PHOTOSYNTHESIS AND TRANSPIRATION IN A DRY-LAND *PINUS RADIATA* FOREST

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Certificate of Supervision

I certify that the experimental work contained in this thesis was planned, executed and written by Adrian Walcroft while under the supervision of Prof. Warwick B. Silvester and Drs. David Whitehead and Francis M. Kelliher.

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ABSTRACT

PHOTOSYNTHESIS AND TRANSPIRATION IN A DRY-LAND *PINUS RADIATA* FOREST

Adrian S. Walcroft

This thesis investigates biotic and abiotic regulation of photosynthesis and transpiration at the leaf and canopy scales in a dry-land *Pinus radiata* D. Don forest by combining gas exchange measurements with biophysical process-based models of photosynthesis, radiation transfer, and soil water balance.

Responses of photosynthesis to leaf intercellular CO_2 concentration in two-year old *P. radiata* seedlings were measured at a range of temperatures and leaf nitrogen concentrations in order to quantify parameters describing photosynthetic capacity and temperature response in a biophysical model of C_3 photosynthesis. Increasing leaf temperature from 8 °C to 30 °C caused a four-fold increase in V_{cmax}, the maximum rate of carboxylation (10.7 to 43.3 μmol m^{-2} s^{-1}), and a three-fold increase in J_{max}, the maximum electron transport rate (20.5 to 60.2 μmol m^{-2} s^{-1}). Foliar nitrogen concentration (N) varied between 0.36 mmol g^{-1} and 1.27 mmol g^{-1}, and there were linear relationships between N and both V_{cmax} and J_{max}. Measurements made throughout the crown of a forest tree, where N varied from 0.83 mmol g^{-1} near the base to 1.54 mmol g^{-1} near the leader, yielded similar relationships.

The leaf-level photosynthesis model was combined with a water balance model to successfully explain a seasonal pattern in stable carbon isotope composition ($\delta^{13}C$) measured within annual rings of *P. radiata* from two sites which differed markedly in annual water balance. Over two growing seasons there was good agreement between mean canopy-level c_i derived from the tree-ring $\delta^{13}C$ data and modelled leaf-level c_i levels. The amplitudes of seasonal $\delta^{13}C$ variation at the wet and dry sites were 1-2 ‰ and 4 ‰ respectively, and mean $\delta^{13}C$ values from the wet site were 3 ‰ more ^{13}C depleted than those from the dry site implying lower water-use efficiency (carbon assimilation per unit transpiration). Seasonal variation in carbon isotope discrimination of leaves in the canopy is therefore reflected directly in the $\delta^{13}C$ of stem wood.

A canopy photosynthesis model was developed by combining the leaf-level model with a model of canopy radiation transfer, and used as a framework to analyse a field experiment designed to quantify the response of photosynthesis and tree growth to a long-term reduction in illuminated leaf area. Shading the lower crown of two young forest trees reduced absorbed radiation and canopy photosynthesis by 11 and 9 % respectively in the first year. Nitrogen was translocated from current year foliage below the shade cloth to that above, and carbon partitioning to the branches increased at the expense of stem growth. In the second year, the effect of the shading on absorbed radiation, canopy photosynthesis and tree growth was less due to a reduction in shaded foliage proportional to total leaf area. Additionally, a prolonged period of soil water deficit during the summer of year 2 reduced photosynthesis, stomatal conductance and growth similarly in both shaded and control trees. Models which scale up processes from the leaf-level to the canopy can provide a framework to analyse and interpret field experiments.

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Symbol	Unit	Description
A	μmol m^{-2} s^{-1}	net photosynthesis rate
A_c	μmol m^{-2} s^{-1}	Rubisco activity limited gross photosynthesis rate
A_q	μmol m^{-2} s^{-1}	RuP_2 regeneration limited gross photosynthesis rate
A_{max}	μmol m^{-2} s^{-1}	photosynthesis rate at saturating irradiance and c_i
a	‰	^{13}C discrimination due to diffusion
a_1	-	coefficient in g_{sc} equation
b	‰	^{13}C discrimination due to carboxylation
c_a	μmol mol^{-1}	ambient CO_2 concentration
c_i	μmol mol^{-1}	intercellular CO_2 concentration
C_i	μmol mol^{-1}	assimilation weighted canopy c_i
c_s	μmol mol^{-1}	CO_2 concentration at the leaf surface
c_p	J kg^{-1} C^{-1}	specific heat of air
D	mmol mol^{-1}	leaf - air saturation deficit
D_s	mmol mol^{-1}	D at the leaf surface
D_0	mmol mol^{-1}	coefficient reflecting sensitivity of stomata to D_s
E_t	mm	evaporation from the canopy
E_u	mm	evaporation from ground surface and understorey
F	mm	soil drainage flux
g_{sc}	mmol m^{-2} s^{-1}	stomatal conductance to CO_2
g_{sc0}	mmol m^{-2} s^{-1}	residual g_{sc} when $A \rightarrow 0$ as $Q \rightarrow 0$
g_{sw}	mmol m^{-2} s^{-1}	stomatal conductance to H_2O
G_c	mm	canopy conductance to water vapour
G_t	mmol m^{-2} s^{-1}	tree conductance from sap flux measurements
H_d	J mol^{-1}	energy of deactivation
H_v	J mol^{-1}	energy of activation
J	μmol m^{-2} s^{-1}	whole-chain electron transport rate
J_{max}	μmol m^{-2} s^{-1}	potential rate of whole-chain electron transport
J_{max0}	μmol m^{-2} s^{-1}	J_{max} at the reference temperature T_0
k	m^2 ground m^{-2} leaf	canopy radiation extinction coefficient
k_N	m^2 ground m^{-2} leaf	canopy N distribution coefficient
K_c	μmol mol^{-1}	Michaelis constant for CO_2
K_o	mmol mol^{-1}	Michaelis constant for O_2
L	m^2 leaf m^{-2} ground	leaf area index (total surface leaf area)
L'	m^2 leaf m^{-2} ground	leaf area index (one-sided leaf area)

Symbol	Unit	Description
L_h	m^2 leaf m^{-2} ground	leaf area index (hemispherical leaf area)
N	mg g^{-1}	leaf nitrogen concentration
N_0	mg g^{-1}	N at the top of the canopy
N_L	mg g^{-1}	N in canopy layer L
N_t	mg g^{-1}	threshold N required for photosynthesis
o_i	mmol mol^{-1}	intercellular O_2 concentration
P	mm	daily net precipitation (precipitation less interception)
Q	µmol m^{-2} s^{-1}	quantum flux density (PAR)
R	J mol^{-1} K^{-1}	universal gas constant
R_a	MJ m^{-2} s^{-1}	available energy at the ground surface
R_0	MJ m^{-2} s^{-1}	available energy at the top of the canopy
R_d	µmol m^{-2} s^{-1}	respiration during the day not due to photorespiration
R_{d0}	µmol m^{-2} s^{-1}	R_d at the reference temperature T_0
s	kPa C^{-1}	slope of saturation vapour pressure *vs.* temperature
S_v	J mol^{-1}	entropy term
T_0	K	reference temperature
T_l	K	leaf temperature
T_{lopt}	K	optimum temperature for photosynthesis
V_{cmax}	µmol m^{-2} s^{-1}	maximum catalytic activity of rubisco
V_{cmax0}	µmol m^{-2} s^{-1}	V_{cmax} at the reference temperature T_0
W	mm	equivalent depth of water in the soil profile
α	mol mol^{-1}	quantum yield of whole-chain electron transport
ε	-	coefficient for scaling g_{sw} to G_c
Γ	µmol mol^{-1}	CO_2 compensation point
Γ_*	µmol mol^{-1}	CO_2 compensation point in the absence of R_d
γ	kPa C^{-1}	psychrometric constant
γ_0	µmol m^{-2} s^{-1}	Γ_* at reference temperature T_0
γ_1	-	coefficient in Γ_* equation
γ_2	-	coefficient in Γ_* equation
λ	J kg^{-1}	latent heat of vapourisation
ϕ	-	soil water limitation factor
Ψ_S	MPa	soil water potential
ρ	kg m^{-3}	density of the air
τ	-	coefficient for turbulent enhancement of E_u
θ	-	shape coefficient for equation relating J to Q
Θ	m^3 m^{-3}	volumetric soil water content

CHAPTER ONE

INTRODUCTION

Concerns about the rapidity of the increase in atmospheric carbon dioxide (CO_2) (Keeling 1993), and the possibility of negative impacts from global warming and climate change, have led to international conferences and workshops aimed at producing agreements to stabilise global net CO_2 emissions (the 1992 Framework Convention for Climate Change, and the 1997 Kyoto Climate Summit). Although highly political in nature, such agreements nevertheless acknowledge the unprecedented scale of the anthropogenic impact on the global ecosystem, and contribute in the least by promoting research into the chemical, biological and physical processes controlling global climate and ecosystem dynamics.

Government policy in New Zealand proposes to reduce CO_2 emissions through the manipulation and extension of natural and plantation forests to increase carbon sequestration. Forest ecosystems cover about one-quarter of the world's land area, and are responsible for about two-thirds of global terrestrial photosynthesis (Eamus and Jarvis 1989). The clearance of forest to make way for agriculture has significantly contributed to the atmospheric CO_2 increase (Dale *et al.* 1991). It is not surprising, therefore, that reforestation by native and exotic plantation and by regeneration of natural forests have been promoted as means of enhancing carbon sequestration (Dixon *et al.* 1994) and thereby reducing net CO_2 emissions. Carbon assimilated in plantation forests cannot be effectively stored in the long term unless soil carbon content increases and the rate of soil carbon turn-over is slow. Any reductions in CO_2 emissions arising from forest planting will therefore only be effective while forests are maturing (Vitousek 1991). This implies that the area of forested land must continue to increase to maintain CO_2 emission reductions, while at the same time maintaining existing carbon pools by conserving forest resources.

A New Zealand perspective on carbon sequestration

As a signatory to the 1992 Rio Accord, New Zealand is committed to reducing, by the year 2000, net CO_2 emissions to the level that existed in 1990. This commitment was made binding at the recent Kyoto Climate Summit. Current government policy in New Zealand states that 80% of the reduction in CO_2 emissions required to fulfil the Rio Accord will be met by a net increase in the rate of uptake of carbon in forest ecosystems. This could potentially be achieved through widespread planting of *Pinus radiata* and other timber species.

New Zealand's exotic forest estate consists of approximately 1.5 million hectares, with around 90% being *Pinus radiata* (New Zealand Forest Owners Assoc. Inc. 1996). Most of the exotic forests are located in relatively mesic sites of the central and southern North Island (51%), Northland and Auckland (18%), and the West Coast, Otago and Southland (14%). It is estimated that a further 5 million hectares of land currently under pasture is suitable for conversion to forestry (MacLaren 1993).

The existing exotic forests are predominantly the result of two major planting periods: the first during the depression years of the 1930's, and the second during the 1970's and 1980's as the original crop was harvested and replanted. The current annual net increase in planted exotic forest area is around 80,000 hectares. It peaked in 1995 at 90,000 hectares which reflected the favourable economic climate for wood products at that time. The greatest proportion of recent planting has occurred on the East Coast of the North Island, a region of generally low summer rainfall, in response to massive soil erosion on hill country caused by the tropical cyclone Bola in 1988. Significant forest expansion has also occurred recently in other dry-land areas such as Hawkes Bay, and Marlborough and Canterbury in the South Island (Fig. 1.1). In these regions, carbon uptake is strongly regulated by summer-time water deficit, and hence productivity is generally lower than at the mesic sites, which formerly were the main sites in which exotic species were planted. Quantification of the limitation imposed by soil water deficit on carbon assimilation and productivity in dryland forests has only recently occurred (Price and Black 1991, Arneth *et al.* 1998a).

The need for an accurate assessment of the potential for dry-land plantation forests to sequester carbon has not been widely recognised (Arneth *et al.* 1998b). However, it is required to determine the effect of the net increase in forested area in dry regions on the current national carbon budget. Moreover, it figures in determining the area of new forestry required to offset predicted carbon emissions in the future because dry-land areas are often most marginal for agriculture, and hence are most available for forestry. This is evident from the increased planting of *P. radiata* in Canterbury.

Current models of forest productivity in New Zealand are largely empirical, and based on long term forest growth measurements from the higher producing, mesic sites (e.g. Hollinger *et al.* 1993). These models are not suitable for predicting growth in dry-land forests. They may also not be suitable for predicting future forest growth

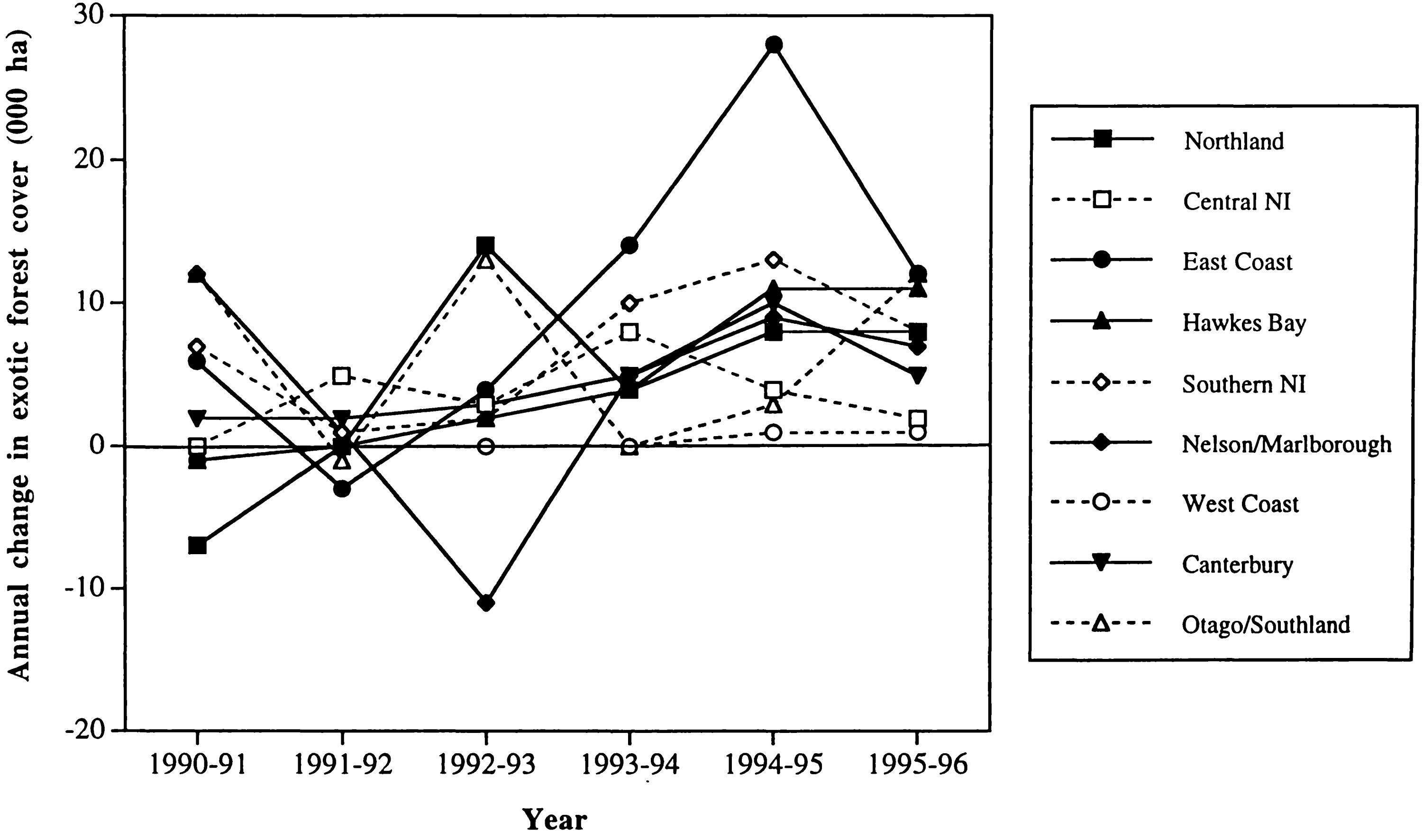

Figure 1.1 Annual change in exotic forest cover (predominantly *Pinus radiata*) by region. Closed symbols with solid lines indicate regions in which summer water deficits are common. (*Source* J Dennis pers. comm., New Zealand Ministry of Forestry)

rates given the likelihood of effects thereon from climate change and elevation of the atmospheric CO_2 concentration. A more mechanistic approach is thus required, where models are principally driven by commonly measured environmental variables connected to biophysical processes.

Modelling forest carbon sequestration

The carbon cycle in a forest ecosystem is complex and dynamic, and consists of pools in the soil, vegetation and atmosphere, fluxes between pools associated with the processes of photosynthesis and respiration, and feedback interactions between fluxes and pools. Carbon is fixed into organic compounds by plants during photosynthesis, and is respired back as CO_2 gas during respiration. To begin to quantify the capacity of plantation forests to sequester carbon therefore requires knowledge of the biophysical processes which regulate photosynthesis. As a caveat, however, it is recognised that non-biological phenomena such as fire, harvesting and wood transport, processing and product shipping and usage may also be significant.

Processes regulating photosynthesis at the leaf level are reasonably well understood for plants growing in the absence of water stress. This has resulted in models which can successfully describe the environmental regulation of stomatal conductance and photosynthesis in well-watered plants (Farquhar *et al.* 1980, von Caemmerer and Farquhar 1981). A current challenge for modellers is to extend the description of processes occurring at the leaf level to those occurring at the whole canopy scale (Leuning *et al.* 1995). Scaling up in space and time is necessary because models of ecosystem carbon and water flux are largely driven by the processes of photosynthesis and respiration which occur at the biochemical, cellular and leaf level over short time periods.

Models which scale processes from the leaf to canopy can be single-layer, where the properties of the whole canopy are ascribed to a single, horizontal plane (the "big leaf") before the fluxes are calculated (e.g. Sellers *et al.* 1992, Williams *et al.* 1997). Alternatively, models may be multi-layered in which the details of canopy microclimate and structure, as well as the vertical distribution of leaf photosynthetic characteristics, are explicitly considered (e.g. Wang and Jarvis 1990, Williams *et al.* 1996). Both approaches are used (Raupach and Finnigan 1988), although suited to different applications.

Big leaf models are appropriate when the focus is on systems in which the spatial scale of interest is much larger than that of the vegetation (e.g. the landscape scale at >10 km resolution). They are computationally less complex than multi-layer models, and so are also suitable when the temporal scale of interest is large (>1 year), as in studies of the long-term response of plants to elevated CO_2 and climate change (Commins and McMurtrie 1993). Parameters for single-layer models cannot be measured directly, nor can they be determined as the arithmetic mean of leaf level parameters, because of non-linear responses of plant processes to environmental variables (McNaughton 1994). Multi-layer models are appropriate when the spatial scale of interest is comparable to, or less than, the canopy height. The problem of defining parameters for multi-layered models is one of determining vertical profiles. Multi-layer models do not include horizontal variability so the vertical profiles are taken to be representative. All non-linearities remain at the leaf level, and fluxes calculated at the leaf level are simply added to determine the canopy flux (Leuning *et al.* 1995).

Scaling photosynthesis from leaf to canopy using nitrogen distribution

Farquhar (1989) showed that simple models which treat the leaf as a homogenous entity can successfully describe responses to light, temperature and CO_2, provided the distribution of chloroplast photosynthetic capacity within leaves is proportional to the distribution of absorbed irradiance. This can be extended to canopies if the distributions of leaf photosynthetic capacity, which is linearly related to leaf nitrogen concentration, and absorbed irradiance are the same throughout the canopy (Sellers *et al.* 1992). Under these conditions, equations describing leaf photosynthesis will also describe canopy photosynthesis, which is the basis of the big leaf model. It has been hypothesised that this condition also represents an optimal distribution of leaf nitrogen concentration (*N*) (Hirose and Werger 1987), where any re-distribution of *N* would reduce total daily photosynthesis.

Non-uniform distributions of *N* have been observed for individual leaves within canopies (Field 1983). Studies which have indicated that more *N* is allocated to foliage in brighter sites than darker ones are consistent with the optimal allocation hypothesis (Hirose and Werger 1987, Evans 1989, Ellsworth and Reich 1993). However, given that the distribution of radiation is always changing, there can be no fixed distribution of *N* that is proportional to absorbed irradiance (de Pury and Farquhar 1997). In the short term, canopy irradiance will change with the diurnal progression of the sun and with changes in cloud cover, illuminating some parts of the canopy and shading others. Over the long term, changes in the distribution of radiation will occur as a canopy approaches closure and the incidence of self-shading, and shading from neighbouring trees, increases. In each case the optimal distribution of N would have to change, requiring a redistribution of N from shaded to illuminated parts of the canopy.

Recent studies suggest that factors apart from irradiance might also influence the distribution of nitrogen within a tree canopy. Hollinger (1996) found less N in brightly illuminated sites throughout a vertical profile in a broad-leaved canopy, and more N in less illuminated sites, than would be expected according to the optimal allocation hypothesis. He argued that this resulted from factors other than irradiance, including herbivory, sunflecks and photoinhibition, which affect carbon assimilation differently throughout the canopy. In a 3-dimensional study, Livingston *et al.*(1998) found a strong correlation between N and height, but not always irradiance, in a young *P. radiata* tree. They argued that branch proximity to the leader, which is a major carbon and nutrient sink, strongly determines the spatial distribution of N.

Assuming that the canopy distribution of N follows that of irradiance therefore may not be correct. However, an alternative scaling mechanism which accounts for factors influencing carbon assimilation apart from irradiance will be complex because of numerous interacting factors, and may explain why one does not exist. Therefore the pragmatic approach suggested by Hollinger (1996) was adopted in this thesis, where N is allocated as a linear proportion of irradiance but is constrained by measurements of N at the top and bottom of the canopy.

Model validation

Models scaling up processes in space and time must be rigorously tested to avoid propagating errors at each increase in scale (Jarvis 1995). Such errors result from non-linearities in physiological responses to driving environmental variables, as well as heterogeneity and patchiness in the spatial and temporal distributions of structures and processes. It is therefore important that models be constrained by measurements at each scale.

It is relatively straightforward to validate models of photosynthesis and water-use at the leaf level with independent measurements of leaf gas exchange. Validating models of canopy photosynthesis is more difficult. Photosynthesis measurements of entire trees can be made using large chambers (Lloyd *et al.* 1995), however such chambers inevitably modify the environmental conditions surrounding the plant and are generally restricted in size for logistical reasons. Fluxes of CO_2, water vapour and heat can be measured at the forest stand scale. However, the net rate of influx or efflux of CO_2 in a forest is the result of a balance between two equally large rates of carbon assimilation by the tree canopy and understorey and respiration by tree and understorey roots and soil micro-organisms. Deconvolution of tree canopy photosynthesis from eddy covariance measurements therefore requires additional measurements of soil respiratory CO_2 fluxes (Arneth *et al.* 1998a).

Carbon isotope analysis of plant tissue provides an independent measurement of physiological activity in plants at a range of spatial and temporal scales, and could be used to test models of photosynthesis and water-use at the leaf and tree canopy scales. Water-use efficiency (WUE) is the ratio of carbon assimilated to water transpired. It is strongly controlled by stomatal conductance since fluxes of CO_2 into leaves and water vapour losses are linked via the stomata. Analysing the stable carbon isotope composition ($\delta^{13}C$) of plant tissue is a technique by which WUE can be determined in intact plants independent of gas exchange measurements. During photosynthesis, plants discriminate against the heavier ^{13}C isotope in favour of the lighter ^{12}C isotope. The extent of the discrimination is linked to the ratio of leaf intercellular to ambient CO_2 concentrations (c_i/c_a) (Farquhar *et al.* 1982). In turn, c_i/c_a reflects the balance between photosynthetic demand for CO_2 due to carboxylation, and supply via diffusion through the stomata. WUE also reflects the balance between photosynthesis and stomatal conductance since transpiration is a linear function of stomatal conductance and the humidity deficit at the evaporating surface (which approximately equals the atmospheric value for needle-leaved species such as *P. radiata*). Thus there is a positive relationship between WUE and ^{13}C discrimination (Farquhar and Richards 1984). Because the ^{12}C and ^{13}C isotopes are stable, the record is preserved in plant tissue.

Stable carbon isotope analysis can provide information on WUE over a range of spatial and temporal scales depending on the source of carbon analysed. In the very short term, the $\delta^{13}C$ of CO_2 in air entering and leaving a gas exchange chamber can be compared to indicate the extent of instantaneous isotopic discrimination at the leaf scale (Evans *et al.* 1986). Soluble sugars can be extracted from leaves which will indicate the assimilation weighted discrimination integrated over several days (Brugnoli *et al.* 1988). Over the longer term, analysis of leaf structural carbon (cellulose and lignin) will indicate WUE integrated over the life of the leaf. In trees, $\delta^{13}C$ of stem wood from growth rings gives a measurement of WUE integrated spatially over the whole canopy and temporally over the year (Livingston and Spittlehouse 1996).

Goal of this thesis

Knowledge about the environmental regulation of carbon assimilation and water-use in dry-land forests is limited, and so the goal of this thesis is to **quantify biotic and abiotic regulation of photosynthesis and water-use from the spatial scale of individual leaves up to the whole canopy, and temporally from instantaneous to the season, in a dry-land *Pinus radiata* forest.** This has not been done before for *P. radiata*, nor has it been done for a tree species in a maritime climate such as that in New Zealand. The goal is achieved by Chapters 2 - 4.

In Chapter 2, parameters are derived for a biophysical model of C_3 photosynthesis and stomatal conductance from measurements made under controlled conditions in the laboratory. The photosynthetic capacity of needles was related to N and to leaf temperature, both of which were experimentally manipulated. Relationships of photosynthetic capacity with N are needed to scale photosynthesis in space, and relationships with temperature to scale in time.

In Chapter 3, the leaf-level model was combined with a sub-model of soil water balance to quantify environmental regulation of leaf-level photosynthesis and transpiration at two contrasting sites over two years. Analysis of $\delta^{13}C$ in wood throughout growth rings was used for the first time to provide an independent measure of the integrated effect of climatic variables and soil water deficit on c_i. This

Chapter represents the first detailed analysis of the factors responsible for the seasonal course in ^{13}C discrimination.

In addition to non-random allocation of nitrogen within canopies, trees show a high degree of flexibility in re-allocating nitrogen between leaves (Hollinger 1996). As a forest canopy approaches closure, the pattern of irradiance will change with the lower foliage becoming increasingly shaded by upper foliage layers. Thus we might also expect the distribution of *N*, photosynthesis and growth to change. In Chapter 4 a field experiment was undertaken to quantify the response of 8-year-old *P. radiata* trees to a long-term reduction in illuminated leaf area. A shading treatment was imposed by which the lower 60 % of the canopy was enclosed in 50 % porosity shade cloth. Growth of shaded and control trees was measured periodically throughout the following two years, and foliage sampled through the canopy was analysed for δ^{13}C and *N*.

To elucidate and quantify the processes regulating growth in the shaded trees, a multi-layer model of canopy photosynthesis was used. The relationship between photosynthetic capacity and *N* determined in Chapter 2 was used to characterise the vertical distribution of photosynthetic capacity from the measurements of *N*. A model of radiation transfer, which incorporated the influence of the shade cloth, was used to calculated the absorbed beam and diffuse radiation for foliage in each of 20-layers through the canopy. Stomatal conductance and photosynthesis were calculated separately for sun and shade leaves. The large impact of summer-time soil water deficit on canopy photosynthesis at this site was incorporated using a site water balance algorithm. The model was validated against independent measurements of canopy radiation absorption, canopy transpiration, and the seasonal course of mean canopy intercellular CO_2 concentration derived from $\delta^{13}C$ measurements within the growth rings.

Chapter 4 thus builds on Chapter 2, where model parameters were derived in relation to N and temperature, and Chapter 3 which quantified the impacts of seasonal variations in climatic variables and soil water content on stomatal conductance and photosynthesis at the leaf level. Chapters 2, 3 and 4 are formatted for publication in scientific journals. Chapters 2 and 3 have been published, and Chapter 4 will shortly be submitted. Chapter 5 is a general discussion integrating elements from the preceding three chapters. It is followed by the overall conclusions and recommendations for future research. All cited references in this thesis are listed together following Chapter 5.

Chapter two

Determination of photosynthetic model parameters in response to temperature and nitrogen concentration in Pinus radiata D. Don

published in the following journal.

WALCROFT, A. S., WHITEHEAD, D., SILVESTER, W. B., & KELLIHER, F. M. (1997). The response of photosynthetic model parameters to temperature and nitrogen concentration in Pinus radiata D. Don. Plant, Cell and Environment, 20(11), 1338–1348. https://doi.org/10.1046/j.1365-3040.1997.d01-31.x

Chapter three

Seasonal changes in stable carbon isotope ratios within annual rings of Pinus radiata reflect environmental regulation of growth processes

published in the following journal

A. S. Walcroft, W. B. Silvester, D. Whitehead, & F. M. Kelliher. (1997). Seasonal Changes in Stable Carbon Isotope Ratios within Annual Rings of Reflect Environmental Regulation of Growth Processes. Functional Plant Biology : FPB, 24(1), 57–68. https://doi.org/10.1071/PP96025

Chapter four

The effects of long-term, partial shading on growth and photosynthesis in Pinus radiata D. Don trees

published in the following journal

Walcroft, A. S., Whitehead, D., Kelliher, F. M., Arneth, A., & Silvester, W. B. (2002). The effects of long-term, partial shading on growth and photosynthesis in Pinus radiata D. Don trees. Forest Ecology and Management, 163(1), 151–163. https://doi.org/10.1016/S0378-1127(01)00540-0

CHAPTER FIVE

DISCUSSION

The phenomena of global environmental and land-use changes have presented scientists and modellers with an important challenge, and a somewhat unique opportunity, to develop measurement techniques and modelling expertise capable of predicting the future response of the bioshpere to such perturbation. Direct measurement of ecosystem functioning is not practical, and the experimental manipulation of ecosystems is not ethical. Thus, predictions must be based on measurements at smaller temporal and spatial scales combined with the simulation of processes and feedbacks occurring at larger scales using models.

Such models must incorporate the scaling up of processes which occur at much smaller scales for two reasons. Firstly, the spatial and temporal scales at which predictions are required are much larger than those which can be practically measured. Secondly, in order for the models to have predictive value, they must be based on the processes upon which the environmental perturbations are known to act (Jarvis 1995). Fluxes of carbon and water between the biosphere and atmosphere occur largely via the processes of photosynthesis and transpiration at the leaf scale, and these processes are regulated by climatic variables such as air temperature, humidity deficit, radiation and rainfall, and by the ambient CO_2 concentration.

The current, widely accepted model of C_3 photosynthesis in leaves was developed by G. D. Farquhar and colleagues during the early 1980's (Farquhar *et al.* 1980, von Caemmerer and Farquhar 1981), and is based on scaling up the biochemical processes of photosynthesis from the sub-cellular to the leaf level. This model has been used in the interpretation of leaf gas exchange data, and more recently in the interpretation of ecosystem CO_2 flux data measured by the eddy covariance technique (Hollinger *et al.* 1994, Arneth *et al.* 1998c). However, prior to the use of this model to address questions of carbon dynamics at the ecosystem scale, it is important to determine the extent to which species differ in their gas exchange characteristics.

Two important conclusions are evident both in the literature and in the results of this thesis (Chapter 2). Firstly, there is a close correspondence between the capacities for carboxylation (i.e. V_{cmax}) and electron transport (i.e. J_{max}) across the majority of species measured (Wullschleger 1993, Chapter 2: Fig. 4). This suggests that over a wide range of habitats and environments plants are able to preserve a balance between carboxylation and light harvesting. Secondly, there is an equally strong and positive linear correspondence between these measures of photosynthetic capacity and leaf nitrogen concentration (Field and Mooney 1986, Evans 1989, Chapter 2: Fig. 8). This indicates that most of the nitrogen in leaves is allocated to photosynthetic proteins and associated molecules, and that photosynthetic capacity may be accurately estimated from simple measurements of leaf nitrogen concentration. Such a relationship will be useful in assigning photosynthetic parameters to different vegetation classes for large scale models (e.g. Schulze *et al.* 1994), particularly given the potential for remotely sensing leaf nitrogen concentration (Prince and Goward 1995).

Extending the temporal scale when modelling photosynthesis requires a description of photosynthetic responses to irradiance and temperature, both of which both change diurnally and seasonally. The relationship between photosynthesis and irradiance is determined principally by the hyperbolic response of the electron transport rate (J) to irradiance, which was modelled using a non-rectangular hyperbola following Farquhar and Wong (1984) (equation 2.A3, Chapter 2). In this equation, J is a function of three parameters: J_{max}, θ, and α (see Chapter 2 for details). J_{max} is determined from the value of photosynthesis at saturating irradiance and c_i. For simplicity, values for α and θ were assumed constant at 0.2 and 0.95 respectively. Leuning (1990) found considerable variation in α in leaves of *Eucalyptus grandis* subjected to different irradiance and nutrient treatments, but suggested this variation may not have been physiologically significant due to interaction between α and θ during the curve fitting procedure. Further detailed laboratory measurements of photosynthetic light responses under varying environmental conditions are required in order quantify the variation in α and θ, and to understand the physiological cause of that variation.

Prediction of the temperature response of *P. radiata* was markedly improved when parameter values derived from measurements of A/c_i response curves at different temperatures were used instead of the only previously available parameters based on studies of *Gossypium hirsutum* (cotton) (Chapter 2, Fig. 9). The contrasting temperature response curves resulted from differences in the activation and deactivation energies for both V_{cmax} and J_{max}. This indicates that it may be necessary to derive parameter values for the temperature dependence of photosynthesis for different species, just as it is necessary to derive the parameters for photosynthetic capacity. However, the activation energy of V_{cmax} for *P. radiata* (45 kJ mol^{-1}) is similar to values derived for other woody perennials: 45 kJ mol^{-1} in *Eucalyptus* *pauciflora* (Kirschbaum and Farquhar 1984), 50 kJ mol^{-1} in *Arbutus unedo* (Harley *et al.* 1986), and 55 kJ mol^{-1} in *Quercus alba* (Harley and Baldocchi 1995). Thus, it may be possible to arrange similar species into functional groups, and thereby use group average parameter values in large scale models of CO_2 and water flux between the land surface and atmosphere.

The spatial scale was extended from the leaf to the canopy in Chapter 3, where the effect of seasonal changes in temperature, irradiance and rainfall on canopy photosynthesis, conductance, transpiration and the soil water balance were investigated. Inter-annual climatic and soil water variations are reflected in tree-ring growth (Fritts 1976), and in the stable carbon isotope composition of wood between years (Dupouey *et al.* 1993, Livingston and Spittlehouse 1993, 1996). Within years, seasonal changes in climate influence the annual course of soil water content in forested catchments (Whitehead and Kelliher 1991a, b). Seasonal changes in $\delta^{13}C$ values within individual tree rings have also been reported (Wilson and Grinsted 1977, Leavitt 1993), but attempts to correlate these with individual climatic variables such as temperature and rainfall gave contradictory results. Annual rings of young *P. radiata* stands growing in New Zealand are often >10 mm across, which allows great precision in wood sampling. Thus, it was possible to measure seasonal cycles in $\delta^{13}C$ within individual growth rings from trees in two forest sites which differed markedly in soil and climatic characteristics (Fig. 3, Chapter 3). The amplitude of the seasonal cycle was 4 ‰ at the dry site, but only 1-2 ‰ at the mesic site. Since the seasonal variation in the concentration and isotopic composition of atmospheric CO_2 is small (Keeling 1993), it was shown that the measured $\delta^{13}C$ cycles were the result of the regulation of c_i, via photosynthesis and stomatal conductance, by climatic variables and by the influence of seasonal soil water deficits.

A combined leaf-level model of photosynthesis and stomatal conductance was run for the two year period at each site which coincided with the tree-rings analysed for $\delta^{13}C$. The model was used to predict the seasonal course of c_i, which determines the extent of ^{13}C discrimination during photosynthesis in the absence of variation in c_a (Farquhar *et al.* 1982). The model predicted a seasonal course of leaf level c_i which closely matched the measured course of canopy c_i in terms of the timing of peaks and troughs, and also correctly predicted the absolute difference between the dry and mesic sites. Thus, it appears the seasonal course in $\delta^{13}C$ reflects the integrated effects of climatic variables and the soil water content, rather than a particular individual climatic variable.

The model overestimated the magnitude of the seasonal variation in c_i, however, particularly at the dry Balmoral Forest site. This is because the model represented only fully exposed needles at the top of the canopy, whereas the measurements based on $\delta^{13}C$ in stem wood represented an integration of c_i in foliage throughout the whole canopy. Exposed foliage is likely to show a greater seasonal variation in c_i compared with the whole canopy, which consists of foliage of different age classes in a range of canopy micro-climates. A quantitative explanation of the measured seasonal course in $\delta^{13}C$ would therefore require the leaf-level model to be scaled up to the canopy.

In Chapter 4, a model of canopy photosynthesis, conductance and transpiration was developed by combining the leaf-level photosynthesis model with a one-dimensional model of radiation transfer based on Beer's law. Output from the model was compared with measurements of absorbed irradiance and canopy evaporation, as well as integrated canopy c_i calculated from the measured seasonal $\delta^{13}C$ patterns. The timing of the seasonal course in predicted canopy c_i was identical to that predicted by the leaf-level model for Balmoral Forest (compare Fig. 6, Chapter 3 and Fig. 4, Chapter 4). However, in contrast to the leaf-level model, the canopy model successfully predicted the magnitude of the seasonal pattern in canopy c_i.

The canopy photosynthesis model comprised a theoretical framework with which to interpret results from the shading experiment. It was thus an essential tool in determining the biophysical processes which regulated carbon assimilation in the trees following imposition of the shading treatment. During the first year there was a large impact of the shade cloth on illuminated leaf area (Table 2, Chapter 4), and an increase in carbon partitioning to branch growth at the expense of the main stem (Table 5, Chapter 4). Further, measurements of leaf nitrogen and $\delta^{13}C$ revealed a reallocation of leaf nitrogen from foliage below the shade cloth to that above and largely explained the resulting physiological response. The canopy photosynthesis model was then used to show the impact of the changes in leaf area and partitioning on absorbed radiation (Table 3, Chapter 4) and canopy photosynthesis (Table 6, Chapter 4).

Two important conclusions resulted from this modelling analysis. Firstly, the comparative growth of shaded and control trees was not a simple function of illuminated leaf area. It was also dependent on the distribution of leaf nitrogen throughout the canopy. The reduction in measured growth was proportionately less than the reduction in leaf area because the upper layers of the canopy, where leaf nitrogen is more concentrated, contribute more to canopy photosynthesis than the lower layers. Secondly, the model showed that tree growth in the dry-land forest is dominated by the overwhelming influence of soil water deficit during the summer. As a result, a large proportion of the annual growth occurs outside of the notional growing season. Soil water deficit reduces the canopy assimilation rate by around 50 % in summer, and changes the seasonality of peak photosynthesis from summer to spring and autumn. The model also revealed that respiration in the foliage is a significant proportion of gross canopy photosynthesis. Low winter temperatures, which reduce the rate of respiration, therefore contribute to maintaining net carbon assimilation throughout the winter.

CONCLUSIONS

In conclusion, the main findings of this thesis are:

- The strong influence of leaf temperature on photosynthesis is successfully described by the currently accepted model of C_3 photosynthesis provided the temperature response parameters for V_{cmax} and J_{max} are quantified.
- The ratio of J_{max}:V_{cmax} is a linear function of leaf temperature in *P. radiata.*
- V_{cmax} and J_{max} are linear functions of leaf nitrogen concentration in *P. radiata.*
- Dynamic seasonal variation of ^{13}C discrimination in canopy foliage is reflected directly in $\delta^{13}C$ values of wood within annual growth rings.
- The seasonal variation in discrimination is driven by the interactive effects of climatic variables and soil water content on photosynthesis and stomatal conductance.
- Forest trees respond dynamically to changes in illuminated leaf area by re-allocating leaf nitrogen to unshaded branches and by partitioning carbon to enhance branch growth.
- Forest tree growth is not a simple function of leaf area, but is also dependent on the canopy distributions of irradiance and leaf nitrogen.
- Extended periods of summer soil water deficit cause large reductions in canopy photosynthesis and tree growth, and change the seasonal course of carbon assimilation.
- Models which scale up processes from the leaf-level to the canopy can provide a framework with which to analyse and interpret experimental results.

FUTURE RESEARCH

The following possibilities for future research originate from this thesis:

- V_{cmax} and J_{max} are being measured in an increasing number of species, yet the literature is sparse with respect to data on the temperature response of these parameters. Research is required to determine if the temperature response is species specific, in which case parameters need to be individually defined, or whether parameters can be defined for functional groups of vegetation.

- Relationships between photosynthetic capacity and leaf nitrogen concentration for functional vegetation groups are required to be defined for large scale modelling of ecosystem carbon assimilation and water-use.

- Analysis of variation in the stable oxygen isotope composition of wood within tree-rings should reveal information on evaporative conditions at the time the wood was laid down. Analysing both $\delta^{13}C$ and $\delta^{18}O$ could therefore reveal separate information on canopy photosynthesis and transpiration.

- Additional research is required to define the dynamic response of stomatal conductance and photosynthesis to soil water deficit, particularly in defining the critical values of soil water content or water potential at which photosynthetic limitation occurs.

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