Photosynthetic acclimation to temperature of four *Eucalyptus* species and *Sequoia sempervirens*

A thesis

submitted to the University of Canterbury

in partial fulfilment

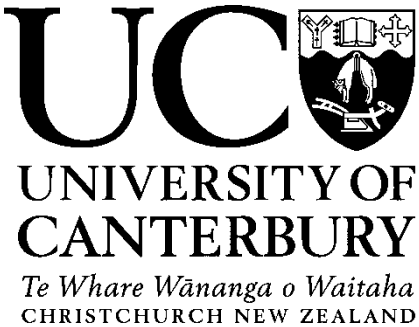
of the requirements for the degree

of

Master of Forestry Science

By

Irene A. Oparah



The New Zealand School of Forestry

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2012

Conditioning of plants in a glasshouse at the University of Canterbury, August 2011

Containerised seedlings of species of eucalypt were repotted in 25 by 17cm pots in a standard potting mix mixed with fertilizer and kept in a well lit glasshouse at a day temperature of 14-20ºC and watered to field capacity daily and excess water allowed to drain out of the pots.

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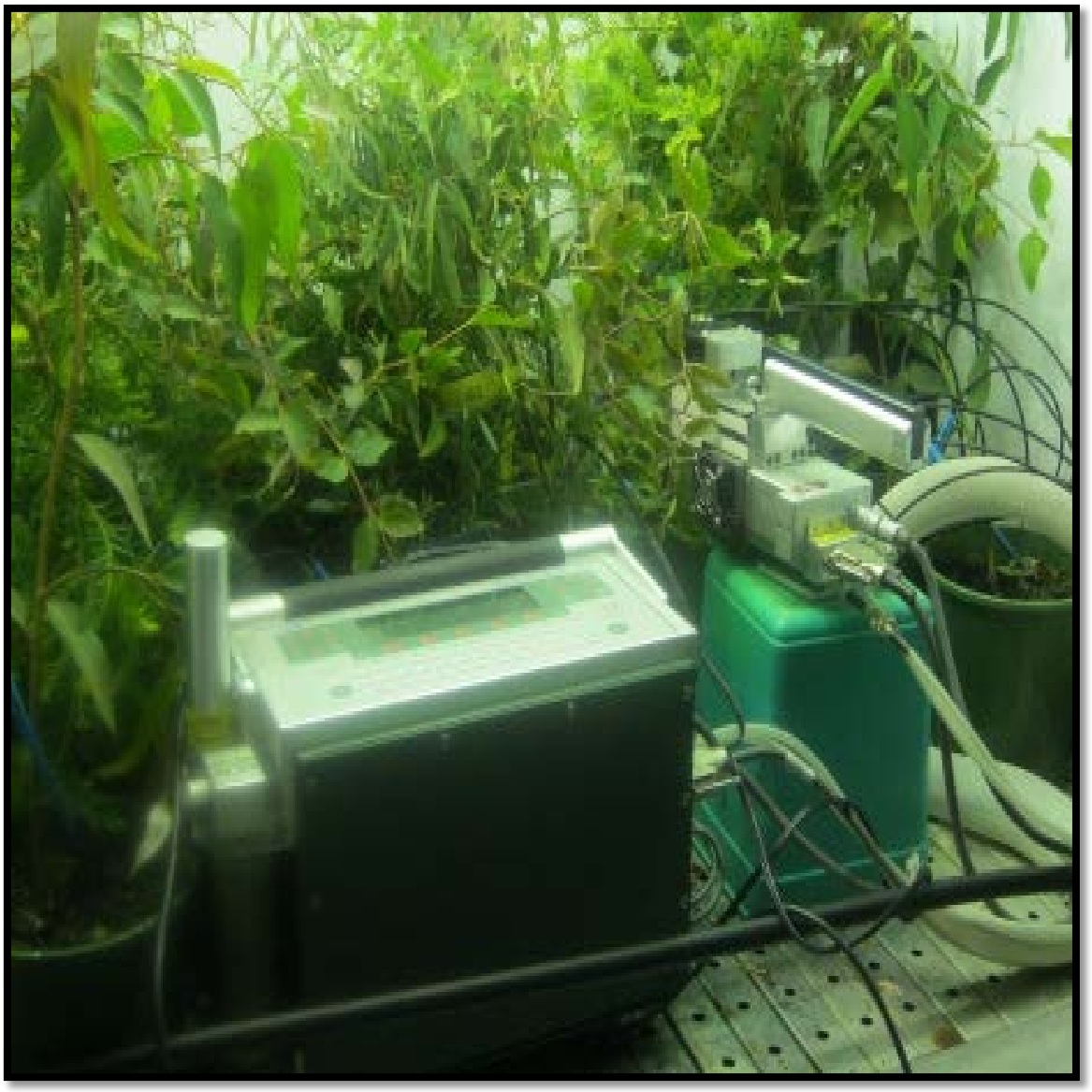
Containerised seedlings of *Sequoia sempervirens* were repotted in 25 by 17cm pots in a standard potting mix mixed with fertilizer and kept in a well lit glasshouse at a day temperature of 14-20ºC and watered to field capacity daily and excess water allowed to drain out of the pots.



Growth cabinet University of Canterbury, September 2011

Gas exchange measurement of the leaves of species of eucalypt and *Sequoia sempervirens* were made with a Li-Cor 6400.

Summary

The 3-PG physiological/mensurational hybrid model is a useful forest management tool capable of producing accurate growth results across a number of parameterised species. The temperature data used in the model are the average maximum and minimum values for photosynthesis above the compensation point (Landsberg and Sands 2011). There is a minimum temperature below which positive net CO_2 exchange will not occur, a maximum temperature above which it will not occur and an optimum temperature at which it is maximised. These parameters are used in the 3-PG physiological model of forest production. However, a species' photosynthetic response to short-term variation may differ from one season to another as species acclimate to temperatures over periods of a few weeks.

In this study, acclimation responses of four species of eucalypt and *Sequoia sempervirens* to long-term temperatures were studied over a wide range of short-term temperature changes in order to identify the minimum, optimum and maximum temperatures of CO_2 assimilation for physiological/mensurational hybrid modelling, and also to identify the sites for which the species would be best suited. In order to achieve the aims of this study, a growth chamber experiment was established.

Seedlings of four eucalypt species and *Sequoia sempervirens* were grown at base-line day/night temperatures of 30/16, 22/12 and 10/5ºC in controlled environment chambers for three months and leaf gas exchange measurements were made of the species at seven short-term temperature levels (5, 10, 15, 20, 25, 30 and 35ºC). The optimum and the maximum temperatures for net photosynthesis increased with an increase in base-line temperature for all species. The highest optimum temperature and net photosynthetic rates recorded were in plants grown at 30/16ºC and the lowest were in those grown at 10/5ºC.

The maximum rate of net CO_2 assimilation increased with the temperature at which plants were grown partly because of acclimation in key photosynthetic processes in the Calvin cycle. Responses of maximal carboxylation rate (V_{cmax}) and also the maximal light-driven electron flux (J_{max}) to short-term temperature change varied with base-line temperature for all species studied. Net photosynthesis and photosynthetic parameters measured did not vary significantly with effects of nitrogen, phosphorus and their interaction ($p = 0.1468$).

The ratio of J_{max} to V_{cmax} decreased with increasing leaf temperatures for all species ($p < 0.001$).

These results indicate that the species studied will adapt to long-run changes in temperature, and the parameters obtained from these studies can be used for models that simulate the physiology and growth of the species.

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Symbol	Description	Units
A	Rate of net photosynthesis	μmol m^{-2} s^{-1}
A_{max}	Photosynthetic capacity	μmol m^{-2} s^{-1}
A_{opt}	Assimilation rate of net CO_2 at optimal temperature	μmol m^{-2} s^{-1}
ATP	Adenosine-triphosphate phosphates	
C_3 plants	Plant that utilize the C_3 carbon fixation pathway as the sole mechanism to convert CO_2 into an organic compound	
CCA	Copper-Chromium-Arsernate	
C_i	CO_2 concentration in intercellular air spaces	μmol mol^{-1}
E	Transpiration	mmol H_2O m^{-2} s^{-1}
E_{aJ}	Activation energy of J_{max}	kJ mol^{-1}
E_{aV}	Activation energy of V_{cmax}	kJ mol^{-1}
g_s	Stomatal (plus boundary layer) conductance to CO_2 diffusion	mmol m^{-2} s^{-1}
H_a	Activation energy	kJ mol^{-1}
H_d	Deactivation energy	kJ mol^{-1}
IRGAs	Infra Red Gas Analysers	
J_{max}	Electron transport driving regeneration of RuBP	μmol electrons m^{-2} s^{-1}
K_c	Michaelis-Menten constants for CO_2	kJ mol^{-1}
K_o	Michaelis-Menten constants for O_2	kJ mol^{-1}
NADPH	Reduced nicotinamide adenine dinucleotide phosphate	
PAR	Photosynthetically active radiation	μmol photons m^{-2} s^{-1}
P_c	Photosynthetic rate limited by Rubisco	

PFD	Photon flux density	μmmol m^{-2} s^{-1}
PPFD	Photosynthetic photon flux density	μmol m^{-2} s^{-1}
P_r	RuBP regeneration	
R	Respiration	μmol m^{-2} s^{-1}
R_d	Dark respiration	μmol m^{-2} s^{-1}
R_g	Universal gas constant	J mol^{-1} K^{-1}
RH	Relative humidity	%
RuBisCo	Ribulose-1,5-bisphosphate carboxylase oxygenase	
RuBP	Ribulose-1,5-bisphosphate	
S	Entropy term	$Jmol^{-1}$ K^{-1}
S_J	Entropy of J_{max}	$Jmol^{-1}$ K^{-1}
S_V	Entropy of V_{camx}	$Jmol^{-1}$ K^{-1}
T_{growth}	Temperature at which plants were grown	ºC
T_l	Leaf temperature	ºC
T_{max}	Maximal temperature	ºC
T_{min}	Minimal temperature	ºC
T_{opt}	Optimal temperature	ºC
TPU	Triose phosphate utilization	μmol m^{-2} s^{-1}
V_{cmax}	*in vivo* maximum rate of ribulose-1,5-*bis*phosphate (RuBP) carboxylase-oxygenase (Rubisco) carboxylation	μmol CO_2 m^{-2} s^{-1}
VPD	Leaf-to-air vapour pressure deficit	kPa

Chapter 1 **Introduction**

1.1 Plantation forest establishment in New Zealand

We need to understand plant responses to temperature in order to model their behaviours in varying environments, particularly when we are introducing exotic species into climatic zones that differ from those in their natural ranges. One of the most important factors that can impact on the survival and growth of plants is the ability of their growing environments to meet their physiological needs (Caemmerer and Farquhar 1999).

With increasing interest of plantation establishers in finding alternative species like eucalypts that will thrive on drylands of New Zealand (Figure 1.1) and also provide durable hardwood timber to meet the needs and aspirations of the country, we need to know more about the environmental tolerance of the species that have been selected for trial on the drylands. Knowledge in the effects of changing temperature on the photosynthetic activities of the species will not only help in matching species to sites and modelling their growth but will also help in identifying species that are likely to adapt to temperature as a result of global climate warming.

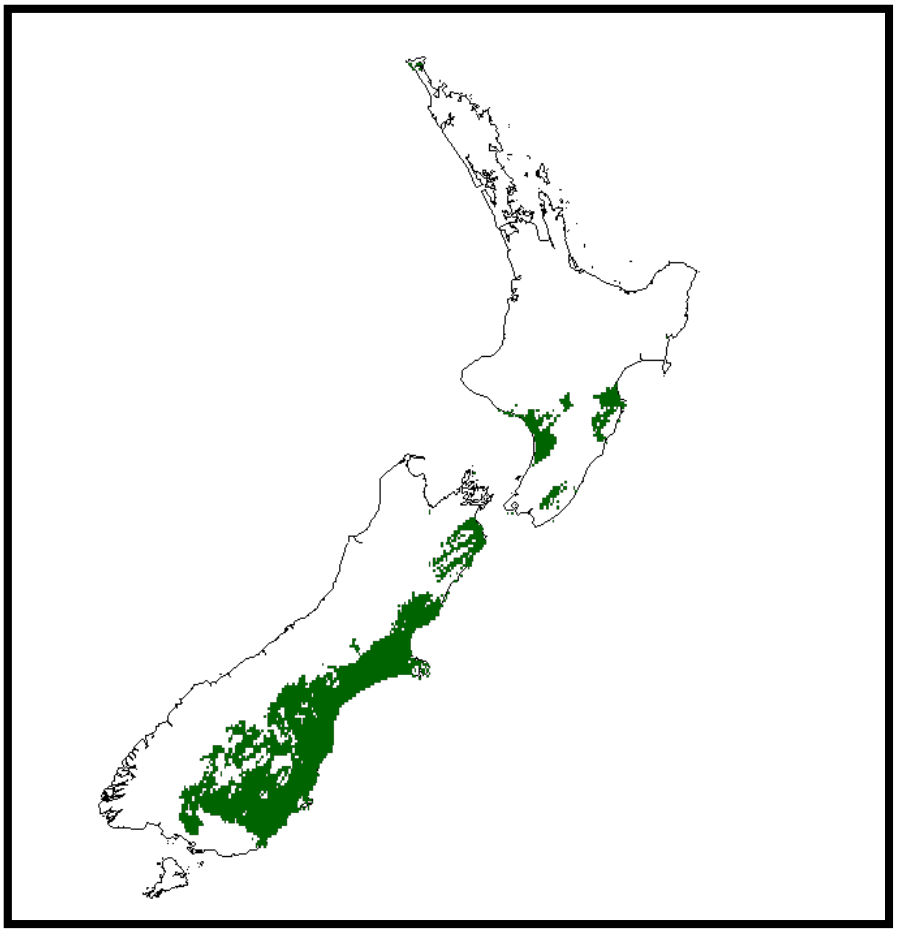


Figure 1.1 Area of New Zealand's Dryland

The area of New Zealand where mean annual rainfall is between 500 and 1000 mm per annum is shown in green. Source: E. G. Mason, plotted from data downloaded from http://www.worldclim.org/current, accessed on 20/09/2012

Temperature is one of the most important factors impacting on the physiology of plants. It does this by regulating the rate of physical and biochemical processes within the plant (Caemmerer and Farquhar 1999; Downs and Hellmers 1975). It directly and indirectly influences photosynthesis by controlling reaction rates in the Calvin cycle, respiration and transpiration (Kozlowski 1971). Temperature determines the rate of diffusion of both organic and inorganic molecules within the aqueous systems of plants, and also affects rates of biochemical reactions (Downs and Hellmers 1975). These biochemical reactions are enzymatically controlled, and temperatures effect on reaction rates of enzyme systems results in changes in the rates of photosynthesis.

The optimal temperature for enzymatic reactions differs between enzyme systems. While a change in temperature may increase the reaction rate of one enzyme, it may simultaneously decrease that of another (Caemmerer and Farquhar 1999; Campbell et al. 2007; Landsberg and Sands 2011). Moreover, the process of changing material from photosynthate to structural or storage products can often occur in more than one way, thus a change in temperature may cause a change to or from a more efficient process (Downs and Hellmers 1975). These sensitive reactions determine optimal temperatures for plant growth. Maximum growth is attained when rates of the majority of enzymatic processes are optimised, when the processing of photosynthate is most efficient, and when the ratio between photosynthesis and respiration is maximised. At temperature extremes, the rate of growth may be limited by the rate of a single reaction (Downs and Hellmers 1975). Respiration generally increases with temperature, eventually exceeding photosynthetic rates and so net primary productivity has clearly defined minima, optima and maxima that vary from species to species.

The temperature requirements of a species can affect its range, its distribution within the range, and its growth rate (Hellmers 1962). It is likely that selection pressures would act upon the temperature requirements of a plant species to maximise its survival competition, and particularly its reproductive capacity in the environment in which it grows. Hence every species may be best adapted to a particular temperature regime (Treshow 1970).

An increase in temperature will increase respiration and possibly reduce the effect of increased assimilation, due to elevated CO_2 concentrations (Caemmerer and Farquhar 1999). Stomatal conductance (gs) is strongly related to stomatal opening, environmental variables and photosynthesis. Stomatal functioning is related to photosynthetically active radiation (PAR), temperature, leaf water potential, air humidity and carbon dioxide concentration in the air (Caemmerer and Farquhar 1999). A physiological model takes into account the relationship between stomatal behaviour and photosynthesis and physiological models of photosynthesis consist of ‘demand and supply functions’. The ‘demand function’ is the description of the biochemical process of CO_2 assimilation by leaves and the ‘supply function’ describes the diffusion of CO_2 inside the cells which largely depends on stomatal conductance. Photosynthesis therefore depends on the opening of the stomata (via the supply of CO_2), but the stomata also react to photosynthesis through a feedback link where opening is done at low internal CO_2.

Biophysical processes (CO_2 transport via the leaf and the stoma) and biochemical processes (occurring in the chloroplast thylakoid membrane, stroma, mitochondria and the cytosol of the cell) have an effect on the net rate of CO_2 assimilation (A) (Sharkey et al. 2007). A combination of both processes with environmental factors (including light intensity and temperature) can impact differently on A (Sharkey et al. 2007). Because A is highly influenced by these factors, predicting the effects of genetic, epigenetics and environment on A is difficult. Careful examination of the biophysical and biochemical factors and estimation of the parameters of photosynthesis is necessary in order to understand the biological principles behind A and also help in the prediction of the effects of environment and genetics on the productivity of plants (Sharkey et al. 2007).

A/C_i curves [net assimilation rate (A), versus calculated internal CO_2 concentration (C_i)] (Figure 1.2) and their analysis has become a valuable tool to estimate leaf photosynthesis under a wide variety of experimental conditions (Manter and Kerrigan 2004) so it was the principal analytical tool that was selected for this study. It is relatively quick, easy to perform, inexpensive (after the initial equipment purchase) and is non-destructive. The relationship between A and C_i depicts the demand for CO_2 (Landsberg and Sands 2011).

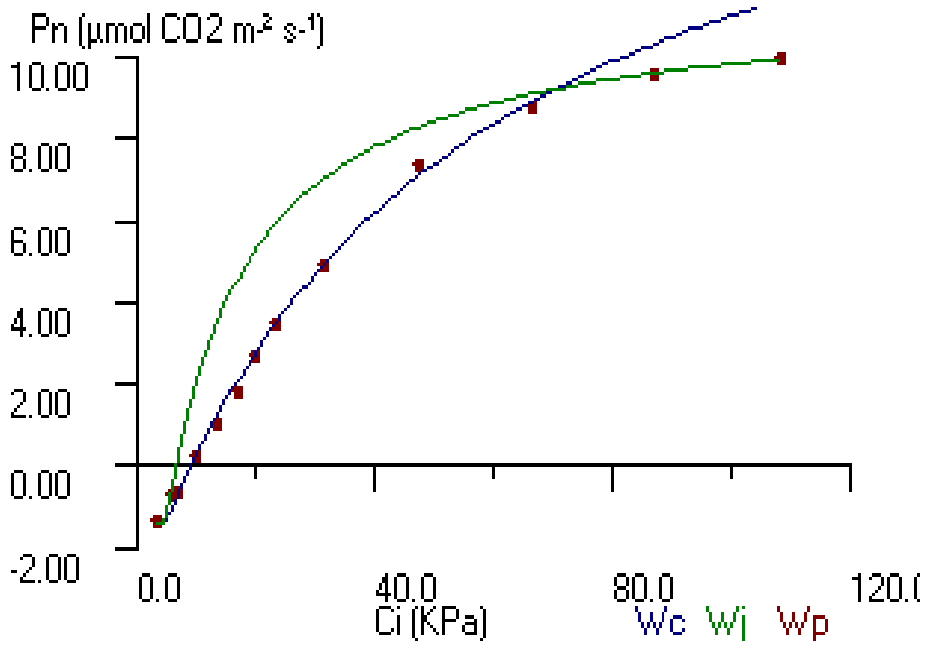


Figure 1.2 A/C_i curve

A/C_i curve; Source: I. A. Oparah plotted from experimental data 02/10/2012

The linear section of the curve (Figure 1.2) conforms to RuBP saturated photosynthesis (Farquhar and Sharkey 1982). In that section, the substrate concentration is high hence, increase in C_i leads to increasing activation of enzymes which subsequently increases the rate of CO_2 fixation (Landsberg and Sands 2011). The ability to generate the substrate gets limited as the rate of RuBP carboxylation is highly increased and extra increase in C_i do not result in a corresponding increases in A (Landsberg and Sands 2011).

1.2 Thesis objectives

The aim of this research was to determine the impact of temperature on carbon exchange in four species of eucalypt suitable for the provision of durable posts and poles in drylands and *Sequoia sempervirens* for physiological growth modelling. Specific objectives included determining:

(i) Optima, minima and maxima temperatures of assimilation rate of net CO_2 of the species acclimated to varying base-line growth temperatures.
(ii) Whether the species differed in their responses to temperature.
(iii) Effects of temperature on the maximal carboxylation rate (V_{cmax}) and the maximal light-driven electron flux (J_{max}).

The null hypotheses of this study were that:

(i) Temperature had no effect on photosynthetic activities of *E. bosistoana*, *E. argophloia*, *E. globoidea*, *E. fastigata* and *Sequoia sempervirens*.
(ii) Temperature had no effect on the photosynthetic temperature minima, optima and maxima of the species.
(iii) The relationship between net photosynthesis and short-term changes in temperature did not vary with long-term temperature conditions.

1.3 Synopsis of experiments

The experiments were conducted in growth chambers in a laboratory at the university of Canterbury New Zealand. It was designed to measure photosynthetic responses of the species in question to temperature in order to model their growth. Three cabinets were allocated with three different day/night growth temperatures and plants were randomly allocated to each of the cabinet. The experiment lasted for four months. *Sequoia semperivirens* was added to the list of species studied because it provided a contrast as a

Gymnosperm, it is increasingly of interest to New Zealand forest managers, and it has received little attention from physiological researchers until now.

1.4 Thesis strategy

This thesis presents an analysis of the extent to which photosynthesis acclimates to seasonal changes in temperature by varying reactions in the Calvin cycle, and the possible impact of leaf nitrogen and phosphorus content on the potential for thermal acclimation. It consists of six chapters with the first two chapters outlining a general introduction and the background of the research.

The third and fourth chapters outline the path to attaining the temperature model for the species and chapter five and six elaborates the discussion and conclusions/further research recommendations respectively.

Chapter 2 **Literature Review**

2.1 Background of the eucalypt genus

Eucalypts emerged between 35 and 50 million years ago in Australia (Keenan et al. 1998; Sewell 1997) but they remained a minor component of the tertiary rainforest until about 20 million years ago when gradual drying of the continent and depletion of soil nutrients led to the development of a more open forest type, predominantly *Casuarina* and *Acacia* species (Sewell 1997). Several eucalypts including *E. regnans, E. globulus, E. viminalis and E. delegatensis* are amongst the tallest trees in the world, yet there are also species that are shrubby (e.g. *E. nitida*) and multi-stemmed (e.g. *E.gunnii*) (Hickey et al. 2000; Nicolle 2006). More than 700 species of eucalypt are recognized and these have been classified in 13 lineages (Potts et al. 2011) occupying a range of environmental conditions (Sewell 1997) with great diversity in form.

Generally, eucalypts have adapted to survive and prosper in low nutrient soils and with fire. A group within the genus is known to have the ability to cope with extremely high temperatures whilst others are restricted to cold temperature conditions (Williams and Woinarski 1997). Three well-proven durable stringybark species *(E. pilularis, E. muelleriana and E. globoidea*) were previously grown in New Zealand by Barr and others for untreated, naturally durable posts and poles, and for high quality durable sawn timber (Barr 1996). Also John Sheppard planted three eucalypt trials in one of New Zealand's driest environments, the Wither Hills near Blenheim, to investigate early survival and growth of some dryland eucalypts and concluded that *E. bosistoana* and *E. camaldulensis* were the best species (Sheppard 1988).

Beside the structural and aesthetic properties of the wood of *Eucalyptus*, it is suitable for high quality, Kraft paper production as the short and slender fibres gives a high number of fibres per gram and low coarseness contribute to softness. *E. globulus* and *E. grandis* are preferred in papermaking compared with other hardwood commonly used as pulpwood species (Bhat et al. 1990; Jorge et al. 200).

2.2 The species used in this study

2.2.1 E. bosistoana

Commonly known as Coast Grey Box, *E. bosistoana* is a tough, highly durable large Australian hardwood (Nicholas 2007). It grows naturally in eastern Victoria and along the southern and central coast of New South Wales (Figure 2.1c) with mean annual rainfalls of 700-1200 mm per year (Table 2.2). It has a rapid growth rate to about 25 metres in height with a straight stem and has a rotation age of 30 to 50 years. It requires a minimum rainfall of 600 mm (Brooker and Kleinig 1999a). Its heartwood is pale brown and the sapwood is paler in appearance (Brooker and Kleinig 1999a; Nicholas 2007). It has a fine and even texture and usually features some interlocked grain (Nicholas 2007).

Gum veins are rarely present in the wood of *E. bosistoana*. It is a high density species so it is quite difficult to work (Bootle 1983). It can be painted, stained and polished. However, it is slow to dry but generally will not develop any surface checking (Nicholas 2007). It is also satisfactory for steam bending and has been used for heavy construction, round timber and sleepers (Bootle 1983). It is a class 1 durable species with a basic density of 900-1200 kgm^3 (Table 2.1) at 12% moisture content (Nicholas 2004) and moduli of elasticity and rupture of 17GPa and 163MPa respectively. This species could be well suited for structures like vineyard posts, power poles and cross arms because of its high durability and high strength. One desirable feature which is of silvicultural utility is its ability to coppice which could be advantageous for forest management and propagation purposes.

2.2.2 E. globoidea

*E. globoidea***,** known by the common name White Stringybark**,** is native to eastern Australia (Jones et al. 2008) with a range and distribution similar to those of *E. bosistoana* (Figure 2.1a). It favours warm humid to sub-humid climates (Jones et al. 2008) with a mean annual rainfall of 650 – 1400 mm per year (Table 2.2). It grows to a height of about 30 m and even under favourable conditions it can attain a height of 120 ft (36 m) with a diameter of about 40 inches (100 m) (Brooker and Kleinig 1999a; Jones et al. 2008). It is locally frequent in dry sclerophyll forest on well-watered sandy or alluvial soil of moderate fertility. It is drought tolerant and can withstand up to about 40 frosts per year (Table 2.2) (Millen 2009). Those growing on poor soils may even reach a height of 80 feet (24 m).

The tree has thick, fibrous bark usually coloured light gray over reddish brown and it is also known for its distinctive glossy green leaves in its adult life. It is a class 3 in ground timber, and class 2 above ground (Bootle 1983). It is well suited to framework and is treated for poles and posts (Jones et al. 2008). The wood is described as brown to pale pink in colour and its grain is reported to be typically straight, but is sometimes interlocked (Jones et al. 2008). The heartwood is naturally resistant to decay, and can last for 15 to 25 years under high decay hazard conditions (Jones et al. 2008) and also the wood has a very good steam bending characteristics (Jones et al. 2008), it is hard, strong, and tough hence well suited as a heavy structural timber. The timber is reported to season without difficulty but the wood is reported to be highly prone to collapse during drying. It has a basic density of 527 - 623 kg/m^3 (Table 2.1) and a mean modulus of elasticity of 14 GPA (Nicholas 2004, 2007).

2.2.3 E. argophloia

E. argophloia, commonly known as Queensland Western White Gum grows naturally in a limited area of southern Queensland, northeast of Chinchilla (Figure 2.1d) with mean annual rainfall of 700 mm per year. It tolerates 10-15 frost occurrences per year (Table 2.2) and copes with saline and heavy clay soils (Lee et al. 2008). It has a high density and grows reasonably rapidly and so can be used for carbon sequestration. It is a medium-sized to tall tree with excellent form and is self pruning. It attains 40 metres in height and 1 metre in diameter (Lee et al. 2008). Its early growth is slow because it has poor root growth with a mean annual increment (MAI) of 0.3-1.4m^3/ha at age three, but it picks up later in the rotation attaining an MAI of 6-10m^3/ha/annum at ages 18 and above (Armstrong et al. 2003).

The wood of *E. argophloia* is of a deep-red colour, hard and durable, and is reported to have a basic density of up to 660 kg/m^3 (Table 2.1) at an age of about 12 years (Nicholas 2007; Sheppard 1988). Its heartwood has a strong colour with a higher basic density than the sapwood. It is good for sawlog production. It is closely related to *E. bosistoana* so it offers the opportunity to develop hybrids with *E. bosistoana* that have a broader site/climatic range while exhibiting greater vigour, and enhanced wood properties such as intense colour and durability (Bush 2011).

2.2.4 E. fastigata

E. fastigata, commonly called Brown Barrel or Cut-Tail is common in south eastern Australia (Figure 2.1b). It is a member of the *Eucalyptus* subgenus Monocalyptus and is quite site-specific, preferring fertile, loamy soils that are moist but well drained (Barr 1996; Jones et al. 2008). It can grow in excess of 60 metres in height, though it generally reaches between 30 and 45 metres tall. It grows in cooler areas of high rainfall from 750 to 2000 mm (Table 2.2) (Brooker and Kleinig 1999b; Jurski and Grigg 1996).

The plant has creamy smooth upper branches and a dark rough bark on the trunk and main branches. Its timber is well regarded and used for building construction (Gindaba et al. 2004; Jones et al. 2008; Lee et al. 2008). It is fast growing, moderately frost tolerant and relatively free from pests and diseases (Jurskis and Grigg 1996). Its timber is not sufficiently durable for external use but is suitable for general construction and pulp production (Bootle 1983; Hills and Brown 1984). It has a basic density of 560 to 610 kg/m^3 (Table 2.1). Relatively, it is tolerant of competition for light, so it is suitable to be grown in comparatively dense stands (Braithwaite et al. 1998; Jurskis and Grigg 1996).

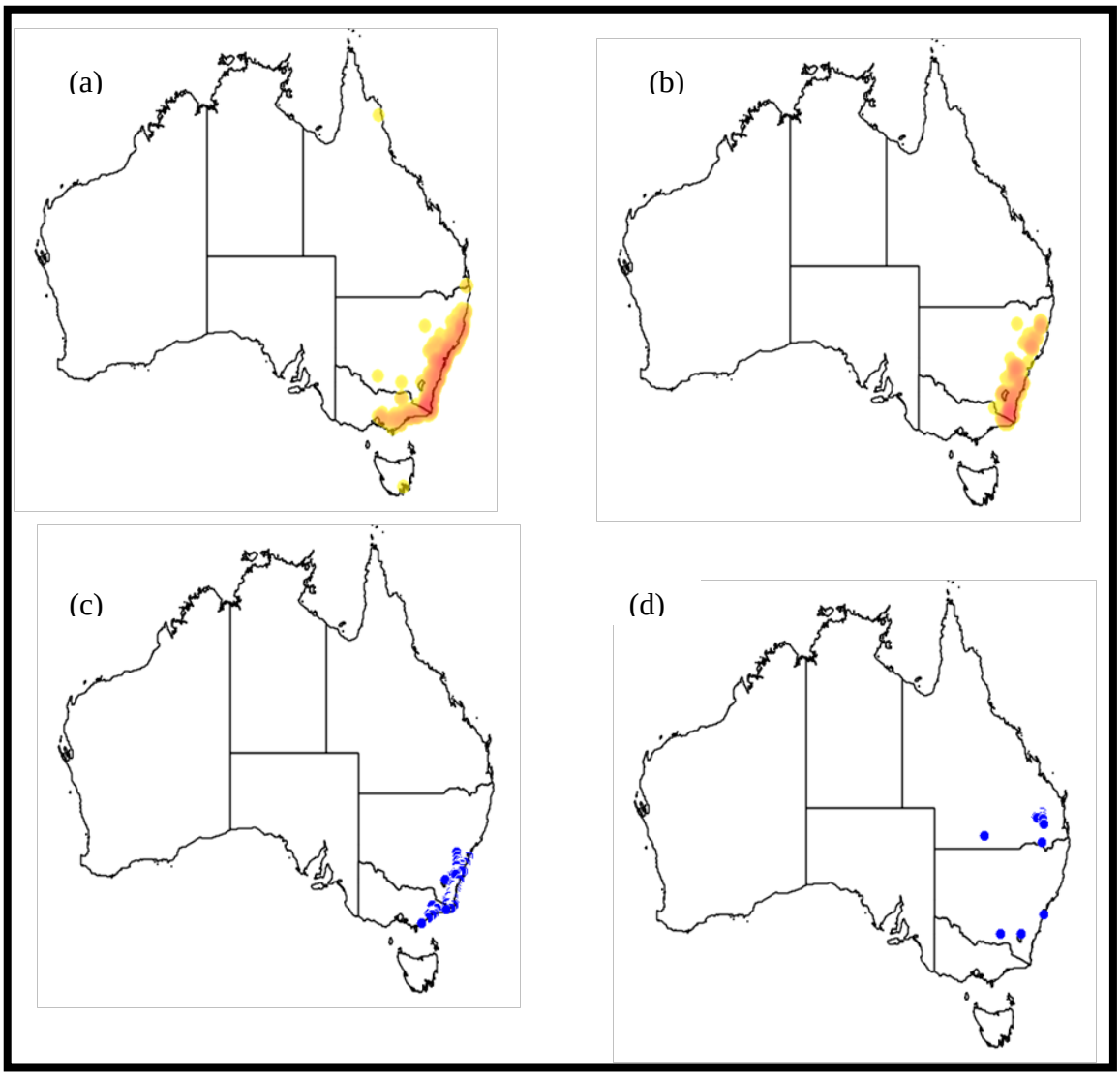


Figure 2.1 Distribution of eucalypt species in Australia

Mapped occurrences of (a) *E. globoidea*, (b) *E. fastigata*, (c) *E. bositoana* and (d) *E. argophloia* in Australia. Source: Atlas of Living Australia

2.2.5 Coastal redwood (Sequoia sempervirens [D. Don] Endl)

Sequoia sempervirens is the only living species of the genus *Sequoia* in the cypress family Cupressaceae (Ahuja 2009) and some common names for it include coast redwood and California redwood. It is an evergreen, monoecious tree able to live for 1200–1800 years or more (Keenan et al. 1998). Before commercial logging and clearing began by the 1850s, this massive tree occurred naturally in an estimated 2,100,000 acres (8,500 km^2) along much of coastal California (excluding southern California where rainfall is not abundant enough) and the south-western corner of coastal Oregon within the United States. It is

locally naturalised in New Zealand, notably at Rotorua (Brown 1982; O'Hara and Berrill 2009). The name Sequoia sometimes refers to the subfamily Sequoioideae, which includes *Sequoia sempervirens* along with Sequoiadendron (giant sequoia) and Metasequoia (dawn redwood). Giant sequoia (*Sequiadendron gigantuem*) reaches up to 379 feet (115.52 m) in height and up to 26 feet (7.9 m) in diameter at breast height so it is included in the list of the tallest trees on earth. On its own, the term redwood usually refers to the coast redwood, which is the focus in this study.

Coast redwoods have a conical crown with horizontal to slightly drooping branches (O'Hara and Berrill 2009). Redwood forests provide habitat for a variety of mammals, birds, reptiles, and amphibians. Fog is of major importance in its ecology (O'Hara and Berrill 2009) by decreasing evaporation and transpiration to protect the plant from drought and heat during summer. The thick, tannin-rich bark, combined with foliage that starts high above the ground provides good protection from both fire and insect damage, contributing to its longevity (Brown 1982).

The species grows well in a mild climatic zone (super-humid and humid) with mean annual temperature varying between 10 and 16°C and a minimum and maximum temperatures of -9 and 38°C respectively (Table 2.2) (Brown 1982; Cown 2008; Knowles and Miller 1993). It receives an annual rainfall in its natural range between 640 and 3100 mm (Table 2.2) and it is tolerant of flooding (O'Hara and Berrill 2009). Its lumber is highly valued for its beauty, light weight, and resistance to decay hence suitable to be used in the construction of railway materials (Brown 1982) and as a good building material in areas of modest decay hazard.

Table 2.1 Durability class and density of eucalypt and *Sequoia sempervirens* woods

Species	Heartwood Durability Class	Density (kg/m^3)
Eucalyptus argophloia	1	660
Eucalyptus bosistoana	1	1100
Eucalyptus fastigata	3	620
Eucalyptus globoidea	2	900
Sequoia sempervirens	3	360

Table 2.2 Climates of the native habitats of eucalypt and *S. sempervirens* species

Species	Locality	Humidity	Mean temperature		Rainfall	Frost
			min	max(ºC)	mm/yr	days/yr
E. argophloia	Southern Queensland	Humid/sub-humid	3.7	32.3	700-900	10-15
E. bosistoana	Victoria/Southen and central coast of NSW	Warm/humid /cooler	1≥6	24 ≥29	≥ 600	5-40
E. fastigata	South-Eastern Australia	Cooler	-2	28	750-2000	slight
E. globoidea	Eastern Australia	Humid/sub-humid			650-1400	40
S. sempervirens	Coastal California	Super-humid/humid	-9	38	640-3100	

As compared to species like *E. pauciphlora, E. globulus, E. niten, E. camaldulensis,* and *E. cloeziana* (Battaglia et al. 1996; Slatyer and Ferrar 1977; Slatyer and Morrow 1977), little is known of the tolerance of eucalypt species selected for this study to changing environmental factors. Photosynthetic light and temperature responses of dryland

provenance of *E. argophloia* has been studied previously by Ngugi et al. (2003a), and Lewis et al. (2011) also looked at its photosynthesis, respiration and stomatal conductance. Much physiological study has been done on *Sequoia sempervirens* in the northern hemisphere (Ambrose et al. 2009; Ambrose et al. 2010; Beerling and Osborne 2002; Ishii et al. 2008; Royer et al. 2005; Way and Oren 2010) but nothing has been done on the species in New Zealand. Radiation-vegetation relations for *E. globoidea* and *E. bosistoana* were studied by Kuma and Skidmore (2000) to confirm that solar radiation had an effect on the distribution of the species because solar radiation influences plant growth through temperature and moisture content in soils.

There is the need for intensive physiological studies of these species especially in the area of leaf net CO_2 assimilation in a wide range of temperature distributions in order to design appropriate silvicultural and management practices for their establishment in plantations in New Zealand.

2.3 Photosynthesis and photosynthetic temperature response

Photosynthesis is highly dependent on temperature (Kositsup et al. 2009). Increasing temperature leads to an increase in most plant physiological processes including respiration and photosynthesis (Downs and Hellmers 1975; Kozlowski 1971). However, beyond the tolerance limit of a plant's phenotypic plasticity, continuous increase in temperature can be harmful or result in changes in the distributions of species (Hellmers 1962) hence, thermal acclimation of photosynthesis is crucial for offsetting harmful effects of high temperatures. Excessive increase in temperature will cause many different types of damage to plants, including growth inhibition or death as a result of denaturation of some protein components of plant cells. On the other hand, temperatures below the optimum alter plant metabolic systems and slow growth (Caemmerer and Farquhar 1999; Campbell et al. 2007; Landsberg and Sands 2011).

Abrupt increases in temperature lead to increases in net photosynthesis up to a point and then it declines (Figure 2.2) and (Figure 2.3) as a result of deviations from the optimum temperature but this may be rapidly normalised as soon as the optimal temperature is restored (Slatyer and Morrow 1977). Contrarily, instantaneous responses of dark respiration tend to correlate positively with temperature up to a deadly point (Figure 2.4). Temperature affects the rate of respiration as well as other biochemical reactions (Ow et al.

2008a; Ow et al. 2008b). There is an exponential increase in respiration rate with increasing temperature. Temperature can affect nutrient availability, nutrient uptake, translocation of solutes within the plant, leaf elongation, protein synthesis and other physiological factors (Wardlaw 1974). Longer term shifts in optimum temperatures for photosynthesis lead to adaptation or acclimation in both photosynthesis and respiration (Mooney and West 1964; Read and Busby 1990; Slatyer and Morrow 1977).

The gradient of the line relating the optimum temperature for net photosynthesis and the acclimation temperature normally ranges from 0.3 to 0.7 (Billing et al. 1971; Read and Busby 1990; Slatyer 1977a) indicating incomplete acclimation due to the inability of the plant to acclimate fully or its inability to regulate the level of acclimation (Sall and Petterson 1994). Theory has suggested that if the maximum rate of photosynthesis is causally linked with the optimum temperature for photosynthesis, then incompletely acclimatized plants can have higher rates of carbon uptake than fully acclimated plants (Sall and Petterson 1994) and extensive studies have shown this to be the case in the field (Slatyer 1977a, b; Slatyer and Ferrar 1977; Slatyer and Morrow 1977). Although photosynthesis and respiration are highly responsive to short-term modifications in temperature, acclimation means longer-term alterations in temperature have less effect (Tao and Zhang 2010).

Many plants exhibit appreciable phenotypic malleability in their photosynthetic attributes. In general the optimal temperatures for net photosynthesis of plants grown at higher temperatures are high (Berry and Björkman 1980). For instance, Slatyer (1977b) detected a linear relationship in *E. pauciflora* between optimal temperatures and those at which plants were growing with a slope of 0.34 and likewise, Battaglia et al. (1996) reported a slope of 0.59 and 0.35 for *E. globulus* and *E. nitens* respectively. Changes in temperature dependence of photosynthesis may be attributed to changes in actions and quantities of components of photosynthesis and/or the concentration of CO_2 in the site of carboxylation. Yet photosynthetic responses to temperature appear to differ from species to species (Berry and Björkman 1980; Ferrar et al. 1989; Hikosaka et al. 1999). The limiting step in the photosynthetic rate of C_3 plants differs with respect to the concentration of CO_2 so that at minimal concentrations of CO_2, carboxylation of Rubisco (RuBP) limits photosynthesis.

The optimal temperature for photosynthesis increases with respect to CO_2 concentration (Berry and Björkman 1980) and the two components involved in this movement are the shift of the limiting step and the other is associated to the kinetics of Rubisco which have a significant influence on the photosynthetic rate limited by Rubisco ($P_{c)}$ activity. For a number of species, the optimal temperature for maximum net photosynthesis is limited by Ribulose-1,5-bisphosphate (RuBP) regeneration (P_r) which is higher than P_c (Farquhar and Sharkey 1982; Hikosaka et al. 1999). The optimal temperature is high at high concentrations of CO_2 because RuBP regeneration limits photosynthesis at higher concentrations of CO_2. At minimal concentrations of CO_2, the carboxylation rate is less sensitive to temperature because a rise in Michaelis-Menten constants for CO_2 (K_c) partially cancels the rise in maximum carboxylation rate (V_{cmax}) (Hikosaka 2005).

The temperature at which plants are growing alters their photosynthetic capacities or their photosynthetic temperature responses or both (Atkin et al. 2006; Berry and Björkman 1980; Kaage and Knorr 2007; Medlyn et al. 2002a; Sage and Kubien 2007). The ability of plants to acclimate to different growth temperatures in order to photosynthesize efficiently varies from species to species (Atkin et al. 2006; Berry and Björkman 1980; Sage and Kubien 2007), within species and to some extent within plants as a result of differences in stomatal conductances of leaves (Atkin et al. 2006).

Photosynthetic acclimation of plants may occur as a result of changes in temperature, soil water, light or the supply of mineral nutrients (Bunce 2000; Delagrange 2011; Dillaway and Kruger 2010; Gea-Izquierdo and Makela 2010; Hikosaka and Terashma 1995; Joseph 2011; Krause et al. 2004; Noguchi et al. 2001; Turnbull et al. 1993; Way and Sage 2008b). Long term changes in temperature could cause a change in the absolute rate of photosynthesis and/or a change in optimum temperature for photosynthesis thereby causing a shift in an entire A/C_i curve. It has been reported that a changes in the optimum temperature for photosynthesis as a result of changes in temperature correlate with changes in the equilibrium between the electron transport and the RuBP carboxylation phase of the Calvin cycle (Hikosaka et al. 1999; Onoda et al. 2005b).

Increases in the rate of photosynthesis with thermal acclimation are accompanied by increases in enzymes regulating the activities of photosynthesis (Campbell et al. 2007; Law and Crafts-Brandner 1999; Luo et al. 2010) and a larger extent of instauration of

membrane lipids leading to alteration of the equilibrium between RuBP regeneration and RuBP carboxylation reactions (Onoda et al. 2005b; Weston et al. 2007). It has been predicted that plant species lacking the capacity to alter the ratio of J_{max} to V_{cmax} may not acclimate due to the exhibition of similar temperature responses of RuBP carboxylation limited photosynthesis and RuBP regeneration limited photosynthesis (Hikosaka 1997). On the other hand plants species having higher degrees of plasticity of the ratio of J_{max} to V_{cmax} have more potential to acclimate than those lacking such capabilities (Onoda et al. 2005c) and this plasticity in the ratio of J_{max} to V_{cmax} has been reported to differ from species to species and even within species (Atkin et al. 2006; Ishikawa et al. 2007; Onoda et al. 2005c).

For instance, photosynthetic acclimation to higher temperature in oak has been reported (Haldmann and Feller 2004) to be as a result of thermal stability of the thylakoid; while a plastic response of electron transport in winter wheat has been attributed to environmental temperature (Yamasaki et al. 2002). Quantities of Rubisco and other enzymes are greater in cold grown plants than hot grown ones because having greater amounts of those enzymes in the cold grown plants offsets the decrease in photosynthetic activities as a result of low temperatures (Hurry et al. 1995).

In practice changes in temperature may have a significant effect on almost all of the biochemical processes involved in photosynthesis and growth (Caemmerer and Farquhar 1999; Campbell et al. 2007). At higher temperatures than optimal ones, net phosynthetic capacity of a leaf may decline probably due to an interruption of the functional character of the photosynthetic apparatus at the chloroplast level (Berry and Björkman 1980). The level and type of damage may be related to the magnitude of temperature change and the duration of exposure (Al-Khatib and Paulsen 1999; Berry and Björkman 1980; Lee and Vierling 2000; Senioniti et al. 1986). However, the photosynthetic capacity is restorable within short or long term periods depending on the type and level of damage. In some instances, the tissue may die completely (Caemmerer and Farquhar 1999). Besides photosynthesis, the rate of respiration, effects of temperature on nutrient availability and uptake and the effects of temperature on senescence are some of the factors that regulate the optimal growth temperature (Kelly et al. 2011; Strauss 2000).

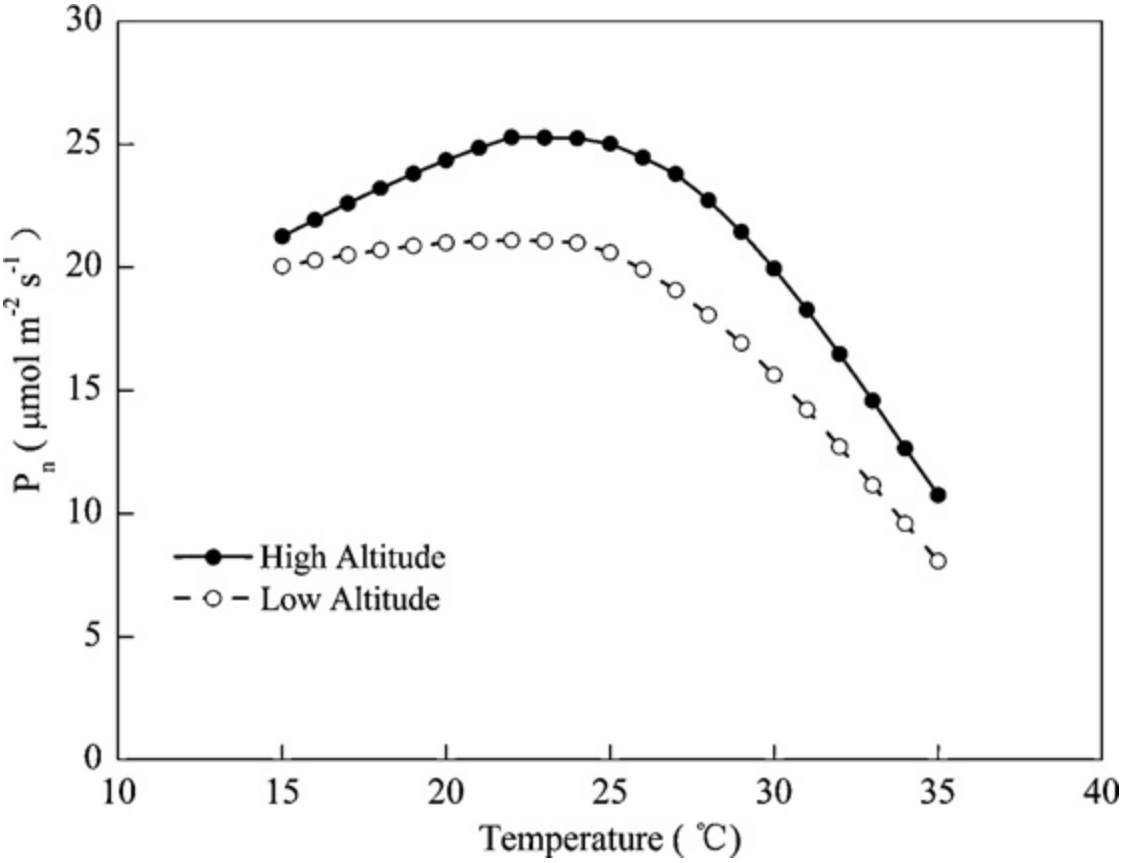


Figure 2.2 Photosynthetic response to temperature

Photosynthetic response to temperature at different altitudes; Source: Fan et al. (2011)

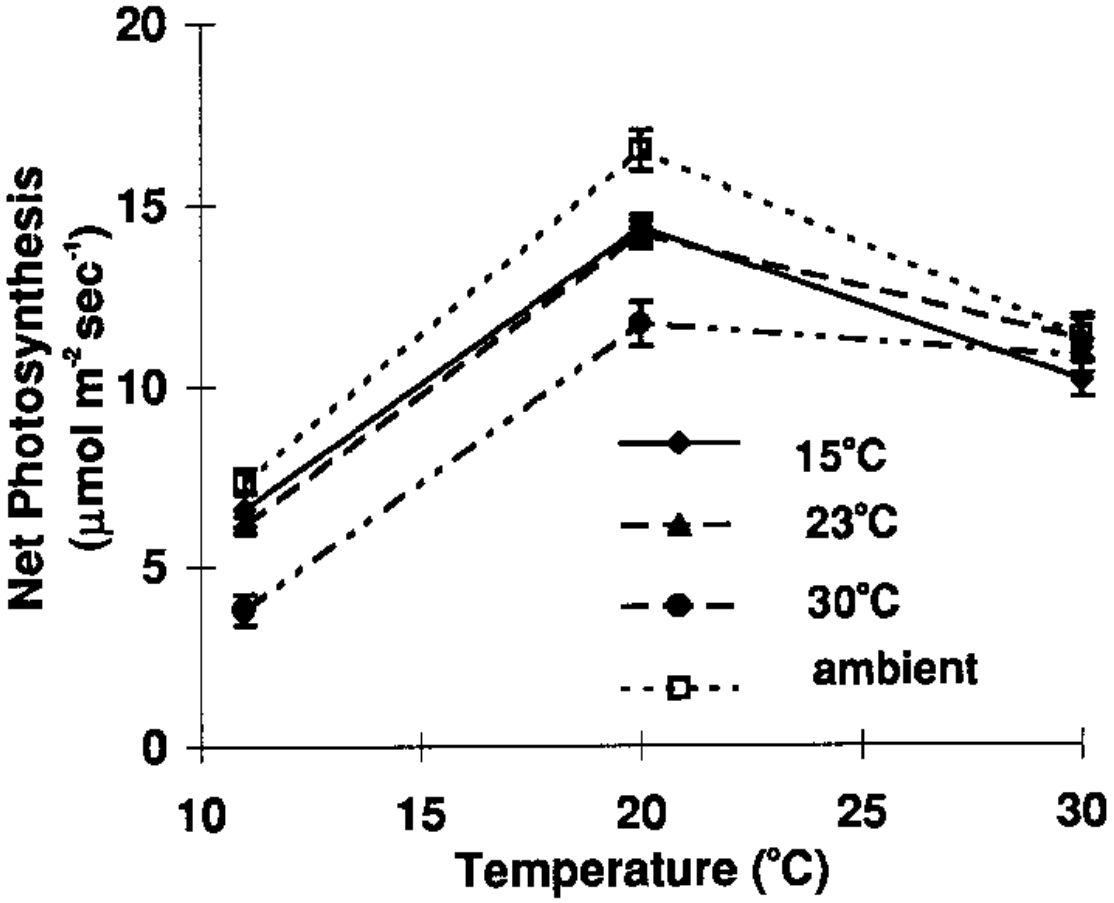


Figure 2.3 Photosynthetic response of *E. globulus* to temperature

Photosynthetic response of *E. globulus* to temperature; Source: Battaglia et al. (1996)

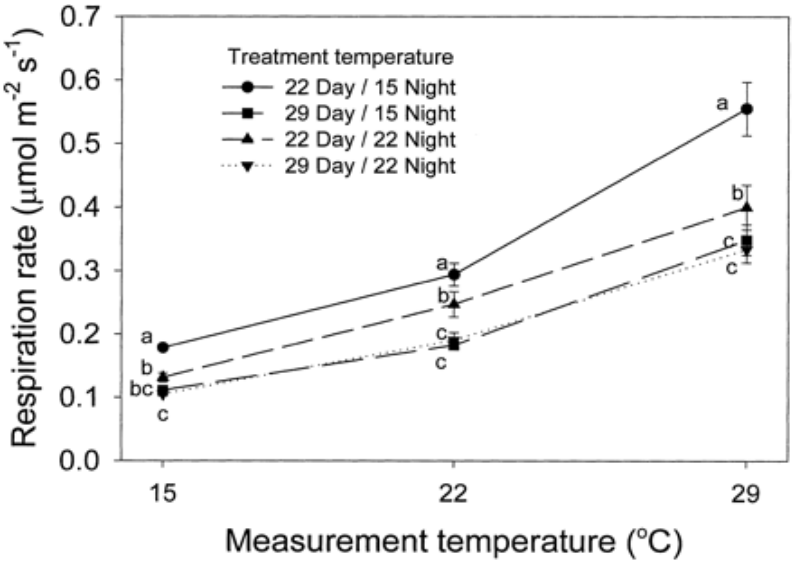


Figure 2.4 Relationship between respiration and temperature

Respiration rates of seedlings of *Pinus taeda* exposed to different temperature regimes measured at three different temperatures; Source: Will, R. (2000)

2.3.1 Research with trees

Battaglia (1996) studied photosynthetic temperature responses of *Eucalyptus globulus* clones taken from four mother plants originating from climatically dissimilar locations within Tasmania and acclimated them at day/night temperatures of 10/15, 18/23 and 25/30°C in temperature-controlled greenhouses. Another set of the clones was acclimated in a shade house where temperatures ranged between 10 and 25°C and with a mean daily temperature of approximately 15°C. It was reported that plants grown at 25/30°C had significantly lower net photosynthetic rates when measured at 10 and 20°C than plants grown at lower temperatures and those at 10/15°C had significantly lower net photosynthetic rates when measured at 30°C than plants grown at higher temperatures (Figure 2.3). Also plants grown at the ambient conditions prevailing in mid autumn in Hobart had significantly higher net photosynthetic rates at 20°C than plants raised in the greenhouses and were equal best performers at 10 and 30°C (Battaglia et al. 1996) (Figure 2.3).

Much research has been done with conifers from the northern hemisphere in identifying the ideal temperature for their growth and a wide range of temperatures have been identified with some species responding to day temperatures while others to night temperature and some to overall heat sums. Photosynthesis could decrease causing a reduction in the production of sugars as a result of extreme temperatures, low light conditions, high humidity or water stress.

Kositsup et al. (2009) measured net CO_2 assimilation rate (A) of rubber saplings grown in growth chambers at 18 and 28ºC in a study aimed at assessing the temperature response of photosynthesis in the species to provide data for physiological growth modelling, and to establish the relationship between photosynthetic capacity and temperature and response of photosynthesis acclimation. It was reported that the optimal temperature (T_{opt}) for A was much lower in plants grown at 18ºC as compared with those at 28ºC. The assimilation rate of net CO_2 at optimal temperature (A_{opt}), maximal carboxylation rate (V_{cmax}) and the maximal light-driven electron flux (J_{max}) at a temperature of 25ºC (V_{cmax25} and J_{max25}) together with the activation energy of V_{cmax} and J_{max} (E_{aV} and E_{aJ}) were found to decrease in plants acclimated at 18ºC. Whilst the ratio of J_{max}/V_{cmax} of plants acclimated to 18ºC leaf was larger, their leaf nitrogen and photosynthetic nitrogen use efficiencies (V_{cmax}/N_a) were

smaller. Ideally the photosynthetic capacity of plants is reduced at elevated [CO_2] and this reduction goes with a lower nitrogen (N) content of leaf (Ainsworth and Long 2005; Ainsworth and Rogers 2007).

2.3.2 Effect of temperature on photosynthetic thermal optima

In some species the optimum temperature for photosynthesis increases with increasing temperature (Figure 2.5). While some plants require a constant temperature others require high day/night temperature differentials (Mahan et al. 1987; Somerville and Browse 1991; Wardlaw 1974). Intensive studies have been made of Douglas-fir seedlings and the species has shown that the temperature for optimal growth lies in a wide range from 18ºC to 24ºC. While a good number of provenances from the north appear to prefer the cooler temperatures in this 18-24ºC range (Brix 1971) the southerly ones prefer summer temperatures that are warmer than those in most of New Zealand (Brix 1971). However, a constant day/night temperature is ideal for growth and development in this species.

Concerning species from areas with similar climatic conditions as New Zealand, redwood seedlings were found to produce optimal growth in a range of 19-15 or 19-19ºC temperature regime compared to 16°C for *E. globulus* (Hellmers 1966; Sands and Landsberg 2002). Western hemlock seedlings have a distinct optimal temperature of 18ºC (Brix 1971). Radiata pine, which is a successful species in the climatic conditions of New Zealand, exhibits maximum growth at day temperatures between 17 and 23ºC and night temperatures of 5ºC with the night temperature thought to have a high influence on growth (Hellmers and Rook 1973). Hellmers and Rook (1973) compared both Californian and New Zealand landrace of radiata pine and reported the same optimum temperatures of growth for both provenances but the Californian seedlings did better than their New Zealand peers at higher temperatures.

Trees from tropical and subtropical climates often show elevated temperature optima compared to those from more temperate climates (Hawkins 1988; Opeke 1982). In Australia, *E. camaldulensis* and *E. grandis* both of which originate from hotter areas of the country yielded optimum growth under a 30/25ºC day/night temperature regime (Battaglia et al. 1996) and this optimum was 5 to 9ºC higher than those of other eucalypts from more temperate regions. A minimum of 12ºC drop in night temperature is desirable for loblolly pine, a species originating from areas with high summer temperature and 30/17 and

23/11ºC regimes was reported to be required for optimal growth (Kramer 1971). Engelmann spruce's optimal growth temperature regime was reported to be 19/23ºC in which most importantly, night temperatures exceeded those of the day (Hellmers et al. 1970) and Opeke (1982) suggested the optimal temperatures of tropical citrus trees to be 28 , 24 to 29 for cashews, 24 to 35 for rubber trees and 27 to 35ºC for coconuts and oil palms.

The majority of eucalypts are intolerant of frost and most of those that are tolerant can withstand down to about -5 ºC (23°F). The hardiest ones commonly known as snow gums including *E. pauciflora* are able to stand up to about -20 °C (-4 °F) (O'Hara and Berrill 2009; Vann et al. 1994).

Species from low temperature climates have been reported to have a reduced ability for photosynthetic acclimation to increasing temperature (Atkin et al. 2006; Ow et al. 2008a). Ow et al. (2010) reported limited evidence of photosynthetic acclimation to temperature in *Pinus radiata* and *Populus deltoides*. On the other hand, Wieser et al. (2010) reported a significantly less net photosynthesis of *Pinus cembra* in fall than in summer with photosynthesis correlating positively with root zone temperature. Slatyer and Ferrar (1977) and Ngugi et al. (2003b) reported high degree of acclimation in *E. pauciflora* and *E. argophloia* respectively. The optimum temperature for net photosynthesis increased as daytime temperature of the growth environment of *E. argophloia* increased from 18 to 33ºC (Ngugi et al. 2003b) with the species exhibiting higher rates of photosynthesis at both 23 and 28ºC acclimation temperature than *E. cloeziana*. Gunderson et al. (2010) reported a shift in the optimal temperature of CO_2 assimilation with changes in air temperature and a thermal acclimation potential of 0.55 to 1.07 per degree change in temperature for five deciduous species (sweetgum [*Liquidambar styraciflua*], northern red oak [*Quercus rubra*], southern red oak [*Quercus falcata*], yellow birch [*Betula alleghaniensis*] and bigtooth aspen [*Populus grandidentata*]).

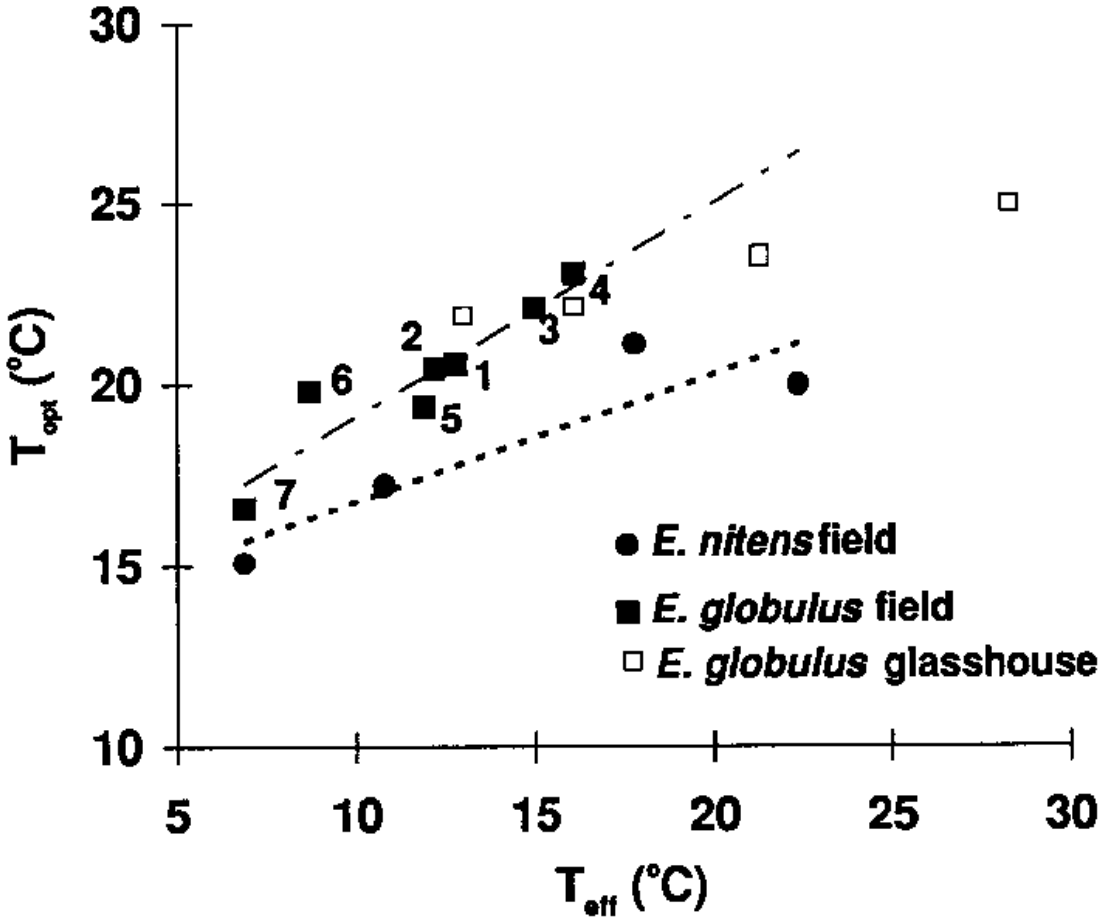


Figure 2.5 Relationship between optimum temperature and growth temperature

Relationship between photosynthetic optimum temperature and average temperature of *E. nitens* and *E. globulus*; Source: Battaglia et al. (1996)

2.3.3 Effect of temperature on photosynthetic parameters

Hawkins (1988) compared the effect of temperature on seedling growth of three indigenous species of New Zealand (rimu, kahikata and totara) in controlled environment cabinets at temperatures regimes of 27/22ºC, 21/16ºC and 15/10ºC and reported that rimu, kahikatea and totara produced maximum height growth and dry weight in the 27/22ºC temperature regime which is higher than temperatures currently common in New Zealand. Ghannaoum (2010) quantified the interactive effects of growth CO_2 concentration and temperature of faster-growing *E. saligna* and slower-growing *E. sideroxylon* grown in a glasshouse at three atmospheric concentrations of CO_2 and reported that photosynthesis of the *eucalyptus* seedlings strongly increased with increasing concentration of CO_2 and temperature provided water and nutrients were not limiting. Long-term effects of CO_2 concentration and temperature on photosynthesis relies on the capacity of the plant to acclimatize to those two growth factors (Ghannaoum et al. 2010).

Photosynthesis may be higher in deciduous leaves than evergreen primarily because of the mechanisms of internal shading and diffusional limitation aimed at strengthening plant tissues and building of defence mechanisms to counter herbivores of the latter at the expense of photosynthesising proteins or reduction in stomatal conductance for water conservation during drought (Reich et al. 1999). For evergreen trees, height would only increase until a temperature above normal growing temperatures, while biomass continued to increase above that temperature. Instead of increasing height, evergreens may be investing in girth and leaves at temperatures more than 5°C above normal. Reduced stem taper could decrease the mechanical stability of tree stems, making them more vulnerable to ice storm and wind damage (Way and Oren 2010). These environmental factors can limit the northern range of some tree species as was in *P. taeda* (Fowells 1965; Wahlenberg 1960).

Osborne and Beerling (2003) measured the seasonal patterns of leaf photosynthesis (A) under CO_2 enrichment in coastal redwood (*Sequoia sempervirens*), dawn redwood (*Metasequoia glytostroboides*) and swamp cypress (Taxodium distichum) and reported that during spring there was a significant increase in A in all the three species at an elevated CO_2 of 80 pa compared with controls at 40 pa. They observed that a rapid acclimatization in V_{cmax} neutralised the CO_2 response of A in all three species in the

presence of six weeks constant illumination and the acclimatization of V_{cmax} correlated with a decrease in leaf nitrogen in summer. The saturation rate of an A/C_i curve relies on the regeneration rate of RuBP which also depends on triose phosphate utilization (TPU) and the rate of electron transport. Photosynthesis is limited by TPU and electron transport capacity but TPU is effective up to higher temperatures and electron transport capacity continues beyond the point at which TPU is limiting (Sage and Kubien 2007).

The biochemical model of photosynthesis by Farquhar et al. (1980) is very useful in reporting photosynthetic responses to environmental variables (Farquhar et al. 1980). The maximal carboxylation rate (V_{cmax}) and the maximal light-driven electron flux (J_{max}) are temperature dependant (Figure 2.6) and are also influenced by nutrients including nitrogen (N) and phosphorus (P) (Hikosaka 1997; Reich et al. 2009). V_{cmax}, J_{max}, the ratio of J_{max} to V_{cmax} and the partial pressure at the site of carboxylation affect the changes in the temperature dependence of photosynthesis (Figure 2.6) and (Figure 2.7) (Hikosaka 1997; Hikosaka et al. 2006; Hikosaka et al. 1999). It has been reported that V_{cmax} is more highly sensitive to temperature than J_{max} (Bunce 2000; Hikosaka et al. 1999; Yamori et al. 2005) and variation among species and within species has been reported for those two photosynthetic parameters (Bunce 2000; Dreyer et al. 2001; Hikosaka et al. 1999; Hikosaka et al. 2007; Medlyn et al. 2002a; Wullscheleger 1993).

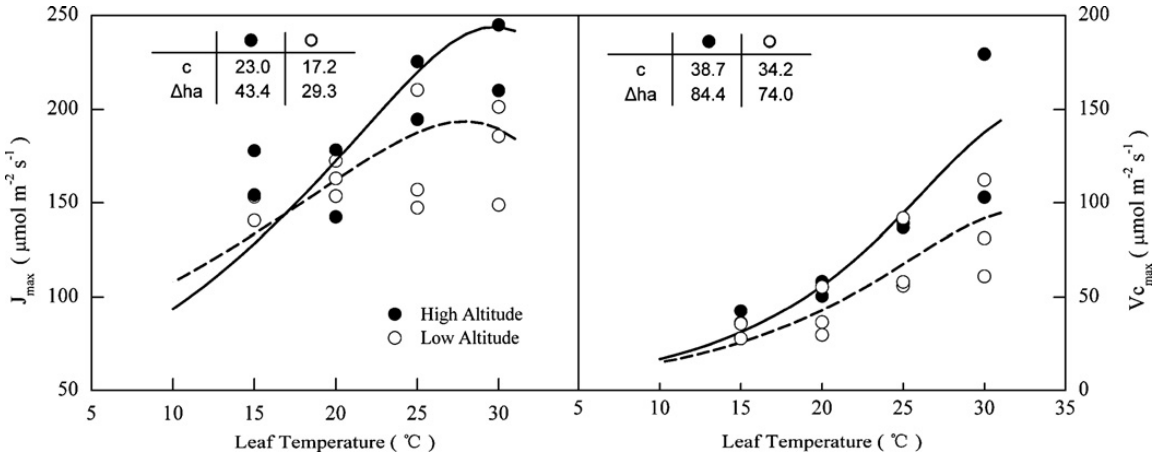


Figure 2.6 Temperature dependence of J_{max} and V_{cmax}

Temperature dependence of J_{max} and V_{cmax} for leaves of plants grown at two altitudes; Source: Fan et al. (2011)

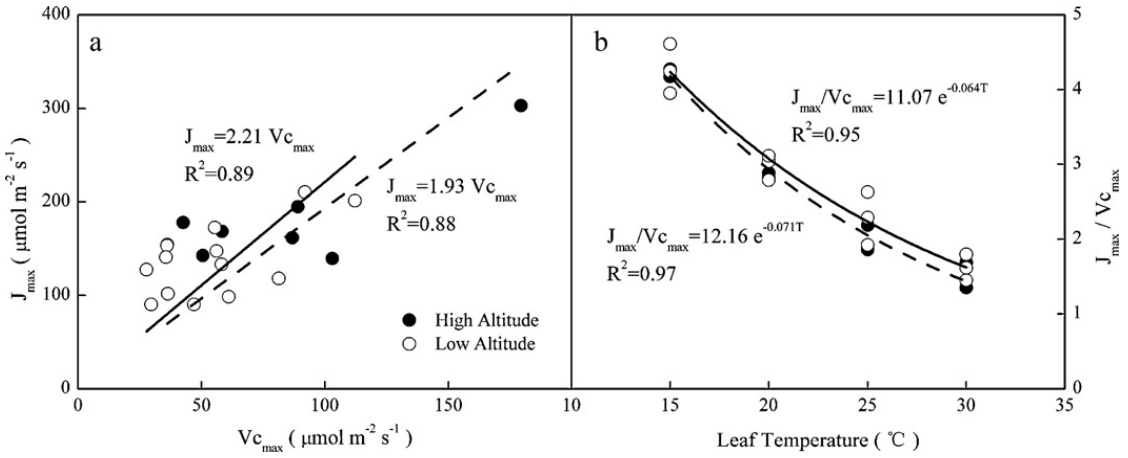


Figure 2.7 Relationship between J_{max} and V_{cmax} and J_{max}/V_{cmax} against leaf temperature

(a) Relationship between J_{max} and V_{cmax} (b) Response of the ratio of J_{max} and V_{cmax} to temperature; Source: Fan et al. (2011)

2.4 CO_2 exchange and mineral nutrition

Nitrogen (N) and phosphorus (P) are important plant nutrients. Their deficiencies restrain leaf area development as well as the rate of photosynthesis and plant growth. Ribulose-1, 5 bisphosphate carboxylase/oxygenase (Rubisco) plays an important role in the biochemical fixation of CO_2 and it is highly resourced with N and the concentration of N plays an important part in leaf photosynthetic capacity (A_{max}) (Bond and Farnsworth 1999; Field and Mooney 1986; Lewis et al. 2004; Reich et al. 1997; Ripullone et al. 2003; Wright et al. 2004; Zhang and Dang 2006). Likewise, P is a constituent of most of the biochemical compounds that play active role in photosynthesis including nucleic acids, sugar phosphates, Adenosine-triphosphate (ATP) and phospholipids (Bielske 1973).

Reich et al. (2009) compiled field data from 314 species to examine the influence of leaf phosphorus on the correlation between photosynthesis and N. They reported that the response of A_{max} to N was inhibited by a decrease in leaf P with A_{max} correlating directly with N and the interaction between N and P. However, variability in leaf photosynthetic rates within or between species may not necessarily correlate to differences in productivity. Similarly, high photosynthetic rates at high temperatures do not necessarily support high rates of plants dry matter accumulation (Way and Sage 2008b) because growth could follow different developmental paths in trees say, allocating more biomass to leaves and less to roots and growing taller for a given stem diameter.

Nitrogen is an important constituent of proteins and chlorophyll and it is important for the establishment of thylakoids and enzymes. There is a close relationship between the amount of nitrogen in the leaves and the amount of chlorophyll (50mol of thylakoid nitrogen/mol chlorophyll [60] and of RuBP-carboxylase (Evans 1989). Proteins of the Calvin cycle and thylakoids represent the majority of leaf nitrogen so photosynthetic capacity is strongly related to leaf nitrogen on an area (N_a) or mass (N_m) basis. Furthermore, for leaves of a given age and for a given nitrogen supply, N_a appears to be strongly related to light exposure (Caemmerer and Farquhar 1999). Research has shown that rates of dark respiration (R_d) and photosynthesis usually correlate with tissue nitrogen (N) content across diverse taxa and environments (Fangmeier et al. 1999).

Ow et al. (2008) assessed the extent of photosynthesis and respiratory acclimation to changing temperatures in pre-existing and new needles of *Pinus radiata* L. and reported a less significant impact of leaf N on the extent of acclimation in the species, although it had emerged from previous work that tissue N influenced the rates of respiration (Zogg et al. 1996). Jull et al. (1999) in an experiment to investigate heat tolerance of selected provenances of Atlantic white Cedar (*Chamaecyparis thyides* [L.] B. S. P) reported that the tissue concentration of mineral nutrients including nitrogen and phosphorus increased with temperature and suggested that mineral concentration might not be a limiting factor at high temperature. Also Whitehead et al. (2004), in a study to determine values for parameters to describe biophysical processes of photosynthesis in mānuka and kānuka leaves and also to investigate the response of photosynthesis to leaf nitrogen concentration, reported that V_{cmax} and J_{max} correlated positively with leaf nitrogen concentration on a unit leaf area basis without a significant relationship between the slopes of the species nor that of individual trees.

2.5 Temperature dependence of respiration

Respiration (R) and glycolysis are the processes by which energy stored in carbohydrates is given out in a controlled way (Caemmerer and Farquhar 1999). The availability of carbon may be high for growth allocation at high temperatures because respiration adapts to temperature more strongly than photosynthesis (Joseph 2011; Ow et al. 2008a; Ow et al. 2008b; Way and Oren 2010). Respiration rates increase as temperature increases and the

most commonly employed respiration versus temperature function is represented by equation 2.1

$$R(T) = R_o e^{K_R(T-T_o)} \qquad 2.1$$

Where K_R is a parameter, R_o is the rate of respiration at a reference temperature T_o (Landsberg and Sands 2011).

Equation 2.2 is an expression of the rate of biological processes in relation to temperature and it is the ratio between the rates of a process at two temperatures that differ by 10ºC (Caemmerer and Farquhar 1999; Landsberg and Sands 2011) and the short-term temperature responses of it range from 2-2.5 (Landsberg and Sands 2011).

$$Q_{10} = e^{10K_R} \qquad 2.2$$

Two types of effects (i.e. type I and II) of temperature on respiration acclimation have been reported by previous research (Atkin and Tjoelker 2003; Billing et al. 1971; Rook 1969; Wager 1941) in plants. Type I respiratory acclimation is caused by changes in the short-term temperature dependence of R that result from changes in substrate supply and/or energy demand (Covey-Crump et al. 2002) and type II thermal acclimation is temperature-mediated changes in respiratory capacity and basal rates of R (Armstrong et al. 2006). Both types have been reported as occurring within plants (Armstrong et al. 2008) but in some plants only type II has been reported (Atkin et al. 2000; Bruhn et al. 2007; Tjoelker et al. 2009; Zaragoza-Castells et al. 2008). Species with both types occurring sustain changes in growth temperature.

Many studies have reported thermal acclimation of leaf respiration. For instance, Ow et al. (2008a) and (2008b) in an experiment to measure dark respiration [i.e. the process by which organic substances are oxidised to CO_2 and water with the production of ATP and NADPH required for biological processes (Landsberg and Sands 2011)] in the leaves of *Populus deltoids* x *nigra* (Veronese') to investigate the extent of acclimation of respiration and photosynthesis to temperature in pre-existing and newly emerged leaves of the species reported a higher degree of dark respiration (R_d) to growth temperature than of

photosynthesis with a significant difference in the responses of leaf photosynthesis and respiration to temperature.

In another study Ow et al. (2010) reported seasonal changes in leaf respiration at a base temperature of 10ºC (R_{10}) in *Pinus radiata* and *Populus deltoides* to be greater in autumn and winter and the short-term leaf respiration to a 10ºC rise in temperature (Q_{10}) was higher during winter. However, long-term responses of respiration to temperature were flat over a wide range of ambient temperatures. Also hourly rate of respiration has been reported to be exponentially related to temperature with $Q_{10} \approx 2$ whist the relationship between daily respirations and mean daily temperature was reported to be linear (Linder and Troeng 1981). Also Pereira et al. (1986) reported Q_{10} of ≈ 2.8 in winter and early autumn but a reduction to ≈ 2.25 in summer and early spring in *E. globulus*.

Acclimation of respiration to temperature has been reported to be higher in young leaves than in older ones (Ow et al. 2008a; Ow et al. 2008b) and leaf nitrogen concentration has been reported to have a huge effect on respiration with respiration reported to increase with increasing leaf nitrogen (Field 1983; Landsberg and Sands 2011; Ow et al. 2008a; Ow et al. 2008b; Sands 1995a, b; Sheriff and Nambiar 1991). Joseph (2011) reported an increase in respiration with increasing temperature in both grass and Kānuka in an experiment to investigate changes in temperature sensitivity of carbon exchange mechanisms in response to soil water content within the species and a significant variation in the R_{10} of Kānuka, which ranged from 0.31 to 0.99μmol m^{-2} s^{-1} and grass, which ranged from 0.15 to 0.43 μmol m^{-2} s^{-1}. Also, the ratio of photosynthetic capacity to dark respiration A_{max}/R_d has been reported to decrease with increasing leaf nitrogen (Turnbull et al. 2005).

Plenty of research has addressed acclimation to temperature for eucalypts as a way of obtaining the necessary information to simulate and predict the growth of the plant but studies have concentrated on just a few species of the genus and relatively narrow temperature ranges. Moreover, the 3-PG model which is designed to model the photosynthetic activities of plants requires estimates of the minimum, optimum and maximum temperatures for photosynthesis (Landsberg and Waring 1997). In the steady described here, durable species of eucalypts having the potential of providing posts for the wine and viticultural industry as well as providing hardwood for other structural application needs of New Zealand were used. These species have received little prior

attention from plant physiologists. Examination of differences in photosynthetic temperature responses of the species will help identify temperature ranges where they could grow and acclimate to temperature and also provide information needed to design daily/seasonal models to predict their net carbon assimilation in a range of conditions. Hence, the objectives of the study were to identify;

(i) the optimum, minimum and maximum temperatures of assimilation rate of net CO_2 of the species acclimated to varying base-line growth temperatures
(ii) whether the species differed in their responses to temperature
(iii) effects of temperature on photosynthetic parameters, maximal carboxylation rate (V_{cmax}) and the maximal light-driven electron flux (J_{max}).

Also, photosynthetic acclimation to changes in temperature has been attributed to changes in CO_2 concentration in intercellular air spaces (C_i,), the activation energies of V_{cmax} and J_{max} and the ratio of J_{max} to V_{cmax}. A further objective was therefore to determine how these parameters would change with changes in growth temperature of the species selected for the study and their effects on photosynthetic acclimation.

Base on previous research findings (Ow et al. 2008a; Ow et al. 2008b) the null hypothesised were;

(i) temperature has no effect on the photosynthetic activities of the species
(ii) the species does not differ in their photosynthetic activities and
(iii) the relationship between net photosynthesis and short-term changes in temperature does not vary with long-term temperature conditions

Chapter 3 **Materials and Methods**

3.1 Plant material and origin of seed source

Containerised nursery seedlings cultivated from seeds selected for high growth rate, good stem form and branch architecture of *E. globoidea, E. bosistoana, E. argophloia* and *E. fastigata* and seedlings of *Sequoia sempervirens* were used in this experiment. The species involved five genotypes of *E. globoidea* (denoted 301, 246, 352, 311 and 247), a genotype each of *E. bosistoana* (996), *E. argophloia* (995), *E. fastigata* and three clones of *Sequoia sempervirens* (denoted Sw002, Sw005 and 04mR) (Table 3.1). The growth mixture in containers consisted of 63% peat soil, 30% vermiculate and 7% perlite and fertilizer.

3.2 Growth conditions and experimental design

Equal sized samples of the containerised seedlings were repotted in 25 by 17 cm pots in a standard potting soil mixed with fertilizer. The potting mix consisted of 80% Horticultural Fine Potting bark and chip Grade 2 and 20% Blood plus Bone (Bio blend). The pH of the mix was adjusted to suit the requirements of the species with a balanced mix of Magnesium Carbonate and Calcium Carbonate with Calcium Sulphate and Iron Sulphate present as trace elements. Osmocote Protect 12/14 month dual coated for delayed release of all nutrients was used in the mix. The seedlings were given 420 millilitres of water daily and excess water was allowed to drain out of the pots.

3.3 Preconditioning growth treatments

The seedlings were kept in a well lit glasshouse (Figure 3.1) at a day temperature of 14-20°C and watered to field capacity daily. Excess water was allowed to drain out of the pots from the beginning of August, 2011 for 6 weeks before the start of the experiment.

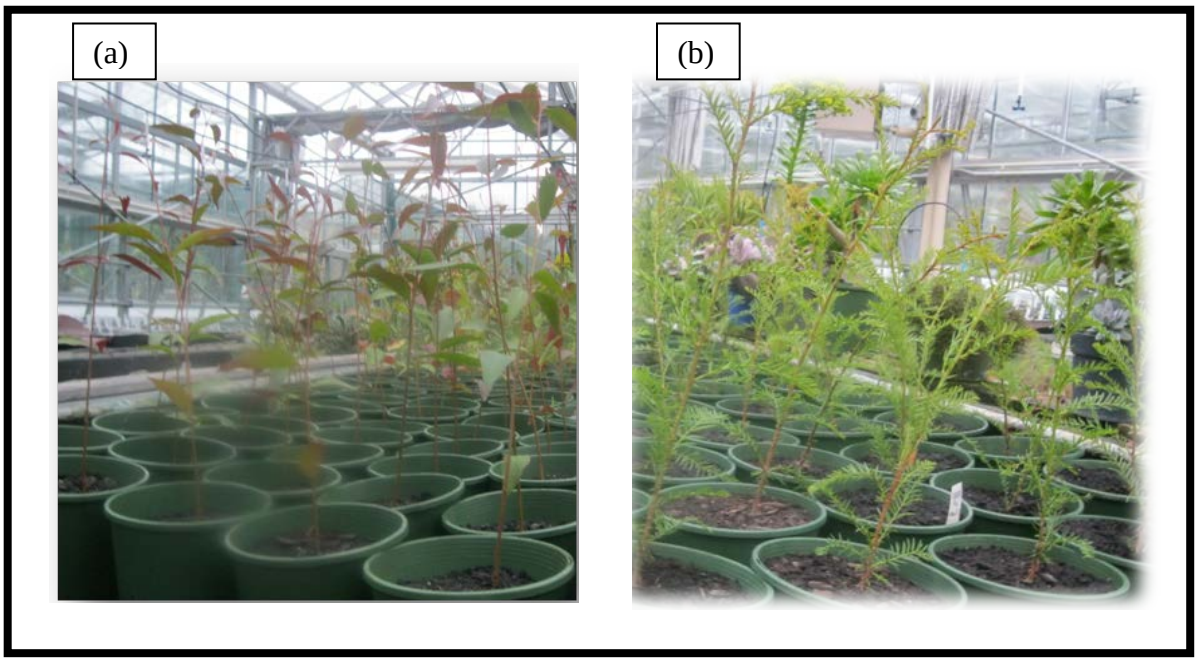


Figure 3.1 Conditioning of plants (a) eucalypt and (b) *Sequoia sempervirens*

3.4 Experiment

The experiment was established in three controlled environment chambers (Contherm 630 climate stimulator) at the University of Canterbury, Christchurch, New Zealand from 15th September 2011 to 15th January 2012. Plants were randomly transferred from the glasshouse to each of the chambers and grown under controlled conditions for day/night. The chambers were set for a 16/8 hours photoperiod at a relative humidity of 70%. All necessary variables including temperature, time, RH, light and CO_2 were regulated to create consistent conditions in the cabinet. The cabinets were artificially illuminated using 400W metal halide lamps with a maximum incident PFD of approximately 720 μmmol m^{-2} s^{-1} at a CO_2 concentration of 400ppm and randomly allocated with temperatures of 30/17, 18/11 and 8/5ºC. The seedlings were allowed to grow under the set growth conditions for three weeks before measurements began. Watering was done near to field capacity throughout the duration of the experiment and so it was assumed to be non-limiting. There were 3 replicates of each genotype in each cabinet and *E. globoidea* and *Sequoia sempervirens* were represented by 5 and 3 clones respectively.

The three tallest trees were randomly allocated to each of the three cabinets successively until each cabinet contained 3 plants of each genotype. This orderly arrangement was to

ensure that any variation in measured parameters result offing from differing initial sizes of plants between treatments could be minimised. The seedlings were re-positioned within cabinets weekly to minimise effects of any internal variation in microclimate (Hawkins 1988).

Table 3.1 Height (h) and ground collar diameter (gld) of plants in growth cabinets

Genotype	30/17ºC cabinet		18/11ºC cabinet		8/5ºC cabinet	
	h/mm	gld/mm	h/mm	gld/mm	h/mm	gld/mm
SW005	400	13	330	14	310	13
SW005	360	13	400	14	350	13
SW005	360	13	340	14	350	12
SW002	220	12	220	13	190	12
SW002	250	12	220	13	280	10
SW002	300	14	221	10	200	10
04MR	240	10	300	11	220	10
04MR	280	10	170	13	320	10
04MR	300	13	300	13	240	11
EG301	310	12	360	10	280	14
EG301	300	10	250	10	350	13
EG301	390	10	290	10	280	12
EG311	300	12	340	11	280	11
EG311	300	12	290	10	330	12
EG311	301	12	310	10	320	11
EG352	430	12	340	11	250	10
EG352	431	12	440	10	250	14
EG352	430	13	439	13	320	12

EG246	300	10	300	13	300	10
EG246	300	10	300	13	280	12
EG246	299	11	301	13	300	12
EG247	300	12	300	12	300	12
EG247	300	12	299	12	300	12
EG247	300	12	300	12	301	13
EA995	260	10	250	12	300	12
EA995	310	11	260	10	311	12
EA995	340	11	380	10	386	12
EB996	300	11	310	10	330	11
EB996	380	10	380	13	260	10
EB996	330	11	340	10	320	10
EF	380	9	340	12	340	12
EF	400	13	360	12	420	13
EF	350	10	401	10	350	12

3.4.1 Leaf gas-exchange measurement

A Licor-6400 photosynthesis system (Li-6400, Li-Cor Inc., Lincoln NE USA) equipped with a standard 2 × 3 cm leaf cuvette and a Li-Cor LI-6400-02B blue-red light source was used for gas exchange measurements of the leaves of the seedlings. The system consisted of Infra Red Gas Analysers (IRGAs) which were microprocessor-based machines that collected and stored physical measurements relating to photosynthesis and it permitted accurate control of cuvette temperature and irradiance. The IRGAs comprised two parts i.e. a leaf cuvette which contained a windowed chamber for the leaf, a clamp and seal, sensors for light and temperature, and a cooling fan. To compensate for changes in temperature, the IRGAs were calibrated to zero on a daily basis. The CO_2 and H_2O span values were calibrated before measurements were made. The two most important measurements made

were CO_2 uptake by a leaf and water loss from the leaf surface. In addition to those two measurements, the instrument measured photon flux density (PAR as µmol photons m^{-2} s^{-1}), leaf temperature (°C), flow rate of gas over the leaf (cm^3 min^{-1}), input CO_2 concentration (µmol mol^{-1}) and input water pressure (mb). Measurements began on the 15th of December 2011. The most recently fully expanded metabolically active leaf of all replicates of each species was used to monitor changes in photosynthetic temperature responses to different intercellular CO_2 (C_i) levels such that temperature response curves were determined for at least one leaf of each plant (Battaglia et al. 1996; Billing et al. 1971). Cuvette conditions were maintained at a photosynthetic photon flux density (PPED) of 1500 µmol m^{-2} s^{-1} and relative humidity >60%. An attempt was made to achieve uniform light levels for all measurements in all the three control environment cabinets, and cuvette air conditions were maintained similar to those of the cabinet.

The Li-6400 was kept in the growth chamber (Figure 3.2) and was controlled externally from a lap-top computer while readings were taken and that maintained a balance between all variables of the chamber and the Licor. Net CO_2 assimilation rates of the leaves which gave an indication of how fast they were photosynthesising (A in µmol CO_2 m^{-2} s^{-1}), the internal concentration of CO_2 in the leaves in the vicinity of rubisco (C_i in µmol mol^{-1}), the stomatal conductance that indicated how open stomata were (G in mmol H_2O m^{-2} s^{-1}) and the evaporation rate which depicted how the leaves were transpiring (E in mmol H_2O m^{-2} s^{-1}) were calculated on a total leaf surface area basis from the measurements taken, and equations were fitted that described the behaviour of leaf photosynthesis and transpiration. Leaf area of species whose surface area was not up to the full chamber value of 6 cm^2 was obtained using digitized images (Figure 3.3) and Image-Pro Plus software (version 4.5.0.19, Media Cybernetics, Silver Spring, MD, USA) (Francisco et al. 2004; Jaya et al. 2010).

Prior to taking measurements, the temperatures and humidities of the cabinets were regulated to suit the various temperatures (35, 30, 25, 20, 15, 10 and 5°C) at which the Li-cor was set to take measurements. The temperatures and relative humidities in the growth chambers were regulated to keep VPD between 0.4 - 0.5 kPa. Combinations of temperatures and relative humidities were 35 - 90, 30 - 88, 25 - 85, 20 - 80, 15 -70, 10 - 60 and 5°C - 50%. Cabinet temperature was set equal to that of the block at which measurements were made such that when block temperature was 20°C, temperature of the

cabinet was equally adjusted to 20°C at a humidity of 80%. Measurements of photosynthetic response (A) to intercellular CO_2 partial pressure (C_i) response curves were made at 13 levels of CO_2 beginning from 1200 to 0Pa (i.e. 1200, 1000, 800, 600, 400, 300, 250, 200, 100, 50, 25 and 0). However before generating A/C_i curves, the leaf samples were kept in the Licor to acclimate at a CO_2 level of 400ppm for about 15 minutes.

Gas exchange was permitted to stabilize for approximately 40 minutes before measurements were made at each C_i set point. VPD was kept between the range of 1.0 and 1.5 kPa. A/C_i response curves automated by the IRGAs were used to generate values for the maximum rate of carboxylation (V_{cmax}), rate of electron transport at saturating irradiance (J_{max}), triose-phosphate utilization (TPU) and respiration (R) using Photosyn Assistant software (version 1.12, Dundee Scientific, Dendee, Scotland, UK) (Jaya et al. 2010; Parsons and Ogston 1999; von Caemmerer and Farquhar 1981). The rate of photosynthesis was taken not to be under estimated based on the assumption that CO_2 exchange processes took place only in the part of the sample enclosed in the chamber.

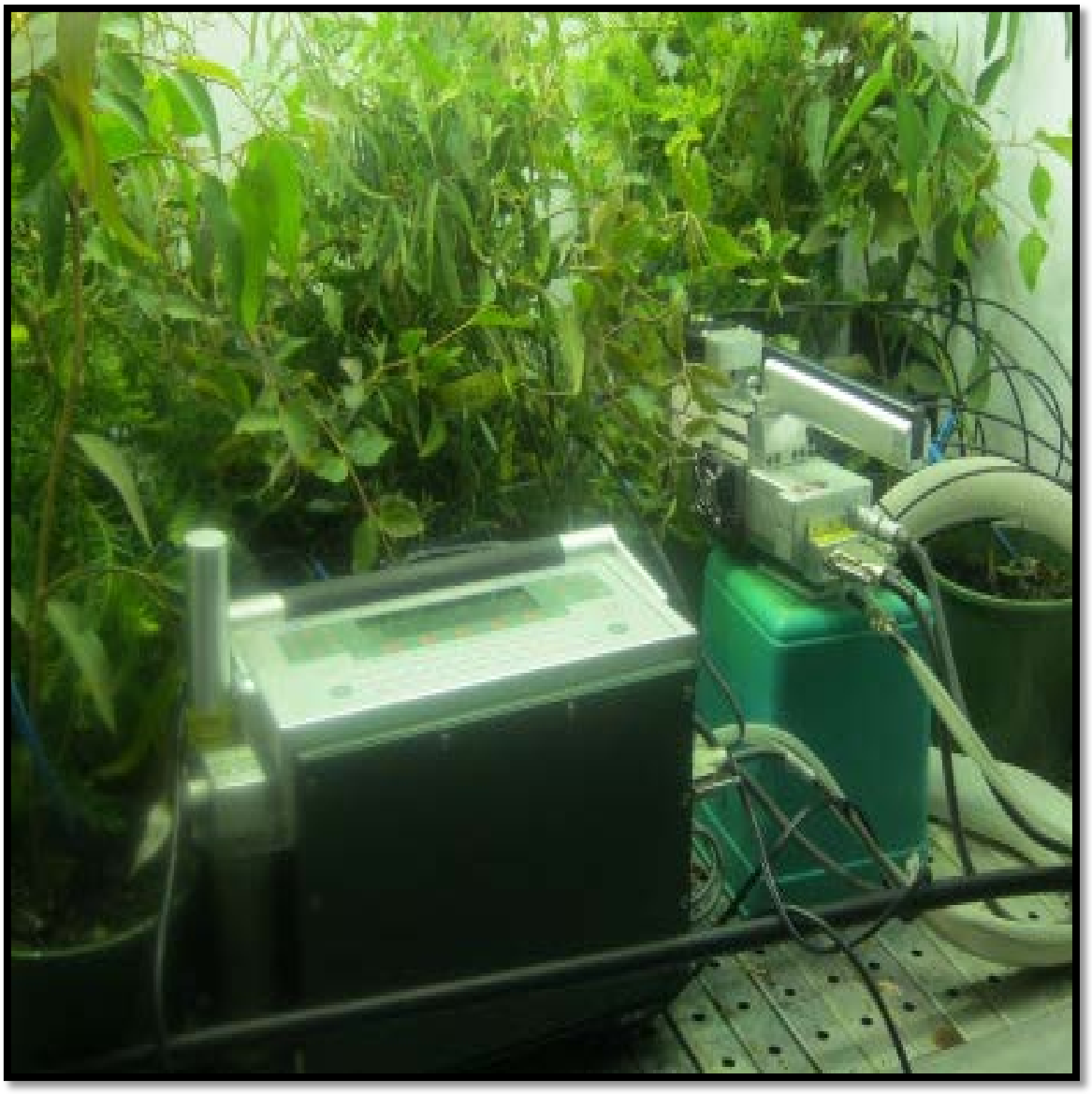


Figure 3.2 CO_2 exchange measurement with Li-6400 in a growth chamber

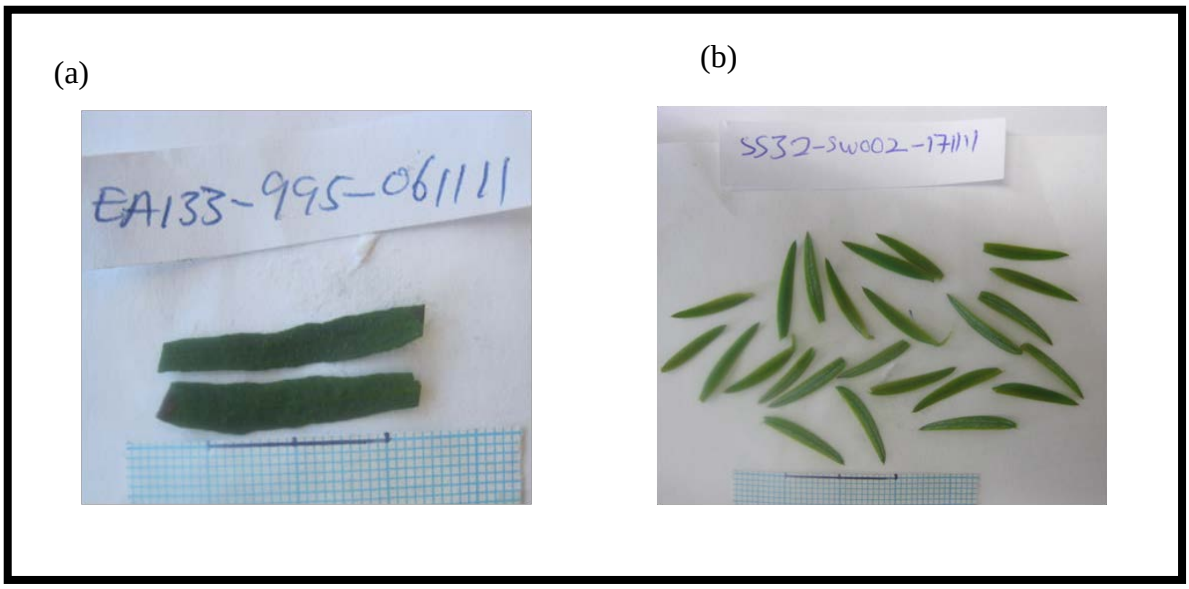


Figure 3.3 Digitized images of leaves

Digitized images of leaves of (a) *E. argophloia* and (b) *Sequoia sempervirens*

3.4.2 Check of cabinet conditions

A set of independent measurements was done inside the growth chambers to confirm that they were performing equivalently using HOBO® Redant, Temperature/Light Data Logger (DOCH 9556-E, Man-UA 002-08,BHE-Pc Version 2.21). The results were unexpected and meant that there was the need to re-evaluate the performance of the chambers and also the results of this study. The growth chambers were apparently overheating when the lights were on, so that the temperatures shown on the control panel were not what the plants were experiencing. Not only that, but they should have sounded an alarm with this malfunction but no alarms sounded.

With plants inside the cabinets, the daytime temperatures were as much as 2ºC above what was wanted, and no alarms sounded. That appeared to be a consequence of heat from the lights. Day time temperatures ranged from 36-30, 17-24 and 4-12 for the 30/17, 18/11 and 8/5ºC cabinets respectively and night temperatures ranged from 18-18.5, 12-22 and 4-10 for the 30/17, 18/11 and 8/5ºC cabinet respectively. Hence the graphs and results were adjusted to reflect the 1-2ºC change in base temperatures.

3.5 Data analysis

The A/C_i mechanistic curve analyst of the Photosyn Assistant software that uses the model proposed by Farquhar et al. (1980) was used for the analysis of A/C_i (CO_2 assimilation

rate against internal leaf CO_2 concentration) curves and the calculation of parameter values that represented the best fit for the data including leaf respiration (R), V_{cmax}, J_{max} and triose phosphate utilisation (TPU) (Sharkey 1985).

Equation 3.1 gives the rate of assimilation limited by carboxylation (A_c) and Equation 3.2 gives the assimilation rate limited by electron transport (A_q)

$$A_c = V_{Cmax}\ \frac{(\mathrm{C_i} - \mathrm{T}^*)}{C_i + K_c\left(1 + \left(\frac{\theta_i}{K_c}\right)\right)} -\ R_d \qquad 3.1$$

$$A_q = J_{max}\ \frac{C_i - T^*}{4(C_i + 2T^*)} -\ R_d \qquad 3.2$$

Where V_{cmax} and J_{max} are the maximum rate of carboxylation by the enzyme Rubisco under conditions of saturating substrate RuBP and the maximum rate of electron transport at saturating irradiance respectively; K_c and K_o are the Michaelis-Menten constants for CO_2 and O_2 respectively. R_d is the rate of daytime respiration as a result of processes other than photorespiration and T* is the CO_2 partial pressure at compensation in the absence of photorespiration.

The V_{cmax} temperature function was calculated using Equation 3.3 Leuning (2002)

$$V_{cmax} = \frac{V_{cmax0} * exp\left[\left(\frac{H_a}{RT_0}\right)\left(1 - \frac{T_0}{T_l}\right)\right]}{1 + exp\left((S_i * T_l - H_d)/\left(R_g * T_l\right)\right)} \qquad 3.3$$

in fitting V_{cmax} data obtained from fitting the model equations of Farquhar et al. (1980) to A/C_i response curves of the CO_2 gas exchange measurement made with the Li6400.

R_g is the universal gas constant, T_o is a fixed temperature (293K), T_l is leaf temperature; H_a and H_d are the activation and deactivation energies respectively and S_i is an entropy term for J_{max} and V_{cmax}.

V_{cmax} and J_{max} values at 20ºC leaf temperature of each of the species at ambient CO_2 of 400 ppm at the three growth temperatures were used to fit J_{max} and V_{cmax} models. A deactivation energy (H_d) of 200000 $Jmol^{-1}$, an activation energy (H_a) of 151779 $Jmol^{-1}$ and an enthalpy term (S_i) of 489 $Jmol^{-1}K^{-1}$ lead to a fit similar to an Arrhenius mode fit.

The relationship between net CO_2 assimilation and temperature for each species and at each base temperature was fitted by equation 3.4

$$y = f(T) = a(T - T_{min})(T_{max} - T)\beta \quad 3.4$$

The constants (α and β) are calculated using equations 3.5 and 3.6. (Landsberg 1977)

$$a = \frac{y_{max}}{(T_{opt} - T_{min})(T_{max} - T_{opt})\beta} \quad 3.5$$

$$\beta = \frac{T_{max} - T_{opt}}{T_{opt} - T_{min}} \quad 3.6$$

Where T_{max}, T_{opt} and T_{min} are the maximum, optimum and minimum temperatures of net CO_2 assimilation respectively and y_{max} is the maximum assimilation.

Equations 3.7 and 3.8 were used to fit J_{max} and V_{cmax} temperature functions

$$V_{cfit} = V_{c20} * exp\left(\left({H_a}/{(R * T_o)}\right) * \left(1 - {T_o}/{T1}\right)\right)/b \quad 3.7$$

$$J_{mfit} = J_{m20} * exp\left(\left({H_a}/{(R * T_o)}\right) * \left(1 - {T_o}/{T1}\right)\right)/b \quad 3.8$$

Where T1 = T+273, T_o = 293, R = 8.314 and, H_a = 151779 $Jmol^{-1}$, b can be calculated from the following equation

$$b = 1 + exp\left(\left(S * T1 - {H_d}/{R * T1}\right)\right) \quad 3.9$$

H_d = 200000 $Jmol^{-1}$, S = 489 and J_{m20} and V_{c20} were the J_{max} and V_{cmax} values at leaf temperature 20ºC for each of the species.

3.5.1 Statistical analysis

All statistical analyses were done using R V2.13.1 statistical programming language (R Core Development Team 2008). A non linear mixed effect model (Crawley 2005; Landsberg 1977) was used to analyse the relation between temperature and net CO_2 assimilation, J_{max} and V_{cmax} and a linear regression model of the form y = a + bx (Crawley 2005; Landsberg 1977) was used to fit the relationship between J_{max} /V_{cmax} ratio and temperature.

Initially both nonlinear least squares (nls) and nonlinear mixed-effects models (nlme) were used to analyse the relation between temperature on J_{max}, V_{cmax} and CO_2 assimilation (A) and the models were compared and the one with the smallest Akaike's Information Criterion (AIC) or Bayesian Information criterion (BIC) were selected as the best fit for J_{max}, V_{cmax} and A. Histogram and scatter plots of residuals of the best fits were made to validate the models. Two way analysis of variance (ANOVA) was used to test for the interactive and non interactive effects of leaf temperature, species and the temperature at which the plants were grown on all the photosynthetic parameters. Where there were no significant interactions between treatment effects, the simplest model that best fitted the data without losing explanatory powers was adopted and TukeyHSD was used to find means that were significantly different from one another.

3.5.2 Biochemical analysis

Leaf weight and nitrogen content were determined on similar leaves taken just above and below those used for the gas exchange measurements. The weight and area of fresh leaves were taken, then oven-dried at a temperature of 70°C for 48 h and then re-weighed. The samples were then ground to minute powder (Figure 3.4) using a ball mill (Retsch: Type MM301-2003, Part No. 20.7410011, Serial No. 123130136B) and were block digested using the Kjeldahl wet oxidation process as described by Blakemore et al. (1987).

Figure 3.4 Powdered samples of oven dried leaves

Chapter 4 **Results**

4.1 Temperature responses and acclimation of net CO_2 assimilation rate

Acclimation of net CO_2 assimilation was sensitive to temperature in all the five species studied. The optimum temperature (T_{opt}) of net assimilation changed significantly with changes in the temperature at which plants were grown (T_{growth}) ($F_{1, 9}$ = 133.899, r^2 = 0.941, $p < 0.001$) and the effect of species was significant ($F_{4, 9}$ = 2.4345, r^2 = 0.941, $p <$ 0.021231). Plants grown at lower temperatures had lower T_{opt} compared to those grown at higher temperatures (Table 4.1). Also as leaf temperature increased, net CO_2 assimilation also increased up to a point beyond which further increases in temperature lead to a decrease in assimilation rate (Figure 4.1). There was a positive linear relationship between T_{opt} and T_{growth} (Figure 4.4).

Among the species studied, *E. argophloia* had the highest T_{opt} (22ºC) for net CO_2 assimilation with *Sequoia sempervirens* having the lowest (20ºC) at T_{growth} 30/16ºC (Table 4.1). The T_{opt} of the remaining three species at 30/16ºC T_{growth} was 21ºC. Also *E. argophloia* had the highest T_{opt} (20ºC) at T_{growth} 22/12ºC and *E. fastigata* had the lowest (17ºC) and the remaining species were 18ºC for *E. bosistoana* and *Sequoia sempervirens* and 19ºC for *E. globoidea*. *E. globoidea* and *E. fastigata* had T_{opt} of 14ºC at T_{growth} 10/5ºC whilst *E. bosistoana* and *E. argophloia* had 16ºC with *Sequoia sempervirens* having 15ºC. However, with the exception of *E. argophloia* whose T_{opt} differed significantly from that of *Sequoia sempervirens* ($p = 0.031$) none of the species varied significantly in T_{opt} at T_{growth} 30/16ºC ($p = 0.0917$).

The minimum temperatures (T_{min}) of net CO_2 assimilation for all the species fell in the range of 3 to 5ºC at the three T_{growth} (Table 4.1) and they were significantly affected by T_{growth} ($F_{1, 9}$ = 66.6269, r^2 = 0.894, $p < 0.001$) but the species did not differ significantly in T_{min} ($F_{4, 9}$ = 2.364, r^2 = 0.894,$p = 0.1306$).

Also T_{growth} had a significant effect ($F_{1, 9}$ = 34.5934, r^2 = 0.8558, $p < 0.001$) on the maximum temperature (T_{max}) for CO_2 assimilation likewise species ($F_{4, 9}$ = 4.7 r^2 = 0.8558, $p = 0.025$). However, apart from *E. bosistoana* which differed significantly from *E. globoidea* ($p = 0.018$), the T_{max} of all others were insignificantly different ($p = 0.19$). It should be noted that the model had to be extrapolated to determine T_{max} (Table 4.1) so care

should be taken in applying these values. The effect of T_{growth} on the net assimilation at T_{opt} (A_{opt}) was significant ($F_{1,9}$ = 405.66, r^2 = 0.9785, p = 0.001) without a significant effect of species ($F_{4,9}$ = 0.9655, r^2 = 0.9785, p = 0.97). *E. globoidea* and *E. fastigata* had the highest rate of CO_2 assimilation (8.9µmol$m^{-2}s^{-1}$) at T_{opt} for T_{growth} 22/12ºC. However, at T_{growth} 30/16ºC it was *Sequoia sempervirens* that had the highest A_{opt} (11.210µmol$m^{-2}s^{-1}$) (Table 4.1).

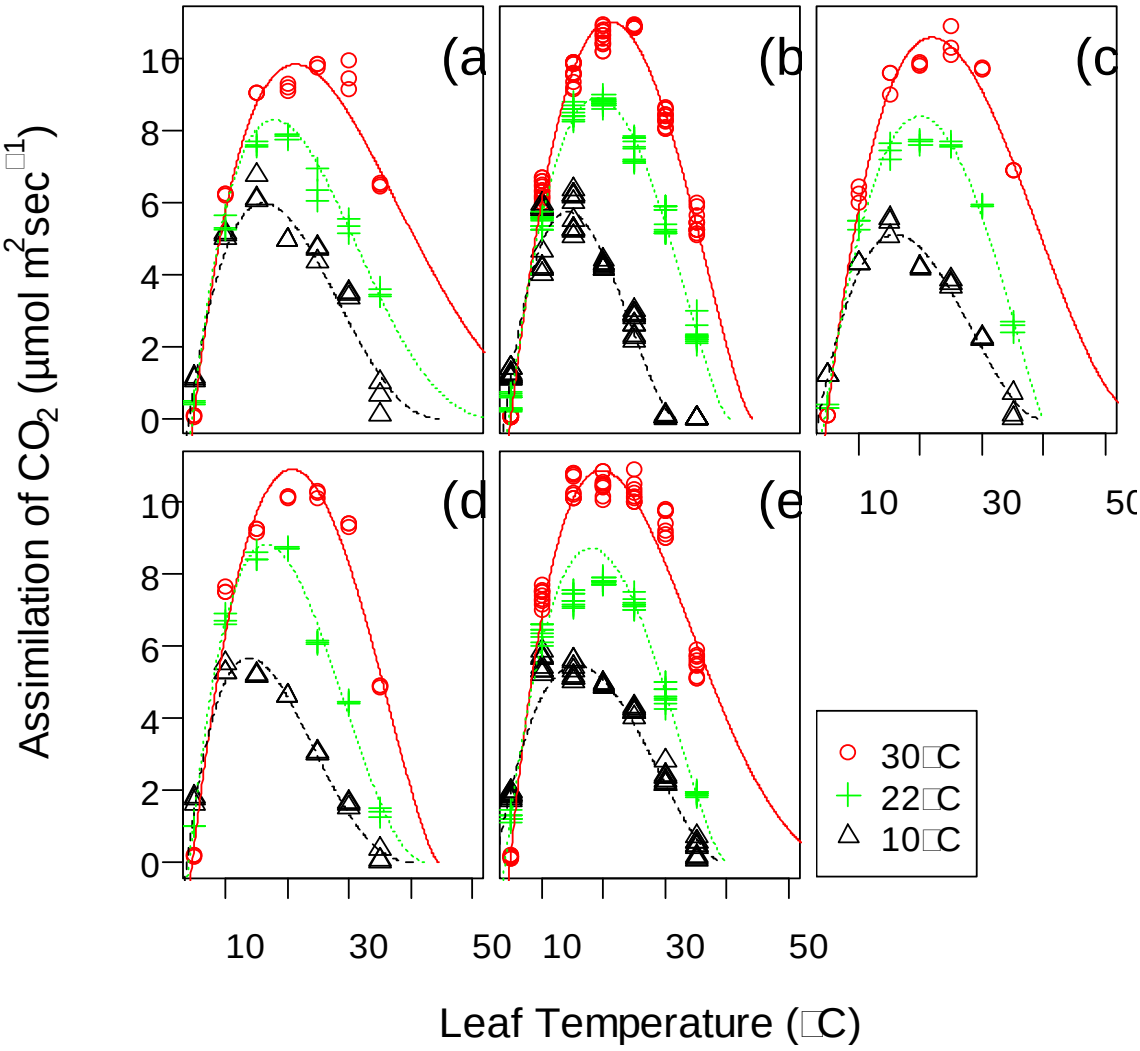


Figure 4.1 Responses of net CO_2 assimilation rate to leaf temperature

Responses of net assimilation rate to leaf temperature 5, 10, 15, 20, 25, 30 and 35^{0}C at CO_2 concentration of 400 µmol m^{-2} s^{-1} of plants grown for three months in growth cabinet at ambient CO_2 and day/night temperatures of 30/16 (o), 22/12 (+) and 10/5^{0}C (Δ) for (a) *E. bosistoana* , (b) *E. globoidea*, (c) *E. argophloia*, (d) *E. fastigata* and (e) *Sequoia sempervirens*. Lines show fit of equation 3.4

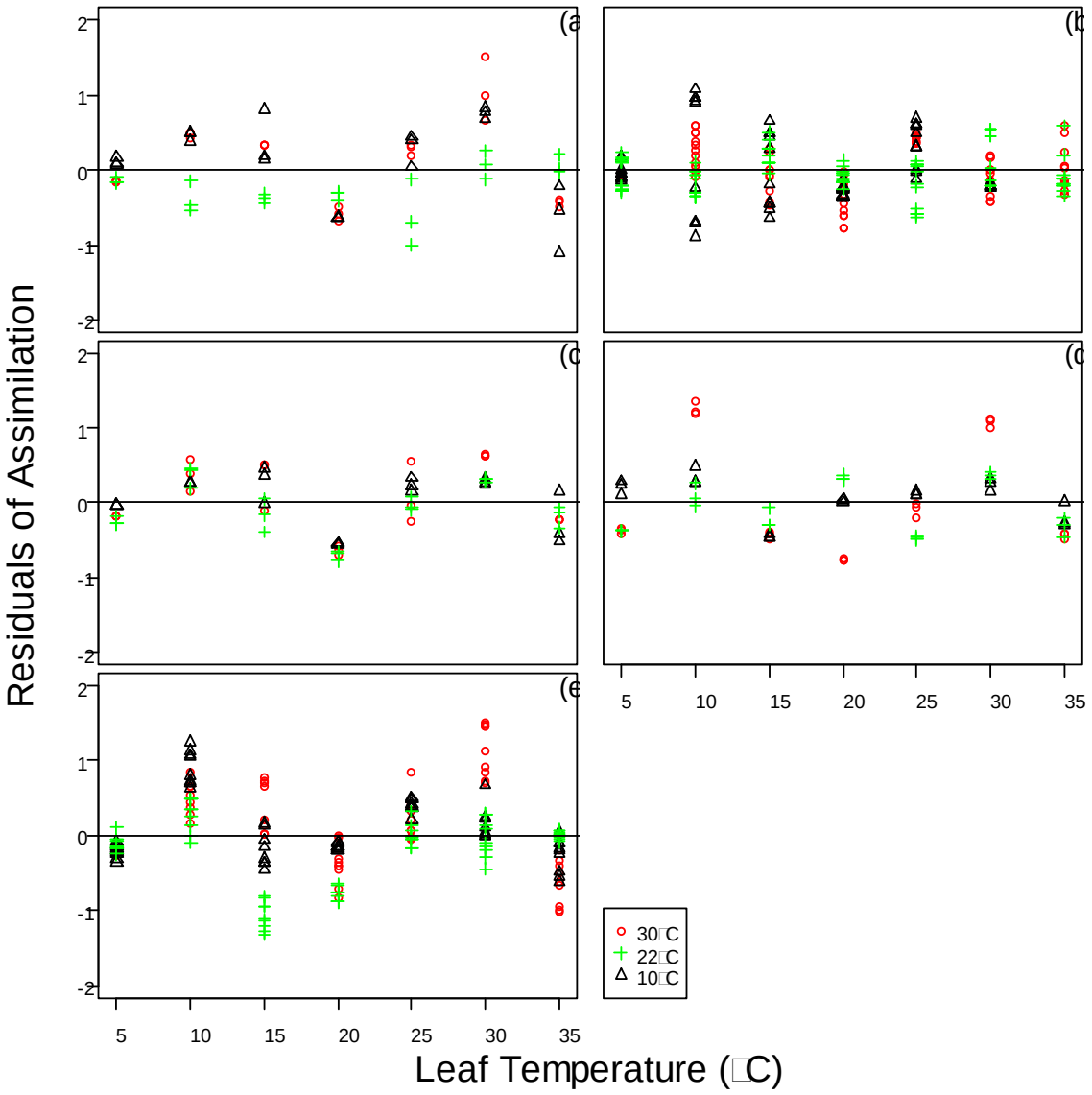


Figure 4.2 Residuals of a model of CO_2 assimilation against leaf temperature

Residuals of a model of CO_2 assimilation plotted against leaf temperature at ambient CO_2 and day/night temperatures of 30/16 (o), 22/12 (+) and 10/5^{0}C (Δ) for (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia*, (d) *E. fastigata* and (e) *Sequoia sempervirens*

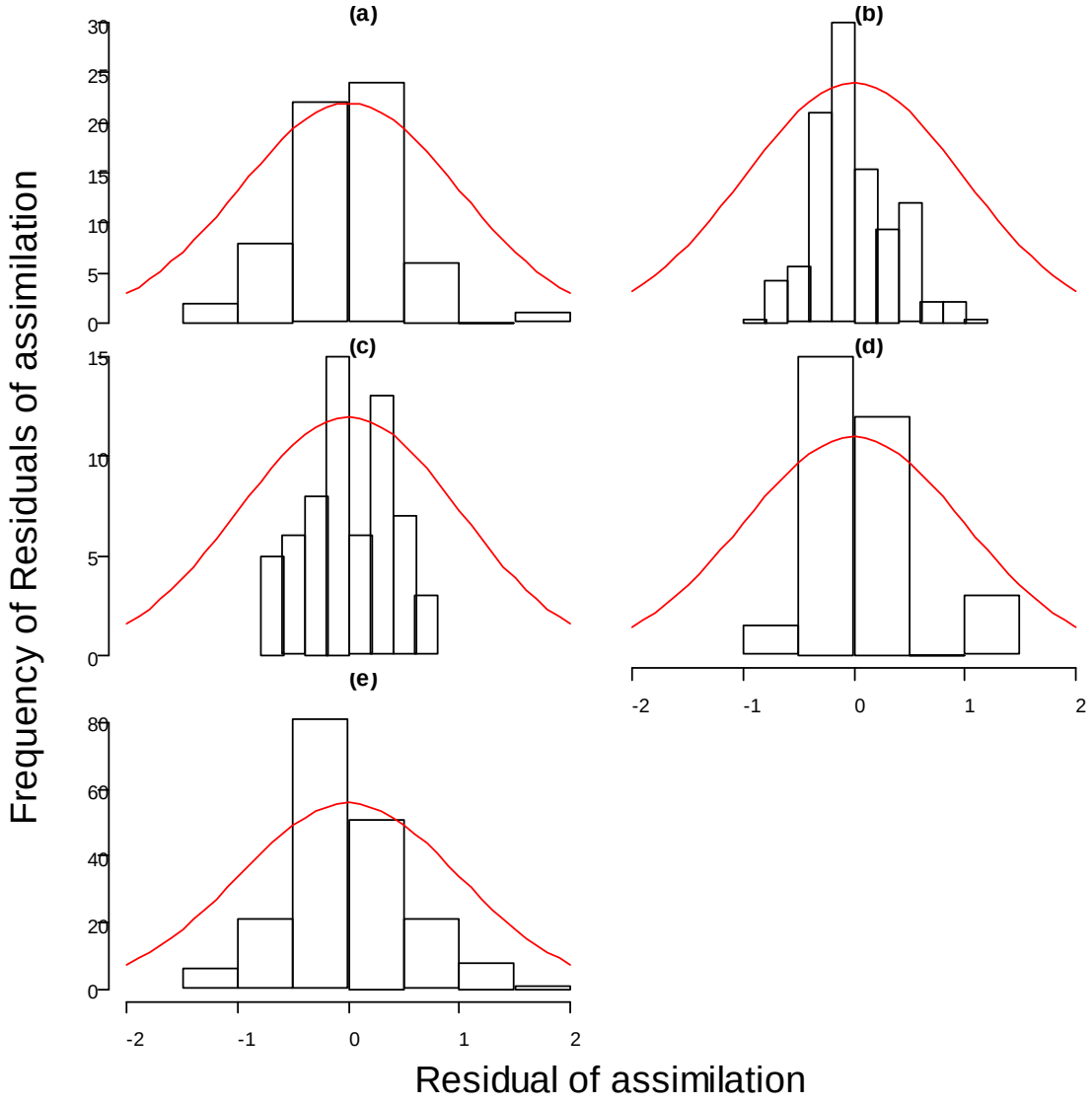


Figure 4.3 Frequency of residuals of CO_2 assimilation against leaf temperature

Frequency distribution of residuals of a model of CO_2 assimilation plotted against leaf temperature for (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia*, (d) *E. fastigata* and (e) *Sequoia sempervirens*

Table 4.1 Optimum, maximum and minimum temperatures of photosynthesis of species T_{opt}, T_{min} and T_{max} for photosynthesis of species acclimated to three day/night T_{growth} and (A_{opt}).

		Growth cabinet temperature, day/night (ºC)			
Species	Parameters	10/5	22/12	30/16	R^2
E. globoidea	T_{min} (ºC)	4***	5***	5***	0.965
	T_{opt} (ºC)	14***	19***	21***	0.96
	T_{max} (ºC)	32***	40***	44***	0.978
	A_{opt} ($\mu molm^{-2}s^{-1}$)	5.7***	8.9***	11.0***	0.909
E. fastigata	T_{min} (ºC)	3***	4***	5***	0.818
	T_{opt} (ºC)	14***	17***	21***	0.747
	T_{max} (ºC)	38***	41***	45***	0.732
	A_{opt} ($\mu molm^{-2}s^{-1}$)	5.6***	8.9***	11.0***	0.903
E. argophloia	T_{min} (ºC)	4***	4***	5***	0.796
	T_{opt} (ºC)	16***	20***	22***	0.834
	T_{max} (ºC)	40***	40***	60***	0.734
	A_{opt} ($\mu molm^{-2}s^{-1}$)	5.3***	8.2***	10.5***	0.896
E. bosistoana	T_{min} (ºC)	4***	5***	5***	0.741
	T_{opt} (ºC)	16***	18***	21***	0.765
	T_{max} (ºC)	42**	52**	57**	0.674
	A_{opt} ($\mu molm^{-2}s^{-1}$)	6.0***	7.9***	10.1***	0.899
S. sempervirens	T_{min} (ºC)	3***	4***	5***	0.834
	T_{opt} (ºC)	15***	18***	20***	0.965
	T_{max} (ºC)	42***	41***	53***	0.731
	A_{opt} ($\mu molm^{-2}s^{-1}$)	5.8***	8.2***	11.2***	0.889

The model extrapolated T_{max} so the values presented may be biased. Statistical significances of growth temperature on the parameters are indicated as ns = $p > 0.05$, * = $p < 0.05$, **= $p < 0.01$ and *** = $p < 0.001$

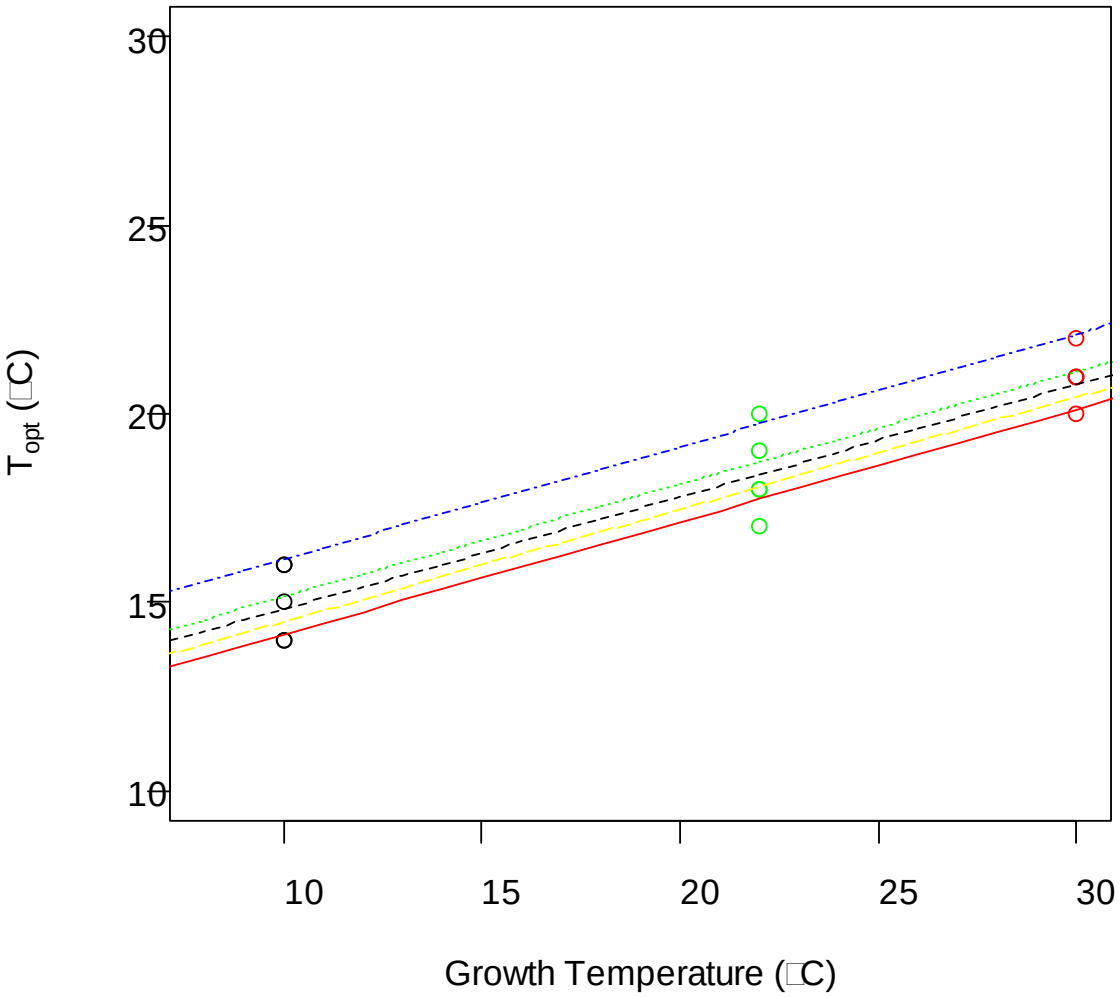


Figure 4.4 Relationship between optimum temperature and growth temperature

Relationship between the temperatures at which maximum CO_2 assimilation were recorded (T_{opt}) and the temperature at which plants were grown (T_{growth}): 30/16, 22/12 and $10/5^0$C for *E. bosistoana* (green line), *E. globoidea* (black line), *E. argophloia* (blue line), *E. fastigata* (red line) and *Sequoia sempervirens* (yellow line)

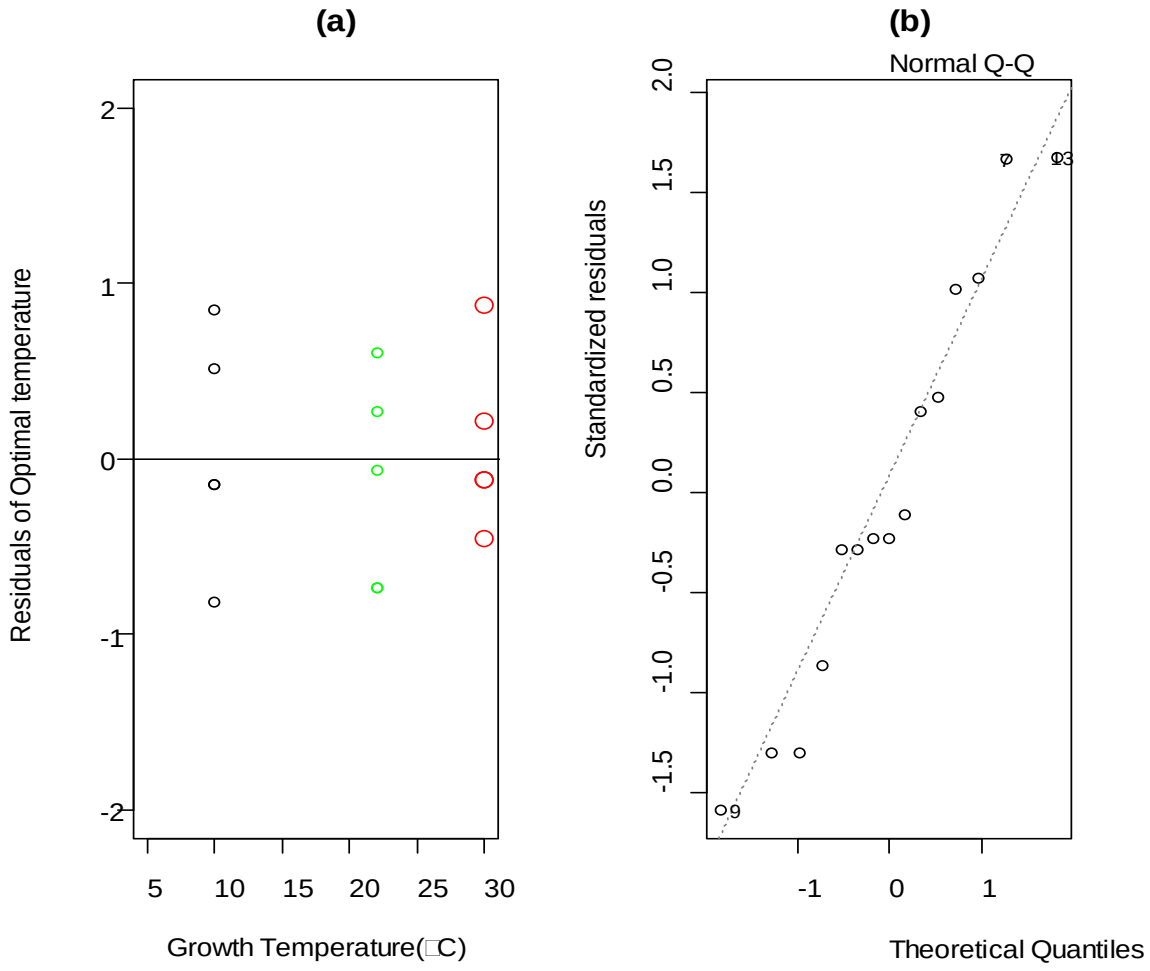


Figure 4.5 Residuals plots of optimum temperature with growth temperature

(a) Residuals of a model of T_{opt} plotted against T_{growth} (b) test of normality of the model of T_{opt} plotted against T_{growth}

4.2 Temperature responses of V_{cmax}

The maximum rate of Rubisco carboxylation (V_{cmax}) increased significantly with increasing T_{growth} ($F_{1, 9}$ = 19.4725, r^2 = 0.8648, p < 0.00168) and leaf temperature (p <0.001), and species had a significant effect on it ($F_{4, 9}$ = 9.517, r^2 = 0.8648, p < 0.0027). V_{cmax} increased exponentially with increasing leaf temperature (Figure 4.6) to an optimum leaf temperature and then declined. The V_{cmax} of *E. argophloia* differed significantly from those of *E. bosistoana* (p = 0.032), *E. globoidea* (p = 0.0042) and *Sequoia sempervirens* (p = 0.00428) otherwise none of the other species differed significantly (p > 0.1024).

V_{cmax} ranged between 40 and 108, 12 and 87, 19.3 and 95, 8 and 86 and 25 and 106.3 μmol CO_2 $m^{-2}s^{-1}$ for *E. argophloia, E. bosistoana, E. fastigata, E. globoidea* and *Sequoia sempervirens* respectively. Low values of V_{cmax20} were recorded at T_{growth} 10/5ºC and for the species, *E. globoidea* (50.922μmol$m^{-2}s^{-1}$). *E. argophloia* had the largest mean V_{cmax} of all the three T_{growth} conditions. The mean value of V_{cmax} for *E. argophloia* at T_{growth} 10/5ºC was larger than those of *E. bosistoana, E. fastigata* and *E. globoidea* at T_{growth} 30/16ºC (Table 4.3). The mean values of V_{cmax} increased with increase in T_{growth} ($F_{1, 9}$ = 19.4735, r^2 = 0.8648, p = 0.001689) and the effect of species was significant ($F_{4, 9}$ = 18.246, r^2 = 0.8648, p < 0.001). Also, there were significant variations in the V_{cmax} for the species studied (p < 0.001).

The T_{opt} of V_{cmax} was significantly affected by T_{growth} ($F_{4, 9}$ = 12.022, r^2 = 0.8715, p = 0.007) and species ($F_{1, 9}$ = 12.225, r^2 = 0.8715, p = 0.00109). T_{opt} of V_{cmax} for *E. argophloia* differed significantly from that for *Sequoia sempervirens* (p = 0.0116) and *E. bosistoana* (p = 0.001) and *E. fastigata* (0.026) also differed significantly in T_{opt} from *Sequoia sempervirens*. Otherwise, all other species were insignificantly different (p =0.0968). T_{opt} of V_{cmax} for *E. bosistoana, E. globoidea, E. argophloia, E. fatigata* and *Sequoia sempervirens* grown at 30/16ºC were 30, 32, 33, 35 and > 35ºC with 31, 30, 30, >32 and >32ºC and 25, 32, 33, 28 and >35ºC for plants grown at 22/12 and 10/5ºC respectively.

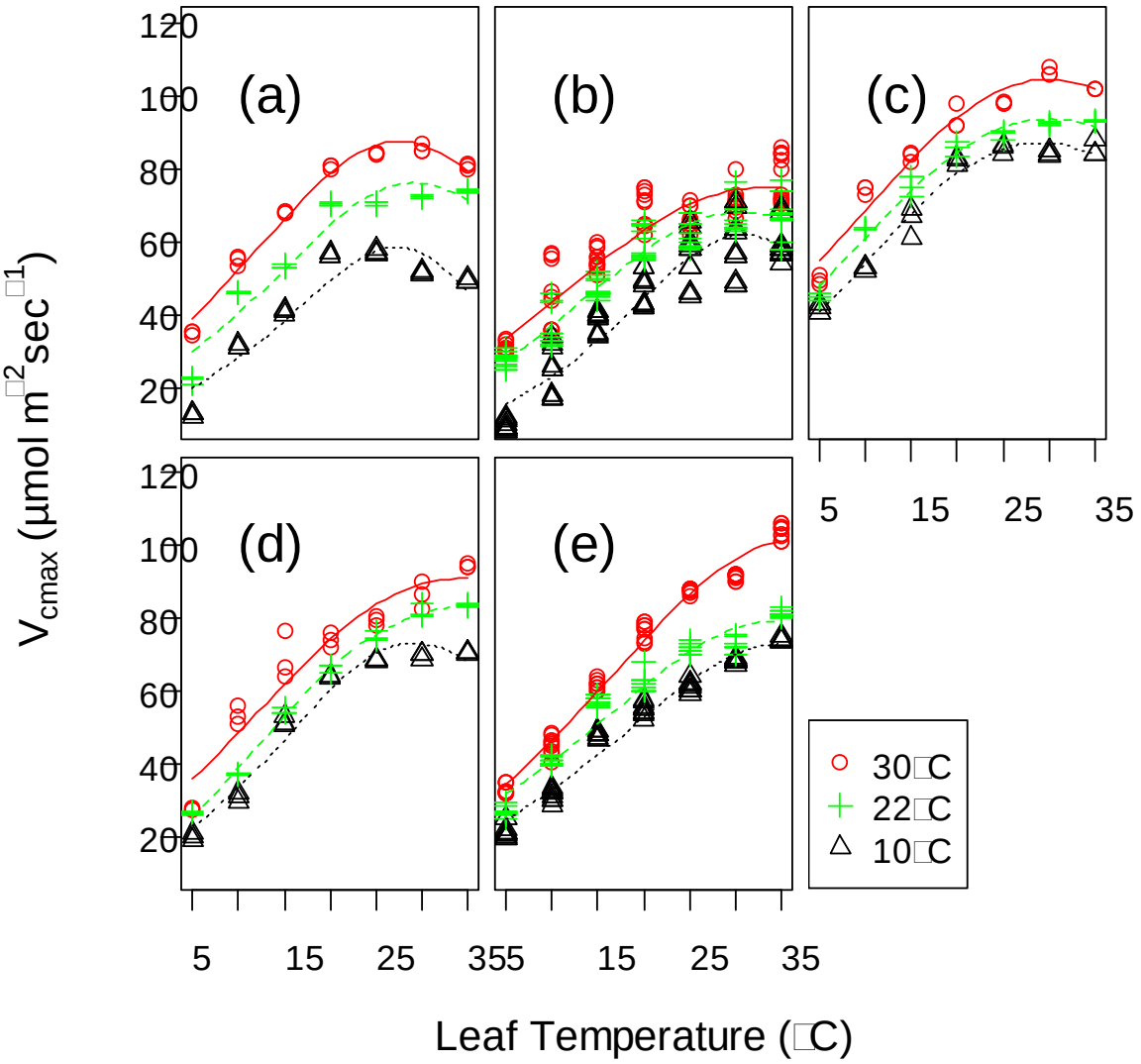


Figure 4.6 Photosynthetic responses of V_{cmax} to leaf temperature

Photosynthetic temperature responses of V_{cmax} at three day/night temperatures: 30/16 (o), 22/12 (+) and 10/5 ^{0}C (Δ) and seven leaf temperatures (5, 10, 15, 20, 25, 30 and 35^{0}C) for (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia* (d) *E. fastigata* and (e) *Sequoia sempervirens*. Lines show fit of Equation 3.7

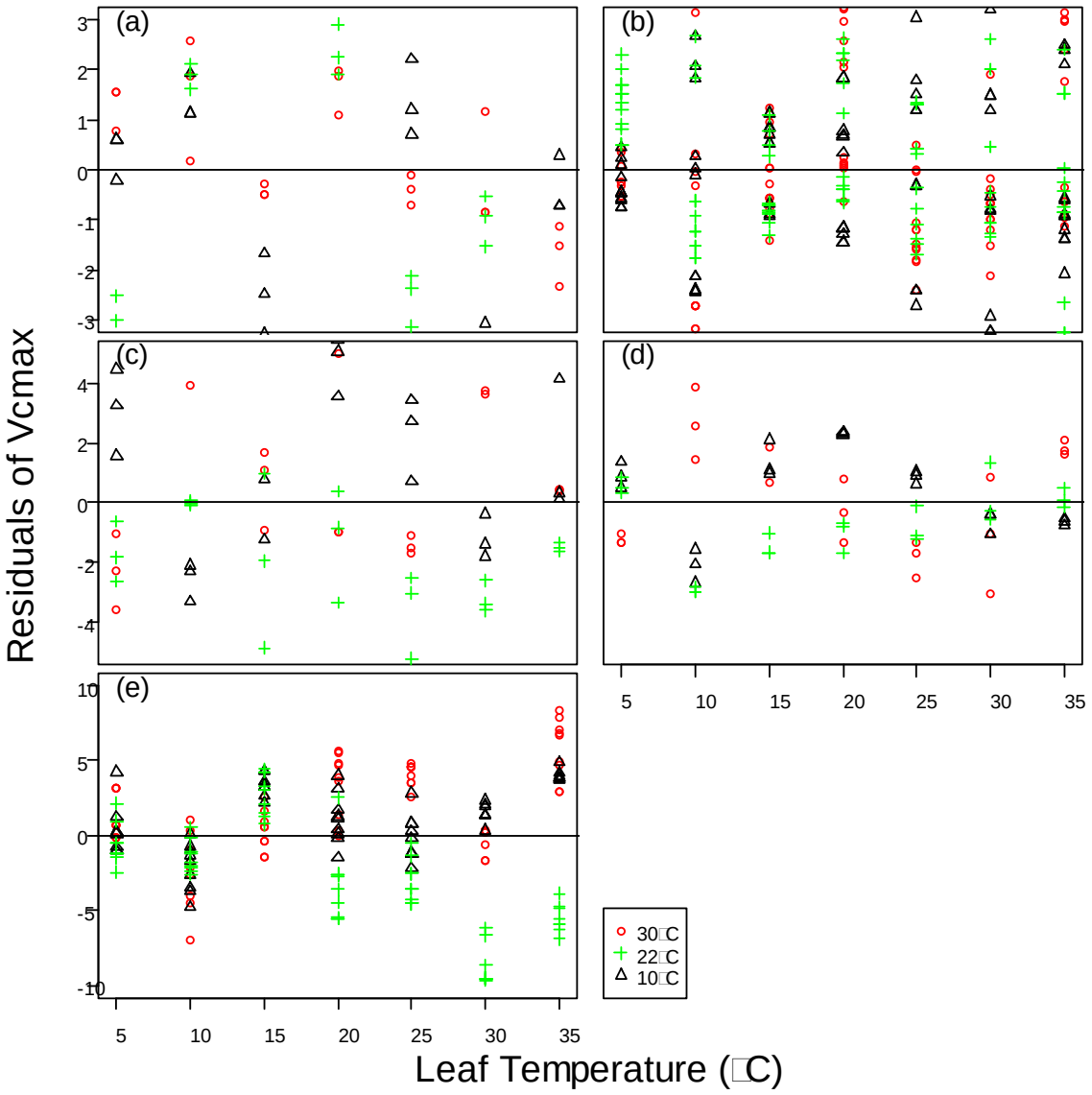


Figure 4.7 Residuals of a model of V_{cmax} against leaf temperature

Residuals of a model of V_{cmax} plotted against leaf temperature at ambient CO_2 and day/night temperatures of 30/16 (o), 22/12 (+) and 10/5^{0}C (Δ) for (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia*, (d) *E. fastigata* and (e) *Sequoia sempervirens*

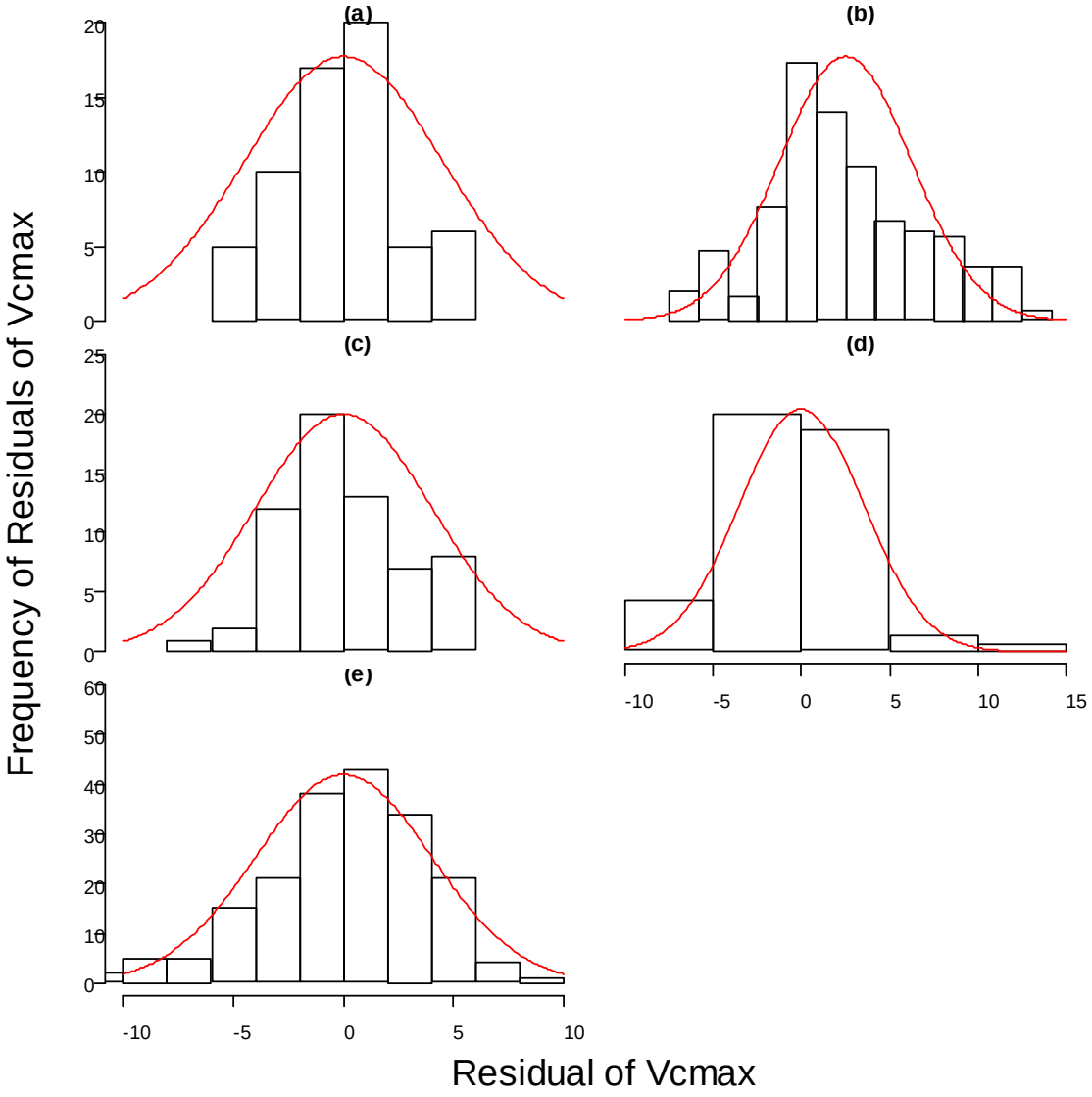


Figure 4.8 Frequency of residuals of a model of V_{cmax} against leaf temperature

Frequency distribution of residuals of a model of V_{cmax} plotted against leaf temperature for (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia*, (d) *E. fastigata* and (e) *Sequoia sempervirens* at ambient CO_2 and day/night temperatures

T_{growth} had a significant effect on the entropy term (S_v) for V_{cmax} ($F_{1,\ 9}$ = 642.41, r^2 = 0.9863, p< 0.00904) but the effect of species had an insignificantly affect on S_v ($F_{4,\ 9}$ = 1.0504, r^2 = 0.9863, p < 0.4338). S_v decreased significantly with increasing T_{growth} for all the species (Figure 4.12 a).

Activation energy for V_{cmax} (H_{av}) increased with increasing T_{growth} (Figure 4.12a) and T_{growth} had a significant effect on it ($_{F1,\ 9}$ = 263.105, r^2 = 0.9795, p < 0.001) with values ranging from 49 to 68, 40 to 58, 43 to 62, 36 to 54 and 36 to 49 kJ mol^{-1} for *E. argophloia*,

E. bosistoana, *E. fastiagata*, *E. globoidea* and *Sequoia sempervirens* respectively with an average of 59, 50, 52.2, 45 and 42ºC for *E. argophloia*, *E. bosistoana*, *E. fastiagata*, *E. globoidea* and S*equoia sempervirens* respectively (Table 4.2). Species significantly affected H_{av} ($F_{4, 9}$ = 37.934, r^2 0.9795, $p < 0.001$). H_{av} of *E. bosistoana* did not differ significantly ($p = 0.431$) from that of *E. globoidea* and that of *E. fastigata* did not differ significantly from that of *Sequoia sempervirens* ($p = 0.271$). All other species differed significantly in their H_{av} ($p < 0.01$).

Deactivation energy of V_{cmax} (H_{dv}) decreased significantly with increase in T_{growth} (F1, 9 = 76.47, r^2 = 0.855, p = 0.00207) (Figure 4.12c) and species also had significantly affect it ($F_{1, 9}$ = 15.38, r^2 0.855, p = 0.00046) and the values ranged from 226 to 246, 211 to 213, 209 to 224, 197 to 218 and 206 to 227 kJ mol^{-1} for *E. argophloia*, *E. bosistoana*, *E. fastiagata*, *E. globoidea* and *Sequoia sempervirens* respectively with an average of 232, 213, 216, 207 and 216 kJ mol^{-1} for *E. argophloia*, *E. bosistoana*, *E. fastiagata*, *E. globoidea* and *Sequoia sempervirens* respectively (Table 4.2). H_{dv} of *E. argophloia* varied significantly from those of *E. bosistoana* ($p = 0.019$), *E. fastigata* (p=0.046) and *E. globoidea* ($p = 0.0019$) but all other species were not significantly different (p =0.0874).

4.3 Temperature responses of J_{max}

The mean values of J_{max} increased significantly with increasing T_{growth} ($F_{1, 9}$ = 61.192, r^2 = 0.9285, $p < 0.001$) and leaf temperature ($p < 0.001$) and species had a significant effect on it ($F_{4, 9}$ = 13.925, r^2 = 0.9285, $p < 0.00068$). J_{max} increased to an optimum leaf temperature and then declined. *E. argophloia* had the highest mean J_{max} value (191.9 ± 9.6 $\mu molm^{-2}s^{-1}$) and *E. globoidea* had the lowest (147.8 ± 7.4$\mu molm^{-2}s^{-1}$) at T_{gowth} 30/16ºC. J_{max} of *E. argophloia* did not differ significantly from that of *E. fastigata* ($p = 0.88$) and that of *E. bosistoana* did not differ significantly from neither *E. globoidea* ($p = 0.99$) nor *Sequoia sempervirens* ($p = 0.9281$). Also, *E. globoidea* and *Sequoia sempervirens* did not differ significantly ($p = 0.88$) in J_{max} but all other species did ($p < 0.001$).

The optimum temperature of J_{max} was significantly affected by T_{growth} ($F_{1, 9}$ = 7.3341, r^2 = 0.8497, p = 0.024) and species ($F_{4, 9}$ = 0.8894, r^2 = 0.8497, p = 0.00168). *E. argophloia* differed significantly from *E. bosistoana* ($p = 0.039$) in the T_{opt} of J_{max} and *E. bosistoana* also differed significantly from *Sequoia sempervirens* ($p = 0.00115$) whiles *E. fastigata* differed from *Sequoia sempervirens* ($p = 0.011$). The remaining species did not differ

significantly (p = 0.468). T_{opt} of J_{max} for *E. bosistoana*, *E. globoidea*, *E. argophloia*, *E. fatigata* and *Sequoia sempervirens* grown at 30/16ºC were 28, 31, 29, 28 and 35ºC with 27, 29, 29, 28 and >31ºC and 24, 28, 29, 27 and 31 for plants grown at 22/12 and 10/5ºC respectively.

J_{max} ranged between 119 - 214, 46.3 – 179, 63.4 - 203.79, 30.2, - 176 and 72 - 106.3 µmol electron m^{-2} s^{-1} for *E. argophloia*, *E. bosistoana*, *E. fastigata*, *E. globoidea* and *Sequoia sempervirens* respectively. J_{max} increased exponentially with increasing leaf temperature (Figure 4.9). Low values of J_{max20} were recorded at T_{growth} 10/5ºC and for *E. bosistoana*.

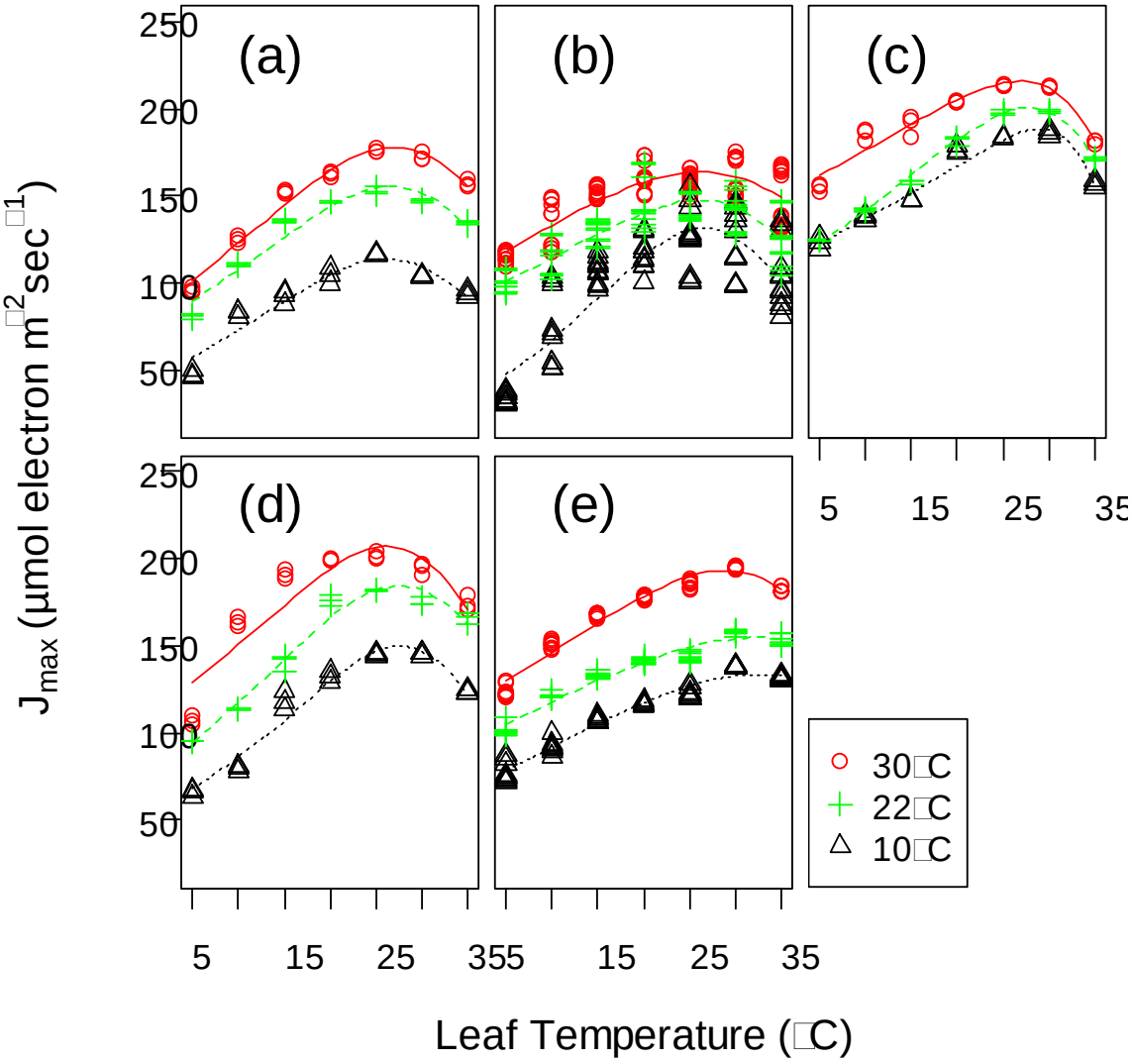


Figure 4.9 Photosynthetic responses of J_{max} to leaf temperature

Photosynthetic temperature responses of J_{max} at three day/night temperatures 30/16 (o), 22/12 (+) and 10/5 ^{0}C (Δ) and seven leaf temperatures (5, 10, 15, 20, 25, 30 and 35 ^{0}C) for (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia* (d) *E. fastigata* and (e) *Sequoia sempervirens*. Lines show fits of Equation 3.8

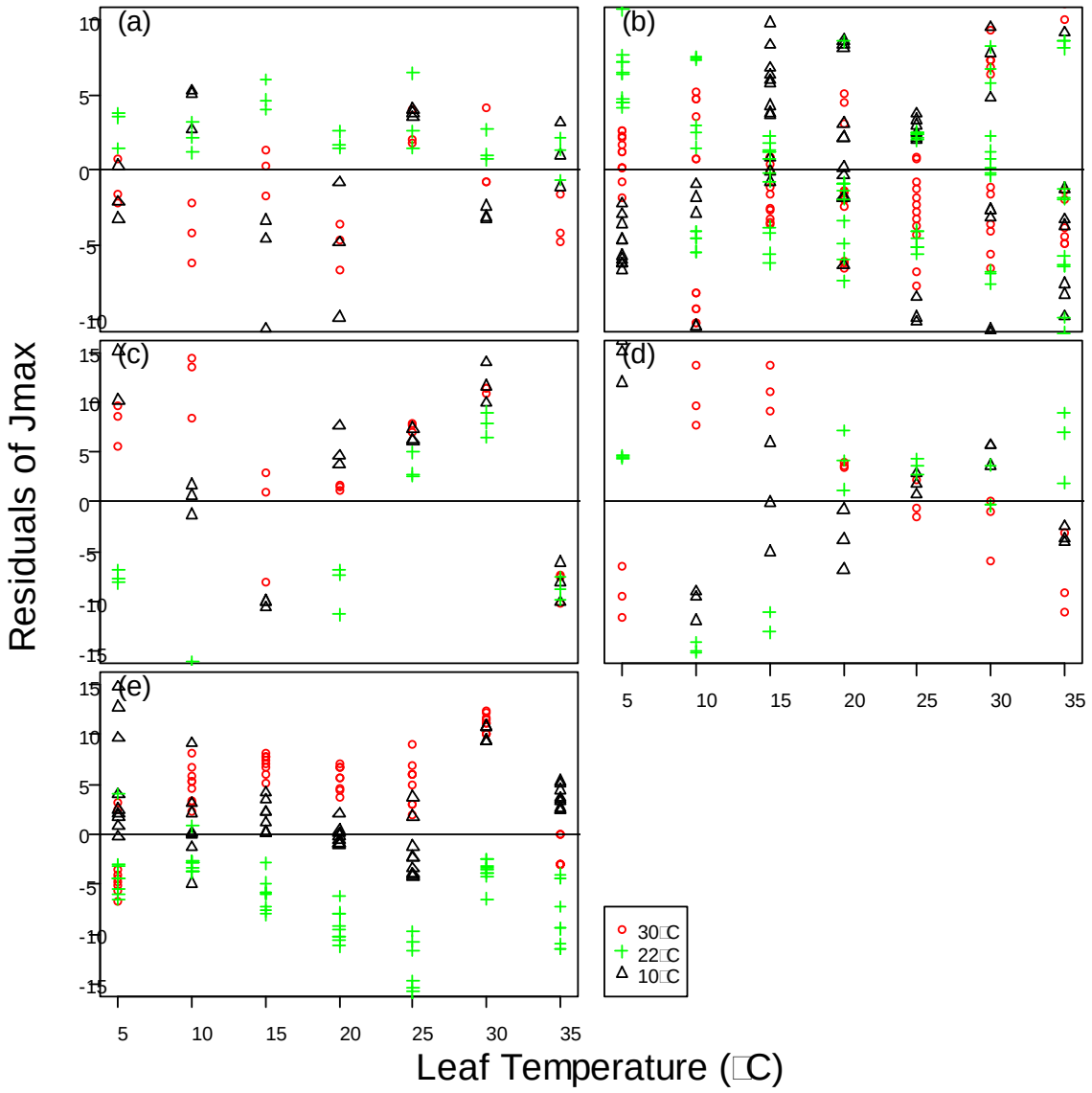


Figure 4.10 Residuals of a model of J_{max} against leaf temperature

Residuals distribution for J_{max} gainst leaf temperature for (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia*, (d) *E. fastigata* and (e) *Sequoia sempervirens* at ambient CO_2 and day/night temperatures of 30/16 (o), 22/12 (+) and 10/5^{0}C (Δ)

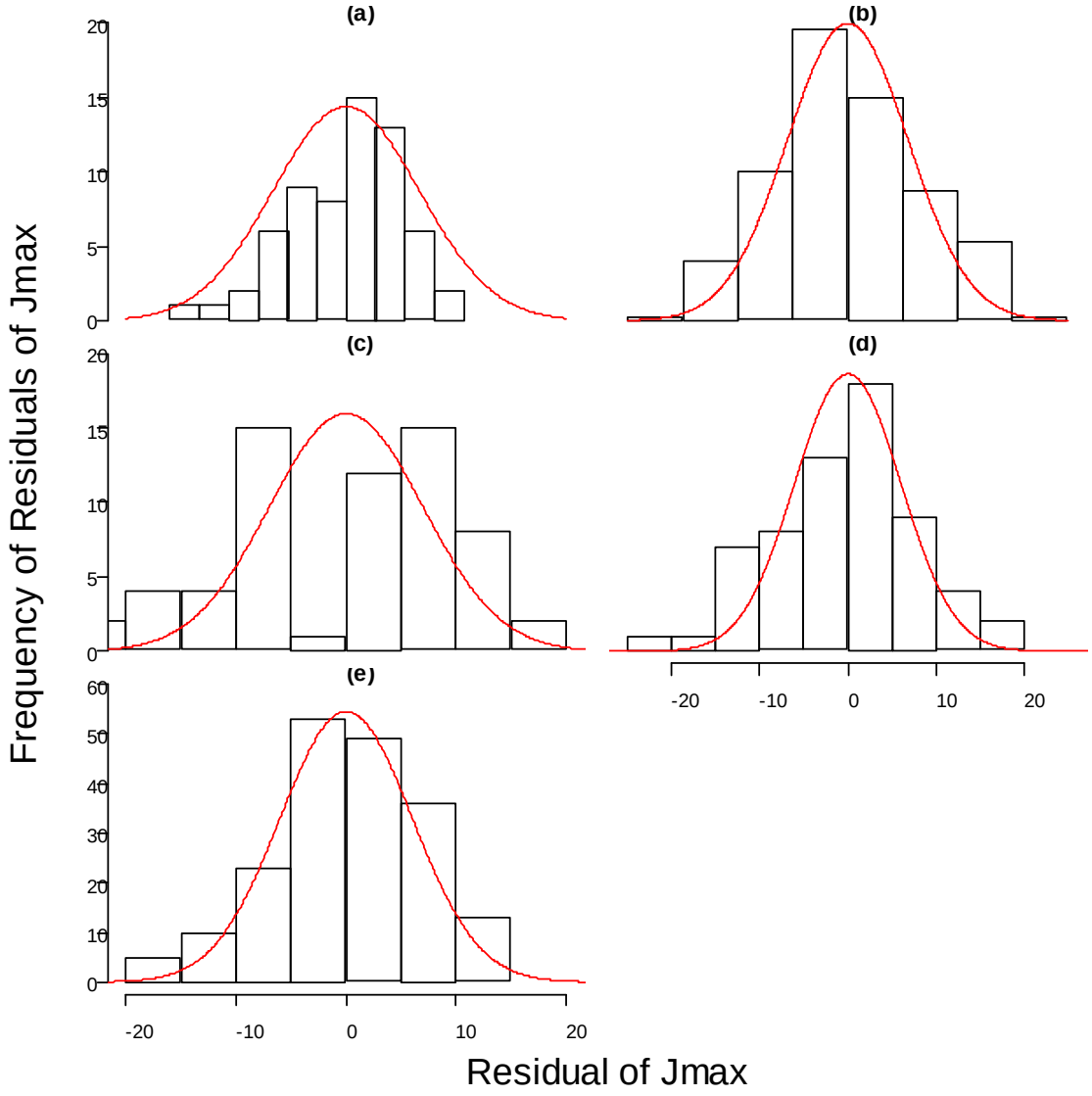


Figure 4.11 Frequency of residuals of a model of J_{max} against leaf temperature

Residuals distribution for J_{max} gainst frequency of the residuals (a) *E. bosistoana*, (b) *E. globoidea*, (c) *E. argophloia*, (d), *E. fastigata* and (e) *Sequoia sempervirens* at ambient CO_2 and day/night temperatures

T_{gowth} had a significant effect on the entropy term, S_J, for J_{max} ($F_{1, 9}$ = 571.788, r^2 =0.7815, $p < 0.001$) but species did not significantly affect S_J ($F_{4, 9}$ = 0.1674, r^2 = 0.7815, p = 0.9496). S_J decreased significantly with increasing T_{gowth} for J_{max} for all the species (Figure 4.12f)

The activation energy of J_{max} (H_{aJ}) decreased with increasing T_{growth} (Figure 4.12b) and T_{growth} significantly affected it ($F_{1, 9}$ = 98.486, r^2 = 0.943 $p < 0.001$). The range of activation energies values for different species were, 41 to 64, 43 to 56, 41 to 56, 34 to 52

and 34 to 45 μmol electrons m^{-2} s^{-1} for *E. argophloia, E. bosistoana, E. fastiagata, E. globoidea* and *Sequoia sempervirens* respectively with an average of 53, 49, 47, 40 and 40 μmol electrons m^{-2} s^{-1} for *E. argophloia, E. bosistoana, E. fastiagata, E. globoidea* and *Sequoia sempervirens* respectively (Table 4.2). The effect of species was significant on H_{aJ} ($F_{4, 9}$ = 12.612, r^2 0.943, p < 0.00098). H_{aJ} of *E. argophloia* differed significantly from those of *E. globoidea* (p = 0.0075) and *Sequoia sempervirens* (p= 0.0085) and that of *E. bosistoana* differed significantly (p = 0.0074) from that of *Sequoia sempervirens* with *E. fastigata* differing from *Sequoia sempervirens* (p = 0.033). All other species did not differ significantly (p = 0.078) in H_{aJ}.

Deactivation energy of J_{max} (H_{dJ}) significantly decreased with increasing T_{growth} ($_{F, 9}$ p = 16.617, r^2 = 0.7916, p = 0.0027) (Figure 4.12d) and the values ranged from 227 to 254, 207 to 217, 225 to 243, 186 to 229 and 205 to 228 for *E. argophloia, E. bosistoana, E. fastiagata, E. globoidea* and *Sequoia sempervirens* respectively with an average of 235, 213.7, 235.9, 214 and 219 for *E. argophloia, E. bosistoana, E. fastiagata, E. globoidea* and *Sequoia sempervirens* respectively (Table 4.2). Species significantly affected H_{dJ} ($F_{4, 9}$ = 4.391, r^2 = 0.791, p = 0.03). However, there were no significant differences in H_{dJ} of any of the species (p > 0.05).

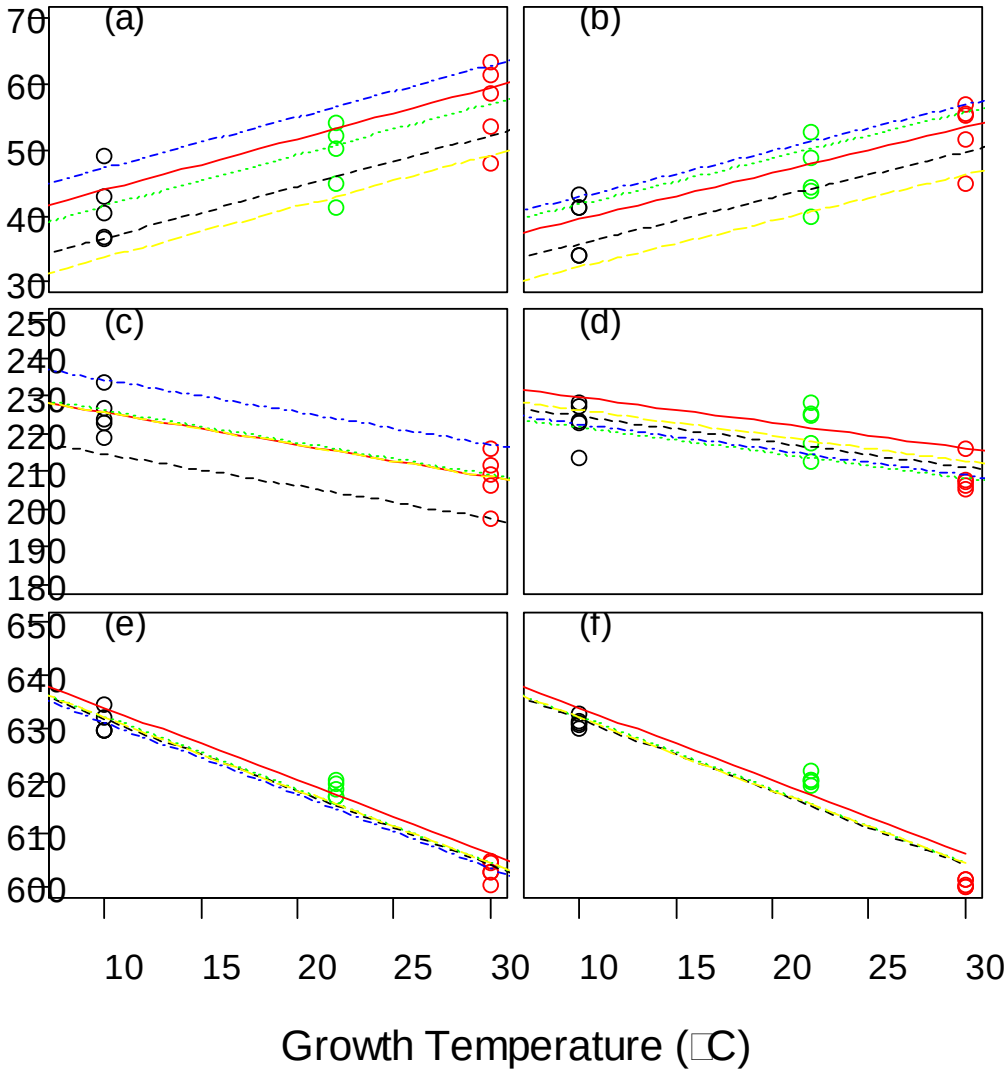


Figure 4.12 Graphs of ΔH and ΔS of J_{max} and V_{cmax} with growth temperature

Plots of (a) the activation energy of V_{cmax} kJ/mol, (b) the activation energy of J_{max} kJ/mol, (c) Deactivation energy of V_{cmax} kJ/mol, (d) Deactivation energy of J_{max} kJ/mol , (e) entropy of V_{cmax} kJ/mol and (f) entropy of J_{max} kJ/mol against growth temperature for *E. bosistoana* (green), *E. globoidea* (black), *E. argophloia* (blue), *E. fastigata* (red) and *Sequoia sempervirens* (yellow).

Table 4.2 Mean values of ΔH and ΔS of J_{max} and V_{cmax}

Mean values of the photosynthetic parameters describing the response of leaf photosynthetic capacity to temperature for *E. bosistoana*, *E. globoidea*, *E. argophloia*, *E. fastigata* and *Sequoia sempervirens* seedlings grown in growth cabinets at three growth temperatures. Values of the activation energy (H_a) and deactivation energy (H_d) are in $kJmol^{-1}$ and the entropy term (S) are in $kJmol^{-1}$ whiles T_{growth} is in ºC

Species	T_{growth}	H_{aj}	H_{dj}	Sj	H_{av}	H_{dv}	S_v
E. argophloia	30/16	63.91	227.34	636.21	67.34	225.71	629.21
	22/12	52.62	225.04	648.23	60.23	226.02	631.52
	10/5	41.34	253.47	658.4	49.16	245.41	642
E. bosistoana	30/16	55.31	207.84	629.24	58.64	211.65	569.7
	22/12	48.86	215.56	631.8	50.2	216.64	578.3
	10/5	43.3	217.81	632.05	40.450	212.9	599.52
E. fastigata	30/16	55.43	225.81	641.5	61.31	209.18	624.8
	22/12	44.37	238.21	636.35	52.28	216.289	631.41
	10/5	41.25	243.74	637.9	43.06	223.9	634.5
E. globoidea	30/16	51.64	186.17	626.4	53.49	197.3	624.47
	22/12	43.86	227.63	632.1	44.89	200.4	627.12
	10/5	34	228.20	637.2	36.45	218.78	629.09
S. sempervirens	30/16	45	205.16	628	48.01	206.19	622.73
	22/12	40	224.67	632.3	41.19	223.41	629.12
	10/5	34	227.08	641.6	36.72	226.57	629.72

4.4 Temperature responses of J_{max}/V_{cmax}

T_{growth} did not significantly affect the ratio of J_{max} to V_{cmax} ($F_{1, 9}$ = 3.5274, r^2 = 0.6717, p = 0.093) but species did ($F_{1, 9}$ = 3.7214, r^2 = 0.6717, p = 0.047). The ratio of J_{max} to V_{cmax} decreased with increase in leaf temperature (Figure 4.13).

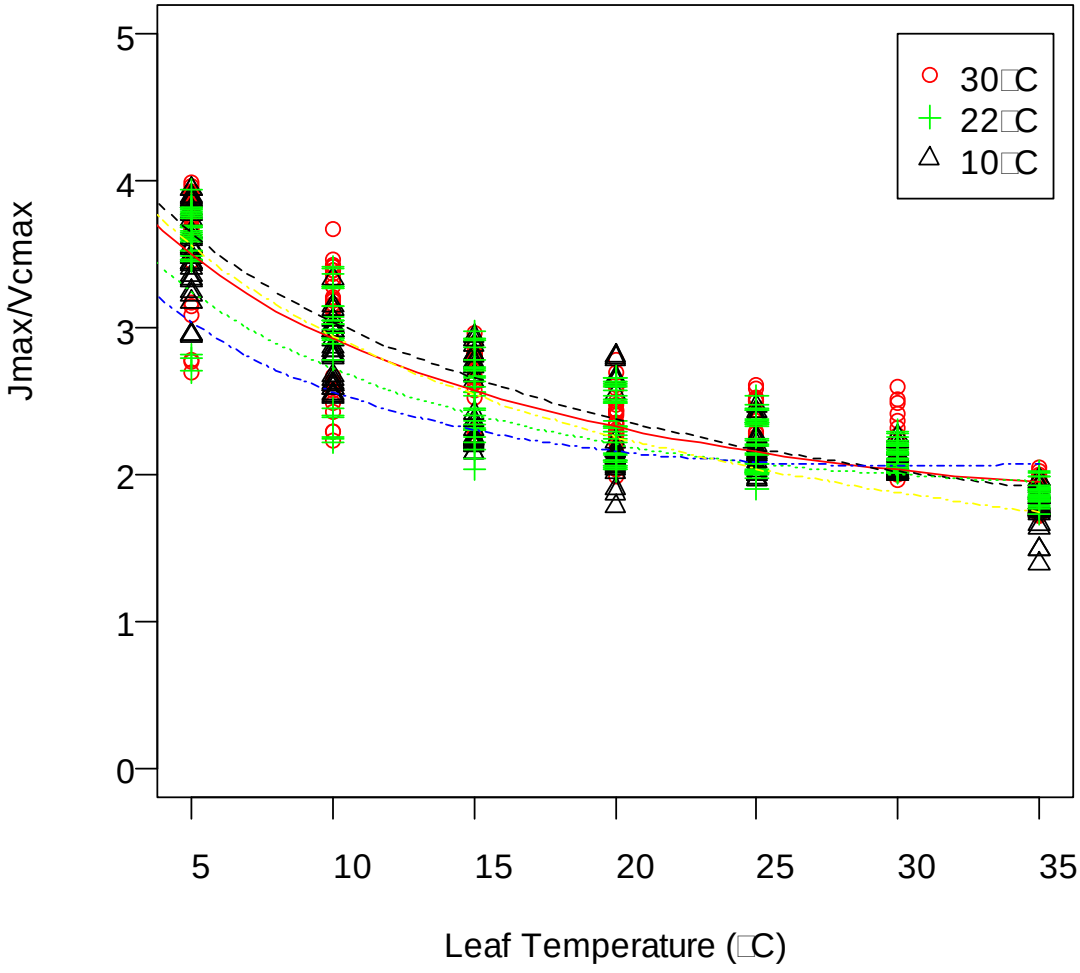


Figure 4.13 Relationship between the ratio of J_{max} and V_{cmax} with leaf temperature

Relationship between the ratio of J_{max} and V_{cmax} with leaf temperature of (black line) *E. globoidea*, (red line) *E. fastigata*, (blue line) *E. argophloia*, (green line) *E. bosistoana* and (yellow line) *Sequoia sempervirens* grown at three day/night temperatures 30/16 (o), 22/12 (+) and 10/5^{0}C (Δ).

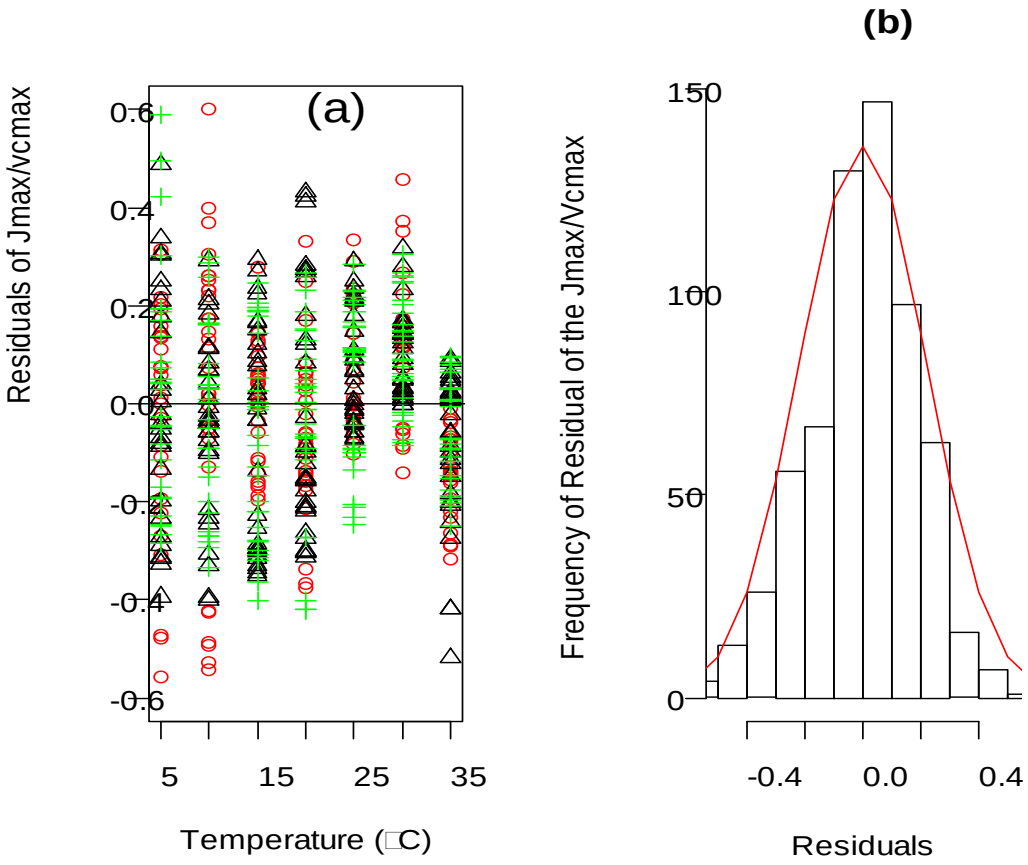


Figure 4.14 Residual plots of a model of J_{max}/V_{cmax} against leaf temperature

(a) Residuals of a model of the ratio of J_{max}/V_{cmax} plotted against leaf temperature (b) test of normality of the model of T_{opt} plotted against T_{growth}

4.5 Effects of temperature on the relationship between J_{max} and V_{cmax}

There was a positive correlation between J_{max} and V_{cmax} (Figure 4.15) and growth temperature ($t_{1,623}$ = 23.558, r^2 = 0.8862, $p < 0.001$) and species (*E. argophloia* $t_{4, 623}$ = 22.554, $p < 0.001$; *E. bosistoana*: $t_{4, 623}$ = -10.830, $p < 0.001$; *E. fastigata* $t_{4, 618}$ = -2.481, $p < 0.0134$; *E. globoidea* $t_{4, 618}$ = -8.857, $p < 0.001$; *Sequoia sempervirens* $t_{4, 623}$ = 23.558, $p < 0.001$) significantly affected the relationship.

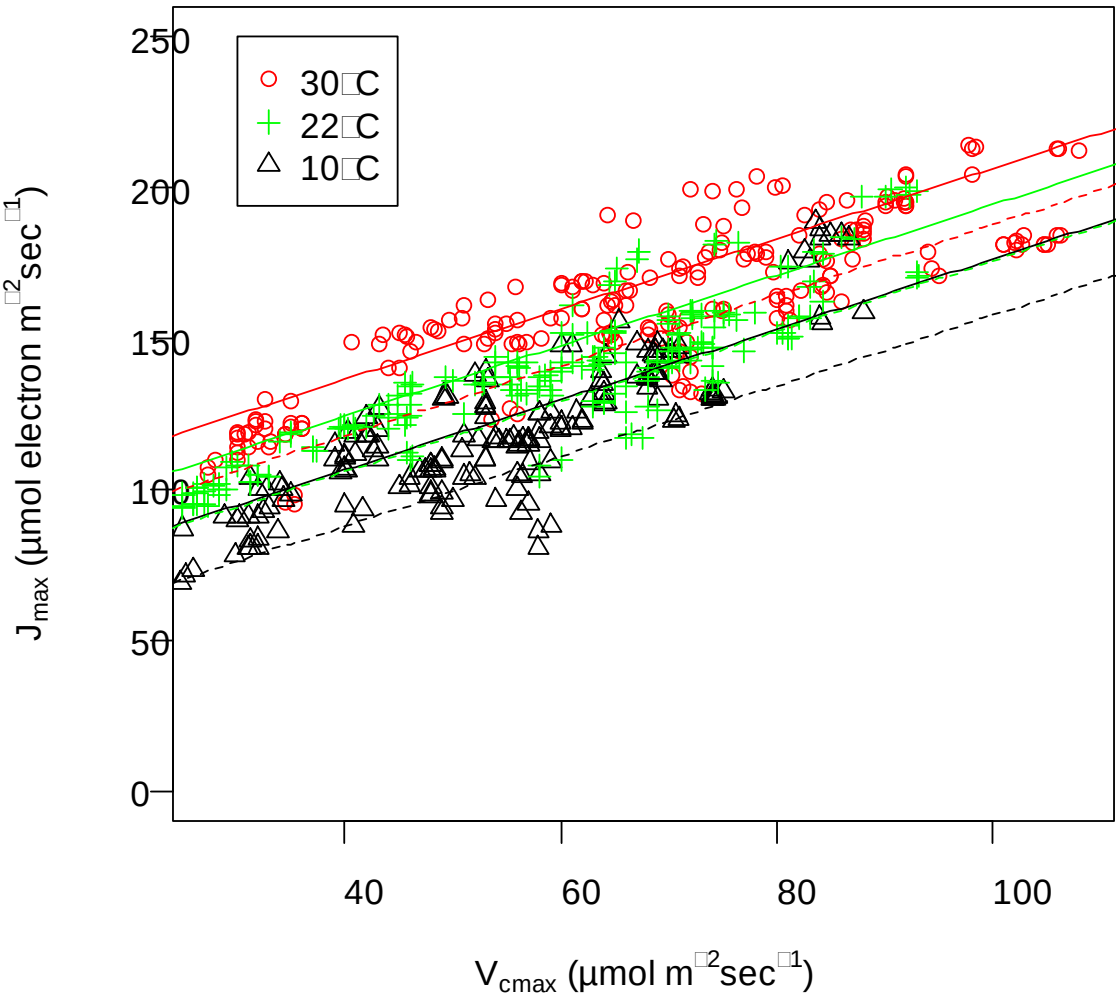


Figure 4.15 Relationship between J_{max} and V_{cmax}

Relation between the maximal rate of electron transport driving regeneration of RuBP (J_{max}) and the maximal rate of Rubiscos carboxylation (V_{cmax}) of *E. globoidea*, *E. fastigata*, *E. argophloia*, *E. bosistoana* and *Sequoia sempervirens* grown at three day/night temperatures 30/16 (o), 22/12 (+) and 10/5^{0}C (Δ). Dotted lines represent *E. bosistoana* while solid lines show *E. fastigata*.

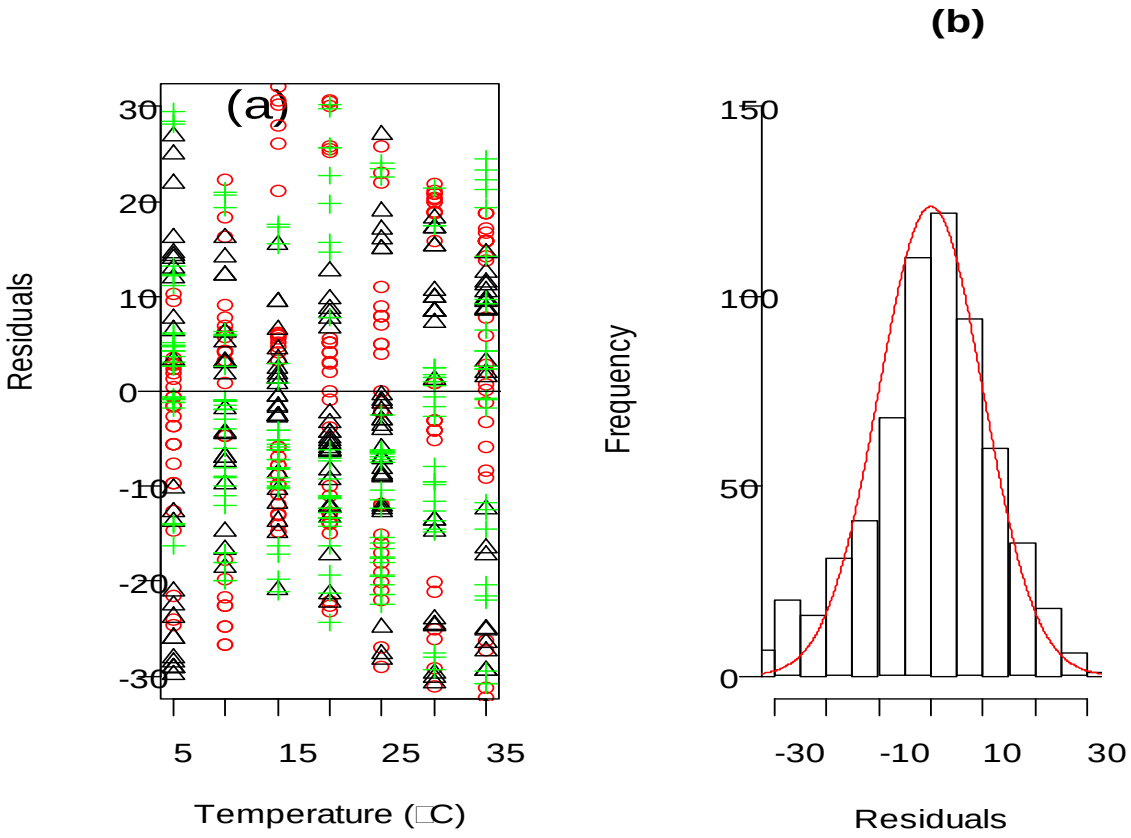


Figure 4.16 Test of normality of a model of J_{max} against V_{cmax}

(a) Residuals of a model of J_{max} plotted against V_{cmax} (b) test of normality of model of J_{max} plotted against V_{cmax}

Table 4.3 Mean values of photosynthetic parameters

Mean of the maximum rate of carboxylation (V_{cmax}), the maximum rate of electron transport (J_{max}), J_{max}/V_{cmax}, the rate of CO_2 assimilation (A) in $\mu molm^{-2}s^{-1}$ and the range of J_{max}/V_{cmax} measured in *E. argophloia, E. bosistoana, E. fastigata, E. globoidea and Sequoia sempervirens* grown at 30/16, 22/12 and 10/5ºC. Standard errors are given in parentheses.

Species	T_{growth}	J_{max}	V_{cmax}	A	J_{max}/V_{cmax}	J_{max}/V_{cmax} limit
	30/16	191.9 (9.6)	86.9 (4.4)	7.5 (0.4)	2.3 (0.1)	3.2 - 1.8
E. argophloia	22/12	167.7(8.4)	77.7 (3.9)	5.3 (0.3)	2.2 (0.01)	2.8 – 1.8
	10/5	159 (8)	71.9 (3.6)	3 (0.2)	2.3 (0.2)	3.0 – 1.8
	30/16	149 (7.5)	70 (4)	7.2 (0.4)	2.2 (0.1)	2.8 – 1.9
E. bosistoana	22/12	130 (6.5)	58.4 (3)	5.4 (0.1)	2.4 (0.1)	3.8 – 1.8
	10/5	91.8 (4.6)	42.7 (2.1)	3.7 (0.2)	2.4 (0.1)	4.0 – 1.9
	30/16	176 (8.8)	69.2 (3.5)	7.4 (0.4)	2.7 (0.1)	3.9 – 1.8
E. fastigata	22/12	149.7 (7.5)	60.7 (3)	5.3 (0.3)	2.6 (0.1)	3.7 – 1.9
	10/5	115.7 (5.8)	53.6 (2.7)	3 (0.2)	2.3 (0.1)	3.4 – 1.7
	30/16	147.8 (7.4)	59 (3)	7.3 (0.4)	2.7 (0.1)	4.0 – 1.8
E. globoidea	18/12	128.4 (6.4)	52.6 (2.6)	5.5 (0.3)	2.6 (0.1)	3.8 – 1.7
	10/5	98.6 (4.9)	42.5 (2.1)	2.7 (0.1)	2.5 (0.1)	3.9 – 1.4
	30/16	168.9 (8.5)	71.3 (3.6)	7.7 (0.4)	2.8 (0.1)	4.0 – 1.7
S. sempervirens	22/12	135.8 (6.8)	58.9 (3)	5.2 (0.3)	2.5 (0.1)	3.9 – 1.8
	10/5	112.1 (5.6)	51.3 (2.6)	3.5 (0.2)	2.4 (0.1)	3.9 – 1.8

4.6 The distribution of temperature in the cabinets

The modal values of the run of day/night temperature were 9.965/4.531, 21.664/11.722 and 30.457/16.427ºC for the cabinets that were set at 8/5, 18/11 and 30/17ºC respectively and the exact distribution of the temperature in the cabinets is shown in Figure 4.17.

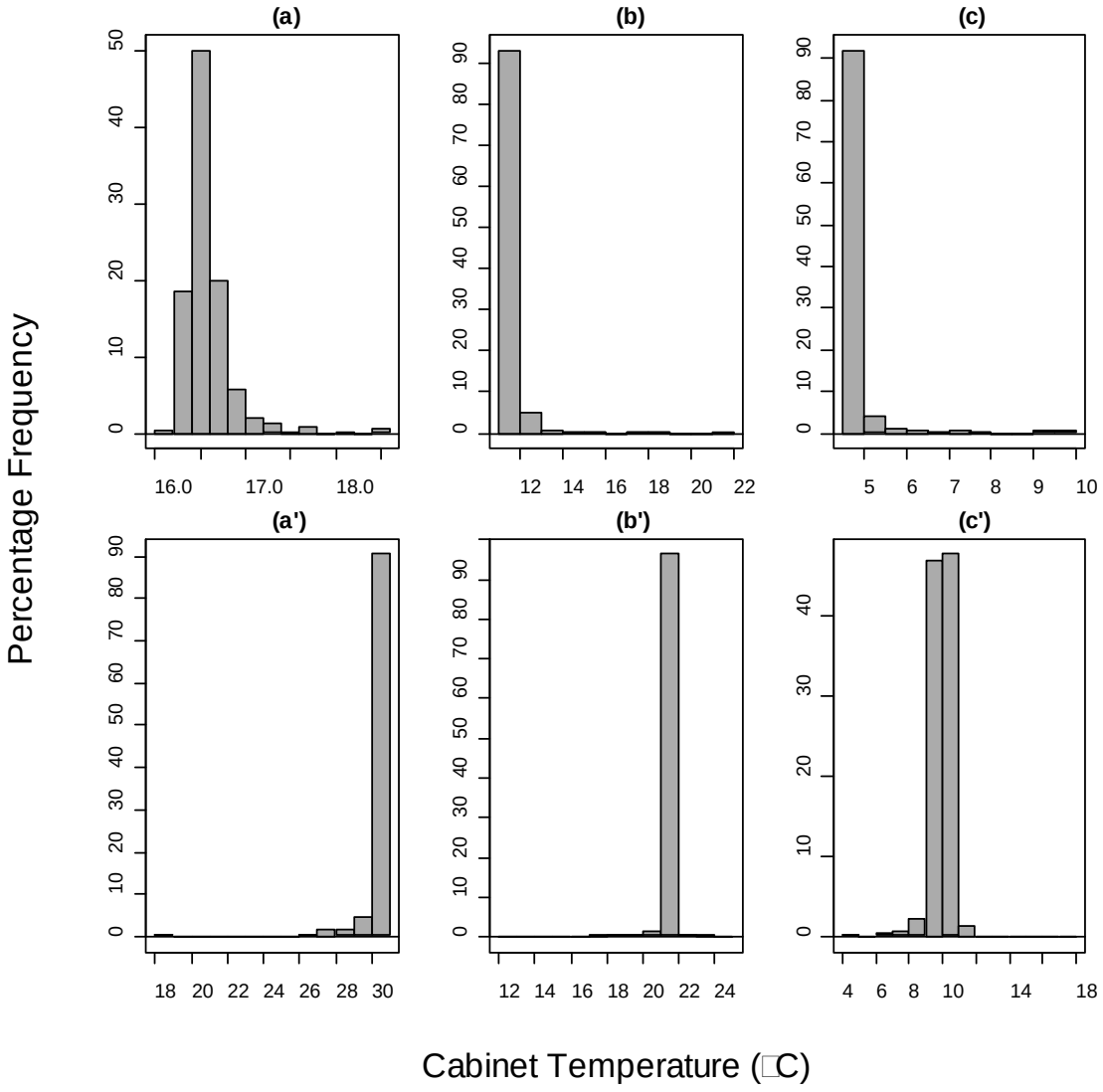


Figure 4.17 Temperature distribution in cabinets

Histogram of percentage frequency distribution of temperature against cabinet temperature (a'/a) 30/17, (b'/b) 18/11 and (c'/c) 8/5ºC

Chapter 5 **Discussions**

Research on acclimation to temperature for eucalypts has concentrated on a limited number of species and temperature ranges. The findings of this research are interesting because not only had the species been little studied but also a wider range of short term temperatures were considered for gas exchange measurement than previously (Battaglia et al. 1996; Lewis et al. 2011; Ngugi et al. 2003a; Ow et al. 2008b). Including *Sequoia Sempervirens* provided both an interesting contrast and also some physiological parameters for a species that has not been studied in this fashion previously, and this permitted an examination of key parameters required for estimating impacts of temperature variation in models such as the 3-PG model of forest production.

5.1 Temperature responses of photosynthesis

The dependence of V_{cmax} on temperature (Figure 4.6) could partly explain net photosynthesis because the activation energy of V_{cmax} (H_{aV}) increased with an increase in optimal temperature (T_{opt}) for net photosynthesis as illustrated by the model of Farquhar et al. (1980). However, increases in temperature activate photorespiration and mitochondria respiration with a reduction of CO_2 solubility in the stroma and together counteract the rise in Rubisco activity which could reduce net photosynthesis at higher temperatures above 25 to 30^0C (Labate and Leegood 1988). Photosynthetic capacity was lower in plants acclimated to lower temperatures a finding conforming to those of other researchers including Medlyn et al. (2002a), Makino et al. (1994b), Warren (2008), Battaglia et al. (1996) and Ngugi et al. (2003a) . The temperature response curves were smooth and unimodal as described by Sall and Petterson (1994).

In general, photosynthetic acclimation to low temperature has been reported to relate to enzymatic processes that limit photosynthesis whilst the ability of the photosynthetic apparatus to withstand heat contributes positively to their acclimation to higher temperatures (Badger et al. 1982; Berry and Björkman 1980; Pearcy 1977). The increase in T_{opt} and A_{opt} with T_{growth} might be result of greater thermal stability of the photosynthetic apparatus (Pearcy 1977) whilst the restricted assimilation at high leaf temperatures might be due to low ability to produce the needed amount of photosynthetic components or the destruction of the photosynthetic components at high temperatures (Wahida et al. 2007).

Hikosaka (1997) speculated that reallotment of nitrogen between J_{max} and V_{cmax} so that both parameters would be simultaneously limited at ambient temperature could be the reason for photosynthetic temperature acclimation in plants. Also temperature acclimation has been associated with variations in cell-wall conductance to CO_2 (Makino et al. 1994b), the effect of stomata conductance on vapour pressure deficit (Medlyn et al. 2002c) and nitrogen partitioning among photosynthetic components (Wilson et al. 2000). Yamori et al. (2006) reported the significance of growth temperature on the dependence of stomatal conductance (g_i) on temperature and the similarity of the variation to those on photosynthetic rate with growth temperature.

A decrease in net photosynthesis at high leaf temperatures could be evidence of a higher respiration rate of low temperature grown seedlings at high temperatures (Way and Sage 2008a). If this is true, then the high respiration rate could explain why *E. argophloia* and *E. bosistoana* in T_{growth} 10/5ºC when transferred to the T_{growth} 30/16ºC cabinet died within a few days. It could also be reasoned from the photosynthetic response curves (Figure 4.1) that nearly all the species growth at 10/5 ºC had reducing amounts of CO_2 assimilation as leaf temperatures rose to 30ºC and above, and so shifting plants that had grown in low temperature conditions to higher temperature conditions placed them in conditions where their respiration greatly exceeded their photosynthetic capacity.

Respiration was not measured in this study but other researchers have reported higher increases in respiration than photosynthesis at higher temperatures (Ow et al. 2008a; Ow et al. 2008b; Ow et al. 2010), and acclimation of respiration to growth temperature has been reported by Ow et al. (2008a; 2008b) with trees acclimated to high temperature having much reduced increases in respiration with increasing temperature compared to those grown in low temperatures. Also it has been suggested that variations in photosynthetic performance as a result of temperature might be due to intercellular CO_2 concentration (Battaglia et al. 1996).

Plants grown at 30/16 and 22/12ºC had comparatively lower net photosynthesis when measured at 5 and 10ºC leaf temperatures as compared with the performances of those grown at 10/5ºC at the same leaf temperatures whilst when measured at leaf temperatures 30 and 35ºC, plants grown at 30/16 and 22/12ºC performed significantly better than those grown at 10/5ºC. These findings are in accordance with the performance of *E. globulus*

where plants grown at 25/30°C had significantly lower net photosynthetic rates when measured at 10 and 20°C than plants grown at lower temperatures and those at 10/15°C had significantly lower net photosynthetic rates when measured at 30°C than plants grown at higher temperatures as shown in (Figure 2.3) (Battaglia et al. 1996).

The ability of the species studied here to acclimate to both cool and hot temperatures is evidence of adaptation to climatic conditions of their natural habitat and the wide ranges of environmental distribution of some of them (Paton 1980). It has been reported that plants originating from environments with a wide range of temperature are able to acclimate better than those from areas where the environmental temperature is reasonably stable during the active growing season (Berry and Björkman 1980).

E. argophloia inhabits environments with mean lowest and highest temperatures of about 3.7 and 32.3ºC respectively coupled with about ten to fifteen days of frost in a year (Lee et al. 2008) and *E. bosistoana* is native to warm, humid and cooler climates of mean minimum temperature in winter months ranging from 1 to 6^0C and mean maximum of 24 to 29^0C in the summer month. The species experiences about five to forty days of frost in a year (Brooker and Kleinig 1999a). Although *E. fastigata* tolerates frost only moderately it is a cold climate plant and it is capable of withstanding frosty conditions up to about -10ºC. The mean minimum and maximum yearly temperatures in its natural habitat are about -2 and 28ºC respectively (Jurski and Grigg 1996). *E. globoidea* is naturally found in humid and sub-humid environments and tolerates frost slightly (Jones et al. 2008). The results of this study support the idea that photosynthetic acclimation might be one of the mechanisms that helps plants to survive cool winter seasons and hot summer climates (Lindenmayer et al. 2005; Sandvea et al. 2011).

There were similarities in the manner in which the species responded to temperature which might not be too surprising in the case of the eucalypts since most of them have a wide range of distribution throughout Australia and might also have large amount of inherent variability (Bootle 1983; Brooker and Kleinig 1999a). However, *Sequoia sempervirens* is an evergreen species and one characteristic of such species is the investment of time and resources into developing tissues to withstand harsh seasons and by so doing, investing fewer resources into promoting photosynthesis (Herms and Mattson 1999). Some studies have reported temperature threshold stretches to developmental processes including leaf

formation and stem expansion besides photosynthesising in evergreen plants (McGoodwin 2008). However this characteristic was not displayed by the plants used in this research since the photosynthetic efficiency of *Sequoia sempervirens* matched those of the eucalypts and at T_{growth} 30/16 ºC *Sequoia sempervirens* assimilation rate (11.2μmol$m^{-2}s^{-1}$) was not substantially different from those of the eucalypt species.

Moreover, because the acclimation of stomatal conductance to temperature also affects photosynthetic rate apart from biochemical processes with similar photosynthetic parameters, leaves may still differ in photosynthetic rate as a result of differences in stomatal conductance which could be caused by internal water stress and external vapour pressure deficit. Stomatal responses have been found to acclimate to the temperature at which plants are grown (Bernacchi et al. 2002).

Ow et al. (2010) reported no clear relationship between nitrogen per leaf area and photosynthesis in pine and poplar but rather attributed variation in phosynthetic parameters to temperature. In this study effects of nitrogen and phosphorus on photosynthetic parameters were insignificant ($p = 0.1468$), corroborating the findings of Ow et al. (2008a; 2008b) but contradicting findings of an interactive effect of P and N on A_{max} (Whitehead et al. 2005). There is a reasonable chance of a type II error in this finding, given the relatively low, but insignificant P value, and so this result should be used with caution.

5.2 Effects of growth temperature on the photosynthetic thermal optimum

The effect of the temperature at which plants were grown (T_{growth}) significantly influenced temperature optima (T_{opt},) and maxima (T_{max}) for photosynthesis in all the five species studied. High T_{growth} lead to high photosynthetic optimal temperatures (T_{opt}) and vice versa which corroborates to previous studies with other species (Berry and Björkman 1980). Although the effects of temperature on stomatal conductance were not modelled in this study, previous research has shown that differences in T_{opt} with changes in T_{growth} and leaf temperatures are partly due to changes in stomatal conductance at different T_{growth} (Bernacchi et al. 2002). Increasing T_{opt} for net photosynthesis at higher T_{growth} has been reported by previous studies (Badger et al. 1982; Berry and Björkman 1980; Hikosaka et al. 1999; Slatyer and Morrow 1977; Yamori et al. 2005).

The difference in T_{opt} for plants that were grown at a day temperature of 10 and those of 22 and 30ºC were 5 and 7, 3 and 6, 4 and 6, 2 and 5 and 3 and 5ºC for *E. globoidea, E.*

fastigata, E. argophloia, E. bosistoana and *Sequoia sempervirense* respectively. Although the design of the experiment did not actually replicate T_{growth} because different growth cabinets were used for each T_{growth}, it could be seen that at different T_{growth}, plants responded differently to temperature variation, and given the regular patterns of behaviour across the three temperature regimes there is no reason to believe that the results were significantly influenced by variations in other conditions within particular growth cabinets. In addition, monitoring of conditions within the cabinets showed that they did not differ significantly in light levels, and both soil characteristics and watering were consistently applied between cabinets.

It has been reported that the T_{opt} for net photosynthesis of *E. globulus* grown in the field increased from 17 to 23ºC as the mean daily temperature increased from 7 to 10ºC whilst in *E. nitens* T_{opt} increased from 14 to 20ºC as the mean daily temperatures increased from 7 to 19ºC (Battaglia et al. 1996). Also, the increase in optimum temperature of *E. argophloia* from 20 to 22°C with respect to increasing day time temperature at which the plants were grown from 22 to 30°C, corroborates a reported increase in optimum temperature of the species as growth temperature increased from 18 to 33°C (Ngugi et al. 2003b).

The results of this current study therefore support evidence of acclimation as reported in many other previous studies for *Pinus taeda* (Teskey and Will 1999), *E. pauciflora* (Slatyer 1977a), *Nothofugus* species (Read and Busby 1990), *Larix decidua Mill*. (Tranquillini et al. 1986), eucalypt species and *Nerium oleanber* (Ferrar et al. 1989), *E. argophloia* and *E. cloeziana* (Ngugi et al. 2003a) and *Quercus crispula* (Hikosaka et al. 2007).

Coefficients of acclimation, α (i.e. the slope of the line relating the T_{opt} for net photosynthesis and $T_{growth)}$ were 0.5, 0.3, 0.4, 0.2 and 0.3 for *E. globoidea, E. fastigata, E. argophloia, E. bosistoana* and *Sequoia sempervirens* respectively. Ngugi et al. (2003a) reported $\alpha = 0.75$ and 0.59 for *E. argopholia* and *E. cloeziana* respectively. The observed slopes indicate that changes in T_{opt} were associated with changes in T_{growth}. Knowledge from previous research has shown that differences in T_{opt} with changes in growth and leaf temperatures are partly due to changes in stomatal conductance at different T_{growth} (Bernacchi et al. 2002).

5.3 Temperature responses of J_{max} and V_{cmax}

Variations in photosynthetic parameters J_{max} and V_{cmax} at 20ºC were clearly defined by changes in the temperature at which plants were grown (T_{growth}) and leaf temperatures in all the species studied. This finding supports previous research on the relationship of these two photosynthetic parameters with temperature (Ghannaoum et al. 2010; Medlyn et al. 2002b; Ow et al. 2010; Warren 2008). A temperature increase led to a larger increase in V_{cmax} and so J_{max}/V_{cmax} ratio decreased with increasing growth temperature (Figure 4.15) and this may explain why plants grown at higher temperature had higher optimum temperatures of net CO_2 assimilation than lower temperature grown plants. This finding corroborates those of previous research reporting V_{cmax} as being more sensitive to temperature than J_{max} (Bunce 2000; Hikosaka et al. 1999; Yamori et al. 2005).

Deactivation of J_{max} (H_{aJ}) began above 30ºC leaf temperatures for all species of the plants grown at 30/16ºC and the optimum temperature for J_{max} was 25 ≤ 30ºC and it varied significantly with T_{growth} ($P = 0.0027$) and species ($p = 0.03$). However, the rapid acclimation in V_{cmax} might have neutralized the responses of net CO_2 assimilation in some of the species particularly *Sequoia sempervirens* as has be reported previously (Osborne and Beerling 2003).

T_{opt} of V_{cmax} was in the range of 31-35ºC for all the species and it was significantly affected by T_{growth} ($p = 0.007$). Findings of this nature were reported by Badger et al. (1982), Mitchell and Barber (1986), and Yamori et al. (2005). In contrast, Hikosaka et al. (2007) reported no change in optimum temperature of J_{max} and V_{cmax} with changes in T_{growth}. Temperature dependence of rubisco activation in spinach leaves varied with T_{growth} in a study by Yamori et al. (2006). The significant effect of growth temperature on temperature optima of J_{max} and V_{cmax} could be attributed to the ability of the photosynthetic apparatus to withstand higher temperatures (Smith and Dukes 2012; Yamori et al. 2010). Low values of V_{cmax} at low temperatures could be due to inactivation of rubisco, decrease in CO_2 diffusion in old leaves (Hikosaka et al. 1998) or the selective degradation of rubisco.

The optimal temperatures for J_{max} were lower than those for V_{cmax}. They varied at different temperatures at which the plants were grown ($p = 0.024$) and species ($p = 0.001683$). The ranges of J_{max} and V_{cmax} optimal temperature fell in 30 to 38 and 35-41ºC ranges reported

for J_{max} and V_{cmax} respectively (Dreyer et al. 2001; Medlyn et al. 2002b; Robakowski et al. 2002). Robakowski et al. (2002) reported the optimal temperature for V_{cmax} and J_{max} as 36.6 and 33.3^{0}C respectively for silver fir seedling and Ghouil et al. (2003) reported 34 and 33.3ºC for V_{cmax} and J_{max} respectively for cork oak seedlings. Adaptation of the photosynthetic apparatus to changes in heat has been suggested to be the reason for the change in the optimum temperature of V_{cmax} at different growth temperatures (Armond et al. 1978). J_{max} and V_{cmax} are also known to be affected by growth temperature, species, nutrition and the availability of light. Low leaf nitrogen content was reported to lead to low J_{max} and V_{cmax} (Onoda et al. 2005a). The mean values of J_{max} and V_{cmax} (Table 4.3) were within the range reported for 19 hardwood species by (Wullscheleger 1993).

The proportion of nitrogen to rubisco and the electron transport in the thylakoid membrane is useful in determining the rate of photosynthesis but contrary to this theory and some previous research findings N and P did not significantly affect J_{max} and V_{cmax} in this study so it was impossible to use them to interpret the lower photosynthetic capacity at very low leaf temperatures. Temperature affects internal conductance of CO_2 transfers (g_i) and previous research has demonstrated the influence of internal conductance of CO_2 transfers (g_i) on the absolute values of photosynthetic capacity and temperature responses of photosynthesis (Warren and Dreyer 2006). Hence the difference in photosynthetic capacity (A), J_{max} and V_{cmax} at different growth and leaf temperatures could be due to differences in g_i caused by differences in temperature. Mesophyll conductance increased with increasing T_{growth} and leaf temperature and it has been reported to affect V_{cmax} and J_{max}.

The linear relationship between J_{max} and V_{cmax} with a positive slope (Figure 4.15) showed how strongly the two parameters were correlated with each other and the y-intercept was higher in low temperature grown plants than in high temperature grown ones, a situation which might be due to a reduction in H_{aJ} than H_{aV} (Bunce 2000; Dungan et al. 2003; Walcroft et al. 1997). This finding corroborates reports from a number of previous studies (Hikosaka et al. 1999; Kositsup et al. 2009; Wullscheleger 1993; Yamori et al. 2005). H_{aJ} and H_{av} correlated positively with T_{growth} (Figure 4.12a and b) an observation also reported previously (Hikosaka et al. 1999; Onoda et al. 2005a; Yamori et al. 2005). Although there was a significant variation in the H_{av} between species ($p < 0.001$), the pattern was similar for all the species with comparable slopes among them indicating that the relationship could be a universal response to T_{growth}.

H_{aV} and H_{aJ} recorded (Table 4.2) were in the range reported by Medlyn et al. (2002a) for conifers. H_{aV} increased with T_{growth} which is a normal response for C_3 plants (Hikosaka et al. 2006). From the model of Farquhar et al. (1980) an increase in H_{aV} is associated with about 0.54 ºC kj^{-1} mol^{-1} of temperature optimum of the net assimilation at optimal temperature (Hikosaka et al. 2006).

5.4 Temperature responses of J_{max}/V_{cmax}

The ratio of J_{max} to V_{cmax} decreased with increasing leaf temperature in all species studied (Figure 4.13) and the values recorded for individual species (Table 4.3) were in the range reported by Dreyer et al. (2001) and conforms to previous findings reported for *E. saligna* and *E. sideroxylon* by Ghannnoum et al. (2010). The thermal response of J_{max}/V_{cmax} ratio shifted in spinach (Yamori et al. 2005) and *Plantago asiatica* (Hikosaka 2005; Hikosaka et al. 2007; Ishikawa et al. 2007) as a result of changes in the temperature at which the plants were grown (T_{growth}). In this study there was no significant shift in the ratio with respect to changes in T_{growth}. This is in line with a previous study of black spruce (Way and Sage 2008b). Hikosaka et al. (2007) found a significant relationship between H_{aV} and the mean daily temperatures in *Quercus crispula* leaves.

There was no significant correlation between the ratio and T_{growth} ($p = 0.6717$) for any of the species which corroborated findings of Hikosaka et al. (2007) where T_{growth} was found not to have been affected by the ratio in *Quercus crispula* and suggested that the seasonal change in the ratio of J_{max} to V_{cmax} could be associated with age rather than an acclimation effect (Onoda et al. 2005b). These findings on the other hand contradict a number of other findings where ratios of J_{max} and V_{cmax} were reported to correlate with temperature (Han et al. 2004; Onoda et al. 2005a) but many other studies yielded similar observations to those reported here (Hikosaka et al. 1999; Kattge and Knorr 2007; Leuning 2002; Medlyn et al. 2002a; Onoda et al. 2005b; Yamori et al. 2005). This relationship has been attributed to higher H_{aV} than for H_{aJ} (Kositsup et al. 2009) and it is evident in this present study since H_{aV} was higher than H_{aJ} for all the species and (Figure 4.12a and b) other previous studies have reported higher H_{aV} than for H_{aJ} with a corresponding decrease in the J_{max}/V_{cmax} ratio with temperature (Kositsup et al. 2009).

Although the effect of species was significant on the ratio ($p = 0.047$) there were no significant differences between them ($p = 0.457$). The effects of T_{growth} did not significantly

influence the relationship between J_{max}/V_{cmax} and temperature in all the species ($p = 0.093$). J_{max}/V_{cmax} ranged from 3.2 to 1.8, 4.0 to 1.8, 3.9 to 1.7, 4.0 to 1.4 and 4.0 to 1.7 for *E. argophloia, E. bosistoana, E. fastigata, E. globoidea* and *Sequoia sempervirens.* Values of 1.7 to 2.0 and 1.0 to 3.0 were reported for J_{max}/V_{cmax} by Kositup et al. (2009) and Kattge and Knorr (2007) respectively.

It has been reported that changes in J_{max}/V_{cmax} with T_{growth} could be due to variations in temperature dependence of J_{max} and V_{cmax} and/or changes in the distribution of nitrogen in the photosynthetic apparatus (Hikosaka et al. 2006; Onoda et al. 2005b). The characteristic of ratios of J_{max}/V_{cmax} has been postulated to compensate for the limitation of RuBP regeneration on photosynthesis whilst a decrease in the ratio of the two parameters as temperature increases has been attributed to a greater H_{aV} than for H_{aJ} (Onoda et al. 2005b).

All the species used in this research have demonstrated their capabilities to alter the ratio of J_{max} to V_{cmax} in response to temperature which is an indication that they will be able to acclimate to seasonal or geographical changes in temperature. This corroborates the prediction that plant species having higher degrees of plasticity of the ratio of J_{max} to V_{cmax} have more potential to acclimate than those lacking such capabilities (Onoda et al. 2005c) and this plasticity in the ratio of J_{max} to V_{cmax} differed significantly among all the species ($p = 0.047$) as has been reported in previous research (Atkin et al. 2006; Ishikawa et al. 2007; Onoda et al. 2005c).

5.5 3-PG model

The data from this study can be extrapolated to a wider region with different temperatures to provide the basis for calculating growth and yield of eucalypt plantations. 3-PG is a suite of biochemically based photosynthesis models (Coops et al. 2011; Coops et al. 2000; Landsberg and Waring 1997; Nightingale et al. 2008; Waring et al. 2010) that has been used in previous studies for the prediction of net primary productivity (NPP) and facilitates selecting favourable sites for the establishment of specific plant species under present and future global climatic condition (Landsberg and Sands 2011). Landsberg and Coops (1999) have postulated that climate change due to global warming may limit the utility of traditional mensurational growth and yield models partially as a result of pure changes in temperature (Mason 2009; Mason et al. 2008).

The results reported here suggest changes to physiological and "hybrid" growth models such as the 3-PG model (Landsberg and Waring 1997) might be required, particularly if they are applied with short recursive periods. The model of net photosynthesis versus temperature at ambient conditions reported here is the same as the one implemented in the 3-PG model, and the fits using that model form were remarkably good, justifying the use of the equation in 3-PG. However, 3-PG assumes that the same parameters apply across all seasons. If the 3-PG model was used on a daily or weekly time-step, then different optimum and maximum temperature parameters could be calculated based on temperature during the previous month or so. This may be required for a monthly time-step as well, but the extent to which this is so and the times required for acclimation to varying temperatures in the real world require further research. 3-PG assumes the same temperature minima, optima, maxima and levels of maximum quantum efficiency regardless of the season and this may not be appropriate for acclimated plants.

5.6 Limitations and areas for further research

Although the results of this research indicate that growth temperature significantly affected photosynthetic responses to immediate temperature change for all the species, individual plant samples were not subjected to all three growth temperature treatments because there was not ample time to swap all the plants around within the three growth environment chambers. More than 900 hours of Licor time was employed in gathering the data described here, and some initial efforts to swap plants resulted in plant death so a gradual change from lower growth temperatures to higher ones would be required in any future studies of this type. Moreover, a limitation might have arisen if individual plants of the species had different inherent characteristics because only one leaf of each plant was measured but different leaves of the same plant could be responding to temperature differently as a result of differences in stomatal conductance. However, the regular patterns observed across three growth temperatures and the corroboration of these patterns with previous studies suggests that this was not a major limitation of the study reported here.

Some of the plants lasted longer in the cabinets than others before being measured which might have affected the result by introducing significant variations in any of the photosynthetic parameters of the species. Although it was assumed that water and nutrients were non-limiting and all other growth factors were constant for all the species in three

cabinets, there was the occasional mechanical breakdown of the cabinets during the period of data collection which might have affected the results of the experiment. However, the regular patterns observed across the three growth temperatures suggest that this was not a major factor in these results.

The eucalypt seedlings that were used were different in ages of about 3 weeks to 3 months so physiological age could also have affected responses of the species to temperature. Due to all these limitations, the outcome of this research should not be relied on solely and should not be extended to cover other species of the genera used in this study. However, the following research areas are recommended on the physiological characteristic of the species:

(i) Measuring the effect of temperature and vapour pressure deficit on stomatal conductance of the species;

(ii) Measuring the effect of different levels of growth nutrient on the rate and net photosynthesis of the species;

(iii) Measuring boundary layer conductance of the species;

(iv) Measuring the effect of temperature on the rate of respiration of the species;

(v) Measuring the joint influences of temperature and CO_2 on photosynthetic responses of the species;

(vi) Measuring the effect of light on photosynthesis of the species.

Chapter 6 **Conclusions**

The minima, optima and maxima temperatures of net CO_2 assimilation rate varied with baseline temperature (T_{min}: $r^2 = 0.834$, $p < 0.001$; T_{opt}: $r^2 = 0.965$, $p < 0.001$; T_{max}: $r^2 = 0.731$, $p < 0.001$) and to a small extent with species (P=0.0436).

The values for the three parameters for each of the species are as shown below;

E. argophlolia

Temp	Min	Opt	Max
10ºC	4	16	40
22ºC	4	20	40
30ºC	5	22	60

E. bosistoana

Temp	Min	Opt	Max
10ºC	4	16	42
22ºC	5	18	52
30ºC	5	21	57

E. fastigata

Temp	Min	Opt	Max
10ºC	4	14	38
22ºC	4	17	41
30ºC	5	21	45

E. globoidea

Temp	Min	Opt	Max
10ºC	4	14	32
22ºC	5	19	40
30ºC	5	21	44

Sequoia sempervirens

Temp	Min	Opt	Max
10ºC	3	15	42
22ºC	4	18	41
30ºC	5	20	53

The nature of acclimation to long–run (>2 months) growing temperature was similar for all the species but rates of key photosynthetic parameters differed among the species. Maximal carboxylation rate (V_{cmax}) and maximal light-driven electron flux (J_{max}) increased with increases in the temperature at which the plants were grown (J_{max}: $r^2 = 0.9285$, $p < 0.001$; V_{cmax}: $r^2 = 0.8648$, $p < 0.00168$) and with instantaneous changes in leaf temperature

(J_{max}: $r^2 = 0.8923$, $p < 0.001$; V_{cmax}: $r^2 = 0.9476$, $p < 0.001$) for all the species and the effect of species significantly affected J_{max} and V_{cmax} ($p < 0.001$). Mean values of V_{cmax} and J_{max} varied with growth temperature for all species studied and the optimal temperatures of J_{max} and V_{cmax} changed with changes in growth temperature ($p = 0.0010$) and the optimal temperature of V_{cmax} was higher (35 ºC) than that of J_{max} (25 – 30 ºC). Species significantly influenced linear relationships between J_{max} and V_{cmax} for all the species ($r^2 = 0.9244$, $P < 0.001$) in exception of *E. fastigata* ($r^2 = 0.9244$, $P < 0.197$). The temperatures at which the plants were grown did not significantly affect the ratio of J_{max} to V_{cmax} ($r^2 = 0.6717$, $p= 0.093$) but leaf temperatures ($r^2 = 0.8775$, $p < 0.001$) and species ($r2 = 0.67$, $p < 0.047$) did.

CO_2 assimilation increased with an increase in leaf temperature up to an optimal level beyond which further increases in leaf temperature lead to a reduction in assimilation. Photosynthetic capacities of leaves increased with increasing temperature at which the plants were grown ($r^2 = 0.9450$, $p < 0.001$). There was little variation among the species in the ratio of J_{max} to V_{cmax} responses to temperature. (*E. argophloia*: $J_{max} = 2.2\ V_{cmax}$, $r^2 = 0.845$, $p < 0.001$; *E. bosistoana*: $J_{max} = 2.1\ V_{cmax}$, $r^2 = 0.9162$, $p < 0.001$; *E. fastigata*: $J_{max} = 2.4\ V_{cmax}$, $r^2 = 0.8796$, $p < 0.001$; *E. globoidea*: $J_{max} = 2.5\ V_{cmax}$, $r^2 = 0.9632$, $p < 0.001$; *Sequoia sempervirens*: $J_{max} = 2.3\ V_{cmax}$, $r^2 = 0.8732$, $p < 0.001$). Nitrogen and phosphorus did not significantly affect the photosynthetic parameters of any of the species ($p = 0.1468$).

The model used in 3-PG to describe photosynthetic responses to temperature was found to be an excellent fit to data within growth temperatures for all five species. Variation in optimal and maximal temperatures and in maximum rates of photosynthesis between growth temperatures indicated that 3-PG's application of the model may need amendment, especially if the model is used with a small timestep.

The results of this research also:

1. show that 3-PG's temperature modifier function fits exceptionally well to the data and provides some parameterization of temperature model for the species studies
2. suggest that 3-PG should be modified to account for temperature acclimation particularly when it is used in daily mode, as some scientists do
3. show there is a remarkably similar temperature acclimation and photosynthetic responses to temperature among the species and may have an implication in

predicting survival and productivity of the five species in areas outside their natural distribution.

References

Ahuja, M.R. 2009. Genetic constitution and Diversity in four narrow endemic redwoods from the family Cupressaceae. Euphytica 165:5-19.

Ainsworth, E.A., and S.P. Long. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the response of photosynthesis, canopy properties and plant production to rising CO_2. The New Phytologist 165:351-372.

Ainsworth, E.A., and A. Rogers. 2007. The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. Plant, Cell & Environment 30:258-270.

Al-Khatib, K., and G.M. Paulsen. 1999. High-temperature effects on photosynthetic processes in temperate and tropical cereals. Crop Sci 39:119-125.

Ambrose, A.R., C.S. Sillett, and T.E. Dawson. 2009. Effects of tree height on branch hydraulics, leaf structure and gas exchange in California redwoods. Plant, Cell & Environ 32:743-757.

Ambrose, A.R., C.S. Sillett, W.G. Koch, R. Van Oelt, M.E. Antoine, and T.E. Dawson. 2010. Effects of height on treetop transpiration and stomatal conductance in coast redwood (*Sequoia sempervirens*). Tree Physiol:1-13 doi:10.1093/treephys/tpq1064.

Armond, P.A., U. Schreiber, and O. Bjo¨rkman. 1978. Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*: II. Light-harvesting efficiency and electron transport. Plant Physiology 61:411–415.

Armstrong, A.F., M.R. Badger, D.A. Day, M. Barthet, P. Smith, J. Whelan, A.H. Millar, and O.K. Atkin. 2008. Dynamic changes in the mitochondrial electron transport chain underpinning thermal acclimation of leaf respiration. Plant, Cell & Environ 31(31:1156–1169).

Armstrong, A.F., D. Logan, and O.K. Atkin. 2006. On the developmental dependence of leaf respiration: responses to short and long-term changes in growth temperature. Am. J. Bot. 93:1633–1639.

Armstrong, M., A. Redman, and G. Hopewell. 2003. *Eucalyptus argophloia* processing study. DPI, Q. (ed.), Brisbane.

Atkin, O.K., C. Holly, and M.C. Ball. 2000. Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. Plant, Cell & Environ 23:15-26.

Atkin, O.K., I. Scheurwater, and T.L. Pons. 2006. High thermal acclimation potentail of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an aipine congeneric. Global Change Biology 12:500-515.

Atkin, O.K., and M.G. Tjoelker. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Science 8:343–351.

Badger, M.R., O. Björkman, and A. Armond. 1982. An analysis of photosynthetic response and adaptation to temperature in higher plants: temperature acclimation in desert evergreen *Nerium Oleander* L. Plant, Cell & Environ 5:85-99.

Barr, N. 1996. Growing eucalypt trees for milling on New Zealand farms. New zealand Forestry Assiciation Report. 140.

Battaglia, M., C. Beadle, and S. Loughhead. 1996. Photosynthetic temperature response of *Eucalyptus globulus* and *Eucalyptus nitens*. Tree Physiology 16:81-89.

Beerling, D.J., and C.P. Osborne. 2002. Physiological Ecology of Mesozoic Polar Forests in a High CO_2 Environment Annal of Botany 89(3):329-339.

Bernacchi, C.J., A.R. Portis, H. Nakano, S. von Caemmerer, and S.P. Long. 2002. Temperature response of mesophyll conductance. Implications for the determination of Rubisco enzyme kinetics and for limitations to photosynthsis in vivo. Plant Physiology 130:1992-1998.

Berry, J., and O. Björkman. 1980. Photosynthetic response and adaptation to temperature in higher plants Annu Rev Plant Physiology 31:491-543

Bhat, K.M., K.V. Bhat, and T.K. Dhamodaran. 1990. Wood density and fibre length of *Eucalyptus grandis* grown in Kerale, India. Wood Fibre Science 22:54-61.

Bielske, R.L. 1973. Phosphate pool, phosphate transpot and phosphate availability. Annu Rev Plant Physiology 24:225-252.

Billing, W.D., P.J. Godfred, B.F. Chabot, and D.P. Bourque. 1971. Metabolic acclimation to temperature in aretic and alpine ecotypes of Oxyria digyma. Arct. Alp. Res. 3:277-289.

Blakemore, L.C., P.L. Searle, and B.K. Daly. 1987. Methods for chemical analysis of soils in New Zealand. Soil Bureau. 103.

Bond, B.J., and R.A. Farnsworth. 1999. Foliage physiology and biochemistry in the response to light gradients in conifers with varying shade tolerance. Oecologia 120:183-192.

Bootle, K.R. 1983. Wood in Australia: types, properties and uses. McGraw Hill Publishing, Sydney.

Braithwaite, L.W., D.L. Binns, and R.D. Nowland. 1998. The distribution of arboreal marsupials in relation to eucalypt forest types in the Eden (NSW Woodchip Concession Area. Australian Wildlife Research 15:363-373.

Brix, H. 1971. Growth response of western hemlock and Douglas-fir seedlings to temperature regimes during day and night Can.J. Bot. 49:289-260.

Brooker, M.I.H., and D.A. Kleinig. 1999a. Field Guide to *Eucalyptus*, South-Eastern Australia.

Brooker, M.I.H., and D.A. Kleinig. 1999b. Field guide to *Eucalyptus* of southern australia. CSIRO Victoria.

Brown, J.E. 1982. Moarchs of the Mist: The story of Redwood National Park and the Coast Redwood. Redwood Natural History Association.

Bruhn, D., J.J.G. Egerton, B.R. Loveys, and M.C. Ball. 2007. Evergreen leaf respiration acclimates to long-term nocturnal warming under field conditions. Glob. Chang. Biol 13:1216–1223.

Bunce, J.A. 2000. Acclimation of photosynthesis to temperature in eight cool and warm climate herbaceous C_3 species: temperature dependence of parameters of a biochemical photosynthsis model. Photosynth Res 63:59-67.

Bush, D. 2011. Selecting and breeding eucalypts for natural durability. P. 12 in Developing eucalypt resource-learning from Australia and elsewhere, Walker, J. (ed.), Blenheim, University of Canterbury.

Caemmerer, S.V., and G. Farquhar. 1999. Processes and resources for growth. P. 634 in Plants in Action. Adaptation in nature, performance in Cultivation Atwell, B., P. Kriedemann, and C. Turnbull (eds.). Macmillan Publishers Australia PTY LTD, South Yarra.

Campbell, C., L. Atkinson, J. Zaragoza-Castells, M. Lundmark, O.K. Atkin, and V. Hurry. 2007. Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. New Phytol. 143:4-10.

Coops, N.C., R.H. Waring, C. Beier, R. Roy-Jauvin, and T. Wang. 2011. Modelling the occurrence of 15 coniferous tree species throughout the Pacific Northwest of North America using a hybrid approach of a generic process-based growth model and decision tree analysis. Applied Vegetation Science 14(3):402-414.

Coops, N.C., R.H. Waring, and F. Moncrieff. 2000. Estimating mean monthly incident solar radiation on horizonatal and inclined slopes from mean monthly temperature extremes. Journal Biometeorol 44:201-211.

Covey-Crump, E.M., R. Attwood, and O.K. Atkin. 2002. Regulation of root respiration in two species of *Plantago* that differ in relative growth rate: the effect of short- and long-term changes in temperature. Plant, Cell & Environ 25:1501–1513.

Cown, D.J. 2008. Redwood in New Zealand – An end-user perspective. New Zealand Journal of Forestry 52(4):35-41.

Crawley, J.M. 2005. Analysis of Variance. in Statistics An Introduction using R. John Wiley & Sons Ltd, Great Bretain.

Delagrange, S. 2011. Light-and seasonal-induced plasticity in leaf morphology, N parttioning and photosynthetic capacity of two temperate deciduous species. Environmental and Experimental Botany 70:1-10.

Dillaway, D.N., and E.L. Kruger. 2010. Thermal acclimation of photosynthesis: a comparison of boreal and temperate tree species along a latitudinal transect. Plant, Cell & Environment 33:888-899.

Downs, R.J., and H. Hellmers. 1975. Environment and the Experimental Cotrol of Plant Growth. P. 145p in Academic Press.

Dreyer, E., X. Le Roux, P. Montrpied, F.A. Daudet, and F. Mason. 2001. Temperature response of leaf photosynthetic capacity in seedlings from seven temperature tree species. Tree Physiology 21:223-232.

Dungan, R., D. Whitehead, and P. Duncan. 2003. Seasonal and temperature dependence of photosynthesis and respiration for two co-occuring broad-leaved tree species with contrasting leaf phenology. Tree Physiology 23:561-568.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_a plants. Oecologia 78:9 19.

Fan, Y., Z. Zhong, and X. Zhang. 2011. Determination of photosynthetic parameters V_{cmax} and J_{max} for a C_3 plant (Spring hulless barley) at two altitudes on the Tibetan Plateau. Agricultural and Forest Meteorology 151:1481-1487.

Fangmeier, A., L. De Temmerman, L. Mortensen, K. Kemp, J. Burke, R. Mitchell, M. van Oijen, and H.J. Weigel. 1999. Effects on nutrients and on grain quality in spring wheat crops grown under elevated CO2 concentrations and stress conditions in the European, multiple-site experiment 'ESPACE-wheat'. European Journal of Agronomy 10(3–4):215-229.

Farquhar, G.D., and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis Annual Review of Plant Physiology 33:317-345.

Farquhar, G.D., S. von Caemmerer, and J.A. Berry. 1980. A biochemical-model; of photosynthetic CO_2 assimialtion in leaves of C_3 species. Planta 149:78-90.

Ferrar, P.J., R.O. Slatyer, and J.A. Vranjic. 1989. Photosynthyetic temperature acclimation in *Eucalyptus* species from diverse habitats and a comparison with *Nerium oleander*. Am. J. Plant Physiol. 16:199-217.

Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. Oecologia 56:341-347.

Field, C., and H.A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. P. 25-55 in The economy of plant form and function Givinish, T. (ed.). Cambridge University Press, London.

Fowells, H.A. 1965. Silvics of Forest Trees of the United States. Forest Service. US Dept of Agriculture. 962.

Francisco, J.S., H.P.d. Moraes, and E.P. Dias. 2004. Evaluation of the Image-Pro Plus 4.5 software for automatic counting of labeled nuclei by PCNA immunohistochemistry. Brazilian Oral Research 18:100-104.

Gea-Izquierdo, G., and A. Makela. 2010. Modelling acclimation of photosynthesis to temperature in evergreen conifer forests. New Phytol. 188:175-186.

Ghannaoum, O., G.N. Philips, A.M. Sears, A.B. Logan, D.J. Lewis, P.J. Conroy, and D. Tissue. 2010. Photosynthetic response of two eucalypts to industrail-age changes in atmospheric [CO_2] and temperature. Plant, Cell & Environment 33:1671-1681.

Ghouil, H., P. Montpied, D. Epron, M. Ksontini, B. Hanchi, and E. Dreyer. 2003. Thermal optima of photosynthetic functions and thermostability of photochemistry in cork oak seedlings. Tree Physiol 23:1031–1039.

Gindaba, A., L. Rozanov, and L. Negash. 2004. Response of seedlings of *Eucalyptus* and three deciduous tree species from Ethiopia to severe water stress,. P. 119-129 in Forest Ecology and Managemet.

Gunderson, C.A., K.H. O'Hara, C.M. Campion, A.V. Walker, and N.T. Edwards. 2010. Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. Global Change Biology 16:2272-2286

Haldmann, P., and U. Feller. 2004. Inhibition of photosynthesis by high temperature in oak (*Quercus pubescens* L.) leaves grown under natural conditions closely correlate with a reversible heat-dependent reduction of the activation state of ribulose-1,5-bisphosphate carboxylation/oxygenase. Plant, Cell & Environment 27:1169-1183.

Han, G., T. Kawasaki, T. Nakano, and Y. Chiba. 2004. Spatial and seasonal variability of temperature responses of biochemical photosynthesis parameters and leaf nitrogen content within a *Pinus densiflora* crown. Tree Physiol 24:737–744.

Hawkins, B.J. 1988. Investigations of the physiology and genetics of the New Zealand Conifers : Rimu, Kahikatea and Totara, Unversity of Canterbury, Christchurch. 278 p.

Hellmers, H. 1962. Temperature effect on optimum tree growth. P. 275-287 in Tree Growth Kozlowski, T.T. (ed.). Ronald Press C., New York.

Hellmers, H. 1966. Growth response of redwood seedlings to thermoperiodism. For. Sci. 12:277-283.

Hellmers, H., M.K. Genthe, and F. Ronco. 1970. Temperature affect growth and development of *Engelmann spruce*. For. Sci. 16:447-452.

Hellmers, H., and D.A. Rook. 1973. Air temperature and growth of radiata pine seedlings. New Zealand Journal of Forestry Science 3:271-285.

Herms, D.A., and J.W. Mattson. 1999. The dilemma of plants: To grow or defend. The quarterly review of Biology 67.

Hickey, J.E., P. Kostoglou, and G.J. Sargison. 2000. Tasmania's tallest trees. Tasfoersts 12:105-105.

Hikosaka, K. 1997. Modelling optimal temperature acclimation of the photosynthetic apparatus in C_3 plants with respect to nitrogen use. Annal of Botany 80:721-730.

Hikosaka, K. 2005. Nitrogen partitioning in the photosynthetic apparatus of *Plantago asiatica* leaves grown at different temperature and light conditions: similarities and differences between temperature and light acclimation. Plant & Cell Physiol 46:1283–1290.

Hikosaka, K., Y.T. Hanba, T. Hirose, and I. Terashima. 1998. Photosynthetic nitrogen-use efficiency in woody and herbaceous plants. Funct. Ecol. 12:896–905.

Hikosaka, K., K. Ishikawa, A. Borjigidai, O. Muller, and Y. Onoda. 2006. Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate, . J Exp Bot 57:291-302.

Hikosaka, K., A. Murakami, and T. Hirose. 1999. Balancing carboxylation and regeneration of ribulose-1,5-bisphosphare in leaf photosynthesis:temperature acclimation of an evergreen tree, *Quercus myrsinaefolia*. Plant, Cell & Environment 22:841-849.

Hikosaka, K., E. Nabeshima, and T. HIura. 2007. Seasonal changes in the temperature response of photosynthesis in canopy leaves of *Quercus crispula* in a cold-temperate forest Tree Physiology 27:1035-1041.

Hikosaka, K., and I. Terashma. 1995. A model of the acclimation of photosynthesis in the leaves of C_3 plants to sun and shade with respect to nitrogen use. Plant, Cell & Environment 18:605-618.

Hills, W.E., and A.G. Brown. 1984. *Eucalyptus* for wood production CSIRO.

Hurry, V.M., S. Asa, T. Marie, P. Gardestrom, and G. Oquist. 1995. Cold hardening of spring and winter wheat and rape result in differential effects on growth, carbon metabilism and carbohydrate content. Plant Physiology 109:697-706.

Ishii, T.H., G.M. Jenny, C.S. Sillett, and W.G. Koch. 2008. Hydrostatic constraints on morphological exploitation of light in tall *Sequoia sempervirens* trees. Oecologia 156:751–763.

Ishikawa, K., Y. Onoda, and K. Hikosaka. 2007. Intraspecific variation in temperature dependence of gas exchange characteristics of *Plantago asiatica* ecotypes from different temperature regimes. New Phytologist 176:356-364.

Jaya, E., D.S. Kubien, P.E. Jameson, and J. Clemens. 2010. Vegetative phase change and photosynthesis in *Eucalyptus occidentalis*:architectural simplification prolongs juvenile traits. Tree Physiology 30:393–403

Jones, T.G., R.M. McCConnochie, C.J.A. Shelbourne, and C.B. Low. 2008. The sawing and grade recovery of 25 year old *Eucalyptus fastigata*, *Eucalyptus globoidea*, *Eucalyptus muelleriana* and *Eucalyptus pilularis*.

Jorge, F., T. Quilho, and H. Pereina. 200. Variability of fibre length in wood and bark in *Eucalytus globulus*. IAWA J 21:24-48.

Joseph, T. 2011. The response of photosynthesis and respiration of grass and native shrub to varying temperature and soil water content. P. 200 in School of biological sciences. University of Canterbury, Christchurch.

Jull, L.G., T.G. Ranney, and F.A. Blazich. 1999. Heat Tolerance of Selected Provenances of Atlantic White Cedar. J. Amer. Soc. Hort. 124(5):492497.

Jurski, V., and A. Grigg. 1996. Flowering and seeding of *Eucalyptus fastigata* in South-eastern New South Wales Forest Research and Development Division, State Forests of NSW.

Kattge, J., and W. Knorr. 2007. Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species Plant, Cell & Environment 30:1176-1190

Keenan, R.J., M.H. Ivory, S. Lawson, D. Lee, W. Leggate, M.J. Lewty, D.G. Nikles, P. Ryan, and S. Walker. 1998. Hardwood plantation research and development: a strategy to support a hardwood plantation industry in Queensland. Queensland Forestry Research Institute. 34.

Kelly, M.J., F.C. Thornton, and J.D. Joslin. 2011. Model Estimates of Nutrient Uptake by Red Spruce Respond to Soil Temperature. Journal of Environmental Protection 2:769-777.

Knowles, F.B., and J.T. Miller. 1993. Introduced forest trees in New Zealand: Recognition, Role and Seed Source13 The redwoods FRI Bulletin 124(13).

Kositsup, B., P. Montpied, P. Kasemsap, P. Thaler, A. Thierry, and E. Dreyer. 2009. Photosynthetic capacity and temperature responses of photosynthesis of rubber trees (*Hevea brasiliensis* Müll. Arg.) acclimate to changes in ambient temperatures Trees 23:357-365.

Kozlowski, T.T. 1971. Growth and Development of trees. P. 514. Academic Press, New York.

Kramer, P.J. 1971. Some effects of various combinations of day and night temperatures and photoperiods on the height growth of loblolly pine seedlings. For. Sci 3:45-53.

Krause, G.H., E. Grube, O.Y. Koroleva, C. Barth, and K. Winter. 2004. Do mature shade leaves of tropical tree seedlings acclimate to high sunlight and UV radiation? Functional Plant Biology 31:743-756.

Kuma, L., and A.K. Skidmore. 2000. Radiation-vegetation relationships in a *Eucalyptus* forest. Photogrammetric Engineering and Rempte Sensing 66(2):193-204.

Labate, C.A., and R.C. Leegood. 1988. Limitations of photosynthesis by changes in temperature. Planta 173:519-527.

Landsberg, J., and P. Sands. 2011. Physiological Processes. P. 49-61 in Physiological Ecology of Forest Production:Principles, Processes and Models, Ehleringer, J.R. (ed.). Academic Press Elsevier inc, Utah, USA.

Landsberg, J.J. 1977. Some useful equations for biological studies. Expl Agric 13:273-286.

Landsberg, J.J., and N.C. Coops. 1999. Modelling forest productivity across large areas and long periods. Natural Resource Modelling 12:1-28.

Landsberg, J.J., and R.H. Waring. 1997. A general model of forest productivity using simplified concepts of radiattion-use efficiency, carbon balance and partitioning. Forest Ecology and Management 95:209-228.

Law, R.D., and S.J. Crafts-Brandner. 1999. Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5 bisphosphate carboxylase/oxygenase. Plant Physiology 120:173-181.

Lee, D., S. Lawson, G. Dickinson, and S. House. 2008. Western white gum (*Eucalyptus argophloia*). Queensland Department of of primary Industries and Fisheries.

Lee, G.J., and E. Vierling. 2000. A small heat shock protein cooperates with heat shock protein 70 systems to reactivate a heat-denatured protein. Plant Physiology 122:189-197.

Leuning, R. 2002. Temperature dependence of two parameters in a photosynthesis model. Plant, Cell & Environment 25:1205–1210.

Lewis, D.J., M. LUcash, D.M. Olszyk, and D.T. Tingey. 2004. Relationship between needle nitrogen concentration and photosynthetic response of Douglas-fir seedlings to elevated CO_2 and temperature New Phytol. 162:355-364.

Lewis, J.D., N.G. Phillips, B.A. Logan, C.R. Hricko, and T.D. Tissue. 2011. Leaf photosynthesis, respiration and stomatal conductance in six *Eucalyptus* species native to mesic and xeric environments growing in a common garden. Tree Physiology 31(997-1006).

Lindenmayer, D.D., J. Fischer, and R.B. Cunning. 2005. Native vegetation cover thresholds assiciated with species responses. Biological conservation dio. org/10.1016/j.biocon.2005.01.038.

Linder, S., and E. Troeng. 1981. The seasonal course of respiration and photosynthesis in stroili of Scots pine. Forest Science 2:267-276.

Luo, Y., X. Zhau, R. Zhou, X. Zuo, J. Zhang, and Y. Li. 2010. Physiological acclimation of two psammophytes to repeated soil drought and rewatering. Acta Physiologiae Plantarum:1-13.

Mahan, J.R., J.J. Burke, and K.A. Orzech. 1987. The 'thermal kinetic window' as an indicator of optimum plant temperature. Plant Physiology 82:518-522.

Makino, A., H. Nakano, and T. Mae. 1994b. Effects of growth temperature on the responses of ribulose-1,5-bisphosphate carboxylase, electron transport components, and sucrose synthesis enzymes to leaf nitrogen in rice, and their relationships to photosynthesis. Plant Physiology 105:1231-1238.

Manter, K.D., and J. Kerrigan. 2004. A/C_i curve analysis across a range of woody plant species: influence of regression analysis parameters and mesophyll conductance. Journal of Experimental Botany 55(408):2581-2588.

Mason, E.G. 2009. Growth and yield modelling in a climate of change: How can we make good use of data from past epochs? . New Zealand Journal of Forestry 54(3):19-25.

Mason, E.G., R.C. Woollons, and B.R. Manley. 2008. Carbon Accounting:Forest Growth Rates and Changing Climates. Ministry of Agriculture and Forestry. 55pp.

McGoodwin, M. 2008. The Physiology Of Higher Plants: An Outline.138.

Medlyn, B.E., E. Dreyer, D. Ellsworth, M. Forstreuter, P.C. Harley, and M.U.F. Kirschbaum. 2002a. Temperature response of parameter of a biochemically based model of photosynthesis II. A review of experimental data Plant, Cell & Environment 25:1167-1179.

Medlyn, B.E., D. Loustau, and S. Delzon. 2002b. Temperature response of parameters of a biochemically-based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster*). Plant, Cell & Environ 25:1155–1165.

Medlyn, B.R., E. Dreyer, and D. Ellsworth. 2002c. Temperature response of parameters of a biochemically based model of photosynthesis II. A review of experimental data Plant, Cell & Environment 25:1167-1179.

Millen, P. 2009. Nz Dryland Forests Initiative: A market focused durable eucalypt R&D project.

Mitchell, R.A.C., and J. Barber. 1986. Adaptation of photosynthetic electron-transport rate to growth temperature in pea. Planta 169:429–436.

Mooney, H.A., and M. West. 1964. Photosynthetic acclimation of plants of diverse origin. Am. J. Bot 51:825-827.

Ngugi, M.R., M.A. Hunt, D. Doley, P. Ryan, and P.J. Dart. 2003a. Photostnthetic light and temperature responses of *Eucalyptus cloeziana* and *Eucalyptus argophloia*. Aust. J. Bot. 51:573-583.

Nicholas, I. 2004. Selecting Durable Eucalypt Tree Species for Evaluation. Report prepared for Vineyard Timbers Ltd, Ensis (Scion).

Nicholas, I. 2007. New Zealand Experience with *Eucalyptus bosistoana* in New Zealand. SCION.

Nicolle, D. 2006. A classification and census of regenerative strategies in the eucalypts (*Angophora*, *Corymbia* and *Eucalyptus*-Myrtaceae), with special reference to the obligate seeders. Aust. J. Bot. 54:391-407.

Nightingale, J.M., W. Fan, N.C. Coops, and R.H. Waring. 2008. Predicting tree diversity across the USA as a function of modeled gross primary production. Ecological Applications 18:93-108.

Noguchi, K., N. Nakajima, and I. Terashima. 2001. Acclimation of leaf respiratory properties in *Alocasia odora* following reciprocal transfers of plants between high-and low light environments. Plant, Cell & Environment 24:831-839.

O'Hara, K.L., and J.P. Berrill. 2009. Epicomic sprout development in pruned coast redwood: Pruning severity, genotype and sprouting characteristics. Ann. For. Sci 66:409-417.

Onoda, Y., K. Hikosaka, and K. Hirose. 2005a. Seasonal change in the balance between capacities of RuBP carboxylation and RuBP regeneration affects CO_2 response of photosynthesis in *Polygonum cuspidatum*. Journal of Experimental Botany 56(412):755–763.

Onoda, Y., K. Hikosaka, and T. Hirose. 2005b. The balance between RuBP carboxylation and RuBP regeneration: a mechanism underlying the interspecific variation in acclimation of photosynthesis to seasonal change in temperature. Functional Plant Biology 32:903–910.

Onoda, Y., K. Hikosaka, and T. Hirose. 2005c. The balance between RuBP carboxylation and RuBP regeneration: a mechanism underlying the interspecific variation in acclimation of photosynthesis to seasonal change in temperature. Functional Plant Biology 56:755-763.

Opeke, L.K. 1982. Tropical Tree Crops. John Wiley and Sons Ltd., New York. 312 p.

Osborne, C.P., and D.J. Beerling. 2003. The penalty of a Long, Hot Summer. Photosynthetic Acclimation to High CO_2 and Continuous light in "Living Fossil" Conifers Plant Physiology 133:803-812.

Ow, L.F., K.L. Griffin, D. Whitehead, A.S. Walcroft, and H.M. Turnbull. 2008a. Thermal acclimation of leaf respiration but not photosynthesis in *Populus deltoides* X *nigra*. New Phytologist 178:123-134.

Ow, L.F., D. Whitehead, A.S. Walcroft, and H.M. Turnbull. 2008b. Thermal acclimation of respiration but not photosynthesis in *Pinus radiata*. Functional Plant Biology 35:448-461.

Ow, L.F., D. Whitehead, A.S. Walcroft, and M.H. Turnbull. 2010. Seasonal variation in foliar carbon exchange in *Pinus radiata* and *Populus deltoides*: respiration acclimates fully

to changes in tgemperature but photosynthesis does not. Global Change Biology 16:288-302.

Parsons, R., and S. Ogston. 1999. Photosyn Assistant Ver. 1.1.2. Dundee Scientific, Dundee

Paton, D.M. 1980. *Eucalyptus* Physiology II, Temperatuer response. Aust. J. Bot. 28:555-566.

Pearcy, R.W. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentformis* (Torr.) Wats. Plant Physiology 59:795-799.

Pereira, J.S., J.D. Tenhunen, and L. Langer. 1986. Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal. Canadian Journal of Forest Research 16:177-184.

Potts, B., M. Hamilton, and D. Blackburn. 2011. Genetics of Eucalypts: Traps and Opportunities. P. 1-26 *in* Developing a Eucalypt Resource: Learning from Australia and elsewhere. NZDFI, Blenheim, New Zealand.

Read, J., and J.R. Busby. 1990. Comparative response to temperature of the major canopy species of Tasmanian cool temperate rainforest and their ecological significance. II. Net photosynthetic and climate analysis. Aust. J. Bot. 38:103-114.

Reich, P.B., J. Oleksyn, and I.J. Wright. 2009. Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. Oecologia 160:207-212.

Reich, P.B., M.D. Walters, and D.S. Ellsworth. 1997. From tropics to tundra:global convergence in plant functioning. Proc natl Acad Sci USA 94:13730-13734.

Ripullone, F., G. Grassi, M. Lauteri, and M. Borghetti. 2003. Photosynthesis-nitrogen relationships: interpretation of different patterns between *Pseudotsuga menziesii* and *Populus x euroamericana* in a mini-stand experiment. Tree Physiology 23:137-144.

Robakowski, P., P. Montpied, and E. Dreyer. 2002. Temperature response of photosynthesis of silver fir (*Abies alba* Mill.) seedlings. Ann. For. Sci 59:163-170.

Rook, D.A. 1969. The influence of growing temperature on photosynthesis and respiration of *Pinus radiata* seedlings. New Zeal. J. Bot. 7:43-55.

Royer, D.L., C.P. Osborne, and D.J. Beerling. 2005. Contrasting seasonal patterns of carbon gain in evergreen and deciduous trees of ancient polar forests. Paleobiology 31(1):141-150.

Sage, R.F., and D.S. Kubien. 2007. The temperature response of C_3 and C_4 photosynthesis Plant, Cell & Environment 30:1086-1106.

Sall, T., and P. Petterson. 1994. A model of photosynthetic acclimation as a special case of reaction norms. Theor. Biol. 166:1-8.

Sands, P.J. 1995a. Modelling canopy production I. Optimal distribution of photosynthetic resources. Australian Journal of plant physiology 22:593-601.

Sands, P.J. 1995b. Modelling canopy production II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. Australian Journal of plant physiology 22:603-614.

Sands, P.J., and J.J. Landsberg. 2002. Parameterisation of 3-PG for plantation grown *Eucalyptus globulus*. Forest Ecology and Management 163:273-292.

Sandvea, S.R., K. Arkadiusz, R. Heidi, F. Siri, R. Marcin, Y. Toshihiko, and O. Rognlia. 2011. Molecular mechanisms underlying frost tolerance in perennial grasses adapted to cold climates. Plant Science 180:69-77.

Senioniti, E., Y. Manetos, and N.A. Gavales. 1986. Co-operative effects of light and temperature on the activity of phosphoenolpyruvate carboxylase from *Amaranthus paniculatus*. *Plant Physiology* 82:518-522.

Sewell, A.J. 1997. Australian timbers. Commercail timber species of eastern subtropical Australia Queensland Dept. Natural Resoueces. 130.

Sharkey, T.D. 1985. Photosynthesis in intact leaves of C_3 plants:physics, physiology and rate limitations. Bot Rev 51:53-105.

Sharkey, T.D., C.J. Bernacchi, D.G. Farquhar, and L.E. Singas. 2007. Fitting photosynthetic carbon dioxide response curves for C_3 leaves. Plant, Cell & Environment 30:1035-1040.

Sheppard, J. 1988. Evaluation of *Eucalyptus*: 1970 Wither Hill Trials.

Sheriff, D.W., and E.K.S. Nambiar. 1991. Nitrogen nutrition, growth and gas exchange in *Eucalyptus globulus* Labill. seedlings. Australian Journal of plant physiology 18:37-52.

Slatyer, R.O. 1977a. Altitudinal variation in the photosynthetic characteristics of *Eucayptus pauciflora* Sieb. ex Spreng IV. Comparison of field and phytotron response to growth temperature Am. J. Plant Physiol 4:583-594.

Slatyer, R.O. 1977b. Altitudinal variation in the photosynthetic characterristics of *Eucalyptus pauciflora* Sieb. ex Spreng. III. Temperature response of material grown in contrasting thermal environment. Aust. J. Plant. Physiol 4:301-312.

Slatyer, R.O., and P.A. Ferrar. 1977. Altitudinal variation in the photosynthetic characteristics of *Eucalyptus pauciflora* Sies.ex Sreng. V. Rate of acclimation to an altered environment. Aust. J. Plant Physiol. 4:595-609.

Slatyer, R.O., and P.A. Morrow. 1977. Altitudinal variattion in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. I. Seasonal changes

under field conditions in the Snowy Mountains area of south-eastern Australia Am. J. Bot 25:1-10.

Smith, N., and J. Dukes. 2012. Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO_2. Global Change Biology doi: 10.1111/j.1365-2486.2012.02797.x.

Somerville, C., and J. Browse. 1991. Plant lipids, metabolism and membranes. Science 252:80-87.

Strauss, E.A. 2000. The effects of organic carbon and nitrogen availabilty on nitrification rates in stream sediments Graduate School of the University of Notre Dame, Notre Dame Indiana. 104 p.

Tao, F., and Z. Zhang. 2010. Adaptation of maize production to climate change in North China Plain: Quantify the relative contributions of adaptation options. European Journal of Agronomy 33(2):103-116.

Teskey, R.O., and R.E. Will. 1999. 1999. Acclimation of loblolly pine (*Pinus taeda* L.) seedlings to high temperatures. Tree Physiol 19:519-525.

Tjoelker, M.G., J. Oleksyn, G. Lorenc-Plucinska, and P.B. Reich. 2009. Acclimation of respiratory temperature responses in northern and southern populations of *Pinus banksiana*. New Phytol. 181:218–229.

Tranquillini, W., W.M. Havranek, and P. Ecker. 1986. Effects of atmospheric humidity and acclimation temperature on the temperature response of photosynthesis in young *Larix decidua* Mill. Tree Physiol 1:37–45.

Treshow, M. 1970. Envoronment and Plant Response. McGraw-Hill Book Co.

Turnbull, M.H., D. Doley, and D.J. Yates. 1993. The dynamic of photosynthetic acclimation to changes in light quantity and quality in three Australian rainforest tree species. Oecologia 94:218-228.

Turnbull, M.H., D.T. Tissue, L. Kevin, K.L. Griffin, S.J. Richardson, D.A. Peltzer, and D. Whitehead. 2005. Respiration characteristics in temperate rainforest tree species differ along a long-term soil-developemt chronosequence. Oecologia 143:271-279.

Vann, D.R., A.H. Johnson, and B.B. Casper. 1994. Effects of elevated temperature on carbon dioxide exchange in *Picea rubens*. Tree Physiology 14:1339-1349.

von Caemmerer, S., and G.D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387.

Wager, H.G. 1941. On the respiration and carbon assimilation rates of some arctic plants as related to temperature. New Phytol. 40:1-19.

Wahida, A., S. Gelania, M. Ashraf, and M.R. Fooladb. 2007. Heat tolerance in plants: An overview. Environmental and Experimental Botany 61:199-223.

Wahlenberg, W.G. 1960. Loblolly Pine. Duke University. 603.

Walcroft, A.S., D. Whitehead, W.B. Silvester, and F.M. Kelliher. 1997. The response of photosynthetic model parameters to temperature and nitrogen concentration in *Pinus radiata* D. Don. Plant, Cell & Environment 20:1338–1348.

Wardlaw, I.F. 1974. Temperature control of translocation. Bull. Royal Soc, Wellington, New Zealand.

Waring, R.H., N.C. Coops, and J.J. Landsberg. 2010. Improving predictions of forest growth using the 3-PGS model with observations made by remote sensing. Forest Ecology and Management 259(9):1722-1729.

Warren, C.R. 2008. Does growth temperature affect the temperature response of photosynthesis and internal conductance to CO_2? A test with *Eucalyptus regnans*. Tree Physiology 28(11-19).

Warren, C.R., and E. Dreyer. 2006. Temperature response of photosynthesis and internal conductance to CO_2 : results from two independent approaches. J. Exp. Bot. 57(12):3057-3067.

Way, A.D., and R. Oren. 2010. Differential responses to changes in growth temperature betwwen trees from differnt functional groups and biomes: a review and synthesis of data. Tree Physiology 30(6):699-688.

Way, A.D., and F.R. Sage. 2008a. Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.]. Global Change Biology 14:624–636.

Way, A.D., and F.R. Sage. 2008b. Thermal acclimation of photosynthesis in black spruce [*Pecea mariana* (Mill) B.S.P.]. Plant, Cell & Environment 31:1250-1262.

Weston, D.J., W.L. Bauerle, G.A. Swire-Clark, B.D. Moore, and W.V. Baird. 2007. Characterization of Rubisco activase from thermal contrasting genotype of *Acer rubrum* (Aceraceae). American Journal of Forestry 94:926-934.

Whitehead, D., N.T. Boelman, M.H. Turnbull, K.L. Griffin, D.T. Tissue, M.M. Barbour, J.E. Hunt, S.J. Richardson, and D.A. Peltzer. 2005. Photosynthesis and Reflectance Indices for Rainforest Species in Ecosystems Undergoing Progression and Retrogression along a Soil Fertility Chronosequence in New Zealand. Oecologia 144(2):233-244.

Whitehead, D., A.S. Walcroft, A.N. Scott, J.A. Townsend, C.M. Trotter, and G.N.D. Rogers. 2004. Characteristics of photosynthesis and stomatal conductance in the shrubland species manuka (*Leptospermum scoparium)* and kanuka (*Kunzea ericoides*) for the estimation of annual carbon uptake. Tree Physiology 24:795-804.

Wieser, G., W. BOberhuber, L. Walder, D. Spieler, and A. Gruber. 2010. Photosynthetic temperature adaptation of *Pinus cembra* within the timberline ecotone of the Central Australia Alps. Ann. For. Sci 67 dio:10.1051/forest/2009094.

Will, R. 2000. Effect of different daytime and night-time temperature regimes on the foliar respiration of *Pinus taeda*: predicting the effect of variable temperature on acclimation. Journal of Experimental Botany 51(351):1733-1739.

Williams, J.E., and J.C.Z. Woinarski. 1997. Eucalypt ecology: overview and outlook. P. 402-410 in Eucalypt Ecology: Individuals to Ecosystems, Williams, J.E.a., J.C.Z. (ed.). Cambridge University Press, Cambridge.

Wilson, K.B., D.D. Baldocchi, and P.J. Hanson. 2000. Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. Tree Physiol 20:565-578.

Wright, I.J., P.B. Reich, M. Wesoby, D.D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-bares, T. Chapin, J.H.C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P.K. Groom, J. Gulias, K. Hikosaka, B.B. Lamont, T. Lee, W. Lee, C. Lusk, J.J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V.I. Pyankov, C. Roumet, S.C. Thomas, M.G. Tjoelker, E.J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.

Wullscheleger, S.D. 1993. Biochemical limitations to carbon assimilation in C_3 plants -a retrospective analysis of the A/C_i curves from 109 species. J. Exp. Bot. 44:907-920.

Yamasaki, T., T. Yamakawa, Y. Yamane, H. Koike, K. Satoh, and S. Katoh. 2002. Temperature acclimation of photosynthesis and related changes in photosystem II electron transport in winter wheat. Plant Physiology 50:203-215.

Yamori, W., K. Noguchi, K. Hikosaka, and I. Terashima. 2010. Phenotypic Plasticity in Photosynthetic Temperature Acclimation among Crop Species with Different Cold Tolerances1[W][OA]. Plant Physiology 152:388–399.

Yamori, W., K. Noguchi, and I. Terashima. 2005. Temperature acclimation of photosynthesis in spinach leaves: analyses of photosynthetic components and temperature dependencies of photosynthetic partial reactions. Plant, Cell & Environ 28:536–547.

Yamori, W., K. Suzuki, K. Noguchi, M. Nakai, and I. Terashima. 2006. Effects of Rubisco kinetics and Rubisco activation state on the temperature dependence of the photosynthetic rate in spinach leaves from contrasting growth temperatures. Plant, Cell & Environment 29:1659–1670.

Zaragoza-Castells, J., D. Sánchez-Gómez, I.P. Hartley, S. Matesanz, F. Valladares, J. Lloyd, and O.K. Atkin. 2008. Climate-dependent variations in leaf respiration in a dry-land, low productivity Mediterranean forest: the importance of acclimation in both high-light and shaded habitats. Funct. Ecol. 22:172–184.

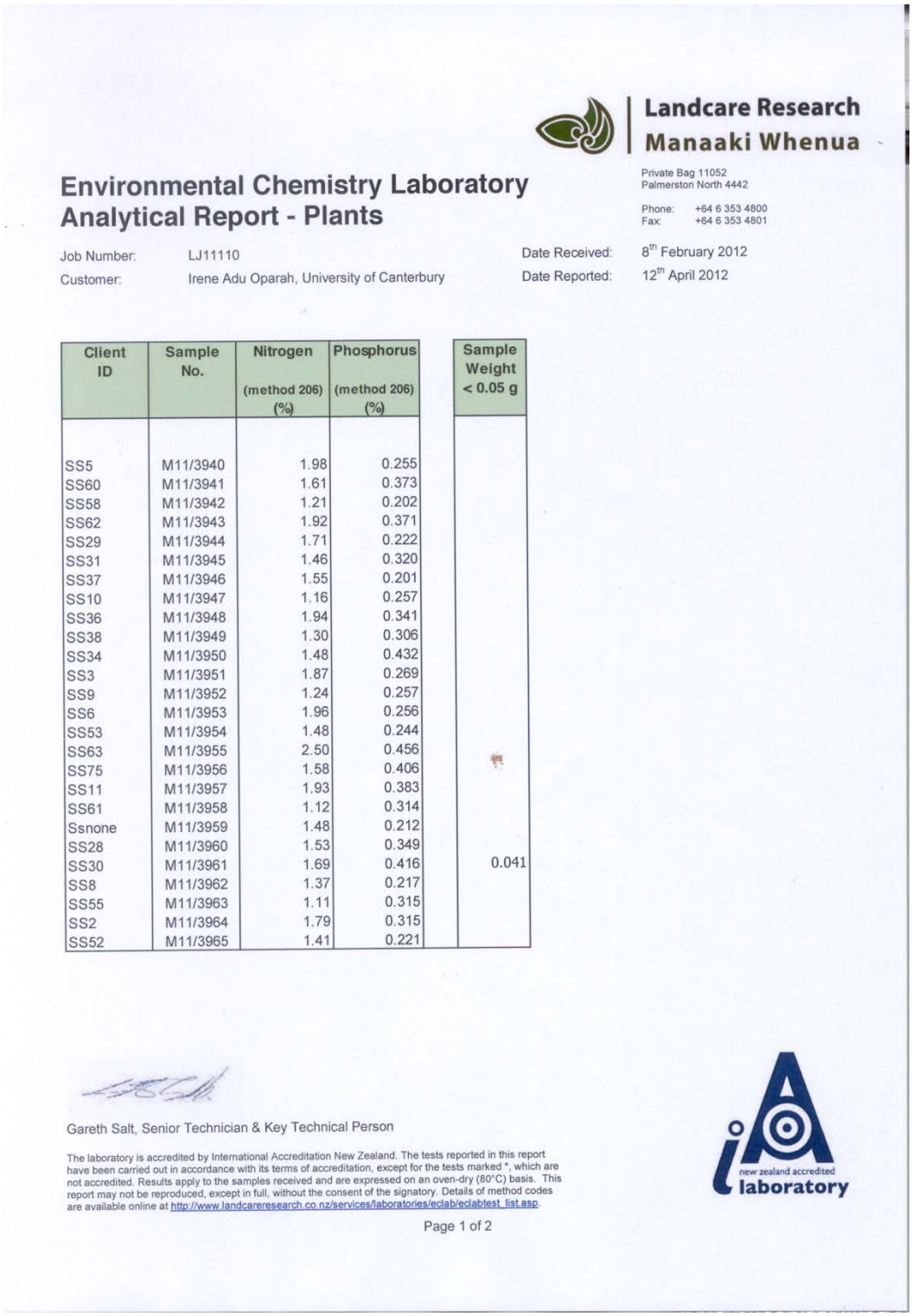
Zhang, S.R., and Q.L. Dang. 2006. Effects of $[CO_2]$ and nutrition on photosynthetic functions of white birch. Tree Physiology 26:1458-1467.

Zogg, G.P., D. Zak, J.A. Burton, and K.S. Pregitzer. 1996. Fine root respiration in northern hardwood forests in relation to temperature and nitrogen availability. Tree Physiology 16:719-725.

Appendices

Appendix A: Laboratory analysis of leaf nutrient

Laboratory results of leaf nitrogen and phosphorus analysis of plants (EF) *E. fastigata*, (EG) *E. globoidea*, (EA), *E. argophloia*, (EB) *E. bosistoana* and (SS) *Sequoia sempervirens*



Landcare Research
Manaaki Whenua

Private Bag 11052
Palmerston North 4442

Phone: +64 6 353 4800
Fax: +64 6 353 4801

Environmental Chemistry Laboratory
Analytical Report - Plants

Job Number: LJ11110
Customer: Irene Adu Oparah, University of Canterbury

Date Received: 8th February 2012
Date Reported: 12th April 2012

Client ID	Sample No.	Nitrogen (method 206) (%)	Phosphorus (method 206) (%)	Sample Weight < 0.05 g
SS5	M11/3940	1.98	0.255	
SS60	M11/3941	1.61	0.373	
SS58	M11/3942	1.21	0.202	
SS62	M11/3943	1.92	0.371	
SS29	M11/3944	1.71	0.222	
SS31	M11/3945	1.46	0.320	
SS37	M11/3946	1.55	0.201	
SS10	M11/3947	1.16	0.257	
SS36	M11/3948	1.94	0.341	
SS38	M11/3949	1.30	0.306	
SS34	M11/3950	1.48	0.432	
SS3	M11/3951	1.87	0.269	
SS9	M11/3952	1.24	0.257	
SS6	M11/3953	1.96	0.256	
SS53	M11/3954	1.48	0.244	
SS63	M11/3955	2.50	0.456	
SS75	M11/3956	1.58	0.406	
SS11	M11/3957	1.93	0.383	
SS61	M11/3958	1.12	0.314	
Ssnone	M11/3959	1.48	0.212	
SS28	M11/3960	1.53	0.349	
SS30	M11/3961	1.69	0.416	0.041
SS8	M11/3962	1.37	0.217	
SS55	M11/3963	1.11	0.315	
SS2	M11/3964	1.79	0.315	
SS52	M11/3965	1.41	0.221	

Gareth Salt, Senior Technician & Key Technical Person

The laboratory is accredited by International Accreditation New Zealand. The tests reported in this report have been carried out in accordance with its terms of accreditation, except for the tests marked *, which are not accredited. Results apply to the samples received and are expressed on an oven-dry (80°C) basis. This report may not be reproduced, except in full, without the consent of the signatory. Details of method codes are available online at http://www.landcareresearch.co.nz/services/laboratories/eclab/eclabtest_list.asp.

new zealand accredited laboratory

Page 1 of 2

Job Number: LJ11110

Date Reported: 12th April 2012

Landcare Research
Manaaki Whenua

Client ID	Sample No.	Nitrogen (method 206) (%)	Phosphorus (method 206) (%)	Sample Weight < 0.05 g
EF190	M11/3966	2.00	0.146	
EF180	M11/3967	1.49	0.165	
EF188	M11/3968	1.85	0.231	
EF179	M11/3969	1.12	0.187	
EF191	M11/3970	0.82	0.109	
EF189	M11/3971	2.11	0.168	
EF196	M11/3972	0.92	0.195	
EF197	M11/3973	0.97	0.341	
EF190	M11/3974	2.14	0.194	
EF198	M11/3975	1.80	0.122	
EB149	M11/3976	2.07	0.181	
EB150	M11/3977	3.10	0.629	
EB161	M11/3978	1.66	0.355	
EB157	M11/3979	2.41	0.278	
EB158	M11/3980	1.70	0.294	
EB156	M11/3981	1.91	0.274	
EB151	M11/3982	2.65	0.273	
EB152	M11/3983	1.41	0.328	
EB155	M11/3984	1.46	0.246	
EA121	M11/3985	1.97	0.284	
EA114	M11/3986	1.90	0.165	0.009
EA117	M11/3987	1.88	0.223	0.030
EA122	M11/3988	1.15	0.167	
EA124	M11/3989	1.13	0.180	
EA115	M11/3990	1.96	0.215	
EA118	M11/3991	1.25	0.178	
EA116	M11/3992	2.31	0.300	
EA117	M11/3993	2.15	0.221	
EA133	M11/3994	2.32	0.310	
EG100	M11/3995	2.84	0.256	
EG80	M11/3996	3.24	0.421	
EG78	M11/3997	2.37	0.428	
EG98	M11/3998	1.31	0.285	
EG111	M11/3999	1.48	0.113	
EG106	M11/4000	2.58	0.258	
EG104	M11/4001	1.04	0.190	
EG109	M11/4002	1.89	0.090	
EG107	M11/4003	1.62	0.298	
EG83	M11/4004	2.47	0.194	
EG80	M11/4005	3.00	0.270	
EG102	M11/4006	1.24	0.195	
EG79	M11/4007	2.92	0.283	
EG109	M11/4008	1.97	0.190	
EG86	M11/4009	1.78	0.260	
EG96	M11/4010	0.75	0.226	
EG102	M11/4011	1.25	0.154	
EG92	M11/4012	2.21	0.257	
EG113	M11/4013	1.51	0.172	
EG89	M11/4014	1.98	0.211	
EG101	M11/4015	1.70	0.095	
EGnone	M11/4016	1.33	0.277	
EG105	M11/4017	1.65	0.206	
EG108	M11/4018	1.88	0.423	
EG103	M11/4019	1.41	0.209	
EG112	M11/4020	1.51	0.281	
EG97	M11/4021	1.39	0.152	
EG88	M11/4022	0.99	0.210	
EG89	M11/4023	1.69	0.134	

Appendix B: Atomic ratio and N and P per leaf mass area

Plant Type	% N	% P	Atomic ratio	LA /m	N/gm^{-2}	P/gm^{-2}
E. globoidea-352	1.62	0.298	5.97099814	35.9630	2.0450984	0.376197
E. globoidea-352	1.62	0.298	5.97099814	35.8684	2.0504945	0.37719
E. globoidea-352	1.62	0.298	5.97099814	35.7962	2.0546314	0.377951
S. sempervirens-sw002	1.55	0.201	8.47000811	8.43489	2.8299112	0.366976
S. sempervirens-sw002	1.94	0.341	6.24878434	9.56294	3.1850010	0.559838
S. sempervirens-sw002	1.71	0.222	8.46040828	8.78922	3.5409270	0.459699
E. bosistoana-996	2.41	0.278	9.52183019	35.7142	2.76668	0.319144
E. bosistoana-996	1.7	0.294	6.35111207	45.9793	2.8728094	0.496827
E. bosistoana-996	1.91	0.274	7.65651239	33.6521	3.9048888	0.560178
S. sempervirens-04MR	2.5	0.456	6.02175874	14.9704	4.0579934	0.740178
S. Sempervirens-04MR	1.92	0.371	5.68428055	13.9708	3.2158315	0.621392
S. sempervirens-04MR	1.41	0.221	7.00769230	14.9631	2.7666380	0.433636
E. globoidea-311	2.92	0.283	11.3329925	11.7679	3.7964213	0.367941
E. globoidea-311	3	0.27	12.2040977	24.7058	3.6792857	0.331136
E. globoidea-311	2.37	0.428	6.08208888	50.1818	2.4653152	0.445213
S. sempervirens-sw005	1.87	0.269	7.63550054	14.0914	3.0123986	0.433334
S. sempervirens-sw005	1.96	0.256	8.40938608	13.1059	5.0847098	0.664125
S. sempervirens-sw005	1.98	0.255	8.52851063	17.2410	3.3074470	0.425959
E. argophloia-995	2.31	0.3	8.45743971	16.9203	2.4710438	0.320915
E. argophloia-995	2.15	0.221	10.6854882	13.5161	2.3224105	0.238722
E. argophloia-995	1.96	0.215	10.0130364	22.8856	2.5778553	0.282775
E. fastigata	1.12	0.187	6.57846550	41.7142	1.4928219	0.249248
E. fastigata	1.85	0.231	8.79646004	37.0728	2.9990952	0.374482
E. fastigata	1.49	0.165	9.91860305	23.1948	3.2247622	0.357105

E. globoidea-246	1.51	0.172	9.64265627	30.8517	2.6968013	0.307185
E. globoidea-246	1.51	0.172	9.64265627	30.8517	2.6968013	0.307185
E. globoidea-246	1.51	0.172	9.64265627	30.8517	2.6968013	0.307185
E. globoidea-301	1.41	0.209	7.41004784	55.3125	2.4140474	0.357827
E. globoidea-301	1.65	0.206	8.79761412	32.9090	3.0985359	0.386848
E. globoidea-301	1.21	0.195	6.81551918	25.7830	3.5573026	0.573284
E. globoidea-301	1.21	0.195	6.81551918	25.7830	3.5573026	0.573284
E. globoidea-352	1.88	0.423	4.88163908	53.0384	1.9211718	0.432264
E. globoidea-352	1.88	0.423	4.88163908	53.0384	1.9211718	0.432264
S. sempervirens-sw002	1.48	0.432	3.76293012	22.6696	0.9988702	0.291562
S. sempervirens-sw002	1.48	0.212	7.66785762	55.4284	1.1134359	0.159492
S. sempervirens-sw002	1.3	0.306	4.66627265	34.5008	1.5109777	0.355661
E. bosistoana-996	1.46	0.246	6.51877414	76.0588	1.7045754	0.287209
E. bosistoana-996	1.41	0.328	4.72164634	40.875	2.8044770	0.652389
E. bosistoana-996	1.66	0.355	5.13603436	45.144	2.6622364	0.569334
S. sempervirens-04MR	1.11	0.315	3.87044241	38.0785	0.8103782	0.229972
S. sempervirens-04MR	1.48	0.244	6.66223694	19.7765	1.6164594	0.266497
S. sempervirens-04MR	1.21	0.202	6.57933782	34.992	1.2379401	0.206664
E. globoidea-311	0.75	0.226	3.64502918	69.0967	1.4946428	0.450386
E. globoidea-311	1.31	0.285	5.04864252	78.4736	1.8212602	0.396228
E. globoidea-311	2.47	0.194	13.9843862	66.1867	3.9856303	0.313041
S. sempervirens-sw005	1.24	0.257	5.29952258	21.9561	0.8866749	0.183771
S. sempervirens-sw005	1.16	0.257	4.95761790	30.9130	1.1970346	0.265205
S. sempervirens-sw005	1.37	0.217	6.93440206	37.9636	1.3604846	0.215493
E. argophloia-995	1.25	0.178	7.71326400	50.1668	0.7001635	0.099703
E. argophloia-995	1.15	0.167	7.56361744	34.7222	1.2684968	0.184208

E. argophloia-995	1.13	0.18	6.89531520	28.5833	1.7987755	0.286531
E. fastigata	0.82	0.109	8.26295790	61.8679	1.8383354	0.244364
E. fastigata	0.92	0.195	5.18204764	53.3142	1.9344158	0.410012
E. fastigata	0.97	0.341	3.12439217	46.3392	1.9320755	0.679214
E. globoidea-246	1.48	0.113	14.3857151	48.1020	3.2214017	0.245958
E. globoidea-246	1.48	0.113	14.3857151	48.1020	3.2214017	0.245958
E. globoidea-246	1.48	0.113	14.3857151	48.1020	3.2214017	0.245958
E. globoidea-301	1.04	0.19	6.01212392	31.5405	1.9784061	0.36144
E. globoidea-301	0.99	0.21	5.17802431	44.7831	2.3366610	0.495655
E. globoidea-301	1.33	0.277	5.27375630	43.8171	1.5874837	0.330626
E. globoidea-352	1.88	0.423	4.88163908	53.0384	1.9211718	0.432264
E. globoidea-352	2.58	0.258	10.9836879	12.5777	1.8666254	0.186663
E. globoidea-352	1.89	0.09	23.0657446	29.5542	1.7586281	0.083744
E. globoidea-352	1.97	0.19	11.3883501	29.5542	1.8330674	0.176793
S. sempervirens-sw002	1.53	0.349	4.81519843	34.6281	1.3652768	0.311426
S. sempervirens-sw002	1.46	0.32	5.01130762	28.2847	0.7742696	0.169703
S. sempervirens-sw002	1.69	0.416	4.46212322	19.6964	1.0467859	0.25767
E. bosistoana-996	2.07	0.181	12.5614552	132.527	0.6247761	0.05463
E. bosistoana-996	2.65	0.273	10.6618216	130.387	0.8820667	0.09087
E. bosistoana-996	3.1	0.629	5.41326432	86.5263	1.1822992	0.239892
S. sempervirens-04MR	1.58	0.406	4.27444013	20.9608	1.6357157	0.420317
S. sempervirens-04MR	1.61	0.373	4.74094841	16.9356	1.5971051	0.370013
S. sempervirens-04MR	1.12	0.314	3.91774856	9.96937	1.1796125	0.330713
E. globoidea-311	2.21	0.257	9.44511686	70.0909	1.7877782	0.2079
E. globoidea-311	1.39	0.152	10.0442935	41.2394	1.8807725	0.205667
E. globoidea-311	2.84	0.256	12.1850288	52.9816	3.1090008	0.280248

S. sempervirens-sw005	1.93	0.383	5.53486102	21.2311	2.3453305	0.465421
S. sempervirens-sw005	1.79	0.315	6.24152426	21.1337	2.5324895	0.445662
S. sempervirens-sw005	1.8796	0.3136	6.1235648	28.8571	2.5321522	0.445672
E. argophloia-995	2.32	0.31	8.220050332	65.10681	1.80663122	0.241403
E. argophloia-995	1.9	0.165	12.64788309	22.58947	0.67287978	0.058434
E. argophloia-995	1.97	0.284	7.618966637	37.74333	1.45101122	0.209181
E. fastigata	2	0.146	15.04614787	47.70732	2.06676892	0.150874
E. fastigata	2.11	0.168	13.79498902	43.6	2.31325688	0.184183
E. fastigata	1.8	0.122	16.20544123	55.13966	1.62242553	0.109964
E. globoidea-246	1.5	0.28	5.90012	34.30714	2.112346	0.39236
E. globoidea-246	1.51	0.281	5.902266475	35.77778	2.11446894	0.393487
E. globoidea-246	1.51	0.281	5.902266475	35.77778	2.11446894	0.393487
E. globoidea-301	1.7	0.277	6.740891518	25.76978	2.38806812	0.389115
E. globoidea-301	1.78	0.26	7.519601746	37.34746	2.34013252	0.341817
E. globoidea-301	1.69	0.134	13.85256166	65.09091	1.34491899	0.106639
E. globoidea-352	2.58	0.258	10.98368794	12.57778	1.86662544	0.186663