3.1 Comparison of mean annual climate, soil chemical and physical properties at the 35 established sites, with those found throughout New Zealand plantation forests. Characteristics of soil physical and chemical properties are shown for the top 100 mm of mineral soil for undisturbed plots sampled prior to planting.

	Trial sites		Plantation forests	
	Mean	Range	Min.	Max.
Mean annual temperature (°C)	11.5	8.6-15.5	8.0	15.6
Solar radiation (MJ m⁻² yr⁻¹)	14.3	12.0-15.4	12.4	15.4
Relative humidity^a(%)	79	69-87	66	87
Rainfall (mm yr⁻¹)	1 560	609-3 718	609	3 718
Soil bulk density (g cm⁻³)	1.0	0.5-1.4		
Total available water (% v/v)	19	9-32		
Soil carbon (%)	6.0	0.7-21.6		
Soil nitrogen (%)	0.29	0.02-0.67		
Total phosphorous (mg g⁻¹)	464	37-937		
pH	5.2	4.1-6.0		
Cation exchange capacity (cmol g⁻¹)	22	2-72		

^aRecorded at 0900 NZST after (Watt et al. 2005)

Weed control was applied one month after planting and then as required to keep plots free of competing vegetation. A mixture of the following selective herbicides in water was broadcast over the trees during the initial spray. Product amounts are given on an area basis and to ensure good coverage the mixture was applied at a calibrated application rate of 200 l ha⁻¹. Terbutylazine (15 l ha⁻¹), Clopyralid (5 l ha⁻¹), Haloxifop (3 l ha⁻¹). Then in the following site visits non selective herbicides were target sprayed at persistent weeds, but because of the close planting this was rarely required.

Dothistroma pini (Hulbary) causes premature defoliation in *P. radiata* (Gadgil 1984). This needle blight has a widely spread distribution throughout New Zealand and around 25% of the forest estate is susceptible during infection periods. Favourable infection conditions include a mean daily temperature of between 16 and 18 degrees with a wet leaf during this period of at least 10 hours. Control efforts using copper fungicide (active ingredient Cu at 5 kg ha⁻¹) and spray oil at labelled rates (2 l ha⁻¹) were applied with a mist blower to all plots during visits in September and January each year until harvest.

Tree growth measurements

Tree height and ground line diameters were measured annually during winter. Final measurements of height, diameter, maximum canopy width and live crown length were made at four years of age, when most sites were at a maximum site LAI. A Schumacher model (Schumacher 1939) which closely predicts the growth of tree diameter, height and volume index over time was compared with LAI development.

Measurements of specific leaf area (cm² g⁻¹) were made at plot harvest to help explain differences between species and sites. Three fascicles from the current foliage of five of the nine sample trees for both undisturbed and fertilised *P. radiata*, and two branches including current foliage from each of three trees in the four *C. lusitanica* plots (undisturbed, undisturbed and fertilised, disturbed and disturbed and fertilised) were collected. Both sets of samples were kept moist until they were processed soon after collection. *Pinus radiata* specific leaf area was measured according to (Johnson 1984) and this is based on volumetric displacement incorporating fascicle length and dry weight. *Cupressus lusitanica* foliage was measured with an automated leaf area meter (LAI 3100 LI-Cor Lincoln NE, USA). The instrument was calibrated with a known sample size (circular disc 50cm²), then *C. lusitanica* specific leaf area was measured by placing the collected foliage on the conveyor of the LAI 3100 to determine the silhouette leaf area. Following this samples were dried at 70 °C and weighed. The specific leaf area was then determined as follows:

$$\text{SLA} = \text{foliage area (cm}^2\text{)} / \text{dry weight (g)} \quad (3.1)$$

Mean values for site and species were compared using a Student-Newman-Kuels means comparison.

Plant canopy analyser measurements

Leaf area index was determined using a LI-COR LAI-2000 Plant Canopy Analyser (LI-COR 1990). Values are predicted from the amount of radiation intercepted beneath the canopy and are based on the Beer-Lambert law (Dalla-Tea and Jokela 1991; Smith et al. 1991). This is basically a probability function that depends on the amount of radiation reaching the ground (Equation 3.2). When less light reaches the ground higher leaf area values are estimated (also see Figure 8.1). This theory should only be assumed valid for continuous canopies and because of this it is well suited to canopies such as those of agricultural crops and plantation forests:

$$\text{LAI} = \log (I_z / I_0) / -k \quad (3.2)$$

where I_z is the photosynthetically active radiation (PAR) 400-700µm transmitted through the canopy, I_0 is the PAR above the canopy and k is called the light extinction coefficient (a constant), which varies with light intensity, different tree species because of the shape and orientation of leaves and the amount of non photosynthetic tissue (Waring 1983).

The LAI-2000 instrument consists of an optical sensor, housed at the end of a lance attached to a data storage unit (Welles and Norman 1991). The optical sensor uses fisheye lens technology to collect and focus diffuse light (<490nm) from five zenith angles onto five concentric detectors. Samples are rapidly collected and a real time assessment of LAI can be provided to the operator as measurements are made. The data is stored at the completion of a designated number of samples for processing later.

The sampling strategy utilised in this study consisted of 24 measurements per plot, 6 below canopy and 2 above canopy samples along each of the four sides of the 3x3m plots. Above canopy measurements helped to account for changing light conditions that may have varied from assessments under clear sky surroundings to evenly overcast at consecutive sites. A 180 degree lens cap prevented interference from

changing shadows cast by the operator and restricted the field of view to the area forward of the lens within the plot. The literature search found several studies that discuss possible errors and violations of the assumptions associated with LAI measurements; some suggest possible corrections for the LAI-2000 (Leblanc and Chen 2001; Pokorny and Marek 2000; Stenberg 1996).

The mean tilt angle which represents the orientation of the foliage is automatically determined by the LAI 2000 using a technique best explained by the manual (LI-COR 1990; Welles and Norman 1991). Horizontal foliage is equivalent to 0 degrees and vertical foliage is represented by 90 degrees. The mean monthly values were calculated from the data collected over the four years. Comparisons of mean values for each plant species across seasons were made.

Site characteristics

During trial establishment soil chemical and physical characteristics were collected by Landcare Research staff. Chemistry samples were taken within plots and soil physical samples were taken from the edge of the planted areas and from an undisturbed profile pit within the trial area (Watt et al. 2005). Five soil chemistry samples were collected from each of the four disturbed and undisturbed plots to a depth of 10 cm. Samples were bulked by disturbance class and mixed before analysis. Landcare Research staff analysed the soil samples following standard methods (Blakemore et al. 1987) for pH in water, total carbon, nitrogen, total phosphorous, Bray P, Olsen P, P retention and exchangeable bases and reported on an oven dried (105°C) basis. Soil physical properties were collected from four small sample pits directly adjacent to the plots in the mineral soil to a depth of 20cm and then from the remaining horizons in the soil pit at greater depth (to 100cm). Intact cores 10cm in diameter and 7.5cm deep were used to sample the bulk density, particle density, air filled porosity (-10 kPa matric potential), macroporosity (-5 kPa matric potential) and total available water according to (Gradwell 1972).

Soil microbial biomass (SMB) was determined from additional soil samples which were collected from beneath the densely planted plots at 16 of the locations during January and February, 2004. Mineral soil samples (0-10cm) were gathered from under both tree species and SMB nitrogen was determined using the Kjeldahl method

(Vance et al. 1987). Comparisons were made between the SMB, soil water content and the plot leaf area at the time of sampling.

Several on-site climatic characteristics were measured. Temperature and relative humidity were measured every 10 minutes with a Hobo Pro series temperature (± 0.1 Deg. C) and relative humidity logger enclosed in a protective screen and fixed at 3m height. Solar radiation was measured at 3.5m height every 10 minutes with calibrated GaAsP photodiodes (300-680 μ m) and logged to a Hobo 4 channel external storage unit and rainfall was measured using a tipping bucket (± 0.1 mm) at each site. However the analysis in the following chapters was based largely on long term climate data (Leathwick and Stephens 1998) because of the efficiency that accurate mean values could be obtained. As, detailed temporal climate characteristics were of little assistance for the following analysis and comparisons. Altitude, aspect and slope were also recorded for each site.

Analysis

Data from 22 sites representing forest soils from 92.6% of New Zealand plantation forest by area were utilised for the statistical analysis in the following chapters. The raw dataset from which the models were developed represent different plots, at different sites, during different times of the year (Fig's. 3.3 & 3.4). A Chapman-Richards 3 parameter non linear equation (Richards 1959) was fitted to both the pooled and individual site data using PROC NLIN (SAS 2000). This sigmoidal function allowed maximum asymptote values, the rate of LAI development (Equation 3.2) and the age at the inflection (Equation 3.3) to be contrasted (see also Equation 2.1), where parameter c = the maximum site LAI ($m^2 m^{-2}$), and the first derivative of the unit-less scale and shape parameters a and b give the slope (or rate = $m^2 m^{-2} yr^{-1}$) of the curve at the inflection point (Lee 2000);

$$\text{rate} = -ab ((c - 1) / c)^{c-1} \quad (3.3)$$

and the age at the inflection point (years), where the slope is at a maximum;

$$\text{inflection age} = \log(c) / b \quad (3.4)$$

SAS non linear convergence criteria were met for 87% (153 out of 176) of the plots across the 22 individual sites. The remaining 13% of plots provided insufficient data to predict an asymptote. Sites and plots removed from the analysis are listed in appendix 3. Significant treatment effects at $p < 0.05$ for species, fertiliser, site disturbance and their interactions on the modelled variables of LAI_{max} , rate of development and age of inflection were tested using ANOVA (SAS 2000) with a split plot design. Mean site values were compared using Duncan's multiple range test. Productivity measures of tree height, root collar diameter and the log transformed volume index were tested using an analysis of covariance because the initial root collar diameter explained a significant amount of variation across sites and seedlings.

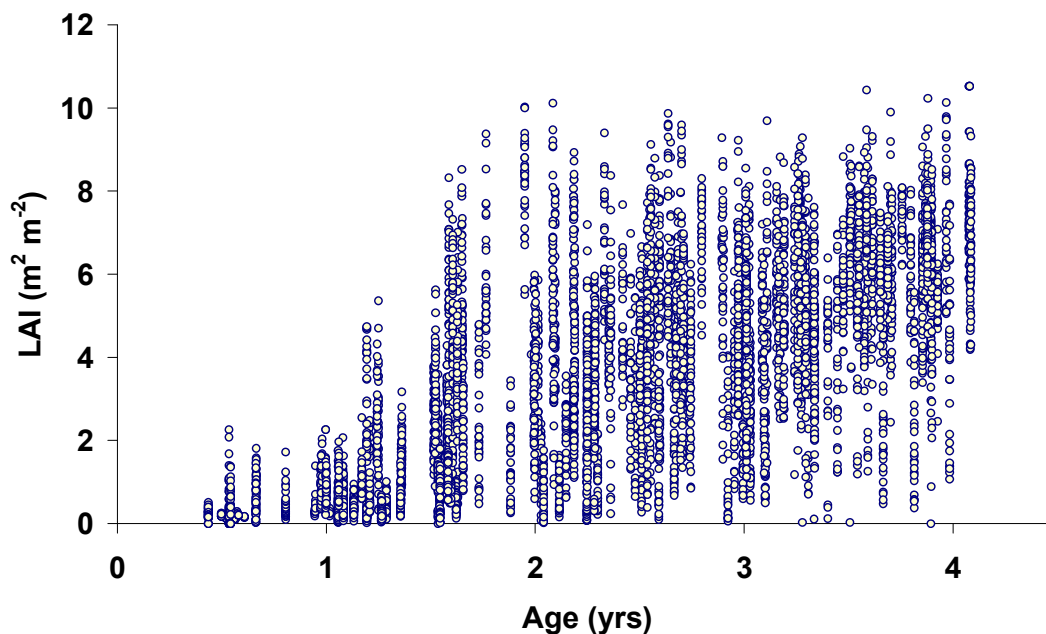


Figure 3.2 Distribution of LAI for plots sampled over the course of the experiment.

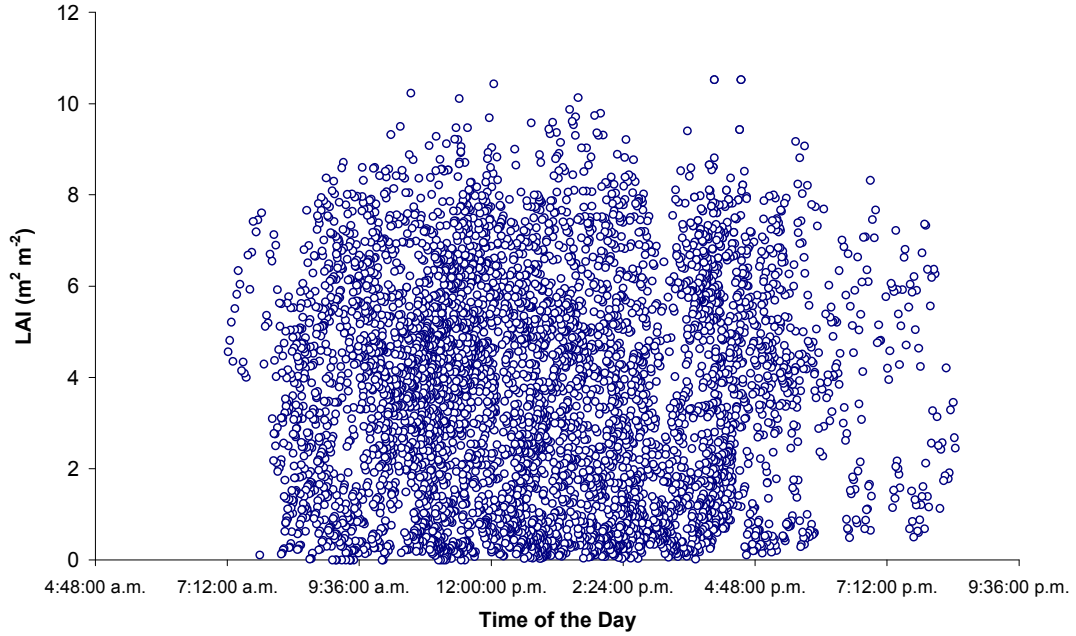


Figure 3.3 Time of sampling for all plots per site, data is pooled across all years and sites.

A seasonal growth pattern was added to the Chapman-Richards LAI function and results are presented in Chapter 5. This modelling is an adaptation of the function developed by Kimberly and Richardson (2004). Variance introduced by individual sites was characterised using site as a dummy variable in the model. The curvilinear relationship has an increasing amplitude until the point of inflection and then reduces as the curve approaches the asymptote (Kimberley and Richardson 2004) (Equations 3.5 & 3.6).

$$\text{seasonal effect} = g * (\sin(2 * \pi * (tstart + age - f)) - \sin(2 * \pi * (tstart - f))) \quad (3.5)$$

$$LAI = c * (1 - \exp(-a * (age + \text{seasonal effect})))^b \quad (3.6)$$

Where the units of the seasonal effect = years, parameter g = the amplitude of seasonal growth (fraction of annual leaf area index) and f = time of the year when the growth is at a maximum, (represented as a fraction of the year e.g. $0.91 = 332^{\text{nd}}$ day of the year). Age = plot age in years, $tstart$ = planting age relative to the 1st of January (e.g. $(10/7/01 - 01/01/01)/365 = 0.5205$).

Multiple linear regression analysis was performed using a forward selection procedure (SAS 2000). The dependent variables; maximum site LAI (LAI_{max}), rate of leaf area development and age of inflection were regressed against a range of climatic, topographic and soil variables. Models for fertilised and non fertilised *P. radiata* and *C. lusitanica* were built by adding the most significant independent variable first and proceeding variables were only incorporated if the parameters and overall model remained significant ($p < 0.05$). Data was pooled across disturbed and undisturbed plots because disturbance was shown to have insignificant affects across sites and species at the harvest age (see results later).

Principle component analysis was used to explore the variation between climatic characteristics across sites. The contributions of average daily solar radiation, average daily temperature, average maximum temperature, average minimum temperature, mean annual relative humidity, and mean annual rainfall and mean annual evaporation rates across sites were compared. A bi-plot of the first two principle components was produced and this is presented in Chapter 4.

Seasonal differences between the locations were subsequently examined with SAS non linear modelling, using the function:

$$\text{Average daily temperature (}^{\circ}\text{C)} = a * \text{COS} (b * (\text{Julian day}-c)) + d \quad (3.7)$$

Parameters a, b, c and d describe the frequency and the amplitude of the curve. A selected number of sites representing the temperature range across all sites are presented graphically.

Further details of specific statistical analysis techniques are described in the course of the relevant chapters.

CHAPTER 4

Effects of Soil and Climate on *Cupressus lusitanica* and *Pinus radiata* Leaf Area Index in Densely Planted Trials across New Zealand Forest Plantations

INTRODUCTION

LAI development of small highly stocked trials of *Cupressus lusitanica* and *Pinus radiata* with split plot treatments of fertiliser and site disturbance were compared with soil, climate and topographic characteristics. Seasonal influences of these characteristics are discussed in Chapter 5 and comparisons between leaf area index and tree growth are examined in Chapter 6.

Leaf area measurements, made with a Li-Cor Plant Canopy Analyser were collected approximately every four months from 22 trials sites. The leaf area index sampling procedure and details on the collection of the soil and climate properties are given in the previous chapters.

In the following chapters it will also be shown that maximum site leaf area can be used to predict site quality and this leaf area measure is dependent on the site conditions when growth is in balance with the ability of the site to provide resources. Additionally, it will be shown that maximum leaf area index can be assessed with a single assessment of leaf area prior to the harvest of a mature crop (such as *P. radiata* or *C.lusitanica*). This is because near harvest, effects of previous management/silvicultural operations are of little consequence (see later chapters).

RESULTS

Treatment effects of site disturbance, species and fertiliser

The calculated maximum site LAI (LAI_{max}) was significantly different across species (Table 4.1). The mean *P. radiata* and *C. lusitanica* values across sites and plots were $6.47 (\pm 2.29 \text{ Std.}) \text{ m}^2 \text{ m}^{-2}$ and $7.28 (\pm 2.59 \text{ Std.})$ respectively. *Cupressus lusitanica* leaf area index was 11% greater than *P. radiata* (Table 4.2). Disturbance did not have an affect on LAI_{max} , but fertiliser did. The species by fertiliser interaction was not significant ($p = 0.1801$) and this may indicate a consistent fertiliser effect across species. Further testing is required. There was a large range in LAI_{max} across sites; values were between 2.9 and $11.8 \text{ m}^2 \text{ m}^{-2}$ for *P. radiata* and $3.1\text{-}12.6 \text{ m}^2 \text{ m}^{-2}$ for *C. lusitanica* (Table 4.3). A Duncan's multiple range comparison distinguished 11 overlapping groups in the *C. lusitanica* and 8 in the *P. radiata* (Appendix 4). LAI_{max} showed a four fold range in values compared with a 3 fold range for site index across New Zealand, this indicates LAI_{max} is likely to be a more sensitive indicator of site quality than site index. Comparisons between growth and LAI are explored in Chapter 6.

Table 4.1 Significance of applied treatments and interaction effects on LAI_{max} , rate of LAI development and age of inflection across 22 plantation forest sites.

<i>Source</i>	<i>df</i>	<i>LAI_{max}</i> ($\text{m}^2 \text{ m}^{-2}$)	<i>Rate of LAI</i> <i>development</i> ($\text{m}^2 \text{ m}^{-2} \text{ yr}^{-1}$)	<i>Age of</i> <i>Inflection</i> (<i>yrs</i>)
<i>mean square values</i>				
<i>Whole plot</i>				
Disturbance (dist)	1	0.37	2.26	0.13
Site	21	18.23***	97.42***	1.32***
error	20	1.72	10.19	0.16
<i>Split plot</i>				
Species (sp)	1	26.64***	11.16**	0.25*
sp*dist	1	0.56	1.68	0.01
Fertiliser (fert)	1	6.00*	57.20***	0.07
fert*dist	1	0.04	15.57**	0.01
fert*sp	1	3.94	144.55***	0.22*
fert*sp*dist	1	0.90	1.96	0.00
error	65	1.18	8.42	0.09

Given a source the mean squares are significantly different from the appropriate mean errors when $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***)

The rate of LAI development was significantly different between species ($p < 0.0001$). Fertiliser significantly ($p < 0.0001$) increased the rate of LAI development across species by around 21%. At sites with low nutrients or significant site disturbance, fertiliser increased the rate of LAI development as shown by the significant ($p < 0.001$) fertiliser by disturbance interaction. A highly significant fertiliser by species interaction for the rate of leaf area development indicated that the rate of response differed for each plant species. On average *C. lusitanica* appeared to better utilise fertiliser and increase the rate of LAI development, but *P. radiata* LAI development rate was consistent with unfertilised (Table 4.2) possibly indicating some other limit on development such as moisture. Consistent insignificant effects of disturbance were shown across the different species.

The age at which leaf area development began to slow was significantly different between species ($p = 0.0060$) and the species by fertiliser interaction ($p < 0.01$). The age of inflection varied across sites from 0.84 – 2.59 years (Table 4.3) and on average leaf area accumulation began to slow 1.49 and 1.62 years after planting for *C. lusitanica* and *P. radiata* respectively. This occurred after peak foliage growth (approximately December) during the second summer season suggesting a self shading effect of the new foliage on the previous year's foliage.

LAI development was slowest at the Hochstetter site. *Cupressus lusitanica* LAI developed fastest at the Glengarry forest site, while *P. radiata* developed fastest at the Woodhill site (Table 4.3).

Table 4.2 Comparison of plot means for LAI_{max} , rate and age of inflection across forest sites. Standard errors are presented in brackets. C = *C. lusitanica*, R = *P. radiata*, F = fertilised, N = no fertiliser, D = disturbed, U = undisturbed.

TREATMENT			LAI_{max} ($m^2 m^{-2}$)	Rate of LAI development ($m^2 m^{-2} yr^{-1}$)	Age of Inflection (yrs)
Species	Fertiliser	Disturbance			
C	F	D	7.12 (0.34)	8.93 (2.36)	1.47 (0.14)
C	F	U	7.06 (0.45)	5.56 (1.51)	1.43 (0.11)
C	N	D	6.89 (0.65)	3.80 (0.66)	1.49 (0.18)
C	N	U	7.98 (0.71)	4.97 (0.95)	1.55 (0.13)
R	F	D	6.85 (0.59)	4.04 (0.82)	1.62 (0.11)
R	F	U	6.85 (1.04)	3.81 (0.46)	1.64 (0.14)
R	N	D	6.55 (0.52)	4.79 (1.18)	1.58 (0.12)
R	N	U	6.55 (0.48)	4.89 (1.00)	1.60 (0.11)

Table 4.3 A comparison of individual site means for LAI_{max} ($m^2 m^{-2}$), rate ($m^2 m^{-2} yr^{-1}$) and age of inflection (yrs) for *C. lusitanica* and *P. radiata*, ranked by mean annual temperature, high to low.

Site	<i>C. lusitanica</i>				<i>P. radiata</i>		
	temp (°C)	LAI_{max} ($m^2 m^{-2}$)	Rate of LAI development ($m^2 m^{-2} yr^{-1}$)	Age of Inflection (yrs)	LAI_{max} ($m^2 m^{-2}$)	Rate of LAI development ($m^2 m^{-2} yr^{-1}$)	Age of Inflection (yrs)
Woodhill	15.3	5.44	5.93	0.93	4.35	15.32	0.75
Riverhead	14.6	3.05	3.47	1.04	2.86	2.50	1.35
Mahurangi	14.2	6.60	10.76	1.07	4.51	8.12	1.07
Tairua	14.1	7.34	7.27	1.51	4.53	5.16	1.26
Bulls	13.2	10.76	2.68	0.78	6.28	3.45	1.30
Tikitere	12.4	6.93	10.15	1.05	6.88	6.29	1.16
Glengarry	12.3	6.97	24.13	1.15	5.68	9.23	1.25
Mangatu	12.1	5.50	2.97	1.03	5.06	3.97	1.35
Kinleith	11.9	6.87	8.39	1.29	5.77	5.33	1.23
Ashley	11.5	6.50	3.63	1.52	6.90	3.14	1.48
Rai Valley	11.5	7.66	2.41	0.84	8.53	3.12	1.67
Ngaumu	11.4	7.33	11.40	1.56	7.31	3.69	1.43
Kaingaroa	11.4	8.43	2.73	2.22	7.28	4.11	2.29
Golden Downs	11.2	6.92	2.66	1.59	6.82	2.72	1.80
Okuku	11.2	7.93	3.93	1.69	6.56	1.80	2.07
Waimarino	11.0	9.61	3.31	1.73	5.30	3.23	1.88
Kaniere	10.9	7.82	2.81	1.40	6.13	2.47	1.51
Hochstetter	9.7	5.64	0.57	1.82	4.44	0.71	1.85
Karioi	9.5	6.96	5.68	1.36	11.76	2.37	1.89
Tekapo	8.6	4.58	1.31	2.40	7.38	2.54	1.92
Catlin's	8.6	12.6	3.34	2.44	9.15	3.12	2.16
Longwoods	8.6	9.43	3.44	1.94	9.94	2.62	3.03

Averaged across sites the leaf area development pattern showed similar trends across fertiliser and disturbance treatments (Fig. 4.1), but differed by species. Fertilised plots showed the highest leaf area by age 4 and *C. lusitanica* showed a greater response to fertiliser. The disturbed *P. radiata* still showed a slight upward trend at harvest indicating a site maximum was not yet achieved.

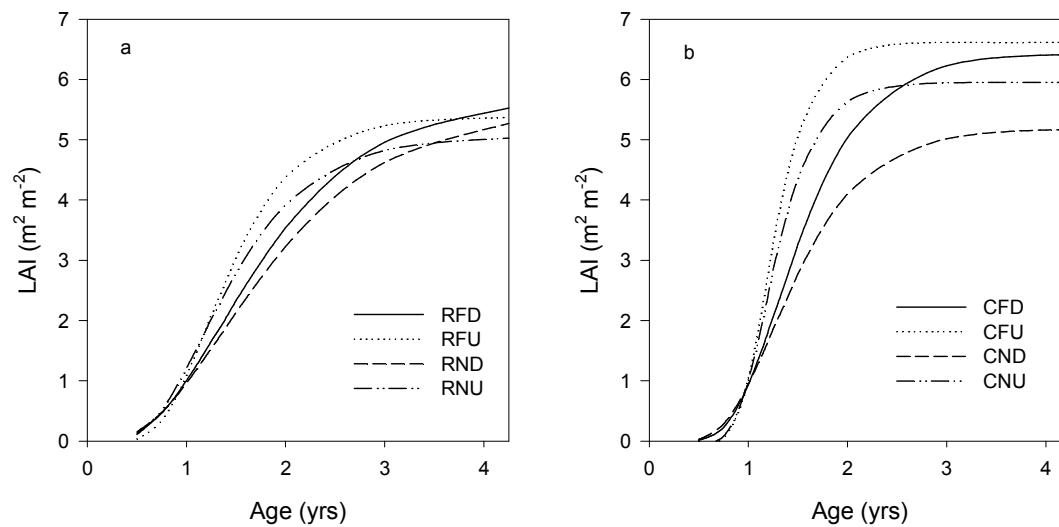


Figure 4.1 Modelled leaf area index development for a) *P. radiata* and b) *C. lusitanica* for each of the four fertiliser and site disturbance combination of treatments over the trial period. R=*P.radiata*, C=*C.lusitanica*, F= fertilised, N=non fertilised, D= disturbed and U = undisturbed.

Climate

Climate differences across sites were examined using principle component analysis and significant components were identified. The first showed that the dominant component was a combination of temperature and solar radiation which explained 50.4% of the climatic variations across sites (Fig. 4.2). The second significant linear component was related to moisture, this explained an additional 35.8% of the variation across sites. A further 13.8% contributes to unexplained climatic variation across sites. A comparison below shows 7 selected sites from the 22 and illustrates the minimum and maximum range and seasonal variation in mean monthly modelled temperatures across each site (Fig. 4.3).

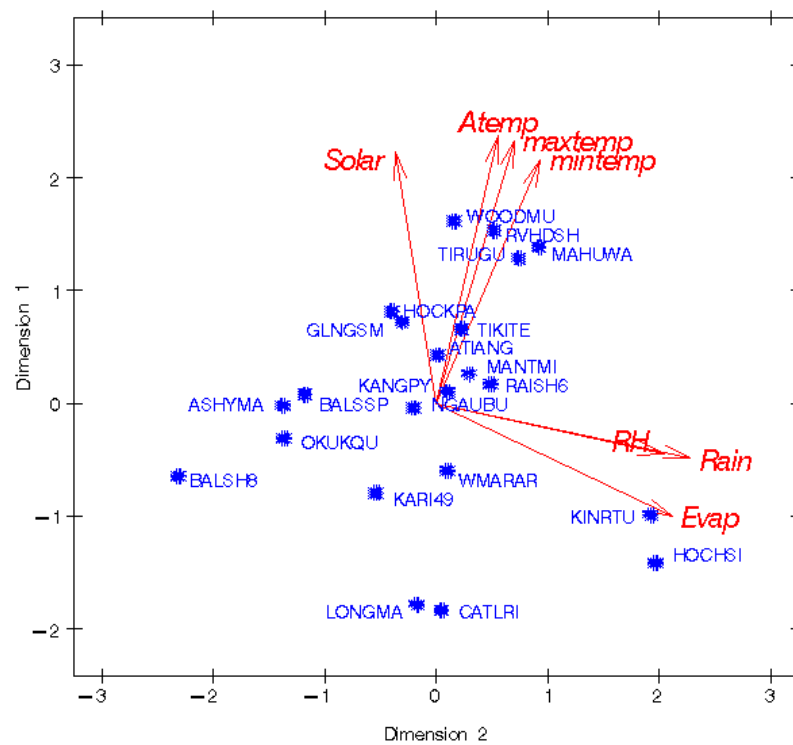


Figure 4.2 SAS principle component bi-plot comparing the influences of temperature and solar radiation with rainfall, relative humidity and evaporation across sites.

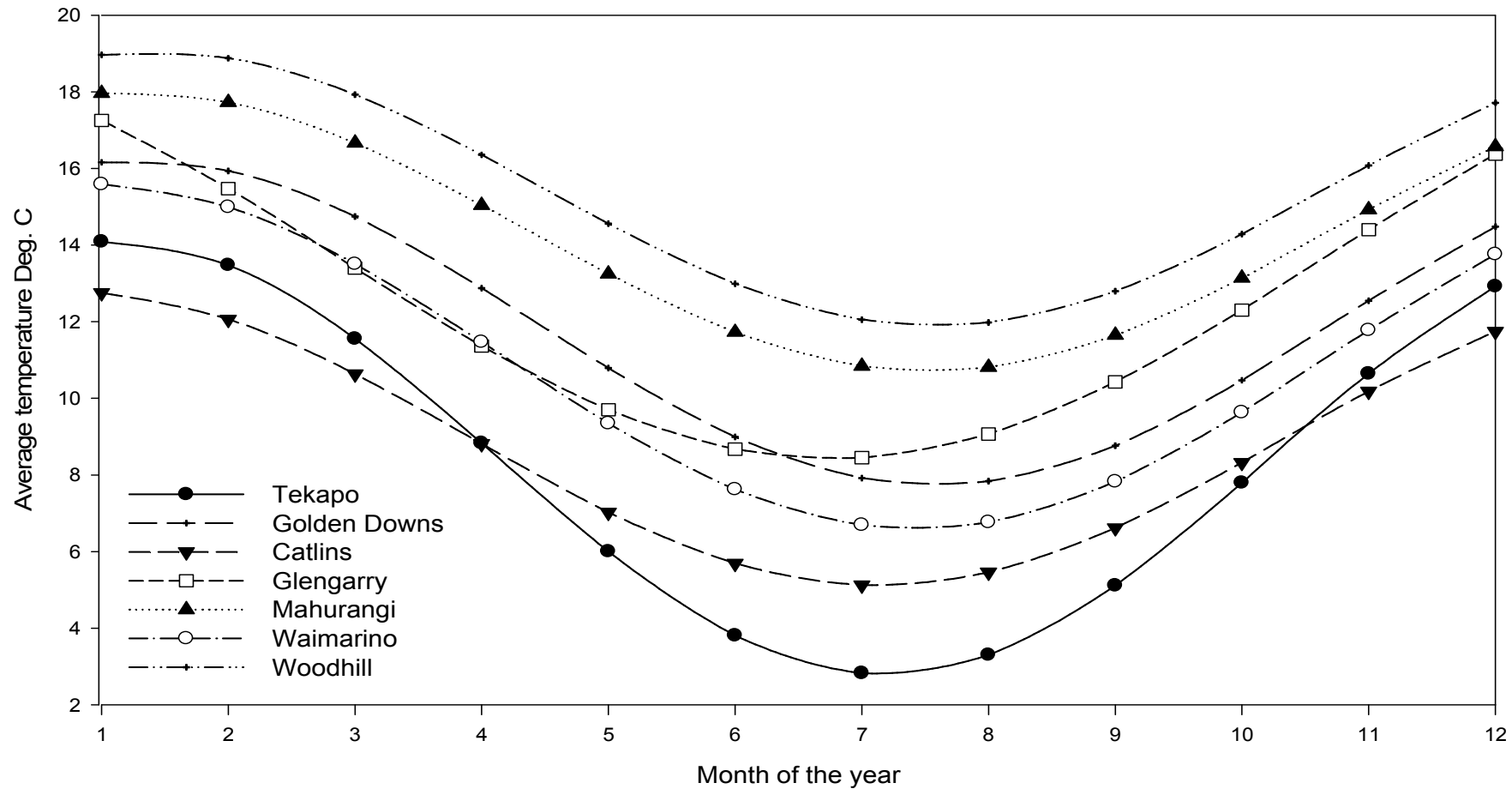


Figure 4.3 Comparison of the average daily temperature from the on-site metrological data, for selected trial sites, over the course of a year. January = 1 All 22 sites fall within the limits shown by the minimum (Tekapo) and maximum (Woodhill) temperatures.

Mean annual temperature was significantly and positively related with the rate of leaf area development (Table 4.4). Both LAI_{max} and the age at inflection showed significant negative correlations with temperature (Fig. 4.4) and light (Fig. 4.5). On average the correlations between temperature and leaf area development were slightly improved compared with PAR (Photosynthetically Active Radiation 400-700 μ m).

Table 4.4 Pearson correlation coefficients and significance in brackets of mean annual temperature, PAR and vapour pressure deficit with LAI_{max} , rate and age of inflection, for *C. lusitana* and *P. radiata* across the 22 trial sites.

	<i>C. lusitana</i> (n=72)			<i>P. radiata</i> (n=81)		
	LAI_{max}	Rate	Age	LAI_{max}	Rate	Age
Annual Temperature ($^{\circ}$C)	-0.5795 (<0.0001)	0.2284 (0.0631)	-0.6082 (<0.0001)	-0.5971 (<0.0001)	0.4948 (<0.0001)	-0.6894 (<0.0001)
PAR ($MJ\ m^{-2}\ d^{-1}$)	-0.6037 (<0.0001)	0.2495 (0.0476)	-0.4809 (<0.0001)	-0.3360 (0.0019)	0.3364 (0.0021)	-0.5290 (<0.0001)
VPD (kPa)	0.5323 (<0.0001)	-0.2767 (0.0234)	0.5576 (<0.0001)	0.5928 (<0.0001)	-0.5184 (<0.0001)	0.6800 (<0.0001)

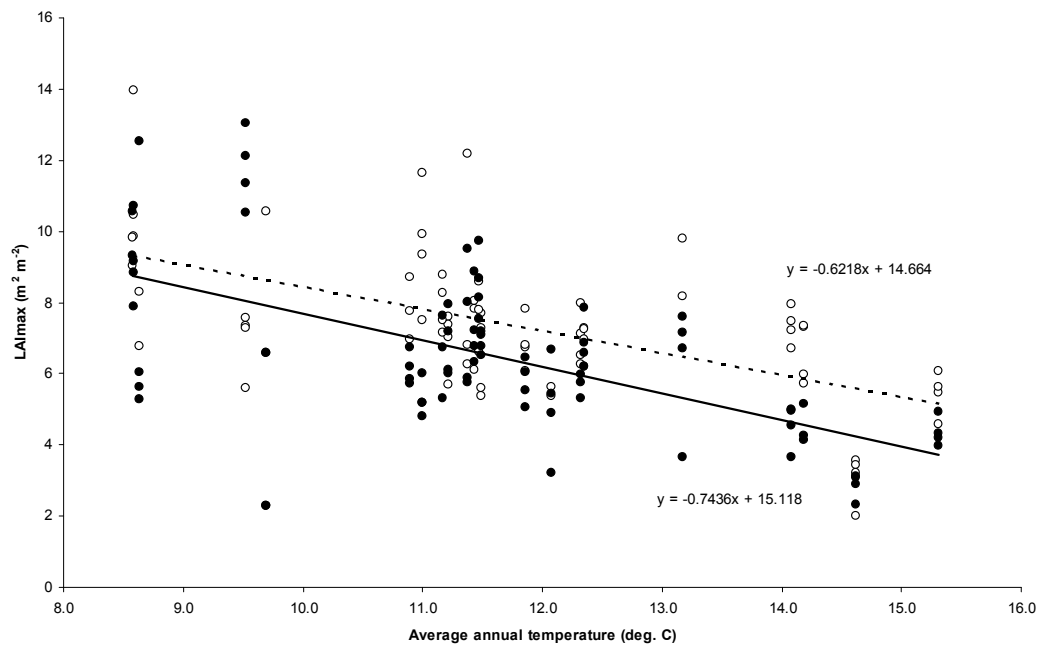


Figure 4.4 Relationships between average annual temperature for sites and LAI_{max} .

P. radiata (●) treatments are represented by the solid line and *C. lusitana* (○) by the dashed line.

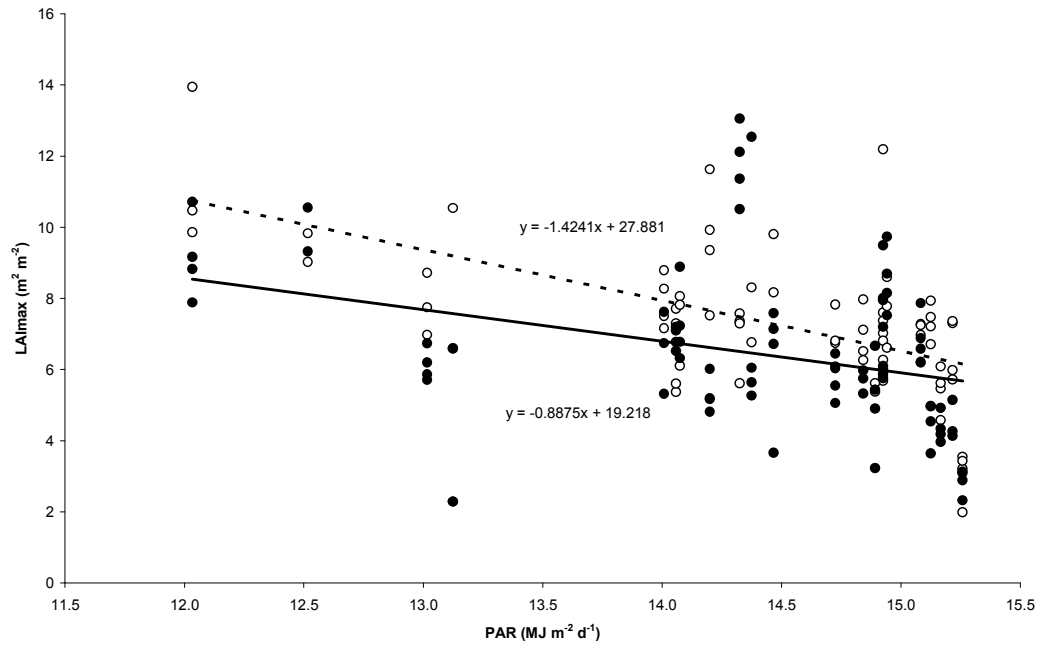


Figure 4.5 Relationships between mean annual PAR across sites and LAI_{max} .

P. radiata (●) treatments are represented by the solid line and *C. lusitana* (○) by the dashed line.

Vapour pressure deficit (VPD) was significantly related to LAI_{max} , rate and age of inflection (Table 4.4). Sites exhibiting a young age of inflection (that is less than 1.5yrs old) were related with a mean VPD of between -1.6 and -0.8 (kPa) (Fig. 4.6).

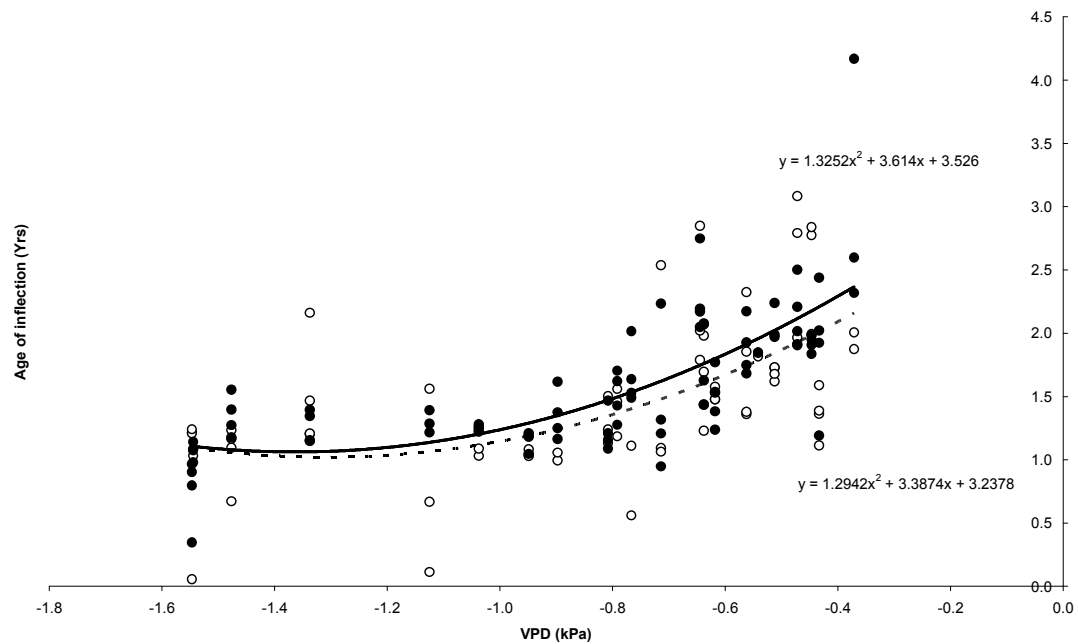


Figure 4.6 Relationships between mean annual VPD across sites and age of inflection. *P. radiata* (●) treatments are represented by the solid line and *C. lusitana* (○) by the dashed line.

Soil microbial biomass (SMB)

At measurement in late summer of 2004, soil microbial biomass was significantly and negatively associated with LAI at the time of sampling ($p = 0.0023$, $r = -0.5275$) and positively with mean annual rainfall ($p = 0.0006$, $r = 0.5806$) for samples across both tree species. Increased LAI was related to lower SMB and both LAI and SMB were positively and significantly influenced by mean annual rainfall. So it is speculated

Physical soil characteristics

Soil physical properties explained 16.8 % of the variation in LAI_{max} across sites. Soil physical characteristics were also related with the rate and age of inflection (Table 4.5). Pearson correlations between the mean water holding capacity and age of inflection were positive and significant for both species, but only when the data was pooled across species was there a significant relationship between soil water holding capacity and LAI_{max} ($p = 0.0022$ with $r = 0.2407$). Soil bulk density was negatively related to LAI_{max} and the age of inflection for both species, which means lower bulk densities were associated with greater LAI_{max} . LAI_{max} for the different species was often correlated with different soil physical characteristics and overall *P.radiata* LAI_{max} was correlated with fewer soil physical characteristics. This may indicate that *P. radiata* is less sensitive to changes in soil physical characteristics compared with *C. lusitanica*.

Table 4.5 Pearson correlation coefficients and probability of significance (below) is presented for soil physical characteristics of *C. lusitanica* and *P. radiata* plots across 22 trial locations. Bold numbers highlight significant correlations.

<i>Soil physical variables</i>	<i>C. lusitanica</i>			<i>P. radiata</i>		
	<i>LAI_{max}</i> (m ² m ⁻²) <i>n</i> = 72	<i>Rate of LAI development</i> (m ² m ⁻² yr ⁻¹) <i>n</i> = 72	<i>Age of Inflection</i> (yrs) <i>n</i> = 67	<i>LAI_{max}</i> (m ² m ⁻²) <i>n</i> = 81	<i>Rate of LAI development</i> (m ² m ⁻² yr ⁻¹) <i>n</i> = 81	<i>Age of Inflection</i> (yrs) <i>n</i> = 81
Water holding capacity (% by mass)	0.3970 0.0006	0.0819 0.5099	0.2369 0.0451	0.1503 0.1751	-0.2081 0.0623	0.4814 <0.0001
Soil bulk density (g cm ⁻³)	-0.4679 <0.0001	-0.2482 0.0429	-0.2742 0.0197	-0.2334 0.0337	0.2296 0.0392	-0.3933 0.0003
Particle density (g cm ⁻³)	-0.1708 0.1514	-0.3293 0.0065	-0.1817 0.1266	-0.1380 0.2133	0.2817 0.0108	-0.2736 0.0135
Total porosity (%,v/v)	0.5354 <0.0001	0.1775 0.1507	0.3162 0.0068	0.2110 0.0555	-0.1336 0.2343	0.4033 0.0002
Macro porosity (%,v/v)	0.3532 0.0023	0.1005 0.4185	0.0194 0.8714	0.1061 0.3396	0.2234 0.0450	0.0888 0.4307
Readily available water (%,v/v)	0.1133 0.3469	0.2796 0.0230	0.3078 0.0090	0.1066 0.3435	-0.0311 0.7855	0.0449 0.6946
Total available water (%, v/v)	-0.0356 0.7684	0.0716 0.5677	0.2413 0.0427	-0.0458 0.6849	-0.1834 0.1058	0.0194 0.8650
Field available water (%,v/v)	0.2009 0.0906	-0.0130 0.9167	0.1534 0.1983	0.0328 0.7688	-0.3719 0.0006	0.3505 0.0013
Penetration (kPa)	-0.2680 0.0260	0.1759 0.1645	-0.0523 0.6697	0.2576 0.0219	0.0465 0.6881	-0.1670 0.1465
Topsoil depth (cm)	0.0787 0.5237	0.0040 0.9751	-0.1638 0.1787	-0.1623 0.1531	-0.0798 0.4901	-0.1451 0.2081
Sand (%)	-0.0357 0.7661	0.0543 0.6628	-0.1152 0.3352	0.1187 0.2850	0.2998 0.0065	-0.1664 0.1376
Silt (%)	0.0956 0.4244	-0.1168 0.3466	0.1386 0.2457	-0.1174 0.2904	-0.3203 0.0036	0.1815 0.1049
Clay (%)	-0.0616 0.6070	-0.0349 0.7792	0.0717 0.5493	-0.0456 0.6823	-0.2502 0.0243	0.1009 0.3700

Nutrients

Soil chemical characteristics explained 18.1 % of the variation in LAI_{max} across sites. Fertiliser significantly ($p = 0.0232$) increased LAI_{max}. For *C. lusitanica* the age of inflection was not significantly correlated with soil nutrients, but the rate of development was positive and significantly related to total phosphorous ($p = 0.0018$) and its organic and inorganic components, nitrogen ($p = 0.0020$) and pH ($p = 0.0109$). LAI_{max} was positively influenced by soil carbon ($p = 0.0028$), nitrogen ($p = 0.0011$),

organic phosphorous ($p = 0.0041$), cation exchange capacity (CEC) and exchangeable K (Table 4.6).

In close association LAI_{max} of the *P. radiata* plots was also significantly related to soil carbon, nitrogen, phosphorous and CEC but not exchangeable potassium, and in further contrast with *C. lusitanica* the age of inflection was correlated with a number of variables such as; pH, carbon, nitrogen, and the CEC (Table 4.6). Like *C.lusitanica* the age of inflection was significantly related to soil acidity and in general as the pH of the soils was less acidic the rate of LAI development increased.

Table 4.6 Significant Pearson correlation coefficients (*p*-values below), for soil nutrient characteristics related to LAI_{max}, rate and age of inflection and for *C. lusitana* and *P. radiata* across trial sites. Bold numbers highlight significant correlations.

Soil nutrient variable	<i>C. lusitana</i>			<i>P. radiata</i>		
	LAI _{max} (m ² m ⁻²) n = 72	Rate of LAI development (m ² m ⁻² yr ⁻¹) n = 72	Age of Inflection (yrs) n = 67	LAI _{max} (m ² m ⁻²) n = 83	Rate of LAI development (m ² m ⁻² yr ⁻¹) n = 81	Age of Inflection (yrs) n = 81
pH	-0.2133	0.3092	-0.1636	-0.0747	0.4074	-0.2882
	0.0721	0.0109	0.1698	0.5023	0.0002	0.0091
C	0.3470	0.09792	0.1771	0.3702	-0.1487	0.4917
	0.0028	0.4305	0.1368	0.0006	0.1853	<0.0001
N	0.3782	0.3702	0.1236	0.3803	-0.1170	0.3417
	0.0011	0.0020	0.3008	0.0004	0.2982	0.0018
C to N	-0.0240	-0.2678	0.1591	0.1079	-0.2107	0.4516
	0.8417	0.0285	0.1820	0.3314	0.0591	<0.0001
P Olsen	0.0835	0.0111	0.0462	-0.0358	0.1165	-0.1261
	0.4856	0.9287	0.6998	0.7479	0.3003	0.2620
P Bray	-0.1167	0.1301	-0.1973	-0.0963	0.2326	-0.2803
	0.3289	0.2939	0.0967	0.3863	0.0367	0.0112
P inOrg	0.0082	0.3278	-0.2150	0.0710	0.3931	-0.2606
	0.9452	0.0068	0.0698	0.5235	0.0003	0.0188
P Org	0.3347	0.3321	0.1921	0.3490	-0.0246	0.1477
	0.0041	0.0060	0.1060	0.0012	0.8275	0.1884
P total	0.2373	0.3741	0.0462	0.2816	0.1564	-0.0088
	0.0447	0.0018	0.7003	0.0099	0.1632	0.9382
P ret	0.2044	0.3050	0.0090	0.2556	-0.1092	0.1607
	0.0850	0.0121	0.9404	0.0197	0.3319	0.1519
CEC	0.3662	0.0106	0.1261	0.3820	-0.2556	0.4901
	0.0016	0.9319	0.2912	0.0004	0.0213	<0.0001
Sumbases	0.1209	0.1131	0.0182	0.1223	-0.0621	0.1627
	0.3119	0.3622	0.8793	0.2708	0.5817	0.1467
BaseSat	-0.1468	0.0566	-0.1049	-0.1188	0.3740	-0.1747
	0.2187	0.6493	0.3804	0.2850	0.0006	0.1187
ExCa	0.0837	0.1225	0.0282	0.0842	-0.0771	0.1034
	0.4845	0.3232	0.8142	0.4493	0.4937	0.3584
ExMg	0.1466	-0.0420	-0.0673	0.1944	0.0095	0.2745
	0.2191	0.7360	0.5744	0.0783	0.9331	0.0131
ExK	0.2824	0.1540	0.1821	0.2010	0.0234	0.2393
	0.0162	0.2135	0.1258	0.0684	0.8354	0.0314
ExNa	0.1360	0.0480	-0.1404	0.02424	-0.0415	0.1235
	0.2546	0.6998	0.2396	0.8278	0.7131	0.2720

Topography

On average topographic characteristics were found to only contribute 3.4 % of the variation in LAI_{max} across locations. Trials sites were established across a range of slopes (Fig. 4.7) and altitudes (Fig. 4.8) and 82% of these were facing either a northerly or a westerly aspect, but LAI at harvest showed only a weak positive relationship with increasing slope. The influence of increasing altitude on mean annual temperature across all sites was calculated to decrease on average by 0.54 degrees Celsius per 100m, illustrating correlations between the climatic and topographic variables, but there was little if any effect of altitude on leaf area at harvest (Fig. 4.8).

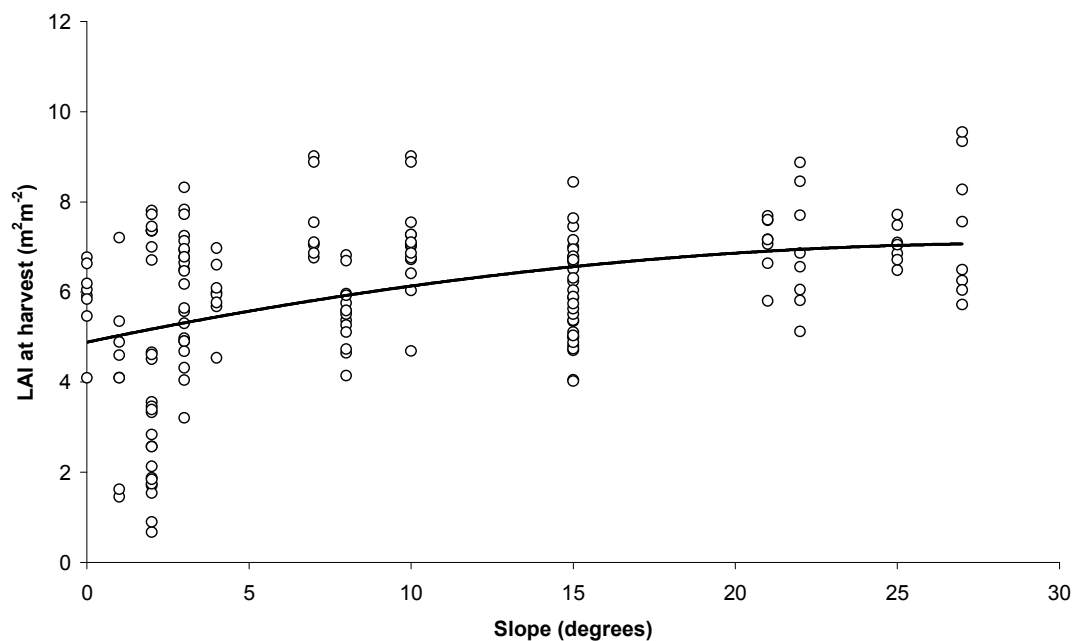


Figure 4.7 Relationship between trial slope and LAI of all plots at harvest. The regression line shows the trend for both the *C. lusitânica* and *P. radiata* treatments across plots at all 22 sites.

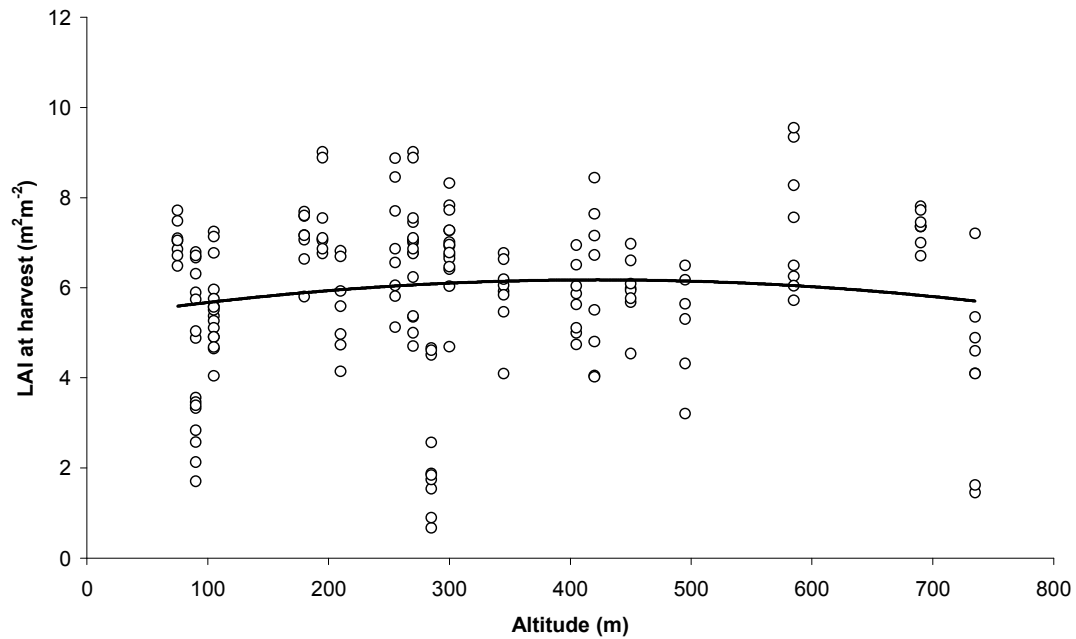


Figure 4.8 Relationship between altitude and LAI of all plots at harvest. The regression line shows the average trend for both the *C. lusitanica* and the *P. radiata* treatments.

Multiple regression analysis

The combined influence of climatic, topographic and edaphic characteristics was determined using a forward selection multiple regression analysis. Models built for individual treatments explained between 44 and 95% of the variation in the data (Table 4.7). Residual plot analysis showed all models to have little apparent bias (data not shown).

Partial R^2 values, measuring the significant relationship of one variable while controlling the effects of others, were grouped by climate, soil chemical, soil physical and topographical characteristics. On average climate explained 53% of the variation in modelled LAI_{max} , 16.8% of the variation was attributed to soil physical characteristics, 18.1% to soil chemical characteristics and 3.4% to topographic properties. Together these variables explained 91.3% of the variation in the data. The modelled values compared well with actual values (Fig.'s 4.9 & 4.10) and little apparent bias was shown by the residual plots produced for these models either (data not shown).

Table 4.7 Linear regression models of LAI_{max} , rate and age of inflection for fertilised and unfertilised plots across 22 New Zealand forest sites. C = *C. lusitanica*, F= fertilised, N = non fertilised, R = *P. radiata*.

Plot	Leaf area attribute	Standardised multiple regression model parameters ⁶	R^2	MSE ⁷
CF	LAI_{max}	7.437 + WHC0.907 + Pen0.314 - CtoN1.286 - Solar1.429	0.94	0.24
	Rate	7.976 + Long1.414 + WHC8.749 + N10.748 - CEC17.347	0.60	46.92
	Age	1.409 + Long0.511 + RAW0.087 + alt0.333 + maxtemp0.271	0.86	0.03
CN	LAI_{max}	6.861 + Lat1.014 + Poro1.793 - RAW0.849 + Pen0.558 - C1.134 - CtoN0.776 - Solar3.090	0.95	0.47
	Rate	4.244 - Field1.824 - pH2.024 + N2.971 + Ptot1.664 + maxtemp3.223 - evap1.118	0.86	2.79
	Age	1.522 - Solar0.336	0.57	0.10
RF	LAI_{max}	6.088 + CEC1.652 - TAW0.545 - Rain1.313 - Solar1.018	0.79	1.00
	Rate	3.542 + RAW2.614 + meantemp6.057 - maxtemp3.775	0.44	8.48
	Age	1.481 + Poro0.172 - Porg0.251 + ExCa0.245 - ExMg0.193 - VPD0.093 - topsoil0.088 - maxtemp0.408	0.95	0.01
RN	LAI_{max}	7.047 + Long1.334 - TAW0.945 - POrg4.058 + Ptot3.087 - meantemp4.605 + mintemp0.938	0.91	0.72
	Rate	4.344 + PinOrg2.781 - VPD2.613	0.55	16.70
	Age	1.630 - RAW0.197 - meantemp0.463 - Slope0.118	0.81	0.06

⁶ See abbreviations and symbols list, page V.

⁷ Mean square error (MSE) is a measure of the deviation of the predicted mean from the true mean. Smaller values are associated with a model that explains more variation in the data. Willmott, C.J. 1982. Some comments on the evaluation of model performance. Bulletin American Meteorological Society. 63:1309-1313.

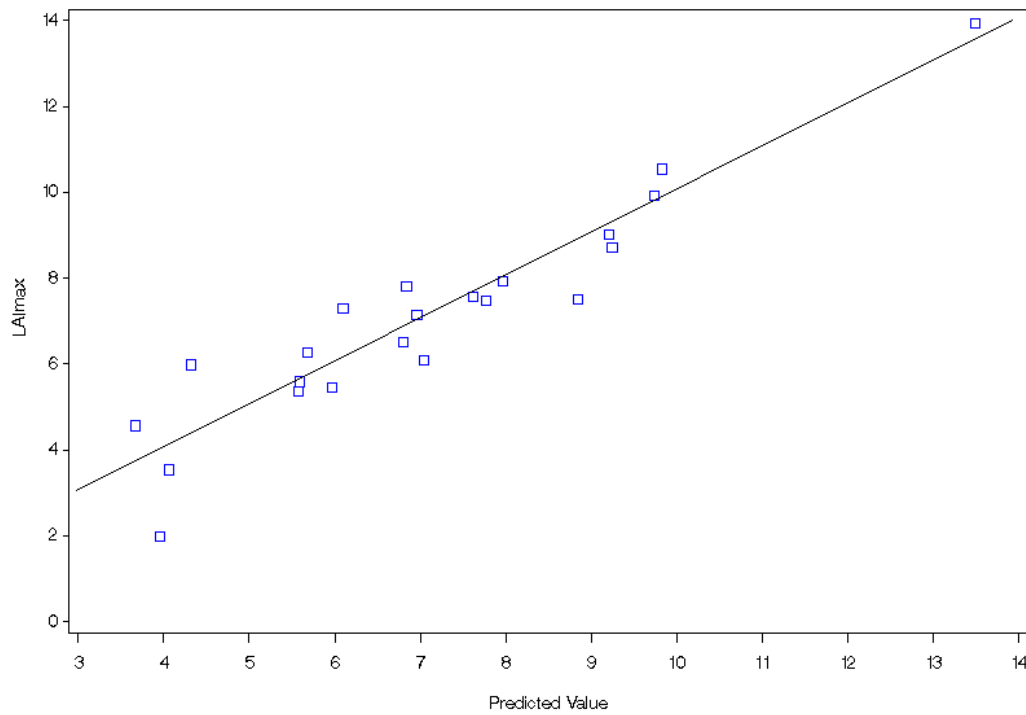


Figure 4.9 Comparing LAI_{max} predicted using soil, climate and topographic characteristics with Chapman-Richards modelled values for the non fertilised *C. lusitana*. $LAI_{max} = 6.861 + Lat1.014 + Porosity1.793 - RAW0.849 + Pen0.558 - C1.134 - CtoN0.776 - Solar3.090$ ($R^2 = 0.95$).

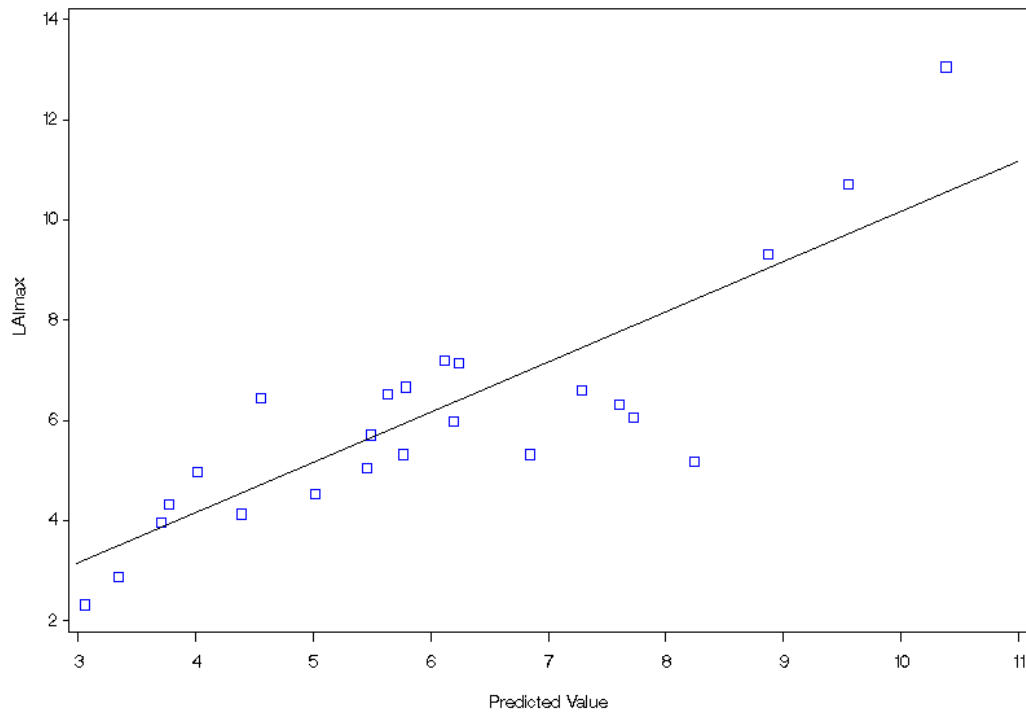


Figure 4.10 Comparing LAI_{max} predicted using soil, climate and topographic characteristics with Chapman-Richards values of the non fertilised *P. radiata*. $LAI_{max} = 7.047 + Long1.334 - TAW0.945 - POrg4.058 + Ptot3.087 - meantemp4.605 + mintemp0.938$ ($R^2 = 0.91$).

DISCUSSION

This study compared 3 characteristics of leaf area development from two commercial plantation tree species, planted at the same density, across 22 plantation forest sites covering a range of New Zealand climate and soil characteristics, over a four year period. *Cupressus lusitanica* and *P. radiata* were introduced to New Zealand, from central parts of Mexico (Bannister and Orman 1960; Miller and Knowles 1996) and from coastal California USA (Burdon 1992) respectively, and because the native habitats in which they have naturally adapted are different, significantly different responses to New Zealand growing conditions might be expected.

Species variations

This study has shown that LAI_{max} was significantly different across sites (Table 4.3) and species. The mean LAI_{max} values of $6.47 (\pm 2.29 \text{ Std.}) \text{ m}^2 \text{ m}^{-2}$ and $7.28 (\pm 2.59 \text{ Std.}) \text{ m}^2 \text{ m}^{-2}$ for *P. radiata* and *C. lusitanica* respectively were recorded across trial locations. Results show that both species were positively and significantly related to soil carbon, nitrogen, phosphorous and CEC (Table 4.6). Soil physical characteristics influenced a number of minor differences between the species see for example penetration resistance (Table 4.5). Similarities between the species were also shown by characteristics such as maximum LAI which was consistently and negatively related with soil bulk density. The age of inflection was positively related with the soil water holding capacity. Species differences were inconsistent but the data suggests that the rate of LAI development in *P. radiata* is more sensitive to the fractions of sand, silt and clay than *C. lusitanica*. However, in general there are more similarities than differences. For example the climatic influences of light, temperature and VPD were similar across species.

The between species variation in LAI_{max} is illustrated across sites (Fig. 4.11). Greater leaf area is represented by larger symbols, these differences may be reflective of a combination of stress induced changes from animal browsing etc. and/or differences in soil exchangeable K concentrations (Table 4.6).

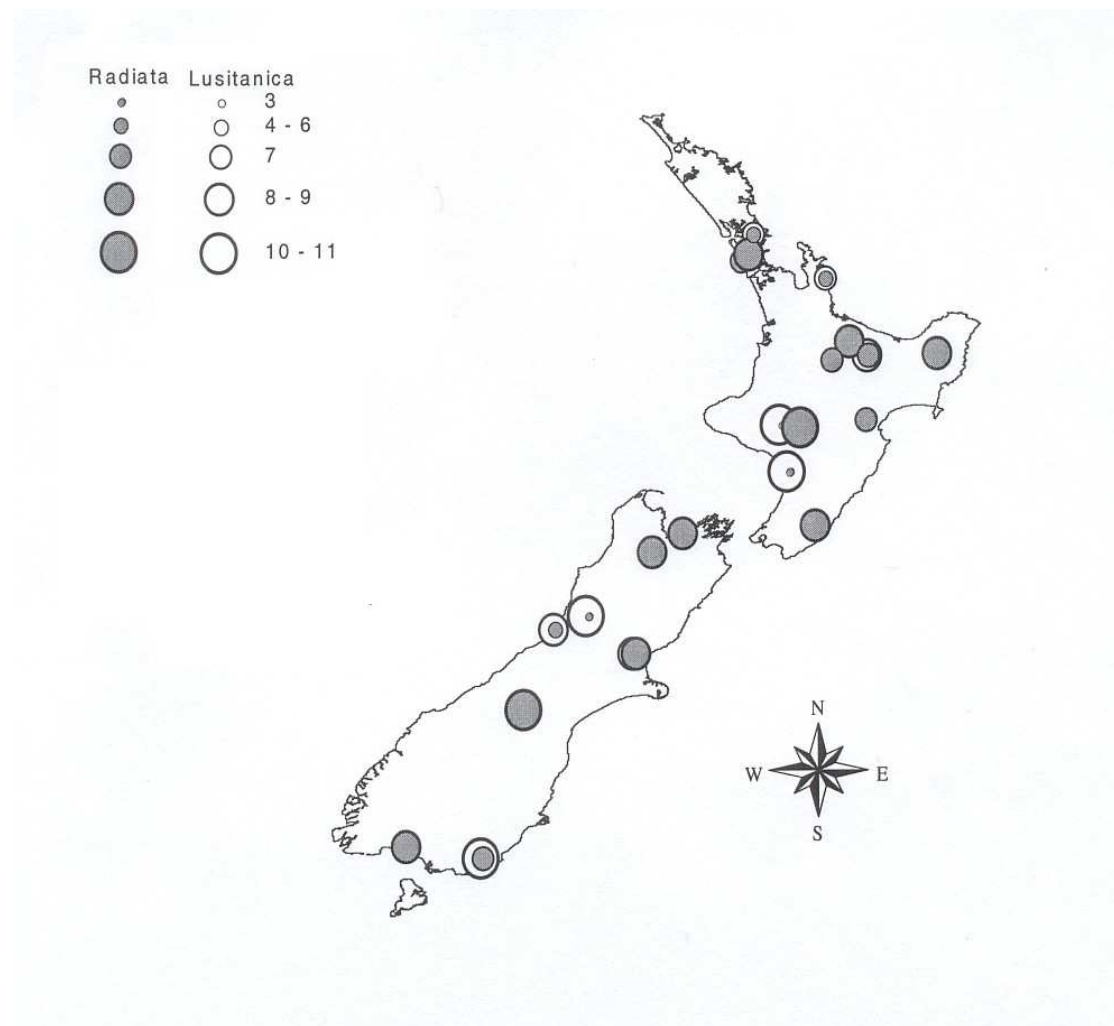


Figure 4.11 LAI_{max} across 22 New Zealand plantation forests for *C. lusitanica* and *P. radiata*. In order to classify the sites into 5 equal divisions the *P. radiata* has been normalised with respect to *C. lusitanica* values so that the relative LAI_{max} size representations are equal.

This study has shown that LAI_{max} was significantly different across sites and species. Mean LAI_{max} was 11% greater in *C. lusitanica* plots on average and fertiliser significantly increased LAI_{max} (Table 4.1 and Fig. 4.1). The age at which leaf area development began to slow in *C. lusitanica* was not related to soil chemistry (Table 4.6): this suggests that water and/or light competition limits the rate of leaf area development.

Additional hypotheses which may explain differences between the species are;

- 1) *Cupressus lusitanica* probably retains comparatively more dead (photosynthetically inactive) foliage in the canopy. Other reports support this belief

by showing that *C. lusitanica* retains foliage longer than several other common species (Lisanework and Michelsen 1994). Reich *et al.* (1999) proposed that leaves of some plant species are built for productivity and others for persistence. As *P. radiata* was shown to be 50% more productive than *C. lusitanica* (see Chapter 6), perhaps *P. radiata* foliage is built more for productivity and *C. lusitanica* for persistence and hence the foliage is retained longer. Additional supporting evidence is a direct relationship between leaf longevity and LAI ($r^2 = 0.82$), which was shown for 5 plantation species in Wisconsin USA (Gower *et al.* 1993) and also by other studies (Reich *et al.* 1992).

2) Shade tolerant trees tend to intercept more light than shade intolerant species by building canopies with greater LAI (Craine and Reich 2005), and this also suggests that *C. lusitanica* may be a more shade tolerant species compared to *P. radiata*.

3) *Dothistroma pini* (Hulbary) causes premature defoliation of infected *P. radiata* (Gadgil 1984). This needle blight has a widely spread distribution throughout New Zealand and around 25% of the forest estate is susceptible during infection periods. This fungal disease may have infected some of the closely spaced seedlings at some sites despite control efforts see Chapter 3.

Site variations

Approximately 90% of the leaf area characteristics calculated (LAI_{max} , rate and inflection) across these New Zealand forest trial sites were explained by the effects of climate, soil and topography.

Climate

In New Zealand more southerly latitudes receive lower light intensities and temperatures. Mean annual temperature varied only slightly over the trial period, 12.6 ± 0.3 degrees C (NIWA 2004), compared with individual site variations that ranged from 8.53 °C to 15.31 (Fig. 4.3). This work demonstrated significant negative relationships between LAI_{max} , and both light and temperature (Table 4.4). This is in agreement with studies that have shown when nutrients and water are not limited but light is, these plants allocate relatively less assimilate to roots and relatively more to structural or foliage components (Montgomery 2004; Shirley 1929).

It was shown that LAI_{max} increased with smaller vapour pressure deficits (Table 4.4). LAI_{max} also tended to increase with greater rainfall and lower evaporation (Fig. 4.2). This finding is similar to that of DeLuca et al., 2000 who found that leaf area in pine species was reduced with greater VPD (DeLucia et al. 2000). Nemani and Running (1989) reported a strong relationship between leaf area and precipitation minus evaporation. These findings and those reported by Gholz, (1982), who tested a range of moisture variables support the findings of this study, because increasing VPD reduces stomatal conductance and photosynthesis, which results in reduced tree growth.

This study found that on average climate explained 53% of the variation in LAI_{max} across forest sites in New Zealand (pg.44). This compares well with Luo *et al.* (2002) who developed regression models of leaf area based on temperature and moisture indices, and their models explained 40 - 90% of the variation in LAI across sites in China.

Soil fertility

Fertiliser increased the rate of leaf area development by 21% across species (Table 4.2). Dalla-Tea and Jokela found that increased nutrition was strongly related with increased levels of LAI in young slash and loblolly pine (Dalla-Tea and Jokela 1991). Fahey *et al.* (1998) found that fertiliser only slightly increased LAI over a range of young hardwood species compared to control plots, while Raison and Myers *et al.* (1992) observed fertiliser effects on LAI up until the point of canopy closure.

Linear regression analysis showed that greater LAI in *P. radiata* and *C. lusitanica* was correlated with increases in the following soil variables: C, N, organic P, total P and CEC (Table 4.6). These findings are in general agreement with Fassnacht and Gower (1997) who reported that LAI was significantly correlated with potassium and nitrogen along with potentially available water in conifer, hardwood and mixed stands. It is highly possible that LAI_{max} is correlated with these nutrients because of a significant interaction with soil moisture which may be the controlling variable (Nambiar and Sands 1993).

Soil physical characteristics

Significant relationships found between soil physical properties and LAI_{max} were associated with the soils ability to store and access water. LAI_{max} of both species increased with both lower bulk density and greater soil water holding capacity (Table 4.5). Hoff and Rambal (2003) studied Mediterranean evergreen oak (*Quercus ilex* L.) and also found that LAI across sites was related with an increase in soil water content. This study also found that only *C. lusitanica* LAI_{max} was positively related to both macro and total porosity, possibly indicating a difference in sensitivities to pore size distribution between species.

CONCLUSIONS

This chapter has demonstrated significant effects of climate and soil on leaf area index. Proportionally more leaf area develops in cooler environments where soil moisture is abundant and the light intensity is reduced. These cooler environments are likely to have influenced changes to the allocation of plant assimilates which increase partitioning to leaves, the findings of other published work support these relationships. The below ground data required to substantiate this is beyond this particular study.

Increased soil water holding capacities illustrated by variables such as macro porosity, soil bulk density and even carbon content were significantly related to leaf area indices and the relationships observed in this study are also in agreement with the findings of others.

These significant effects of climate and soil on leaf area suggested by this study advocate that a site quality indicator utilising properties of leaf area development could be utilised to take into account many major and complex interacting influences of the climate and soil environment (see also Chapter 7). Plants respond to an environment so that an optimal use of site resources are made and leaf area is an important plant attribute which is used to optimise plant growth. Maximum site leaf area index is a potential measure of this environmental equilibrium and this chapter has shown significant links with many variables that are correlated with the maximum leaf area index, rate of leaf area development and the age of inflection.

CHAPTER 5

A Seasonal Model of Leaf Area Development in Highly Stocked Forestry Trials

INTRODUCTION

Like tree height and diameter growth, leaf area develops at a variable rate during each growing season (Kimberley and Richardson 2004). The data-set collected during this study has allowed seasonal development patterns to be examined. The modelling approach is an adaptation of the function developed by Kimberly and Richardson (2004) and is described in more detail in Chapter 3. A sine function with increasing amplitude until the point of inflection is introduced into a Chapman Richards 3 parameter equation.

RESULTS

The average growth pattern of leaf area index, across all 4 years of the experiment, for both *C. lusitanica* and *P. radiata* were similar in shape. The peaks and troughs of the seasonally modelled trends coincided during the same month for most plots, although the magnitude was considerably different (Fig. 5.1). The maximum rate of leaf area accumulation across the trial period occurred in December for all plots except the disturbed and unfertilised *P. radiata* (RDN) (see appendix 5), which reached a maximum earlier in November. There was minor LAI loss in 3 out of 4 *P. radiata* treatments during the winter period. This trend contrasted with the *C. lusitanica*, only one treatment consistently lost LAI, the undisturbed and unfertilised treatment (CDN). It is speculated that the 4% decrease in *P. radiata* LAI over the winter period may have been caused by either a combination of frost, severe wind, and hail or animal and insect browsing or changes in foliage orientation (see later). These climatic and animal browsing factors are fairly typical in *P. radiata* plantations (Burdon 1992) and these results suggest that *C. lusitanica* may be more resistant to this type of environmental exposure.

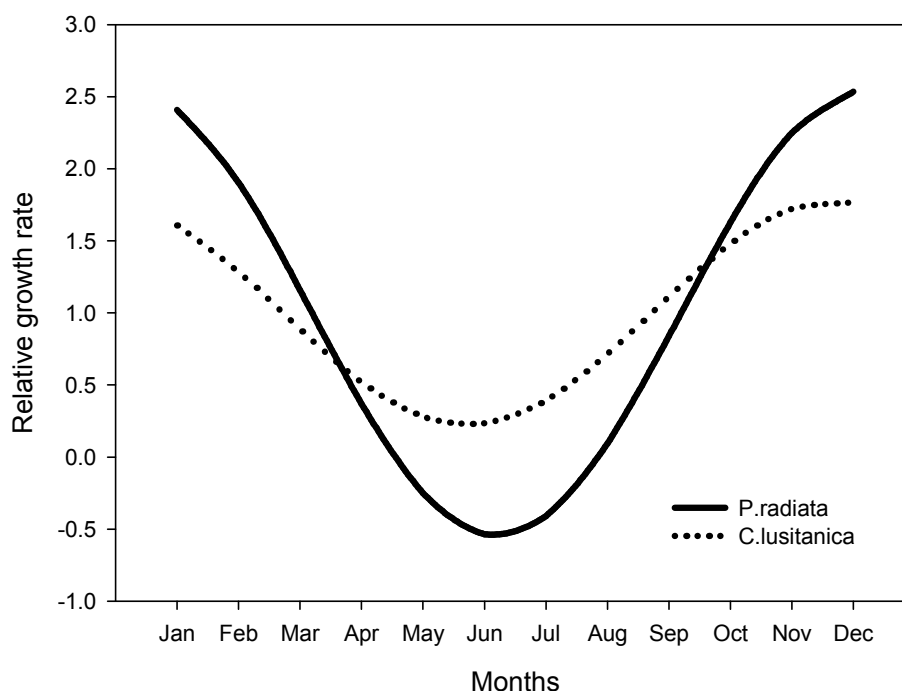


Figure 5.1 Modelled annual relative growth rates of *P. radiata* and *C. lusitanica* LAI across the 22 trial sites.

A seasonal pattern in specific leaf area ($\text{cm}^2 \text{g}^{-1}$) was also determined from plots harvested over the corresponding winter periods in both 2004 and 2005. There was a strong relationship between harvest month (pooled for both years) and foliage weight for both *P. radiata* and *C. lusitanica* (Table 5.1). *Cupressus lusitanica* had greater specific leaf area during the months of May and June. *Pinus radiata* specific leaf area was highest in May and declined through till September. These results mirror the points when leaf area growth is at its lowest and therefore support the trends of the modelled relative seasonal growth patterns illustrated in Figure 5.1.

Table 5.1 Mean specific leaf area ($\text{cm}^2 \text{g}^{-1}$) across trial sites, standard deviation in brackets, a Student-Newman-Keuls means comparison is shown for each species and sampling months, different letters indicate significantly different SLA at $p < 0.05$.

	<i>C. lusitanica</i>	<i>P. radiata</i>
Harvest month	SLA ($\text{cm}^2 \text{g}^{-1}$)	SLA ($\text{cm}^2 \text{g}^{-1}$)
April	18.34 (3.43) b	-
May	21.15 (4.54) a	66.35 (13.37) a
June	21.56 (4.04) a	63.01 (11.63) a
July	17.47 (2.34) b	61.61 (10.02) a
September	-	56.23 (6.02) b

By incorporating the seasonal effect (Equations 3.5 & 3.6), with site as a dummy variable, the LAI development trends across sites for individual treatments were determined. Trends across species (Fig. 5.2) and between treatments were shown to be fairly consistent. Disturbed plots accumulated LAI at a slower or an equivalent rate during the initial years compared with undisturbed, then over the later years disturbed plots continued to accumulate LAI at a greater rate than undisturbed plots (Fig's. 5.3 a&b).

Fertiliser assisted tree growth and LAI development of both species (Fig's. 5.4 a&b). In the fertilised *P. radiata* treatment, annual peaks of LAI tended to be higher than the non-fertilised, but differences between these treatments diminished with time as the LAI built to an equilibrium point (Fig. 5.4a). In contrast to the *P. radiata* treatments the differences between *C. lusitanica* fertilised and non-fertilised treatments increased with time suggesting *C. lusitanica* has a much higher demand for nutrients (Fig 5.4b) or that finer roots⁸ more efficiently capture fertiliser nutrients.

⁸ From personal observations made during harvesting and coarse root washing procedures

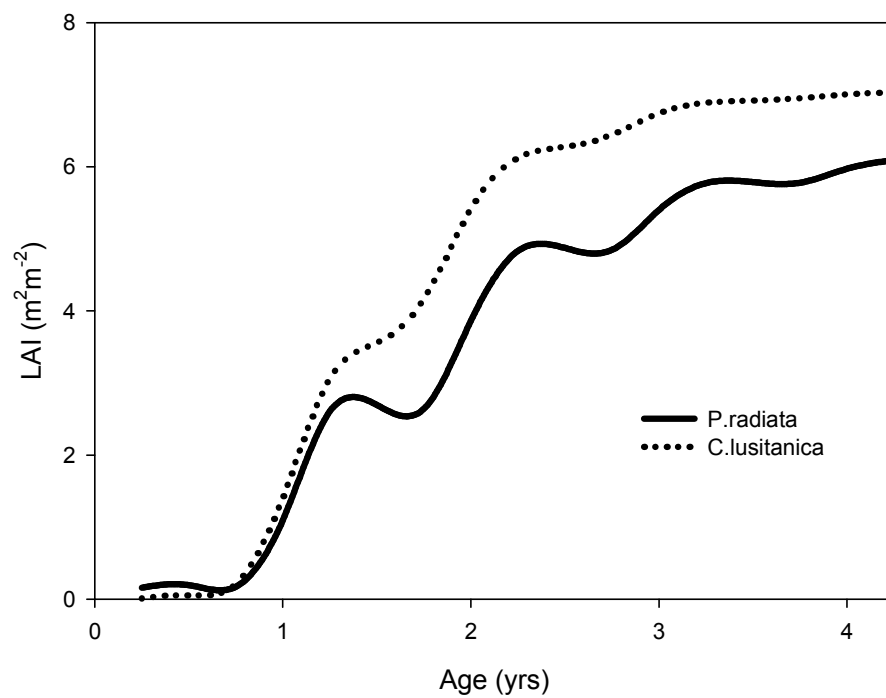


Figure 5.2 Modelled seasonal LAI patterns for *P. radiata* and *C. lusitanica* species across sites.

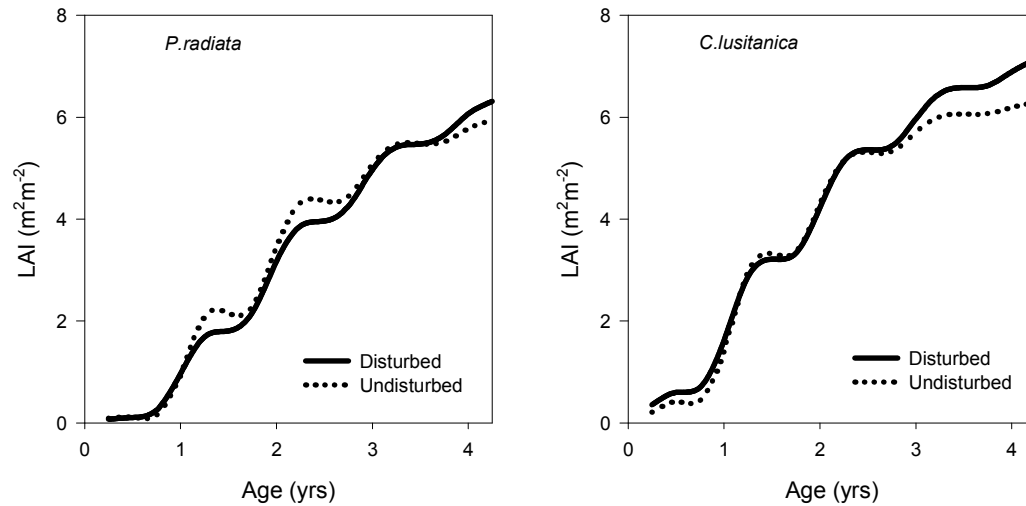


Figure 5.3 Modelled seasonal LAI patterns for disturbed and undisturbed treatments across sites.

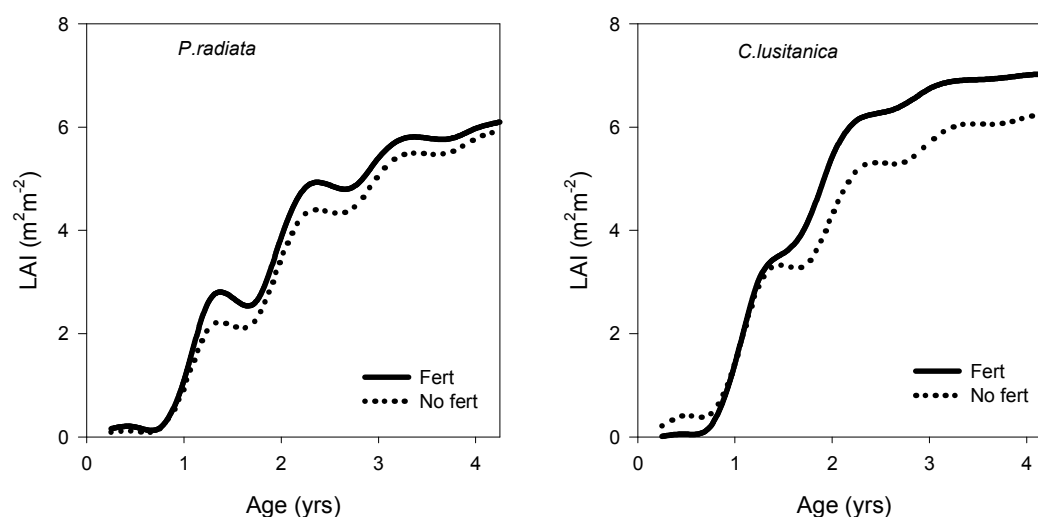


Figure 5.4 Modelled seasonal LAI effects of fertiliser on treatments.

To examine factors which may influence seasonal changes in LAI, foliage orientation was assessed. The mean tilt angle (MTA) is estimated during calculations by the Plant Canopy Analyser and represents the orientation of the foliage (LI-COR 1990). Horizontal foliage is equivalent to 0 degrees and vertical foliage is represented by 90 degrees. Like seasonal relative growth MTA was averaged across the four years of the trial duration. These calculations showed there was a strong linear decrease in MTA as the age (yrs) of plants increased $MTA = -9.82(\text{age}) + 77.88$, ($R^2 = -0.9916$). As the seedlings matured, heavier branches developed and grew with a more horizontal inclination. MTA demonstrated considerable variation across sites and a seasonal pattern within the pooled data is barely evident because of this (Fig. 5.5), but the pooled site data suggests a 17 or 28 degree seasonal change in MTA for *C. lusitanica* and *P. radiata* respectively. This indicates that the orientation of the branches and needles is likely to have an influence on the seasonal LAI trends and further studies are required to confirm links with the seasonal availability of water which is speculated to affect plant turgor and hence young branch and foliage orientation.

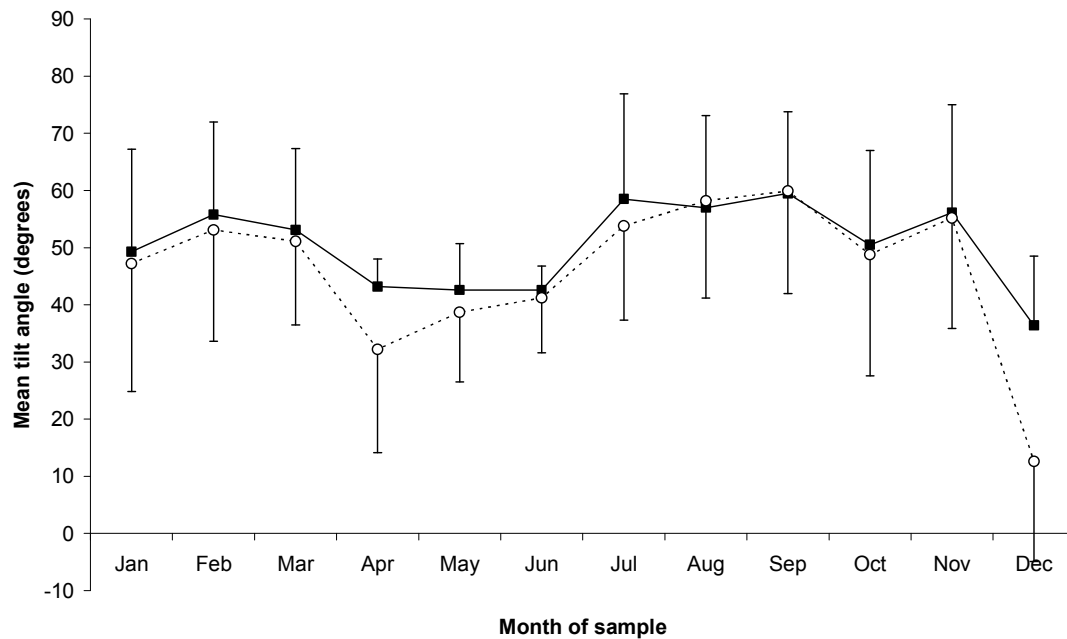


Figure 5.5 Mean tilt angle of *P. radiata* (○) and *C. lusitana* (■) foliage by sampling month across sites. Error bars represent standard deviations.

Seasonal site patterns

Each site had a unique development pattern. LAI at Glengarry (Eastern North Island) grew rapidly from planting and reached a plateau around 1.8 years after establishment following the classical sigmoidal shape (Fig. 5.6a). This plateau coincided with the late summer period of the second growing season. The Kaingaroa (Central North Island site with low fertility) took longer to establish; in general there was a constant but slower development of LAI at this site (Fig. 5.6f). The Okuku (wet winter and dry summer) site had even seasonal dips and peaks with relatively large amplitude (Fig. 5.6d). This site dramatically illustrates how a seasonal influence of moisture availability might affect foliage and branch orientation. The relatively cool and wet Catlin's site developed a greater LAI_{max} despite a slow start during the first year (Fig. 5.6b).

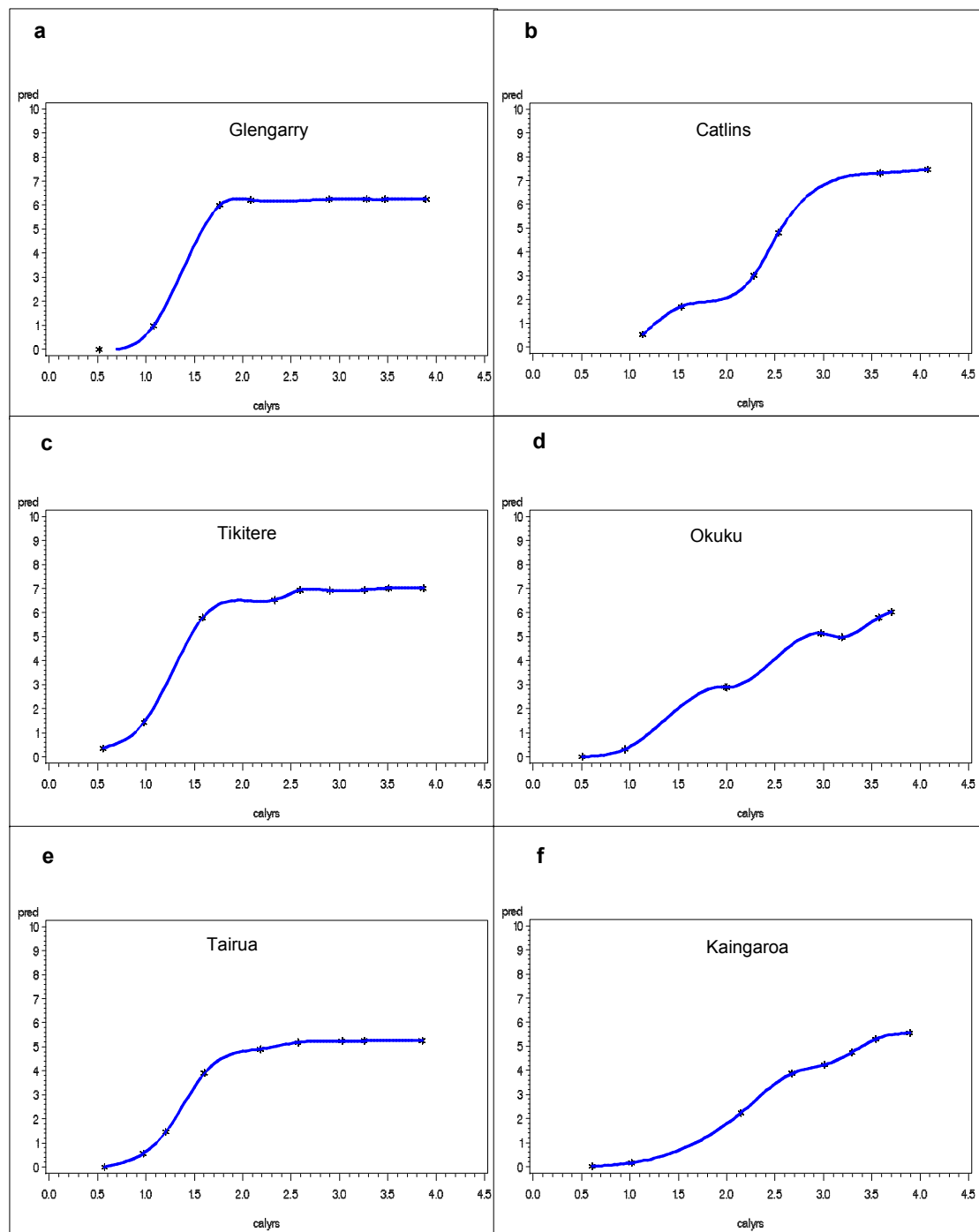


Figure 5.6 Modelled seasonal leaf area indices of pooled treatments for forests trial sites. Predicted LAI (m^2m^{-2}) is represented on the Y axis and trial age in years is represented on the x axis.

DISCUSSION

This study showed leaf area index was at a maximum in December (Fig. 5.1). These findings are consistent with those of a previous New Zealand study also reporting the seasonal leaf area growth of *P. radiata* (Whitehead et al. 1994). A peak in LAI for both *C. lusitanica* and *P. radiata* during late December coincides with the peak in solar intensity around the summer equinox. Luo *et al.* (2002) reasoned that seasonal patterns of leaf development were controlled by temperature and light, and the changing patterns of specific leaf area in this study support these theories (Table 5.1).

A change in young branch and foliage orientation was suggested by this study to have an effect on seasonal patterns (Fig. 5.5), as the mean tilt angle was found to vary by 17 to 28 degrees for *C. lusitanica* and *P. radiata* through the season. These changes were slightly offset compared with relative leaf area index growth, although a dependent link between the two is still conceivable.

Across sites treatments and years this study showed an average seasonal LAI increase of $2.21 \text{ m}^2\text{m}^{-2} \text{ yr}^{-1}$ with a smaller seasonal fluctuation of $0.188 \text{ m}^2 \text{ m}^{-2}$. This is equivalent to an 8.5% seasonal fluctuation in an established canopy. Seasonal changes have been observed in several other studies. For example the changes in leaf area of 15 year old *P. radiata* was shown to be equivalent to 1-3 units of projected leaf area (Raison and Myers 1992). Dalla-Tea and Jokela (1991) found that the LAI of 6 year old slash and loblolly pine at 1543 stems per hectare varied by about 20-25% during a season and suggested this reflected needle fall and sun angle changes.

Remotely sensed data has also observed seasonal changes and measurements collected from the Thematic Mapper on the Landsat-5 satellite, across an Oregon transect (east-west at about 45°N), showed a seasonal change in LAI which ranged from 20-30.1% across different forest ages, types and variable stand densities (Spanner et al. 1994).

This study demonstrated similar but slightly reduced seasonal leaf area trends compared with mature trees at conventional planting densities. Mixed stands and

other variations at a broader scale such as a more diverse genetic base are likely to explain some of these differences. However, the LAI development trends of the following reports also show that in mature stands patterns are generally similar to those found by these trials (Ryan et al. 2004; Vose et al. 1994; Waring and Schlesinger 1985; Whitehead et al. 1994).

This work has also shown that there is considerable variation in LAI development patterns across trial locations in New Zealand plantations. These findings may be consistent with the large variation of site specific climate and soil characteristics (see Chapter 4), but further detailed water balance analysis may provide a greater understanding.

CHAPTER 6

Comparing Leaf Area Development with Productivity of *Pinus Radiata* and *Cupressus Lusitanica* across New Zealand Forest Soils and Climates

INTRODUCTION

To be widely used, an indicator of site quality should ideally be linked with properties which are easily measured and have a physiological basis. Chapter two reviewed the use of productivity to assess site quality, and discussed its wide use by forest managers for economic and logistics planning. This chapter compares productivity, as measured by tree height, root collar diameter and volume index with leaf area index at age four or modelled maximum leaf area index (LAI_{max}) in miniature plantations.

Light energy and growth efficiency

Prior to the 1980's, variations in crop growth rates were often explained by the amount of leaf area multiplied by the net assimilation rate. A different approach was developed after Monteith's ideas around 1973, when a linear relationship was discovered between the quantity of dry matter produced and the amount of light energy intercepted by plant foliage (Medlyn 1998). Simplified process models using this idea are now widely used in models such as 3-PG (Landsberg and Waring 1997) and FOREST-BGC (Running and Gower 1991) amongst others.

These process based models predict growth by utilising variations of the following equation:

$$\Delta W/\Delta t = \epsilon J \eta - V \quad (6.1)$$

where, $\Delta W/\Delta t$ = rate of woody dry matter production with time, for example on a daily basis (g d^{-1}); ε = efficiency which light is used to produce dry matter (g d^{-1}); J = intercepted light energy ($\text{J m}^{-2} \text{d}^{-1}$); η = the daily proportion of growth partitioned to wood (a unit-less fraction) and V = the rate of dry matter loss ($\text{g m}^{-2} \text{d}^{-1}$) (Cannell 1989).

Climate, nutrients and water all influence crop productivity by affecting leaf area which is then reflected through changes in J (intercepted light). Management operations which modify leaf area will have an effect on productivity according to this model. It therefore follows in that a reduction in site quality from harvesting disturbance, nutrient loss, climate change etc. may also affect leaf area.

METHODS and ANALYSIS

Annual measurements of tree height, root collar diameter and volume index were compared with either leaf area index of the trial plots at age four (harvest) or modelled maximum leaf area index (LAI_{max}). LAI 's were measured at approximately quarterly intervals at each site and both sets of data were modelled using a Chapman-Richards function, as detailed in Chapter 3.

Tree height (h), root collar diameter (D) and a volume index (D^2h) were modelled using a sigmoidal function (Schumacher 1939). LAI_{max} measurements were compared with volume index using Pearson correlation coefficients, following this a linear regression was determined. Then the efficiency with which foliage produced volume increment was calculated and correlations with associated variables were examined.

RESULTS

Tree size and shape

Pinus radiata trees at harvest had smaller live crown lengths in proportion to total tree height, and *C. lusitanica* had wider crown widths (Table 6.1). Because seedlings were planted at 0.5 m intervals and the maximum crown widths were greater than the available space for both species, this suggests a difference in canopy shape, light attenuation and light capturing efficiency between the species.

Table 6.1 Mean tree crown height, length and width of *C. lusitanica* and *P. radiata* seedlings at harvest across 22 trial sites. Standard deviations are presented in brackets.

Mean crown descriptors (cm)	Tree species	
	<i>C. lusitanica</i>	<i>P. radiata</i>
Tree height	299.7 (105.8)	385.2 (119.2)
Live crown length	232.5 (75.9)	278.9 (83.4)
Live crown width	93.6 (35.2)	60.1 (21.4)

Treatment responses

Tree height, root collar diameter and volume index increment showed significant differences across treatments and slight changes over time (Table 6.2). Appendix 6 shows a comparison of mean treatment affects over time on tree height and diameter values across individual sites. The effects of site disturbance on tree volume diminished over time. However, on average, across treatments site disturbance decreased mean plot volume by 5% and fertiliser increased tree height and volume index by 6.6% and 30% respectively.

Table 6.2 Comparison of species, fertiliser and site disturbance on tree height, root collar diameter and volume index increment over time, significant responses are indicated by the probability values in bold.

Parameter	Source	Trial age (yrs)			
		1	2	3	4
Height	Site	<.0001	<.0001	<.0001	<.0001
	Disturbance	0.0039	0.0163	0.0583	0.2018
	Species	<.0001	0.3966	0.0065	0.0002
	Fertiliser	0.3888	0.0018	0.0005	0.0008
	dist*fert	0.5777	0.6261	0.2106	0.4530
	site*dist	<.0001	<.0001	<.0001	<.0001
	dist*sp	0.0050	0.1987	0.1326	0.0403
	site*fert	<.0001	<.0001	<.0001	<.0001
	sp*fert	0.4547	0.6744	0.5811	0.7887
	site*sp	<.0001	<.0001	<.0001	<.0001
	dist*sp*fert	0.3278	0.0012	0.0056	0.0447
Root collar Diameter	Site	<.0001	<.0001	<.0001	<.0001
	Disturbance	0.1212	0.3462	0.6987	0.7799
	Species	<.0001	0.0579	0.0025	0.0057
	Fertiliser	0.0248	<.0001	<.0001	<.0001
	dist*fert	0.1687	0.5762	0.5797	0.4795
	site*dist	<.0001	<.0001	<.0001	<.0001
	dist*sp	0.0105	0.0143	0.0245	0.0545
	site*fert	<.0001	<.0001	0.0160	0.0068
	sp*fert	0.6422	0.0934	0.0047	0.0026
	site*sp	<.0001	<.0001	<.0001	<.0001
	dist*sp*fert	0.9809	0.1180	0.2107	0.4005
Volume increment index	Site	<.0001	<.0001	<.0001	<.0001
	Disturbance	0.0637	0.2479	0.4484	0.6042
	Species	0.0440	0.4361	0.0044	0.0031
	Fertiliser	0.15464	0.0007	<.0001	<.0001
	dist*fert	0.1414	0.6232	0.3858	0.6539
	site*dist	<.0001	<.0001	<.0001	<.0001
	dist*sp	0.0029	0.0064	0.0077	0.0071
	site*fert	<.0001	<.0001	<.0001	<.0001
	sp*fert	0.5115	0.1148	0.0022	0.0012
	site*sp	<.0001	<.0001	<.0001	<.0001
	dist*sp*fert	0.3678	0.0009	0.0024	0.0194

A Schumacher model closely approximated growth of tree height, root collar diameter, and volume increment over time (Fig's. 6.1 a - f). The model of *C.lusitanica* root collar diameter explained 92% of the variation in the actual data and the *P.radiata* model explained 96%. The tree height model explained 92% and 94%

of the variation in the *C. lusitanica* and *P. radiata* respectively. A volume index increment model explained 98.9% and 99.1% of the variation in growth of *C. lusitanica* and *P. radiata* respectively. At harvest the stem volume index of *P. radiata* was 55.4% greater than *C. lusitanica*. However, after the first growing season *C. lusitanica* tree height was greater than *P. radiata*. This trend lasted until plots were approximately 2.5 years old, after which *P. radiata* trees grew taller than *C. lusitanica*. The fertilised and disturbed *P. radiata* treatment showed greater volume increment compared with the undisturbed and fertilised treatments at harvest.

DISCUSSION

Comparisons with conventional stand development

Up until the point when measurements were ceased the leaf area and tree growth development patterns showed similar trends to those reported for stands at conventional densities in New Zealand (Garcia 1999; Kimberley et al. 2005; Maclaren et al. 1995; Mason et al. 1997; Turner and Lambert 1986; Whitehead et al. 1994) and elsewhere (Landsberg 1986; Turner and Lambert 1986; Vose et al. 1994; Zeide 1999; Zeide 2004).

Differences between mature stands at conventional planting densities and the time taken for these highly stocked plots to reach the inflection point were observed. These differences were consistent with the original objectives of the trial design that aimed to speed up treatment responses. On average trees planted at a conventional stocking would close canopy after approximately 7 years growth. This period is equivalent to 1.5 year old seedlings in the miniature plots and because there is no tree thinning within the miniature plots the current annual increment when converted to a per hectare basis at age 4 is considerably greater than that found in conventional regimes.

Some of the development trends of productivity (Fig's. 6.1 a - f) and LAI (Fig's. 6.2 a&b) were similar, but the data from both species indicates that LAI would reach a distinctive maximum asymptote earlier than tree height, root collar diameter or volume index. Because this asymptote reflects a point in time when site resources

become limiting to growth (see Chapter 4), it could also theoretically suggest a measure of site quality or carrying capacity much earlier than productivity measures.

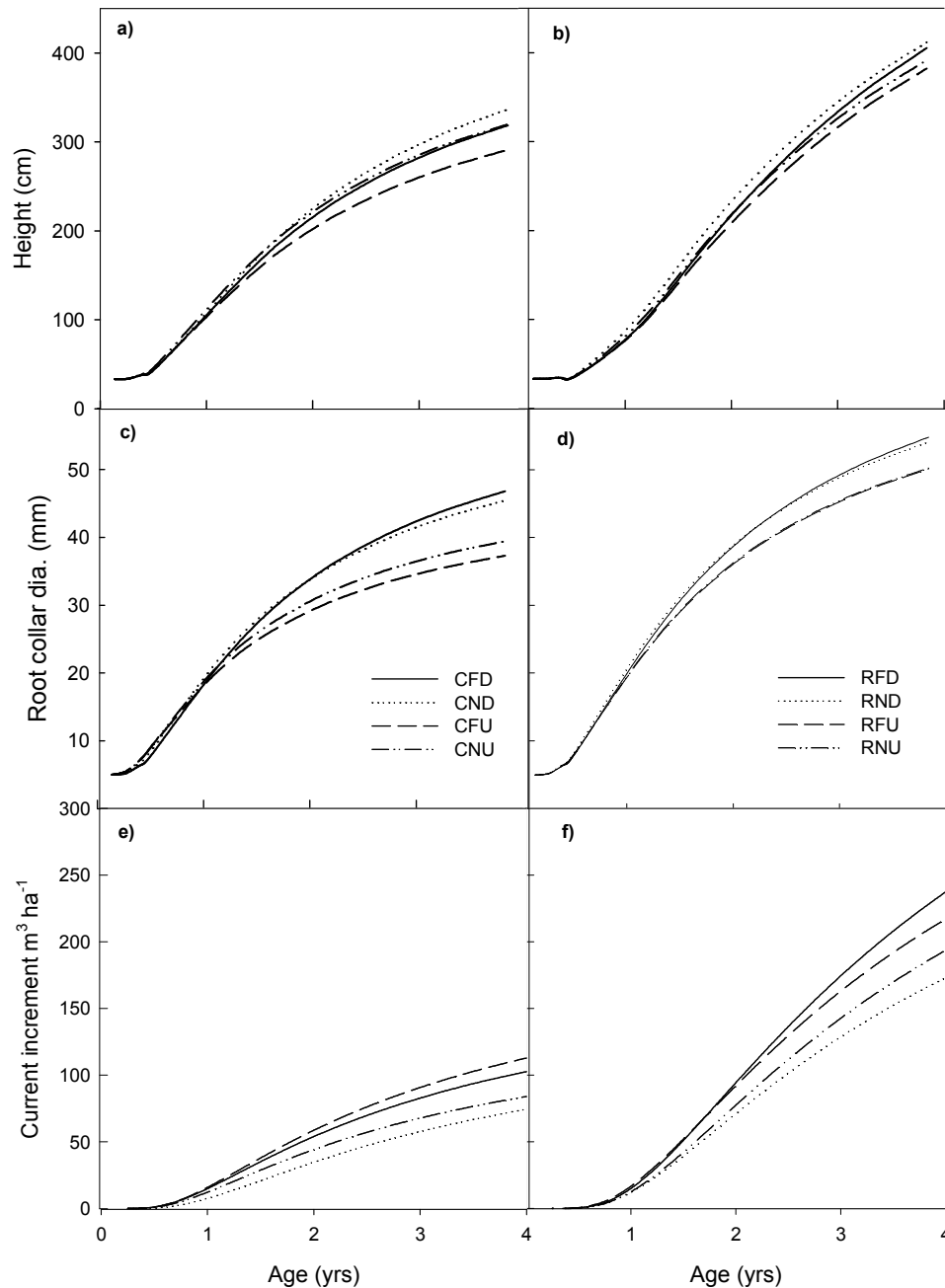


Figure 6.1 Modelled influence of site disturbance and fertiliser on development of tree height, root collar diameter and volume index increment over time in *C. lusitanica* (a,c,e) and *P. radiata* (b,d,f). C = *C. lusitanica*, R = *P. radiata*, F = fertilised, N = unfertilised, D = disturbed, U = undisturbed.

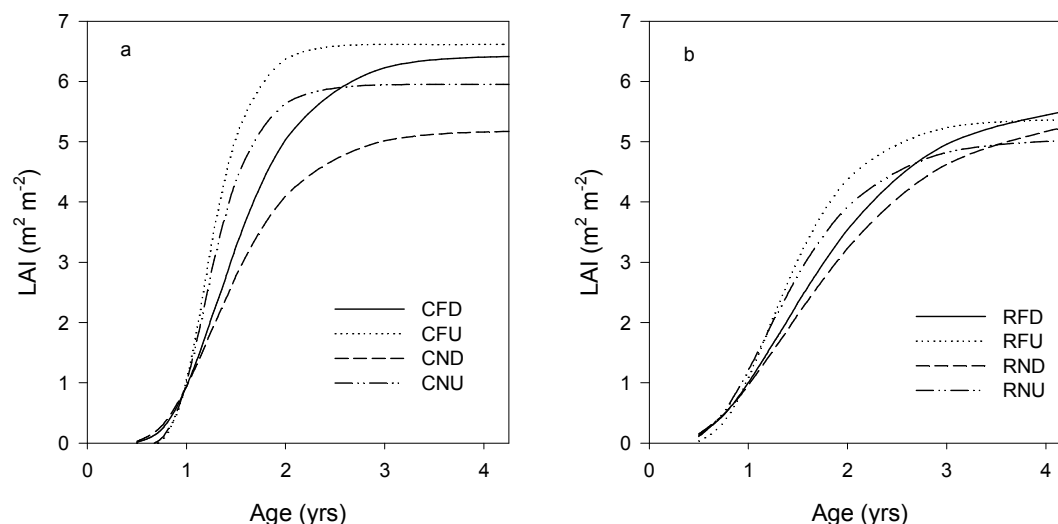


Figure 6.2 Modelled leaf area index for a) *C. lusitanica* and b) *P. radiata* for each of the four fertiliser and site disturbance combination of treatments over the trial period. R=*P. radiata*, C=*C. lusitanica*, F= fertilised, N=non fertilised, D= disturbed and U = undisturbed.

Species comparison

Cupressus lusitanica produced greater crown widths and live crown lengths in proportion to tree height, and *C. lusitanica* reached a maximum site LAI more rapidly than *P. radiata*. LAI of both species illustrated a typical type 1 response to fertiliser, which is characterised by just a temporary increase in growth (Mason and Milne 1999; Snowdon 2002). In comparison, fertiliser increased tree height and root collar diameter according to a type 2 response, which has a sustained growth characteristic, and the fertiliser affects were more easily distinguished by measures of root collar diameter compared to tree height.

Significant correlations between mean plot volume index and LAI at harvest ($p = 0.0007$, $p = 0.0004$) for *C. lusitanica* and *P. radiata* were shown, with Pearson correlation coefficients ($n=86$) of $r = 0.3572$ and $r = 0.3733$ for *C. lusitanica* and *P. radiata* respectively. A log transformation of volume index slightly improved the relationship with leaf area index but the inclusion of the interaction between temperature and LAI provided substantially more improvement to predictions of volume index. Linear regression models incorporating the temperature * LAI interaction with fixed intercepts explained 77.6 % of the variation in *C. lusitanica* and 84.2 % of the variation in *P. radiata* volume index (Fig's. 6.3 & 6.4). Application of a fixed intercept assumed that at zero LAI (or a mean annual temperature of 0°C) there

is no resulting plant volume and this assumption would seem justified. The regression equation for *C.lusitanica* was:

$$\text{volume index (m}^3\text{ha}^{-1}\text{)} = 2.72 * (\text{mean annual temperature} * \text{LAI}) \quad (6.2)$$

Conversion factors

The constant (equation 6.2) equates to the conversion factor of LAI to actual leaf area, amongst other things. The plant canopy analyser measures a one sided projected leaf area. To convert from this to total leaf area a conversion factor is required, and the constant, determined above, compares well with conversion factors from one sided projected leaf area to actual leaf area for similar species such as *Abies grandis* (Dougl. Ex D.Don) Lindl. and *Thuja plicata* Donn ex D.Don (2.86) (Barclay and Goodman 2000). The conversion factor estimated for *P. radiata* was 5.34. In theory the constant is mathematically equivalent to π (Grace 1987), however the conversion factor is a function of stand density and tree size (Barclay and Trofymow 2000). Un-thinned stands have lower conversion factors because of the greater proportion of stem wood to foliage. Thinned stands have increased foliage clumping and hence greater conversion factors, so predicting conversion factors for different planting density needs to account for differences in canopy structure. Comparison of actual biomass with LAI at harvest will provide the most appropriate conversion factors for both *P. radiata* and *C. lusitanica* at these high planting densities across these New Zealand trial sites.

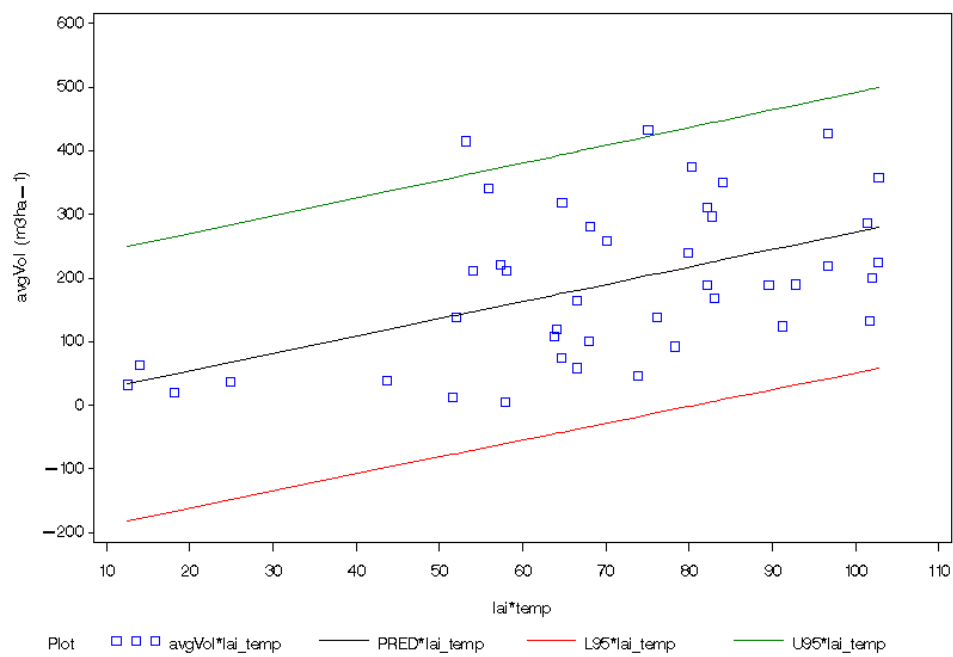


Figure 6.3 Relationship between temperature*LAI compared with actual volume index for non fertilised *C. lusitanica* treatments. The linear regression line and the upper and lower 95% confidence limits of the mean are shown.

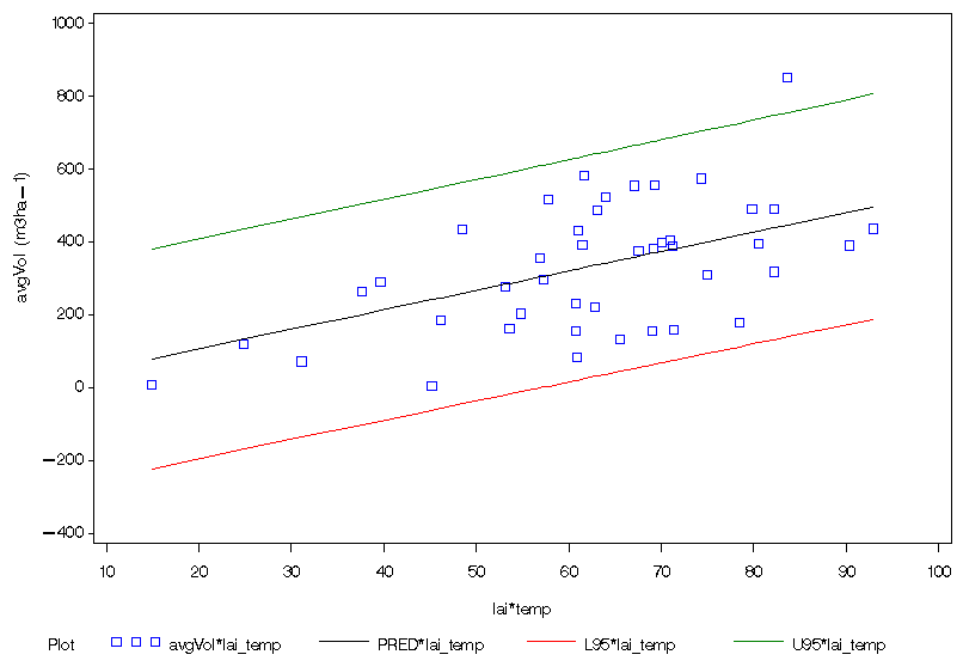


Figure 6.4 Relationship between temperature*LAI compared with actual volume index for non fertilised *P. radiata* treatments. The linear regression line and upper and lower 95% confidence limits of the mean are shown.

Foliage efficiency

The stem volume index produced for every unit of LAI at age four was calculated (equation 6.3). This is considered a measure of foliage efficiency or tree vigor (Waring et al. 1980). Waring and colleagues suggested their version (basal area/sapwood area) could be used to determine optimum stocking levels. They found that LAI values at around half the maximum site LAI was approximately an optimum. Calculated values from equation 6.3 compared with climate and soil variables (which have been detailed in previous chapters) to determine significant Pearson correlations for each species.

$$E = \text{vol/LAI}_{\text{harvest}} \quad (6.3)$$

Where, E = amount of stem volume index produced per square meter of foliage, vol = annual volume index increment $\text{m}^3 \text{ ha}^{-1}$ and LAI at harvest = $\text{m}^2 \text{ m}^{-2}$.

Correlation analysis showed that efficiency was positively related to soil bulk density, temperature and solar radiation intensity, and negatively with a range of nutrient characteristics for both species (Table 6.3).

Table 6.3 Pearson correlation coefficients between efficiency and listed variables for *P. radiata* and *C. lusitanica* (n = 86), *p*- values are shown in brackets.

Variable	<i>P. radiata</i>	<i>C. lusitanica</i>
Mean annual temperature	0.5015 (<.0001)	0.2039 (0.0597)
Solar radiation	0.3462 (0.0011)	0.2530 (0.0187)
Soil bulk density	0.2712 (0.0116)	0.2649 (0.0137)
Carbon	-0.2784 (0.0095)	-0.2583 (0.0163)
Nitrogen	-0.2725 (0.0112)	-0.2592 (0.0160)
P retention	-0.1501 (0.1676)	-0.2590 (0.0160)
CEC	-0.3572 (0.0007)	-0.2757 (0.0102)
Exch. Mg	-0.3155 (0.0031)	-0.3037 (0.0045)
Exch. K	-0.2373 (0.0278)	-0.2462 (0.0223)

Across sites the efficiency that LAI produced tree volume index ranged from 1.12 to 9.14 $\text{m}^3 \text{m}^{-2} \text{yr}^{-1}$ for *P. radiata*, and 0.33 to 7.0 $\text{m}^3 \text{m}^{-2} \text{yr}^{-1}$ for *C. lusitanica*. Despite this range there were hardly any significant differences across most sites for the combined fertilised and non fertilised treatments. Appendix 7 compares the efficiency of both *P. radiata* and *C. lusitanica* plots across sites. A paired species comparison taking into account the different volumes indicates that on average *P. radiata* is more efficient across sites except for the Tekapo location and the performance of the two tree species at Golden Downs, Okuku and Waimarino are similar to one another (Fig. 6.5). This possibly suggests that *P. radiata* has better stomatal control and is more suited to the climatic conditions in which the two species were growing.

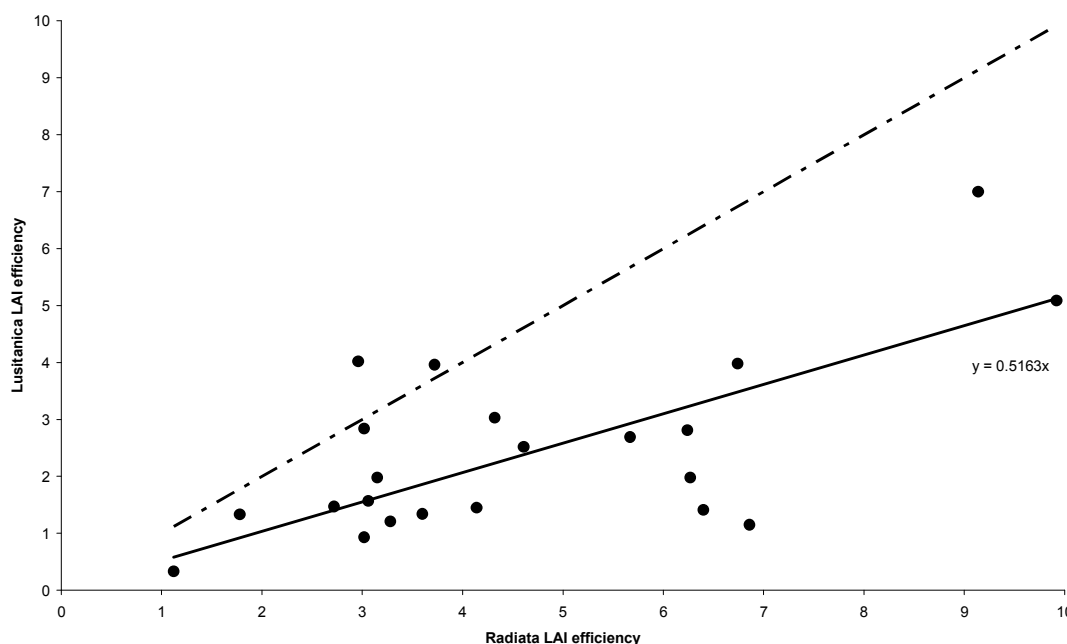


Figure 6.5 Paired site comparison of LAI efficiency. The 1:1 relationship (dotted line) is shown for comparison with the trend line (thick black line).

Relationships between leaf area and productivity

Fassnacht and Gower (1997) found that annual net primary production (ANPP) was closely correlated with conifer LAI ($R^2 = 0.62$). Gholz, (1982) found strong relationships between LAI and stand basal area across a small number of sites ($R^2 = 0.92$) and also noted that factors other than moisture and temperature limited LAI_{max} .

Romanya and Vallejo, (2004) produced several multiple regression models that explained between 85 and 97% of the variation in site index across 10 Mediterranean and 12 Atlantic locations in Spain. The contributing variables were: soil depth, carbon/nitrogen content and phosphorous concentrations in the L horizon, effective CEC, foliar nutrients and altitude (Romanya and Vallejo 2004). Romanya and Vallejo also found that pine litter fall had the best correlation with site index, a measure of site quality. This is significant in relation to this study because litter fall is shown to be closely associated with leaf area (Gower et al. 1993; Reich et al. 1992) and this supports the belief that leaf area is related to site quality (site index), see Chapter 4.

Relationships between productivity and site characteristics

Hunter and Gibson, (1984) developed a model of site index based on relationships between climate and soil characteristics which explained 57.7% of the site variation across the North Island, New Zealand. A large data set using 299 sample plots in the North Island were collected and site index was predicted from the following variables, most of which were linearly transformed: pH, temperature, soil fertility, depth to the A horizon, penetration resistance, rainfall and Bray phosphorous (Hunter and Gibson 1984).

There was a great deal of similarity between the variables identified by Hunter and Gibson and those identified by Watt *et al.* (2005) temperature, rainfall, soil C to N ratio, total nitrogen, total phosphorous, organic phosphorous and the depth to the A horizon. This chapter has also shown that a simple linear regression model using the interaction of LAI and mean annual temperature was closely correlated with *P. radiata* volume index ($R^2 = 0.84$). This suggests that maximum LAI and site mean annual temperature may provide an effective and simple predictor of site quality, and this interaction has explained a larger proportion of the variation in volume growth across the 22 sites tested.

CONCLUSIONS

In Chapter 4 the modelled maximum leaf area index exhibited highly significant species differences ($p < 0.0001$), significant fertiliser ($p = 0.0232$) but not site disturbance differences (Table 4.1). The greater separation of *C. lusitanica* LAI development trends (Fig's. 6.2 a&b) suggests that *C. lusitanica* LAI is more sensitive to the treatments than *P. radiata*. In comparison, measures of productivity show a much greater range in treatment effects over time. Root collar diameter was the most responsive measure of fertiliser effects (Table 6.2). The affects of site disturbance on productivity diminished over time, but tree height showed the greatest response to site disturbance. These results suggest that productivity may better account for the fertiliser and disturbance effects over the long term compared with leaf area index.

The development trends of both productivity and leaf area index are shown to be relatively similar when modelled across sites, although leaf area index reached a maximum asymptote earlier than productivity measures. This may show that LAI is a more sensitive temporal measure of site quality. This is probably because of a lag between canopy responses to the environment and stem wood production. Because sensitivity to changes in site conditions is stated as a critical attribute of site quality measures (Schoenholtz et al. 2000), leaf area index may provide a more useful measure of site quality especially if measures are able to be made more quickly and cost effectively than productivity.

Development trends in the densely planted trials are similar to stands at conventional tree spacing with 3 exceptions: 1) the period over which the canopy development has occurred is dramatically condensed, 2) no silvicultural operations were carried out and 3) the leaf area conversion factor for the densely planted trials will be greater than that for conventional stands because of the greater foliage clumping associated with wider spaced trees, further study is required to quantify this. Ideally long term studies of mature crop development at these sites are required to compare the LAI development patterns fully and an alternative would be to take LAI measurements of mature stands

that have had initial soil chemical and physical factors determined at planting. These measurements would also allow a suitable comparison with the findings of this study.

The interaction of mean annual temperature and LAI provided a simple linear regression model that was highly correlated with productivity and calculations showed that the efficiency with which LAI produced tree volume index was within a 7-8 fold difference for both species but analysis suggested sites were hardly different apart from the extremes. The leaf area efficiency of *P. radiata* foliage was approximately twice that of *C.lusitanica* across all sites and foliage efficiency for both species was related to similar climate factor, soil physical and chemical properties.

CHAPTER 7

A National Model of LAI_{max} across New Zealand *Pinus radiata* Plantation Forests

INTRODUCTION

Monitoring identified indicators of plantation forests over time should allow changes in site quality to be identified and poor management practices to be targeted using specific forest management operations. A national model of maximum leaf area index (LAI_{max}) could provide a standard or benchmark from which site quality can be assessed rapidly across large areas and over a number of stand rotations. In the previous chapters it has been shown that LAI_{max} like productivity is significantly related to a number of key variables that contribute to a description of site quality such as temperature, soil physical properties and a range of soil nutrients. This chapter proposes a model and then discusses the challenges and benefits of a national LAI_{max} model for *Pinus radiata*, New Zealand's most economically important plantation species.

National forest leaf area models are not well reported in the literature. Most leaf area patterns are incorporated into process-based models and based on small intensive studies. However, Lou *et al.* 2002 studied a seasonal leaf area distribution across China. Their sophisticated "PhenLAI" model was based on a combination of field and satellite data covering a range of forest types. They predicted LAI_{max} from annual temperature and rainfall statistics and then modified it by seasonal water balance. Unfortunately they did not have ground-based seasonal data like this study to compare with their model estimates. Their work demonstrated many of the capabilities and benefits of a national LAI_{max} model by producing maps and explaining 56% of the LAI_{max} variation across the 16 forest types found in China (Luo *et al.* 2002). The work of Lou *et al.* 2002 strongly supports the reasoning behind a New Zealand LAI model and by targeting one species rather than a range of species more accurate estimates of site quality and the monitoring of changes in site quality are possible.

METHODS and ANALYSIS

A multiple linear regression model was developed for *P. radiata* LAI_{max} from data collected across 22 forest trial sites. These sites cover a wide range in climate, fertility and topographic characteristics encompassing 92.6% of the soils planted with this species.

Prior to construction, variables were checked for linearity. Location was considered a relatively important component of the model because a response surface would have distinct advantages when incorporated into geographic information systems as shown by Lou *et al.* 2002, and this could lead to a greater understanding of relationships between site quality and LAI across New Zealand. Significant variables which have indicated their importance during analysis in the previous chapters were introduced with an overall aim of creating a simple model based on easily collected variables with little apparent bias.

RESULTS

A national LAI_{max} model (Equation 7.1) was developed for non fertilised *P. radiata* which explained 96% of the variation in the original dataset, by incorporating 5 input variables (Table 7.1). Negative relationships were shown between LAI_{max} and mean annual temperature and readily available water. Of the 5 variables listed in the model, all are commonly collected from the field or from long term climate records (Leathwick and Stephens 1998). The model predictions provide a good fit (Fig. 7.1) when the variation across sites is considered, and the residuals appear unbiased (Fig. 7.2). Latitude and mean annual temperature are auto-correlated so incorporation of one in the model insures the other is less significant, but was retained for reasons outlined above.

Table 7.1 Variables identified for a national model of *P. radiata* LAI_{max}, estimated parameters and standard errors are given (3dp) Adjusted $r^2 = 0.9612$, with MSE = 2.141.

Variable	Parameter	Std err	<i>p</i> value	<i>partial R-squared</i> %
mean annual temperature	-1.417	0.231	<.0001	92.89
Longitude	0.181	0.040	<.0001	1.28
Readily available water	-0.235	0.059	0.0003	1.13
P inorganic	0.006	0.002	0.0278	0.74
Latitude	0.168	0.112	0.1415	0.08

$$\text{LAI}_{\max} = \text{Temp}(-1.417) + \text{Lat}(0.168) + \text{Long}(0.181) + \text{PinOrg}(0.006) + \text{RAW}(-0.235) \quad (7.1)$$

Where Long = longitude (degrees), Temp = mean annual temperature (°C), Lat = latitude (degrees), PinOrg = inorganic phosphorous (mg g⁻¹) and RAW = readily available water (% v/v).

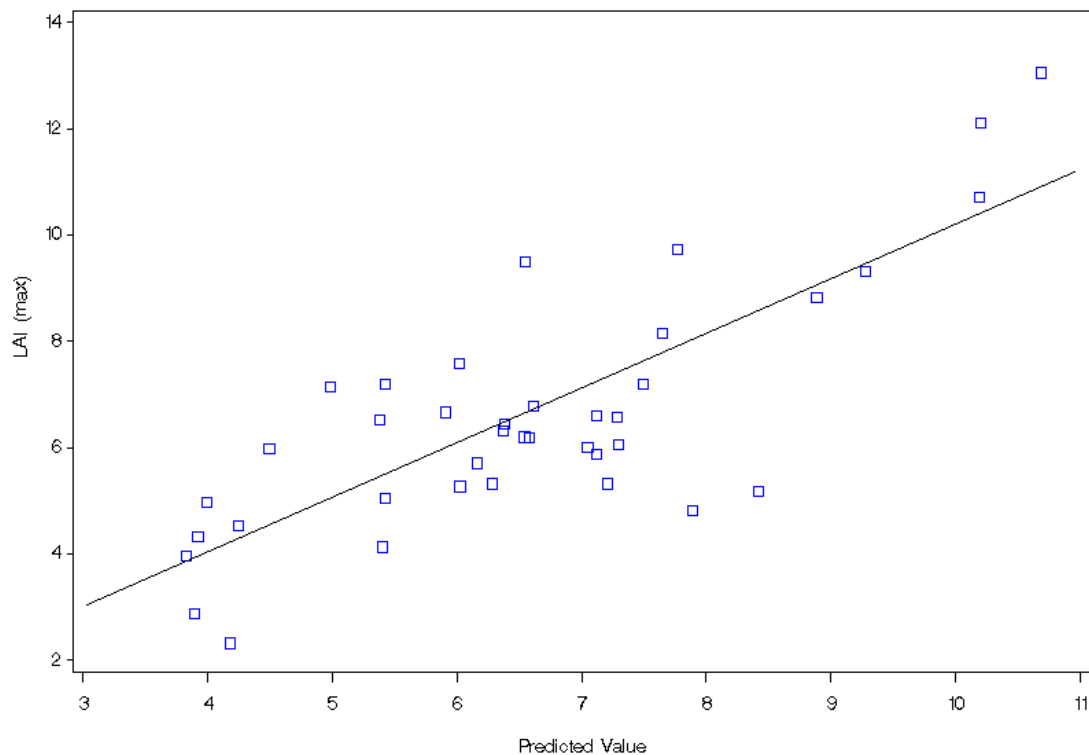


Figure 7.1 Comparison of LAI_{max} with the predicted national *P. radiata* LAI_{max}. The 1:1 comparison (line) is shown.

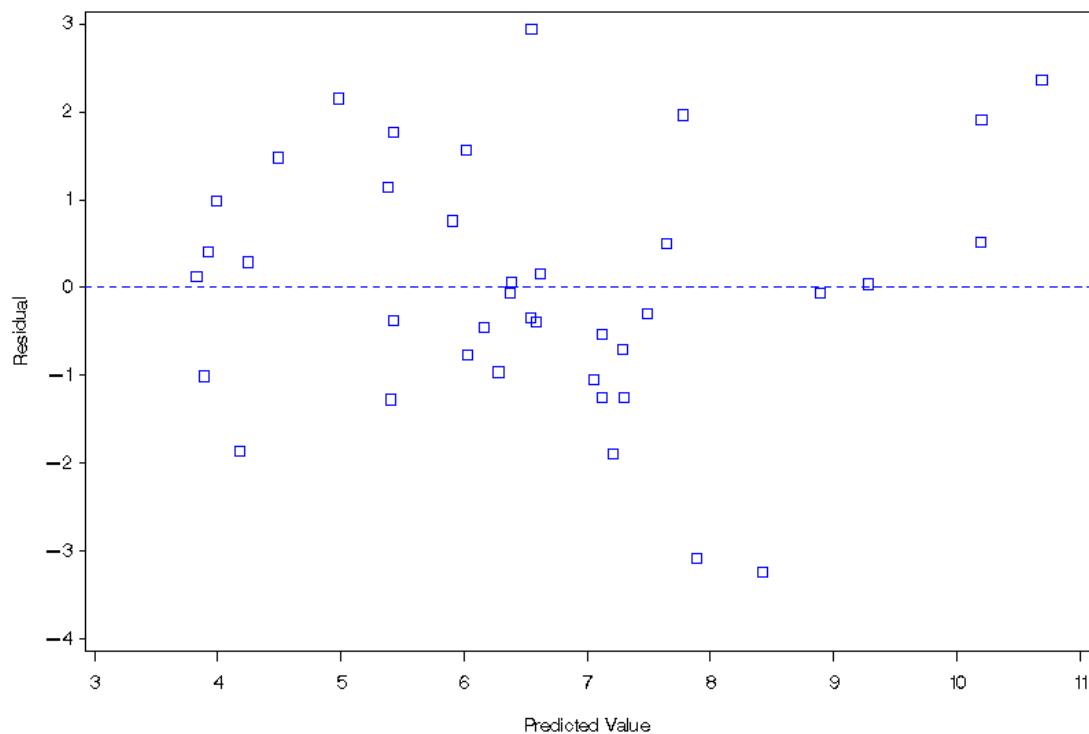


Figure 7.2 Residual plot of the national *P. radiata* LAI_{max} model.

DISCUSSION and CONCLUSIONS

Benefits of a national LAI_{max} model

Compared with empirical growth models such as site indices (Garcia 1999) a national LAI_{max} model is more useful in explaining variation across sites because it incorporates processes that are known to affect stomatal control and hence growth. Building a national LAI_{max} model to make comparisons across sites is an important first step for an integrated site quality monitoring programme. A robust national LAI_{max} model should contribute data to a response surface of site quality, and which can be incorporated into geographic information systems for mapping and interrogation. The proposed national model of LAI_{max} (Equation 4.1) incorporates both climate and soil variables and it is likely that the development of a national model such as this could also lead to a greater understanding of relationships between site specific management operations and site quality across New Zealand plantation forests.

Building a site quality index from a national *P. radiata* LAI_{max} model

In New Zealand the maximum leaf area index of temperate forests typically ranges from 4 to 10 depending on species, canopy age, stocking, soil nutrients solar radiation and rainfall, although there are very few published reports quoting values. Whitehead et al (1994) gave reference to a 6 year old *P. radiata* stand at 450 stems per hectare with a leaf area index between 3.2 and 5.3 m²m⁻². However, this stand was unlikely to be exhibiting closed canopy attributes.

It is proposed that deviations from the recommended national model, that accounts for temperature, moisture, solar radiation, fertility and location affects could provide quantitative estimates of site quality (Equation 7.2).

$$\text{Site Quality Index} = ((\text{actual} - \text{predicted})/\text{predicted}) * 100 \quad (7.2)$$

Where predicted = LAI_{max} (m²m⁻²) predicted from the input variables of the national *P. radiata* model and actual = measures of mature *P. radiata* LAI (m²m⁻²) from the field at a particular site of interest.

Using measures of leaf area index to estimate an index of site quality will provide a slightly improved sensitivity using a greater range in values than estimates from site index. Whether this sensitivity is warranted can be debated, and perhaps a set of bounds that encompasses the inaccuracy of the model and seasonal sampling variation can be calculated from the following Equation (7.3). These bounds were determined using the seasonal influences calculated in Chapter 5.

$$\text{Significant deviation from the model (baseline)} = -0.16 * \text{LAI}_{\text{max}} + 2.37 \quad (7.3)$$

National models of leaf area are not well reported in the literature, although results from this study compare well with the findings of Luo *et al.* (2002) that determined LAI_{max} values which ranged from 4.31m² m⁻² in temperate to 12.41 m² m⁻² in alpine fir forests, and found that leaf area expansion was at a maximum in the April to May period for the northern hemisphere.

A simple national model explaining 96% of the variation in *P. radiata* LAI_{max} was developed. Appendix 8 shows a *C. lusitanica* LAI_{max} model and provides additional support for the *P. radiata* model in the fact that the dominant contributor explaining the variation in the data was temperature and that different but rational variables were chosen during the statistical analysis. The national model of *P. radiata* LAI_{max} showed significant negative relationships were determined between LAI_{max} and both mean annual temperature and readily available water. Positive relationships were determined between LAI_{max} and latitude, longitude and inorganic phosphorous.

CHAPTER 8

Use of LAI_{max} as a Site Quality Monitoring Tool

INTRODUCTION

The specific goals of this study were to determine:

- 1) The variation in LAI across New Zealand plantation forests,
- 2) the likely causes of variation in LAI and
- 3) compare predictions of maximum LAI (LAI_{max}) with productivity measurements.

This chapter summarises the findings of this thesis and examines the potential challenges and sources of error likely to be experienced while attempting to utilise LAI as a component of a site quality monitoring tool.

DISCUSSION

This chapter will argue that LAI could be a useful component of site quality indices that monitor changes across New Zealand plantation forests, because it fulfils the criteria identified in Chapter one, providing calibration is undertaken.

The two opposing views of site quality indices

Many researchers and political organisations believe that site quality monitoring tools are required to address concerns about the effects of forestry on the environment and a changing global environment on forest productivity. However, there are also researchers who believe there are deficiencies in the soil (or site) quality concept and its application through an index (Letey et al. 2003). Examples are given, one of nitrogen, which showed that high concentrations led to an improved N-mineralization index but this was accompanied by detrimental affects on water quality. This demonstrates that maximising one index may have a counter affect on another, and to

combat these Letey *et al.* (2003) suggests that technical information rather than indices are required to motivate and educate management practices in order to optimise crop production and sustain soil resources. This is based on the belief that we can not accurately foresee new technology or management adaptations that are likely to modify the levels of sustainable productivity.

However, across other parts of the world and in particular Australia and New Zealand there is a commitment to the site quality monitoring concept (Letey *et al.* 2003; Sparling and Schipper 2004; Sparling *et al.* 2004). At present there are a range of site quality techniques which are being developed, but they are not widely applicable across diverse environments at a global scale, or at a national scale in New Zealand as reviewed in Chapter one.

Why and how can LAI help?

Leaf area index is influenced by the accumulated effects of climate, nutrients and moisture over the preceding period. LAI can also be influenced by management practices and is sensitive to changes from year to year and within a season. Measurements of leaf area provide a perspective of the underlying processes that affect plant growth and these allow a greater understanding of site characteristics. Because there are a number of processes that effect LAI, many influencing variables may be incorporated into a monitoring programme or a national model of LAI_{max}.

Not only can these LAI measures be used to demonstrate changes in site quality over time, but comparisons with a national model may provide a benchmark to enable sites with resource limitations to be identified and highlight the factors contributing to this.

Satellite or aerial LAI measurements

At present, LAI based on satellite or air-borne devices are likely to provide the best and most efficient assessment tools for long-term site quality monitoring programmes, because it is possible to obtain a snap shot in time across large areas from unobtrusive measurements combined with large scale cost efficiencies. A snap shot of large areas at one time is an important feature because comparisons are best made when conditions are relatively constant across sites, even though measurements may be

subject to minor seasonal influences; over time trends can be observed like the treatments effects were discernable in this study.

Satellite or aerial data can be acquired at various scales and resolutions. It is proposed that a national programme would require fine resolution (50m²) over large areas (~1 800 000 ha). Remotely sensed stand data of alternative management practices across the forest estate in combination with ground based validation could be used to account for improved management practices in a national LAI model.

At present remotely sensed data for New Zealand is distributed across a number of government organisations (pers. comm Peter Stephens MfE). There is a need and a desire to collate data for a wide range of research applications (pers comm. Kimberly Cullen, Official Statistics Research and Data Archive Centre (OSRDAC)).

Model calibration

To monitor changes in site quality over time, given that management practices may alter levels of sustainable productivity at a site, a continual process of calibration is foreseen. LAI measurements are well suited to such a process because research studies can quickly test changes in management practices as demonstrated by the miniature plot design. LAI can account for management practices if these characteristics are examined and then incorporated into the model. Differences induced by improved genetic material (St. Clair 1993; Xu 2000) or different tree species (as demonstrated by this study) require calibration. Differences due to plant age and stand density will also need to be determined before a national model can provide definitive recommendations. With cooperation from growers a great deal of this data is possibly available from ongoing trials. These are generally scientific or operation trials established to determine productivity gains and all that may be required is authorisation, some geographic information work to locate the relevant sites, a site visit and then access to recent LAI measures. Any remaining requirements may be achieved by establishing a limited number of arboretum type trials covering the extremes of climate across New Zealand.

A range of conversion factors could be calculated from the above work; some have already been determined for environments and species which are commonly planted in New Zealand (e.g. *Eucalyptus Nitens* (Medhurst et al. 1999) *Pseudotsuga menziesii* (Mirb. Franco) (Smith 1993)).

It will also be possible to calibrate the effects of numerous insect and fungal infestations (Chapman 1998) on leaf area with the Plant Canopy Analyser, and investigating changes over the short term are distinctly possible, although the sensitivity to levels of infestation is yet to be tested.

Study findings compared with conventional stand densities and older trees

This study was undertaken using miniature plantations for two fundamental reasons: 1) to control within site variation and 2) establish rapid treatment effects. This approach uses miniature plots at high density and seems quite controversial, yet it is not unique (Amateis et al. 2003; Kelting et al. 1999; Ryan et al. 2004). This study has demonstrated that the development trends of leaf area index and tree growth have shown similar patterns, but LAI reaches an asymptote earlier than measures of productivity, and these sigmoidal trends are similar to those reported for stands at conventional densities in New Zealand (Garcia 1999; Kimberley et al. 2005; Maclaren et al. 1995; Mason et al. 1997; Whitehead et al. 1994) and elsewhere (Landsberg 1986; Vose et al. 1994; Zeide 1999; Zeide 2004).

Within the scope of this study it was not possible to compare LAI measurements over long periods such as decades but it is speculated that patterns of development would follow the findings of previous studies which show a gradual decline in LAI with age (Luo et al. 2002; Vose et al. 1994). This function would also be important to investigate and incorporate in a national model.

Sources of error

The identification of possible sources of error arising from LAI measurements is an important process that may guide future calibration and validation programmes. Errors occurring during the LAI measurement process were controlled as much as possible through the use of a pilot study that determined the best technique for

measuring LAI in the highly stocked plots, but there is little doubt that techniques will need to be modified in order to assess mature stands and field sampling regimes need to keep this in mind in order to protect against potential inaccuracies. A recommended sampling strategy for homogenous canopies under pines suggests at least 10 measurements are required, and for heterogeneous canopies samples are best derived from individual gap fraction measurements then averaged for the site (Weiss et al. 2004).

It is important to note the form of the relationship between the fraction of light measured beneath a canopy and the calculated LAI so the capabilities of the instrument are better understood (Fig. 8.1). In dense canopies of mature tree crops small changes in the fraction of light coming through the canopy can lead to large differences in the estimated LAI. From the relationship shown in Figure 8.1 it is possible to see how the most accurate estimates of LAI are made for crops with foliage densities below $3 \text{ m}^2 \text{ m}^{-2}$, where relatively large changes in the light fraction lead to small increments in LAI estimates.

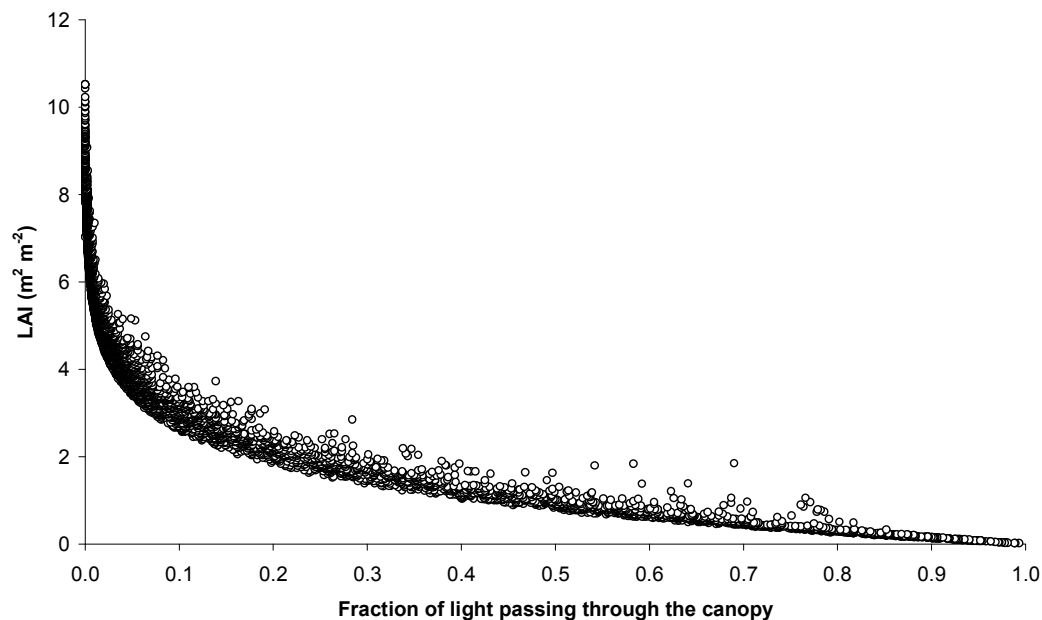


Figure 8.1 Relationship between the fraction of light passing through the canopy and leaf area index using actual sample data across the 35 forest sites.

Factors that lead to over-estimation of LAI

Optical measurements using a device such as the LAI-2000 Plant Canopy Analyser have been reported to slightly over estimate LAI measurements as the branch area increases (Kucharik et al. 1998). This trend is found in older stands and consistent relationships are expected across stands of a similar age and stocking. However, over-estimation of LAI is reported to contribute an insignificant amount because more than 90% of branches are shaded by foliage anyway (Kucharik et al. 1998). This depends on species because of the different allocation of biomass to stems, branches and foliage (Kucharik et al. 1998).

Factors that lead to under-estimation of LAI

Measurements of LAI in mature stands are also reduced due to foliage clumping which occurs in the outer portions of a canopy (Smith et al. 1991; Stenberg 1996), so over-estimation of LAI is partially negated by under-estimation. The effect of stems is more significant, especially in very dense stands (Jack and Long 1991) and further work is required to compare the effects of stocking (Smith 1991) and pruning levels on LAI to quantify these differences as discussed in the calibration requirements.

Lighter coloured foliage has greater reflective properties and the scattered light within a canopy can lead to an under-estimation of LAI. For example, a fully sun lit canopy can lead to an under-estimation of LAI by approximately 11% in mature forest canopies (Welles and Norman 1991). This emphasises the need for measurements to be taken during overcast conditions to minimise these effects.

Other monitoring tools

The use of productivity as a component of a national monitoring tool of site quality is the current basis for site comparisons. Productivity calculations provide a wide range in values which are responsive to different site conditions as demonstrated by the treatment effects, see Chapter 6. Productivity is an empirical measure and a series of benchmark trials must be linked to models based on soil characteristics affecting growth (Richardson et al. 2001; Richardson et al. 1999). However, the productivity of various tree species differs widely across environments and a single benchmark species is unlikely to function across environments at a global scale, so a time consuming calibration process would be required, as productivity measures are generally based on long term responses.

Critical examination of the relative stocking index (Bergusson et al. 1994) showed it was not likely to be a practical tool for use in plantations because of the manipulation of stand densities that occur in New Zealand and because of the young age at which stands are harvested.

Using soil quality indicators to monitor changes and benchmark site quality has many merits because of the mechanistic links with productivity, such as the effects of nutrient supply on productivity (Schoenholtz et al. 2000). Generally vast datasets of soil properties are being collated (Lilburne et al. 2004; Sparling and Schipper 2004; Sparling et al. 2004), but cost effective assessment over large areas on a frequent basis is not one of the advantages at present.

Table 8.1 Subjective comparisons between the source of data, costs of acquisition, ease of measurement and estimated likelihood of errors from different assessments of site quality.

<i>Measure of Site Quality</i>		<i>Probable data source</i>	<i>Indicative costs</i>	<i>Ease of measurement</i>	<i>Errors in measurement</i>
Productivity (empirical)	Height & Dbh	field	medium	simple	low
	“ “	modelled	low	simple	medium
other key components	Soil chemistry	field	high	medium	low
	Soil physical	field	high	medium	low
	Soil chem. & physical	historical	low	simple	unknown
	Soil biological	new survey	medium	difficult	medium
	Invertebrates	new survey	high	simple	medium
	Climate data	historical	low	simple	low
Leaf area (physiological)	Remote	aerial	medium	medium	medium
	Remote	satellite	medium	medium	medium

Is leaf area index a helpful monitoring tool?

LAI can be a useful component of a site quality tool because it fulfils all three of the criteria which have been identified as important. It is 1) sensitive to changes over time and across environments, 2) it is relatively inexpensive to measure over large or diverse areas and 3) it is also easy to measure in the field, although further calibration is required.

The first criterion is satisfied across a range of measurement periods. Foliage is responsive to both relatively short term changes such as moisture deficits and also seasonal changes in the medium term, or long term changes such as soil fertility over a stand rotation. Over varying periods of time LAI_{max} is shown to be correlated with changes in vapour pressure deficit, mean annual temperature, soil carbon, nitrogen, and inorganic phosphorous. The sensitivity of LAI_{max} across a wide range of environments is supported by this study and by other studies which showed that leaf properties of more than 100 species across 6 biomes in the Americas exhibited predictable leaf traits across a wide range of vegetation types (Reich et al. 1999) and Luo *et al.* (2002) who showed a model of LAI explained 56% of the variation across 16 forest types in China.

The second and third criteria are satisfied because LAI is a rapid and relatively simple assessment made with a number of available measurement devices. Indirect measurement of LAI is a rapidly evolving science (Hyer and Goetz 2004) that is at the forefront of research focuses. Because of the efficient manner in which LAI can already be collected, the cost of using LAI for monitoring in the future is likely to be relatively inexpensive compared with current techniques used to measure key components of site quality.

Whether leaf area index is a better measure of site quality than productivity will be debated for a while yet. But if soil attributes hold the key to measures of soil quality as reported (Kelting et al. 1999; Schoenholtz et al. 2000) then perhaps another argument in favour of LAI is the large and significant contribution that soil properties exhibit to the variation in LAI across New Zealand sites (34.9%, see Chapter 4).

SUMMARY

Chapter one provides an introduction and rationale for this study. Chapter two discusses the need for a widely applicable, cost effective and rapidly assessed site quality monitoring tool, alternative methods were reviewed. Chapter three describes

the scope of this study and outlines the trial series details and characteristics, along with descriptions of the datasets and analysis methods.

The influences of soil and climate characteristics on *P. radiata* and *C. lusitanica* leaf area index are discussed in Chapter four. The sensitivity of LAI_{max} to differences across sites and seasons was demonstrated in Chapter five. In Chapter six the relationships between leaf area index and productivity were shown to be relatively strong when the effects of temperature and actual leaf area index were introduced together. Differences between LAI and productivity were attributed to changes in efficiencies and allocation across contrasting environments and these were positively associated with nutrients and temperature but negatively with soil moisture. It was also argued that plants respond to the environment so that optimal use of site resources are made and that leaf area is an important attribute used to optimise plant growth which is occurring both above and below the ground.

Chapter seven proposed a model of LAI_{max} across New Zealand. It showed that for the 22 sites analysed in this study there were strong relationships that varied across New Zealand *P. radiata* plantations and this final chapter has drawn attention to the calibration requirements and the need for more work in mature stands at different densities and to compare different genetic material of important species.

The specific goals of this study were met when the variation in maximum leaf area index across New Zealand plantation forests was shown to be between 2.9 and 11.8 m²m⁻² for *P. radiata* and 3.1 to 12.6 m²m⁻² for *C. lusitanica*, and the variation in leaf area index was shown to be correlated with changes in vapour pressure deficit, mean annual temperature, soil chemistry such as inorganic phosphorous and soil physical factors such as readily available water. The final specific goal was achieved when predictions of maximum LAI for both species compared favourably with productivity measurements when combined with temperature and especially when particular site efficiency or allocation influences were accounted for.

IMPLICATIONS

Models provide helpful research tools from which predictions and comparisons of changing conditions or effects can be observed. They are compiled at various levels of complexity to explain and explore functions of interest. Modelling of site quality is an attempt to simplify the complex functions and processes that occur at a site. This study shows that the major factors that influence site quality across New Zealand plantation forests in order of importance are climate, soil chemical, soil physical characteristics and topographic properties. The proposed national LAI_{max} model for *Pinus radiata* provides a simplified foundation on which some of the complex climate and soil characteristics across New Zealand plantation forests can be taken into account in an attempt to assess site quality and on this basis this model can offer a benchmark to monitor changes in site quality over time, particularly once further calibration is carried out.

APPENDIX 1

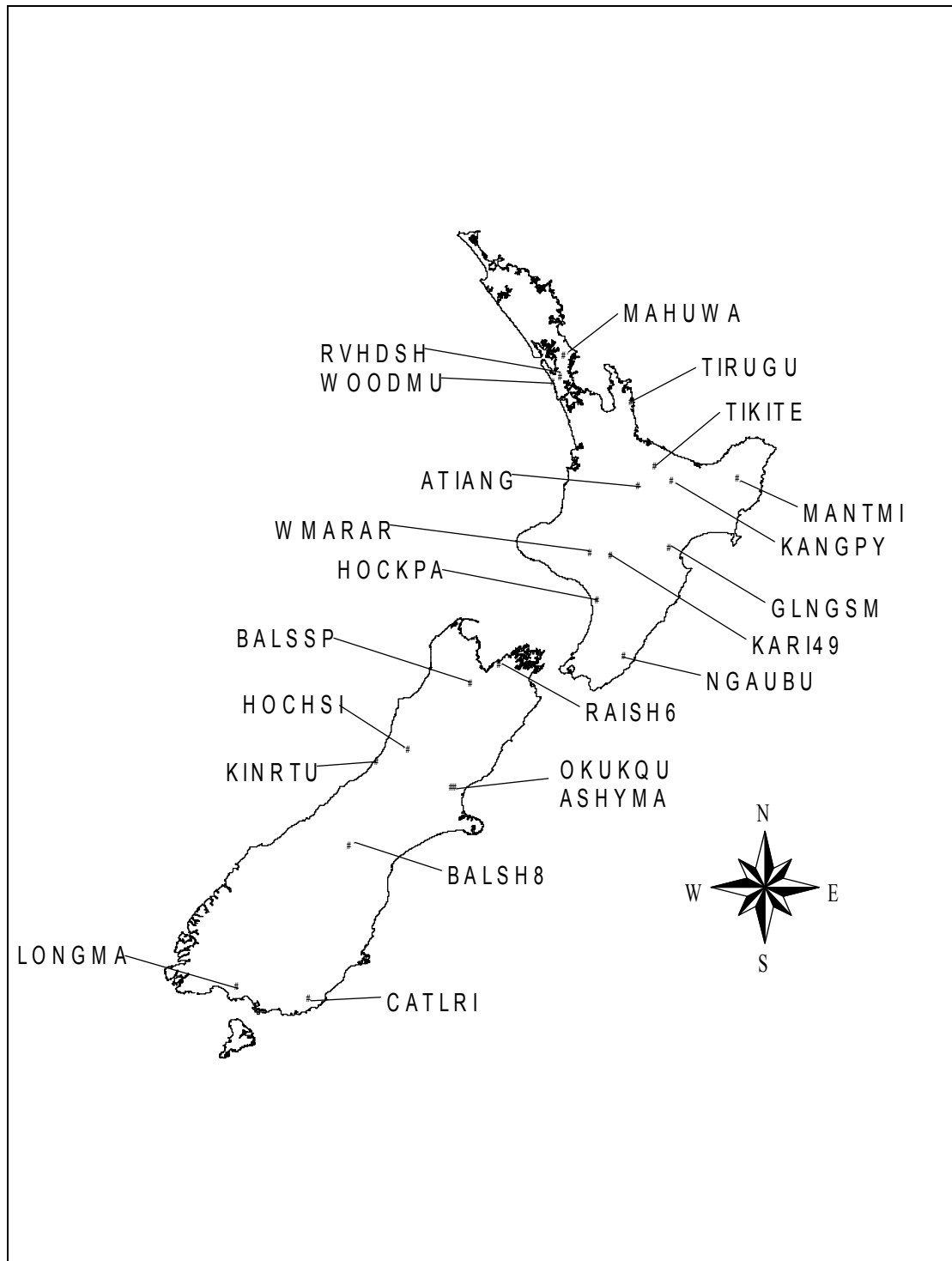


Figure A 1.1 Map of the 22 trial locations examined in this study.

APPENDIX 2

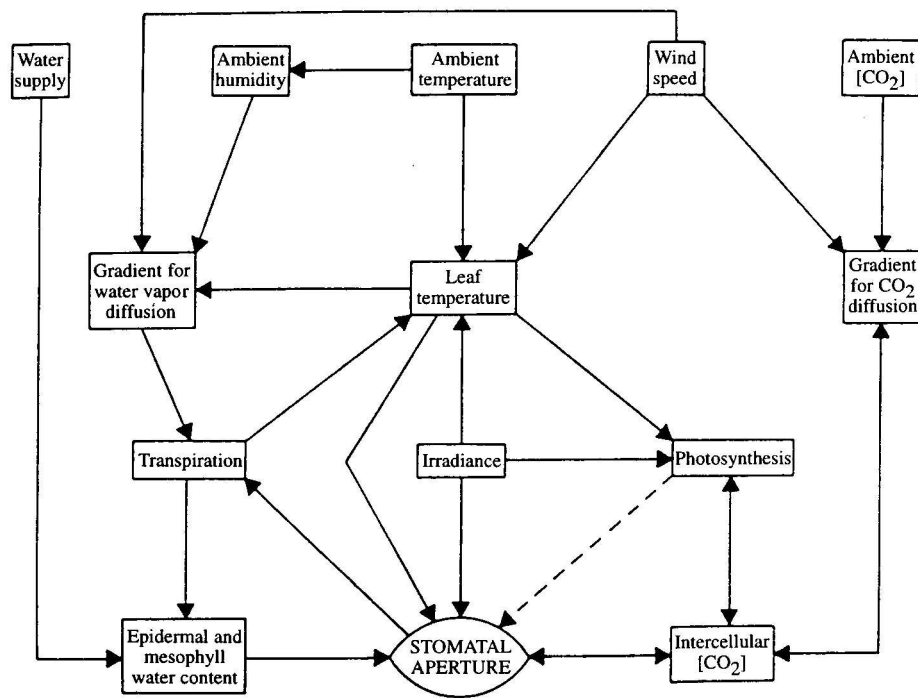


Figure A 2.1 Relationships between environmental variables and physiological processes controlling stomatal aperture: Source (Kozłowski and Pollardy 1997).

APPENDIX 3

Table A 3.1 List of sites with plots that were removed from the analysis. D = disturbed, U = undisturbed, C = *C.lusitanica*, R = *P.radiata*, N = no fertiliser, F = fertilised.

<i>Site</i>	<i>LAI_{max}</i>	<i>Rate of development</i>	<i>Age of inflection</i>
<i>Bulls</i>	DCN	DCN	DCN
<i>Catlins</i>	DCN		
<i>Hochstetter</i>		UCN	UCN
<i>Hochstetter</i>		URN	URN
<i>Hochstetter</i>	DCF	DCF	
<i>Hochstetter</i>	DCN	DCN	DCN
<i>Hochstetter</i>	DRN	DRN	DRN
<i>Hochstetter</i>	UCF		
<i>Kaingaroa</i>	DCN	DCN	DCN
<i>Kaniere</i>	DCN	DCN	DCN
<i>Kinleith</i>		UCF	UCF
<i>Longwoods</i>	DCF	DCF	DCF
<i>Longwoods</i>	DCN	DCN	DCN
<i>Longwoods</i>	DRN	DRN	DRN
<i>Longwoods</i>	URF		
<i>Mahurangi</i>		UCF	UCF
<i>Ngaumu</i>		DCF	
<i>Okuku</i>	DRN	DRN	DRN
<i>Rai Valley</i>		DCF	DCF
<i>Rai Valley</i>	DCN	DCN	DCN
<i>Tikitere</i>		UCF	UCF
<i>Woodhill</i>		DCN	

APPENDIX 4

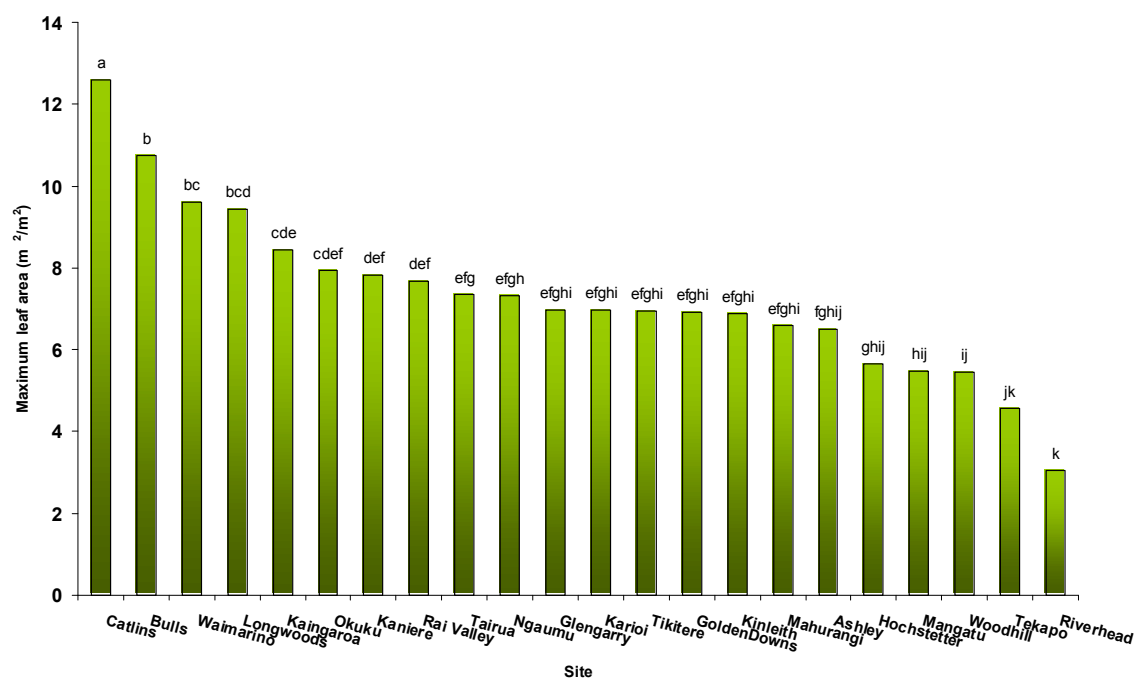


Figure A 4.1 Variation in LAI_{max} across sites for *C. lusitanica* plots. Bars with a similar letter indicate no significant difference between sites according to Duncan's multiple range test ($p=0.05$).

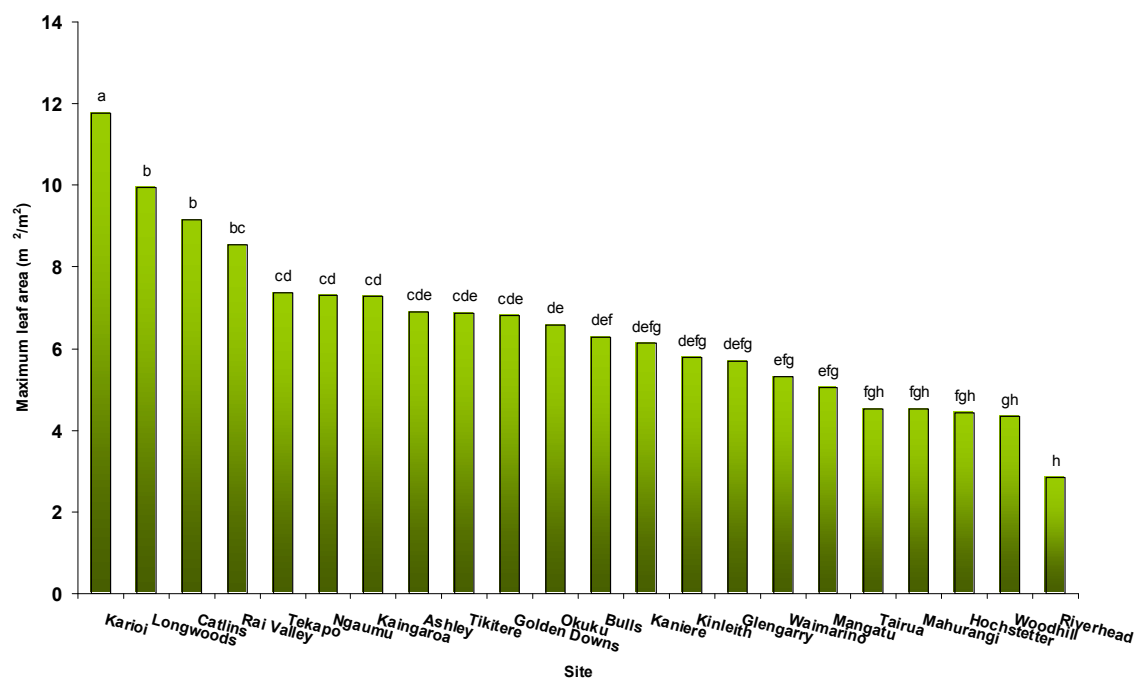
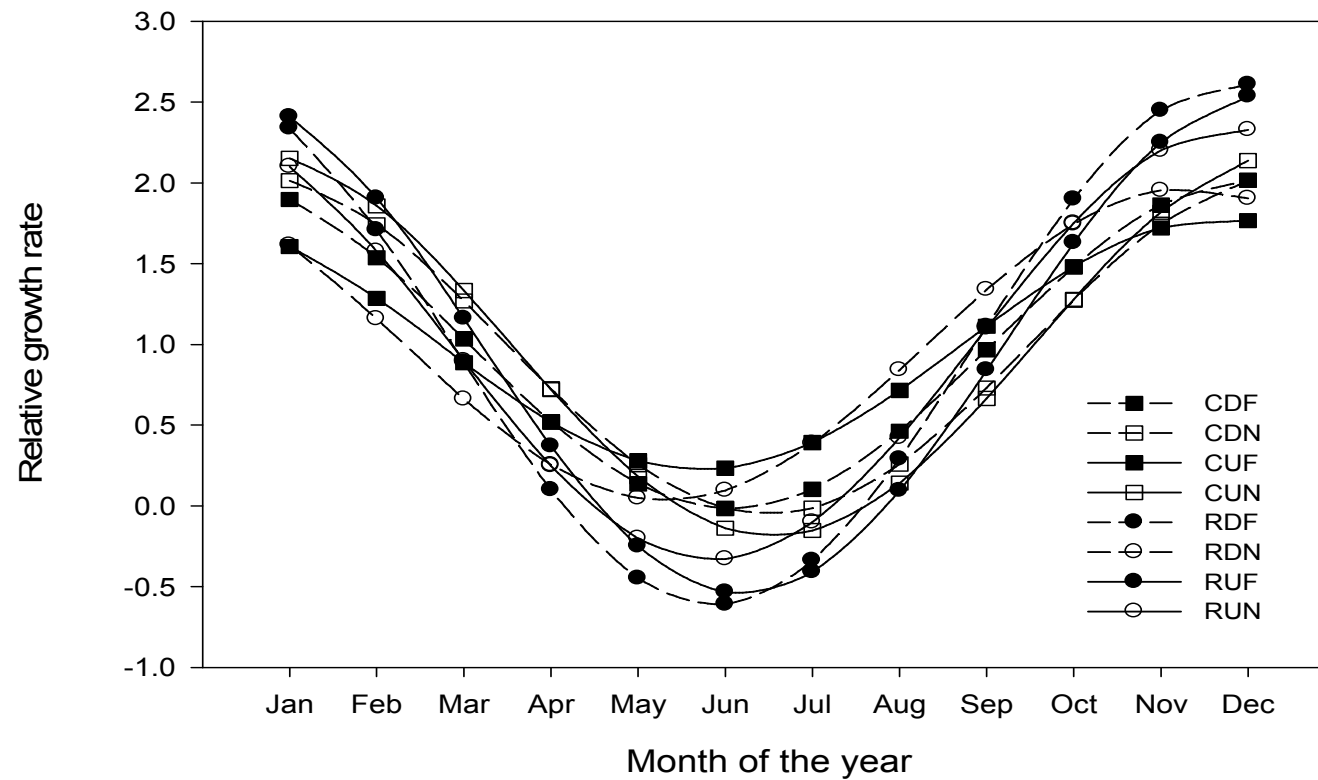


Figure A 4.2 Variation in LAI_{max} across sites for *P. radiata* plots. Bars with a similar letter indicate no significant difference between sites according to Duncan's multiple range test ($p=0.05$).

APPENDIX 5

Figure A 5.1 Relative seasonal growth patterns averaged across 4 years of growth for treatments across sites. D = disturbed, U = undisturbed, C = *C. lusitanica*, R = *P. radiata*, N = no fertiliser, F = fertilised.



APPENDIX 6

Table A 6.1 Mean tree height by treatment and sites by age. Standard errors are presented in brackets.

Tree Height (cm)	Trial Age			
	1	2	3	4
Disturbed	74.6(1.05)	164.9(2.29)	255.0(3.40)	346.3(4.68)
undisturbed	83.6(1.08)	179.1(2.23)	269.8(3.28)	359.5(4.61)
Fertilised	79.2(1.09)	178.4(2.29)	272.4(3.31)	364.9(4.61)
Non-fertilised	79.3(1.07)	166.5(2.24)	253.2(3.35)	341.9(4.65)
C. lusitânica	87.5(1.22)	169.7(2.26)	238.5(3.10)	311.1(4.01)
P. radiata	71.4(0.83)	174.9(2.28)	285.8(3.33)	393.7(4.66)
ASHYMA	67.8(1.96)	155.4(2.94)	234.9(4.61)	293.5(7.35)
ATIANG	98.7(2.76)	231.4(5.21)	342.7(8.63)	464.8(13.47)
BALSSP	78.6(2.68)	163.6(3.76)	259.4(5.93)	351.2(8.39)
CATLRI	56.7(1.71)	134.87(3.16)	218.9(5.87)	298.1(8.93)
GLNGSM	87.9(1.66)	211.9(4.24)	327.2(7.50)	404.9(13.84)
HOCHSI	52.1(1.97)	101.8(4.55)	149.0(6.72)	200.1(10.53)
HOCKPA	94.8(2.30)	174.2(3.98)	299.3(8.14)	415.4(12.06)
KANGPY	63.0(2.12)	137.5(4.54)	215.2(8.02)	314.3(12.96)
KARI49	68.6(1.84)	150.3(4.79)	236.8(8.72)	318.8(10.99)
KINRTU	81.8(2.84)	178.4(5.93)	269.6(10.58)	357.3(13.56)
LONGMA	50.5(1.34)	96.7(3.53)	148.7(5.77)	203.4(7.55)
MAHUWA	113.5(3.87)	250.3(5.89)	359.3(7.51)	478.3(11.69)
MANTMI	91.9(4.09)	181.0(6.85)	285.3(9.52)	384.4(11.51)
NGAUBU	91.6(4.02)	198.4(7.67)	309.9(11.14)	405.8(14.38)
OKUKQU	50.8(2.20)	122.4(5.78)	199.3(7.33)	257.7(9.56)
RAISH6	83.3(2.20)	173.2(2.92)	273.0(6.21)	364.0(9.06)
RVHDSH	73.3(2.98)	133.1(5.89)	201.2(7.80)	288.2(11.80)
TIKITE	114.8(3.01)	253.4(4.68)	353.1(7.84)	484.9(10.43)
TIRUGU	74.73(2.66)	184.8(6.05)	269.3(7.68)	364.4(10.99)
WMARAR	66.8(2.95)	161.2(5.49)	255.6(9.08)	368.8(11.26)
WOODMU	97.6(2.04)	215.4(4.99)	295.7(8.25)	393.1(13.90)

Table A 6.2 Mean root collar diameter by treatment and sites by age. Standard errors are presented in brackets.

Tree Diameter (mm)	Trial Age			
	1	2	3	4
Disturbed	14.2(0.20)	27.8(0.39)	37.8(0.54)	43.4(0.62)
undisturbed	15.0(0.19)	28.5(0.37)	38.2(0.51)	43.7(0.60)
Fertilised	14.9(0.20)	29.8(0.38)	40.5(0.53)	46.5(0.62)
Non-fertilised	14.4(0.19)	26.6(0.37)	35.6(0.50)	40.7(0.58)
C. lusitanica	13.9(0.20)	25.3(0.35)	33.3(0.48)	38.3(0.56)
P. radiata	15.3(0.18)	30.9(0.38)	42.5(0.50)	48.6(0.59)
ASHYMA	11.9(0.34)	28.8(0.78)	37.7(1.06)	44.4(1.32)
ATIANG	15.6(0.42)	31.4(1.08)	40.3(1.59)	43.9(1.89)
BALSSP	14.6(0.35)	27.4(0.82)	38.1(1.13)	43.7(1.36)
CATLRI	12.4(0.35)	25.9(0.86)	36.22(1.29)	44.8(1.70)
GLNGSM	19.4(0.53)	35.5(1.24)	45.9(1.84)	48.8(2.34)
HOCHSI	8.7(0.32)	14.5(0.71)	21.2(1.09)	25.8(1.40)
HOCKPA	15.4(0.40)	28.0(0.90)	39.4(1.36)	44.6(1.65)
KANGPY	12.2(0.41)	23.4(0.92)	33.6(1.55)	40.2(1.92)
KARI49	13.5(0.52)	29.1(1.05)	39.7(1.38)	45.9(1.68)
KINRTU	14.0(0.41)	26.1(1.04)	35.6(1.54)	40.7(1.85)
LONGMA	9.7(0.33)	19.2(0.72)	27.8(1.14)	35.2(1.46)
MAHUWA	22.3(0.54)	37.0(1.17)	47.3(1.83)	50.3(2.19)
MANTMI	17.4(0.60)	29.6(1.36)	42.3(2.10)	50.0(2.47)
NGAUBU	14.2(0.58)	29.4(1.22)	39.2(1.82)	46.2(2.11)
OKUKQU	9.7(0.36)	23.8(1.27)	34.7(1.77)	41.5(2.18)
RAISH6	16.7(0.40)	30.5(0.66)	41.5(1.03)	46.7(1.36)
RVHDSH	13.7(0.50)	23.8(1.02)	32.3(1.61)	38.1(2.04)
TIKITE	20.1(0.39)	37.8(1.03)	48.3(1.58)	53.2(1.84)
TIRUGU	15.7(0.63)	31.1(1.32)	40.4(1.69)	44.7(1.92)
WMARAR	10.8(0.41)	26.7(1.26)	37.3(1.65)	45.1(2.22)
WOODMU	18.3(0.6)	31.9(1.13)	39.6(1.43)	43.1(1.70)

APPENDIX 7

Table A. 7.1 Efficiency ($\text{m}^3\text{ha}^{-1}\text{yr}^{-1}$) of LAI (m^2m^{-2}) to produce stem volume (m^3ha^{-1}) index for each site and species. Data is pooled across fertilised and disturbed treatments. Student-Newman-Kuels means comparison for each species by site.

Site	Efficiency of <i>P.radiata</i>	Efficiency of <i>C.lusitanica</i>
LONGMA	1.12 bc	0.33 b
HOCHSI	6.74 abc	3.98 ab
KARI49	3.02 bc	0.93 b
RAISH6	3.15 bc	1.98 b
OKUKQU	3.02 bc	2.84 ab
BALSSP	3.72 bc	3.96 ab
TIRUGU	6.27 abc	1.98 b
CATLRI	2.72 bc	1.47 b
WMARAR	1.78 bc	1.33 b
MANTMI	4.32 abc	3.03 ab
KINRTU	4.14 abc	1.45 b
NGAUBU	3.28 bc	1.21 b
ASHYMA	4.61 abc	2.52 b
HOCKPA	3.60 bc	1.34 b
KANGPY	3.06 bc	1.57 b
BALSH8	2.96 bc	4.02 ab
WOODMU	6.86 abc	1.15 b
ATIANG	6.24 abc	2.81 ab
TIKITE	5.67 abc	2.69 ab
MAHUWA	9.92 a	5.09 ab
GLNGSM	6.40 abc	1.41 b
RVHDSH	9.14 ab	7.00 a

APPENDIX 8

Table A 8.1 Model of *C. lusitánica* LAI_{max}. ($r^2 = 0.9827$, MSE = 1.266)

Variable	Parameter	Std err	<i>p</i> value
Latitude (Degrees south of the equator)	-0.206	0.031	<.0001
Mean annual temperature (°C)	-0.531	0.084	<.0001
Macro porosity (% V/V)	0.131	0.031	0.0006
Annual rainfall (mm yr ⁻¹)	0.0037	0.0007	<.0001
Depth of topsoil (cm)	-0.121	0.0534	0.0369

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