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Research Facility

An Assessment of the Vulnerability of Australian Forests to the Impacts of Climate Change

2. Biophysical impacts of climate change on Australia's forests

Image: Ann Penny

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Emer O'Gara, Giles Hardy, Thomas Lyons, Li Li and Bradley Evans

FOREST VULNERABILITY ASSESSMENT

Biophysical impacts of climate change on Australia's forests

Contribution of Work Package 2 to the Forest Vulnerability Assessment

Macquarie University and Murdoch University

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Executive Summary

The assessment of the vulnerability of Australian forests to climate change is an initiative of the Natural Resource Management Ministerial Council (NRMMC). The National Climate Change Adaptation Research Facility (NCCARF) was approached to carry out a comprehensive Forest Vulnerability Assessment (FVA). NCCARF engaged four research groups to investigate distinct aspects in relation to the vulnerability of forests, each of which has produced a report. In addition a fifth group was engaged to create a summary and synthesis report of the project.

This report – Biophysical impacts of climate change on Australia's forests - is the **second** in the series. It presents a review of the primary literature on evidence of impacts of climate change on Australian forests. Existing evidence for climate change impacts in relation to direct stresses (CO_2, temperature and rainfall), indirect stresses (fire, pests, pathogens and weeds) and plant processes (growth, transpiration and phenology) is discussed. The report concludes with a discussion of the overall impact of climate change on vegetation and the ecosystem services provided by forests. It should be noted that there have been several excellent reviews of climate change impacts on Australian forests as well as reports on climate change impacts on natural heritage and biodiversity. Conclusions drawn from these earlier reviews are not repeated. Instead, the report focuses on drawing evidence from the primary literature, including grey literature. Relevant literature was identified by bibliographic searches and in consultation with experts across Australia.

This review highlighted a number of uncertainties involved in assessing forest vulnerability to climate change. These include uncertainty over changes in the climate, the ecosystem-scale responses to climate change, and interactions of climate change impacts with other global change processes. There is, however, clear evidence of the impact of some individual factors. These are summarised below.

Impacts

The most certain change is the global rise in atmospheric CO_2 concentration. Increased atmospheric CO_2 has been demonstrated to increase productivity and increase water use efficiency. However, in Australia’s forests, the availability of nutrients may restrict this benefit which will result in shifting species distributions, with largely negative consequences for biodiversity.

Rising temperature has the potential to increase productivity in cool and cold forests, but will also negatively impact on biodiversity, with cool-climate specialists being edged out of these areas. In warmer ecosystems, rising temperatures could cause decreases in productivity, and combined with lower rainfall cause more severe droughts.

Reductions in water availability and increased drought frequency are of major concern for many forest systems and pose a significant threat to most aspects of ecosystem functioning.

In contrast, the limited evidence on the direct effects of climate change on phenology suggests that flowering and reproduction of forest systems in Australia are relatively robust under climatic variability.

Fire occurrence was identified as a factor positively influenced by temperature rise and the projected changes in most other climate variables. However, fire occurrence was found to be highly location specific, and dependent on the ability of the vegetation to build up a critical fuel load. Fire will stay an important stressor, affecting native and plantation forests, and under the projected changes in climate is most likely to increase in frequency and severity in dry temperate forest systems found in the southeast and southwest of Australia.

Temperature rise was generally found to positively influence insect pest species. Pest outbreaks can therefore be considered as an important stressor of native and plantation forest that will likely increase under the projected changes in climate.

Pathogens and invasive weeds are likely to continue to have an impact on forest systems, but the available direct evidence indicates no general strong positive influence of temperature rise on these stressors. However, the responses were found to be highly species dependent. Based on climate suitability there is a likely range shift for most species. However, in general the overall impact of these stressors on native and plantation forests is unlikely to worsen with the projected changes in climate.

Knowledge gaps

There are very significant gaps in our knowledge. At this point we do not have credible predictions for impacts of climate change for most of the Australian forest estate, and we are not yet in a position to make such predictions. There are major research gaps in relation to climate projections, ecosystem scale data, process understanding and research integration and modelling.

Water availability has been shown to be the key environmental factor structuring Australian forests and woodlands, but there are major uncertainties surrounding future projections of water availability with regard to rainfall, evapotranspiration and drought frequency. Researchers around the world use ecosystem scale data sets to develop and test ideas about controls on forest productivity. The availability of data for Australian forests lags well behind other countries. Such data are a fundamental requirement for scientific research into forest vulnerability to environmental factors. We critically need better measurements and monitoring of current and past forest processes if we are to project into the future. There are significant gaps in our understanding of major response processes including effects of rising atmospheric CO_2 concentration on productivity and water use of Australian forests and effects of long-term drought on ecosystem processes, particularly mortality.

There are also more fundamental questions. There is a real mismatch between predictions of vulnerability coming from bioclimatic and ecophysiological models. Bioclimatic models, based on observed climatic niches, found that many Australian species have narrow ranges and concluded they are very vulnerable to climate change. On the other hand, ecophysiological models, based on mechanistic understanding of climate impacts on plant processes, predicted widespread increases in forest production. The difference between these two approaches reflects the fact that we do not understand, at a very fundamental level, what limits species distributions. Basic ecological and ecophysiological research is needed, targeted at apparent climatic limits identified by bioclimatic models, to better understand how climate limits species distributions.

Overall, we found that research was very fragmented, with many individual research groups doing very fine work, but few attempts to integrate across different strands of research, or to scale up from existing research to make quantitative projections for climate impacts on native Australian forests and woodlands. To achieve such projections would require that the wide range of research surveyed in this review be synthesised in a modelling framework. We strongly recommend the development of a dynamic vegetation model for Australia that could be used as a quantitative framework to draw together the large body of research discussed here and make informed projections for the future.

1. Introduction to the Forest Vulnerability Assessment project

The Natural Resource Management Ministerial Council (NRMMC) identified the need for a national assessment of the vulnerability of Australia's forests to climate change and a framework for adaptation to the potential impacts. The National Climate Change Adaptation Research Facility (NCCARF) through the Commonwealth Department of Climate Change and Energy Efficiency (DCCEE) was approached to carry out such a comprehensive assessment of the vulnerability of Australia's forests. This Forest Vulnerability Assessment (FVA) has been carried out by four research groups each of which has produced a report. In addition a Synthesis Report (Boulter et al. 2011) has been produced which summarises and synthesises the outcomes from the four narrowly focussed reports. A summary for policy makers for the whole project has also been prepared..

A Steering Committee of federal and state government and university stakeholders involved in forest management, policy and research was engaged to adopt the NRMMC brief and set the parameters for this study. Here we scope the FVA and introduce the general terms of reference for the project.

1.1 Purpose and approach

The primary aim of the Forest Vulnerability Assessment project is to provide forestry policy makers and forest managers in Australia with information that assists the sector to adapt to climate change. In particular, the project sought to provide governments, natural resource managers and the business sector with:

- *an improved understanding of current knowledge of the likely biophysical and socio-economic consequences of climate change for Australia's native and planted forest regions;*
- *an assessment of the vulnerability of Australian forests from the perspectives of both resource use and ecosystem services - identifying particularly vulnerable forests and communities in major forest areas;*
- *an understanding of what is already being done in Australia in relation to understanding and managing climate related risk in relation to forests; and*
- *guidance on key gaps to assist climate change adaptation.*

The project has sought to enhance awareness of forest managers and policy makers to climate change risk by providing up-to-date information about likely climate change impacts on forests and vulnerability to these impacts. As outlined above, the project was undertaken by a consortium of research groups with specific aspects of the project allocated to five separate Work Packages (WP) based on four major research themes and a synthesis. Work

Packages 1 to 4, through an extensive review of literature and policy from a range of sources (including peer reviewed journals and technical reports) and through engaging with stakeholders, provide a critical analysis of the vulnerability of Australia's forests to climate change impacts. (see Table 1.1 for a list of reports).

A fifth Work Package (Boulter et al. 2011) summarises and synthesises all Work Packages, draws some broader conclusions on regional variability and vulnerabilities, and provides a review of the legal issues surrounding forest management under climate change.

Table 1.1 The Work Package reports delivered as part of the forest vulnerability assessment (Abbreviations: JCU – James Cook University, Macquarie – Macquarie University, Murdoch – Murdoch University, QUT – Queensland University of Technology, USC – University of the Sunshine Coast, USQ – University of Southern Queensland, GU - Griffith University and NCCARF, National Climate Change Adaptation Research Facility).

WP	Report title	Authors and affiliations
1	Establishing the need and consultation with key stakeholders in forest policy and management under climate change. Contribution of Work Package 1 to the Forest Vulnerability Assessment (Wood et al. 2011)	Helen Wallace, Kathleen Wood, Anne Roiko and Peter Waterman (USC)
1	The scenarios of climate change: Tools, methods, data and outputs. Supplementary Materials of Work Package 1 to the Forest Vulnerability Assessment	Richard Warrick (USC and CLIMsystems Ltd)
2	Biophysical impacts of climate change on Australia's forests. Contribution of Work Package 2 to the Forest Vulnerability Assessment (This report)	Belinda Medlyn and Melanie Zeppel (Macquarie), Tom Lyons, Giles Hardy Niels Brouwers, Kay Howard, Emer O'Gara, Li Li and Bradley Evans (Murdoch)
3	Socio-economic implications of climate change with regard to forests and forest management. Contribution of Work Package 3 to the Forest Vulnerability Assessment (Cockfield et al. 2011)	Geoff Cockfield and Tek Maraseni (USQ), Laurie Buys and Jeffrey Sommerfeld (QUT), Clevo Wilson and Wasantha Athukorala (QUT)
4	Climate change adaptation options, tools and vulnerability. Contribution of Work Package 4 to the Forest Vulnerability Assessment (Wilson and Turton 2011)	Steve Turton and Robyn Wilson (JCU)
5	An assessment of the vulnerability of Australian forests to the impacts of climate change (Boulter et al. 2011)	Sarah Boulter (GU & NCCARF), Roger Kitching (GU), Frank Stadler (NCCARF)
5	An assessment of the vulnerability of Australian forests to the impacts of climate Change. Supplementary Material: Forest resources, climate change and the law	Douglas E. Fisher (QUT)

1.2 Definitions of forests and forest uses for the purpose of the project

The scope of the project is largely set by the definition of forests used. We adopted the definition in the 2008 *Australia's State of the Forests Report* (SOFR) (Montreal Process Implementation Group for Australia 2008). This definition includes both native forests and plantations:

> *A FOREST is an area, incorporating all living and non-living components, that is dominated by trees having usually a single stem and a mature or potentially mature stand height exceeding two metres and with existing or potential crown cover of overstorey strata about equal to or greater than 20%. This includes Australia's diverse native forests and plantations, regardless of age. It is also sufficiently broad to encompass areas of trees that are sometimes described as woodlands.*

Based on this definition, the assessment includes a large part of Australia's mallee ecosystems (defined as dominated by multi-stemmed eucalypts - any one of about 25 species depending upon location) and encompasses very large areas of tropical savannah and woodland (also referred to as rangelands), where trees are spread out in a more open landscape and grazing is the predominant landuse. Inter-tidal, salt tolerant forests, often referred to as mangroves, also fall within this definition of forests. What many people would traditionally regard as forests – expanses of tall, closely spaced trees – are a relatively small part of the country's total forest estate.

Australia's forests are dominated by eucalypt forests (including the genera *Eucalyptus, Corymbia* and *Angophora*) and acacia forests making up about 89% of all native forest types (see Table 13). Both these forest types support an enormous diversity of species with over 700 eucalypt species and almost 1000 *Acacia* species (Montreal Process Implementation Group for Australia, 2008) as well as other plant species. Other important forest types cover smaller areas. These include rainforest, as well as *Melaleuca* wetlands and mangroves.

The SOFR 2008 report also used the National Forest Policy Statement (Commonwealth of Australia 1992) definition of plantations:

> *Intensively managed stands of trees of either native or exotic species created by the regular placement of seedlings or seeds*

which has also been adopted for the Forest Vulnerability Assessment.

In summary, Australia's forests are a continuum of large-scale industrial plantations at one extreme and native forests (including mallee, savannah, woodland and mangroves) at the other. In order to place the Australian forest estate firmly into a management context, we superimpose a set of forest type categories, reflecting the way forests are used:

- Plantation or farm forests
- Productive native forests
- Conservation native forests
- Environmental plantings

Table 1.2 Total area ('000 hectares) under three of the four categories of forest type used in this report including the percentage of Australia's total area under each type. The coverage of environmental plantings has not been quantified. Source: Montreal Process Implementation Group for Australia (2008).

Forest Type	ACT	NSW	NT	QLD	SA	Tas	Vic	WA	Aus	% of forest area
Plantation/farm forests	10	345	26	233	172	248	396	389	1818	1
Productive native forests	5	21060	30994	48005	4826	1996	4332	13797	125052	83
Conservation native forests	108	5148	16	4576	4029	1121	3505	3868	22371	16
Total forest	133	26553	31036	52814	9024	3364	8233	18054	149215	100

Table 1.3 Important vegetation types and their representation in the Australian forest conservation estate.

Forest vegetation type	**Area ('000 ha)**	**Portion of forest type in conservation area (%)**	**Description**
Acacia	10,365	5	Australia's second most common forest type; predominantly woodlands (average annual rainfall <750mm); can form open forests in wetter areas; found in all states and the Northern Territory; Mulga (*Acacia aneura*) dominant species in arid and semi-arid zone; Brigalow (*A. harpophylla*) widespread in Queensland and northern New South Wales.
Callitris	2,597	8	Found in a wide variety of climates; tolerant of temperatures ranging from below 0°C to more than 40°C; areas of annual rainfall > 300 mm, but can be as low as 200 mm; wide range of soil types, but commonly nutrient-poor soils associated with mycorrhiza.
Casuarina	2,229	39	Woodlands or open forests; all states and territories of Australia; semi-arid zone; coastal areas; Belah (*Casuarina cristata*) forests have the widest distribution; Belah and river she-oak (*C.*

			cunninghamiana) common inland; Coast she-oak (*C. equisetifolia)*, rock she-oak (*Allocasuarina huegeliana*) and drooping she-oak (*A. verticillata*) form pure stands.
Eucalypt	116,449	18	Three genera – *Eucalyptus*, *Corymbia* and *Angophora* – are usually referred to as eucalypts; found throughout Australia except in the most arid regions; variety of dominant structures.
Mangroves	980	18	Mangroves are important and widespread coastal ecosystems in the intertidal zone of tropical, subtropical and protected temperate coastal rivers, estuaries and bays. Can form dense, almost impenetrable stands of closed forests providing coastal protection from storm and wave action.
Melaleuca	7,556	11	There are hundreds of species in the genus *Melaleuca* and many other species in closely related genera, such as *Callistemon.* About 75% of Australia's melaleuca forest occurs in Queensland, particularly on Cape York Peninsula.
Rainforest	3,280	55	'Rainforest' is a general term for a range of broad-leaved forest communities with closed canopies; do not depend on fire for their regeneration; account for most (77%) of Australia's closed crown cover forest; extend across the top of northern Australia from the Kimberley to Cape York and down the east coast to the cool temperate zone in Tasmania.

Plantation/farm forests

In this category are those planted forests which are destined to be harvested for economic benefit at some time in the future. They include major broad-acre plantings of exotic species such as pines as well as smaller farm forestry plantings utilising a variety of species from construction to cabinet timbers.

In the 2010 National Forest Inventory update (Gavran and Parsons 2010), there were a reported 2.02 million hectares of plantations of which 1.02 million hectares was pine (softwood) and 0.99 million hectares of hardwoods of various species and mixtures. This is an increase of 49 658 hectares of new plantations from that reported in the 2008 State of the Forests Report (Montreal Process Implementation Group for Australia 2008). The area of plantation estate in Australia has continued to expand, with planting of hardwoods the greatest area of expansion (from 29% of all plantations in 1999 to 49% in 2009). There are several regions of plantation activity (Figure 1.1) with the largest proportion of the national estate being in Victoria and Western Australia. The majority of plantations are privately owned (62%). One-third are publicly owned and a further 5% are jointly owned (Gavran and Parsons 2010).

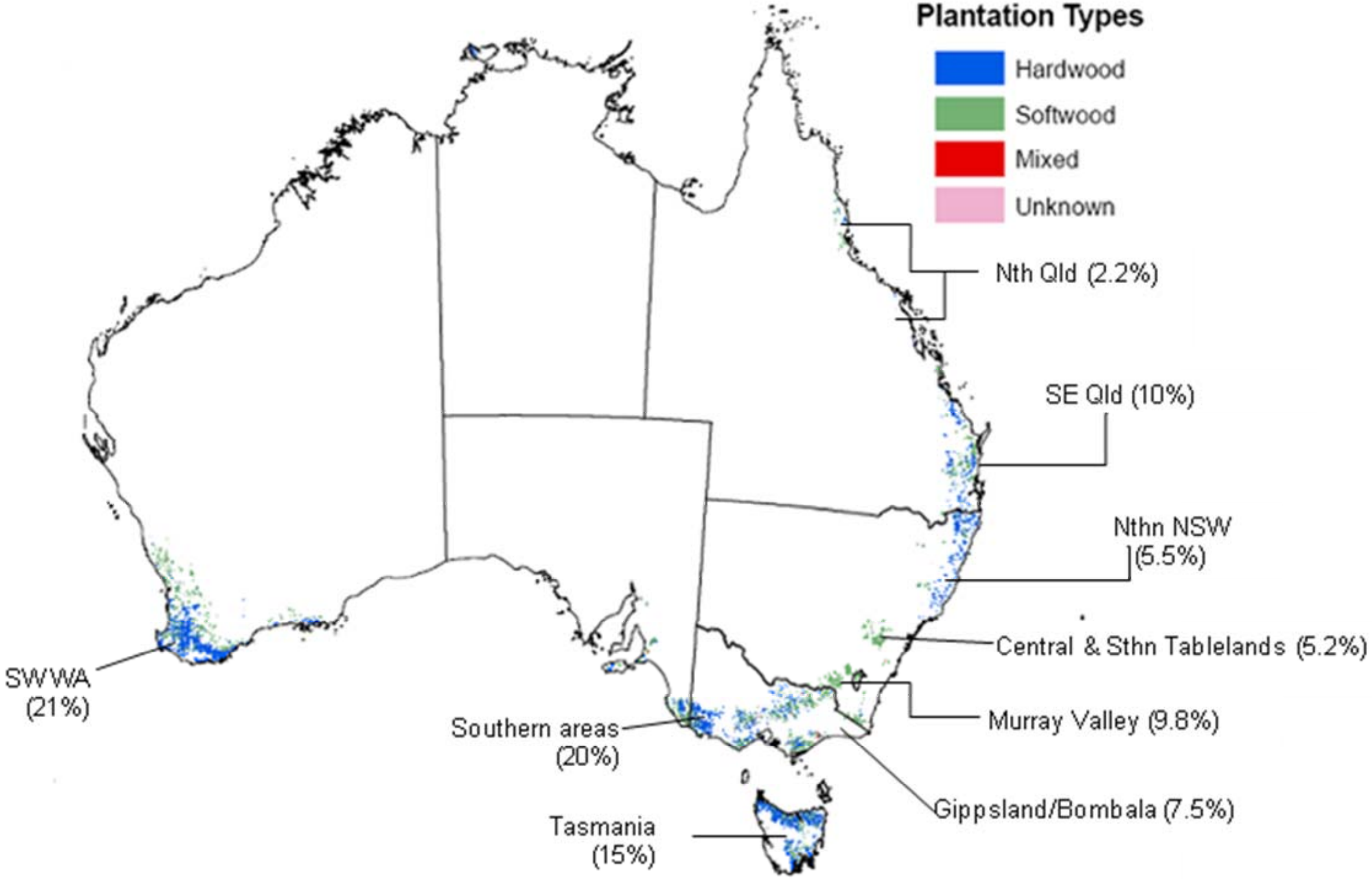

Figure 1.1 Major Australian plantation regions. The percentage area each region makes up of the national estate is shown in brackets. Source: Bureau of Rural Sciences

Productive native forests

Under this category we include those naturally occurring forests which may be periodically harvested for timber or other forest products or used for other agricultural purposes while retaining the essential ecological characteristics of their undisturbed predecessor forests. Therefore, ‘productive’ refers to the narrow economic use of forest resources such as timber, for example. In contrast, the much broader ecological understanding of productivity is applied to all ecological systems.

Of the 149 million hectares of forest in Australia, 147 million hectares are native forest (Montreal Process Implementation Group for Australia 2008). Under the Montreal Process definition, native forests available for harvesting (wood and non-wood products) are defined as “those native forests in which harvesting is not illegal” and some 112 million hectares or three-quarters of Australia’s native forests were classified as not legally (in a strict sense) excluded from timber harvesting or tree clearing in the 2008 State of the Forests Report, (Montreal Process Implementation Group for Australia 2008). Only forests in nature conservation reserves are specifically excluded from tree removal.

For the purposes of the FVA, we have categorised those forests in which “harvesting is not illegal” as productive native forests. In practice, however, very little of this area is currently used for timber supply, with more than half (65 million hectares) being leasehold land used for grazing. In addition, in Queensland and New South Wales the clearing of vegetation is controlled legislatively (Vegetation Management Act Qld 1999 and Native Vegetation Act NSW 2003) with permits required for tree clearing and areas under remnant vegetation in “endangered” or “of concern” or “threatened” categories prohibited from tree clearing but available for other land uses such as grazing. Productive native forests, as defined here, are represented by three tenure types – multiple-use public forests, leasehold and freehold (private) lands.

Harvesting of native forests is largely restricted to multiple-use public forests with some contribution from leasehold and private lands. There is relatively limited commercial harvesting of native forests in the Northern Territory and none in South Australia or the Australian Capital Territory (Montreal Process Implementation Group for Australia 2008). The Queensland government has signalled its intention to phase out native forest harvesting in favour of hardwood plantation development (Montreal Process Implementation Group for Australia 2008) with the South-East Queensland Forests Agreement providing for the ending of timber harvesting in native State forests and timber reserves in the South East Queensland Bioregion by 2024. Although wood products can be harvested from native forests on private land, this is distinguished from farm forestry, in which seed or seedlings are purposefully planted for future harvest.

Much of the land that can be classified as productive native forests makes up the arid area of Australia commonly referred to as “the rangelands”. The rangelands are those areas where the rainfall is too low or unreliable and the soils too poor to support regular cropping (Bastin and ACRIS Management Committee 2008). The area traditionally defined as rangelands includes savannah, woodlands, shrublands and wetlands that fall under the definition of forest used in this assessment. The primary use of these areas is grazing, with the trees or forests providing services such as shade and shelter, nutrient input, salinity control, biodiversity and amenity rather than any harvestable product.

Conservation native forests

Native forests on which no harvesting is legally permitted and over which conservation controls are in force are defined here as conservation native forests. This includes the many categories of forest reserves designated to serve as areas for the maintenance of environmental quality, biodiversity conservation and/or tourism. In some states this also includes forests designated as ‘wilderness’. Forests in nature conservation reserves are located around Australia and cover a broad range of vegetation types. Australia has 22.37 million hectares of nature conservation reserve (Montreal Process Implementation Group for Australia 2008).

Environmental plantings

This last category encompasses artificially constructed forests with a diverse set of roles from restoration and maintenance of environmental health to provision of shelter belts, biodiversity corridors, erosion control or amenity.

Amenity plantings are for human enjoyment and comfort and seek to provide shade, screening and windbreaks. Amenity plantings may also be used along roadsides.

Ecological plantings use species local to an area (indigenous species) and provide habitat to native animals. The use of locally indigenous species conserves the character of a region both biologically and visually.

Environmental plantings may also be established for the purpose of carbon sequestration (carbon offsets) and the management of soil salinity. Environmental plantings can serve a number of these purposes simultaneously.

1.3 Classifying Australia’s forests

In addition to the forest use classification introduced earlier, the FVA applied a second layer of landscape classification using the 10 zones (Figure 1.2) proposed by Hobbs and McIntyre

(2005). These zones were developed using both climate and vegetation. Climate was based on an agro-climatic classification incorporating a moisture index, growth index and seasonality. The climate classes were aligned to the existing Interim Biogeographical Regionalisation for Australia (IBRA) bioregions (Environment Australia 2000). Vegetation was broadly classified on the presence or absence of a tree layer and whether the understorey was grassy or shrub-dominated. A more extended discussion of these overlapping concepts of forest classification and their role in evaluating likely impacts and adaptation strategies is given in the FVA Synthesis.

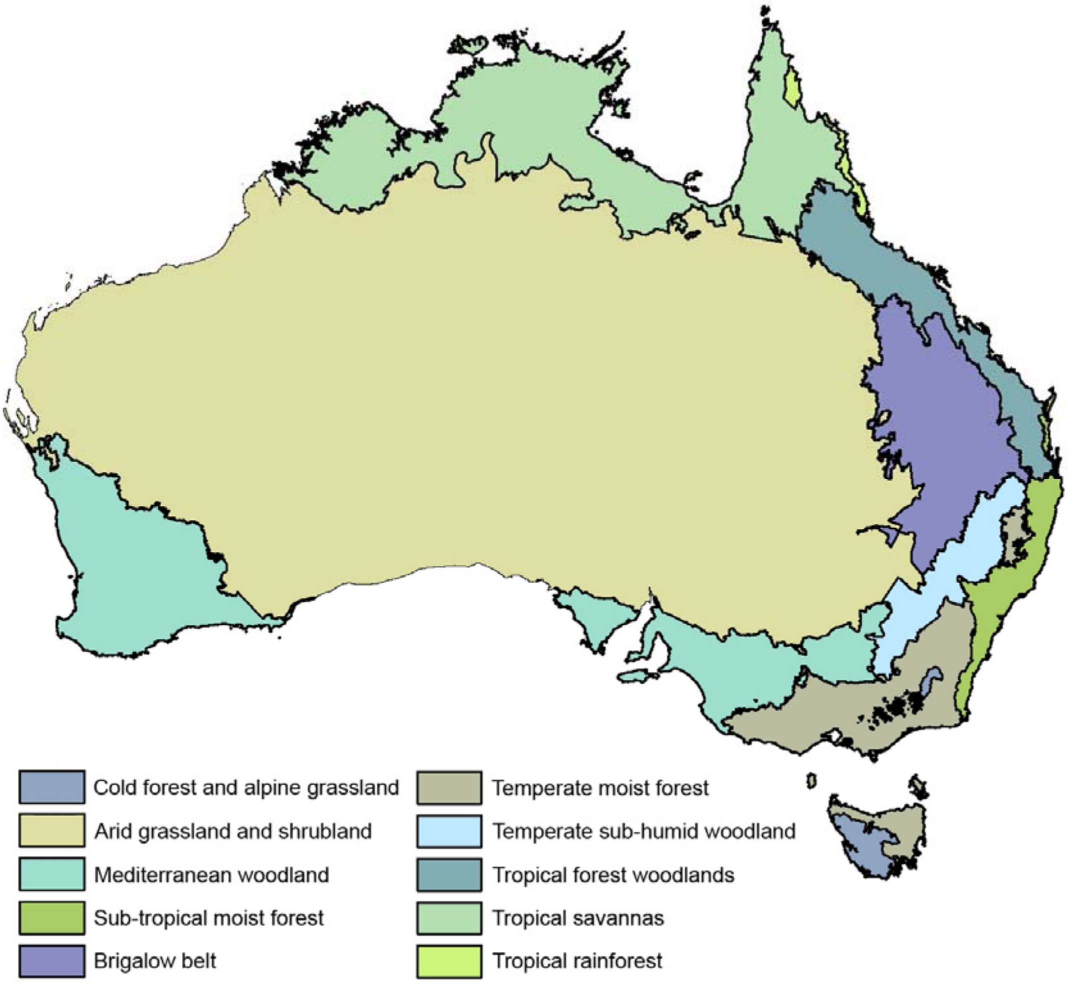

Figure 1.2 Agro-climatic biomes developed by Hobbs and McIntyre (2005) and used here as a framework to assess the regional impact of climate change on Australia's forests

1.4 Ecosystem services

Ecosystem services are defined as goods and services acquired from ecosystems as a result of the functions and processes which occur in these ecosystems. Forests supply a wide range of ecosystem services that are essential for human well-being (Table 1.4). Maintaining these ecosystem services requires maintaining healthy ecosystems in a changing climate (DAFF 2008; Norby and Luo 2004). The most obvious ecosystem service of forests is providing wood resources to the forestry industry. Forestry makes a significant contribution to rural and regional employment (Forests Australia, viewed November 2010). Storage of carbon is likely to become an increasingly valuable ecosystem service, as economies move towards pricing carbon.

Forests also participate in the shaping of weather, climate, and atmospheric composition (Norby and Luo 2004). Not only are forests influenced by climate, but forests can also influence local and regional climates. Regulation of climate and weather is a service of particular benefit in the water-limited and drought-prone continent of Australia (Deo et al. 2009; Mcalpine et al. 2009). Land-use change studies have demonstrated that large-scale clearing of vegetation in the past has led to statistically significant increases in surface temperatures of 0.1 - 0.6 °C and decreases in summer rainfall in southeast Australia (McAlpine et al. 2007). Vegetation clearing is thought to have increased the number of hot dry days, decreased daily rain intensity, and increased drought severity, particularly during El Nino conditions (Deo et al. 2009). The removal or addition of forests alters the radiation balance of a site, influencing local temperatures.

Forests have an important role as regulators of water tables. This role helps to prevent and/or ameliorate dryland salinity, provide clean water, mitigate floods, and prevent soil and nutrient loss through surface flows. The value of ecosystem services provided by forested catchments is demonstrated by the cost of damage by the effects of dryland salinity. The replacement of deep-rooted native vegetation with shallow-rooted, annual crops is one of the main causes of increases in dryland salinity. Salinity affects more than 2.5 million hectares and 220 towns across the Murray Darling basin, and significant areas within Western Australia. The Murray Darling Basin commission estimated the cost of salinity was $304 million per year in lost productivity, repairing damage and lifestyle adjustments (DAFF 2008).

Australian forests have a recognised high biodiversity conservation value (Lindenmayer and Franklin 2002). Australia has a globally unique flora and fauna with many national and internationally recognised biodiversity hotspots (Australian National University 2009; Steffen et al. 2009), and forested systems harbour a large part of this biodiversity (Australian National University 2009; Dunlop and Brown 2008; Howden and Gorman 1999; Steffen et al. 2009). For instance, forests of the wet tropics in the north and the Mediterranean temperate forest systems in the southwest of Australia are recognised for their biodiversity values (Abbott and Le Maitre 2010), which has resulted in their inclusion into areas designated for biodiversity conservation (Australian National University 2009; Dunlop and Brown 2008). Many important ecosystem services are provided by this biodiversity including pollination, nutrient cycling/decomposition, and natural pest control, as well as recreational values related to tourism (Australian National University 2009; Dunlop and Brown 2008; Howden and Gorman 1999).

Thus, there is clear and demonstrable value in maintaining healthy forests and ecosystem services (IUFRO 2009). Australia has a large number of projects underway measuring and accounting for various ecosystem services (Maher and Thackway 2008). A major aim of this report is therefore to consider climate change impacts on ecosystem services specifically for Australian forests and woodlands.

Table 1.4 Ecosystem services provided by forests globally (adapted from IUFRO 2009)

Ecosystem service	***Description***	***Potential Impact of Climate Change***
Productivity	Carbon storage and nutrient cycling	Changes in forest growth and biomass, changes in species/site relationships, changes in ecosystem nitrogen dynamics
Carbon cycles	Carbon sequestration, oxygen cycles, climate regulation	Alteration of forest sinks and increased CO_2 emissions from forested ecosystems due to changes in forest growth and productivity
Biodiversity	Habitat provision, recreation, tourism, cultural and spiritual values	Alteration of plant and animal distributions, loss of biodiversity, invasive species, changes in plant dispersal and regeneration
Soils and water	Clean water, flood protection, prevention of soil erosion, nutrient cycling	Changes in seasonality and intensity of precipitation, altering the flow regimes of streams, changes in salinity of coastal forest ecosystems, increased probability of severe droughts, more/earlier snow melt resulting in changes in the timing of peak flow and volume in streams
Wood products	Production forests and plantation, timber, fuelwood.	Altered productivity and mortality of forests. Changes in wood density and timber quality. Changes in availability of specific forest products (timber, fuelwood).
Additional tangible benefits of forests for people	Non-wood products: pollination, clothing, medicinal services	Alterations in plant species distribution and composition, loss of pollination, changes in insect species distribution and composition.

1.5 Climate change projections and scenario modelling

Actions to mitigate and adapt to ongoing climate change rely on modelling to predict how the climate will respond to changing atmospheric levels of greenhouse gases. There are four main areas of uncertainty in climate models (Steffen et al. 2009):

- The projected rate of production of greenhouse gases (emissions scenarios, see below)
- The relationship between the rate of greenhouse gas emissions and their atmospheric concentrations
- The rate and magnitude of the global warming for a given change in concentration in greenhouse gases
- Identifying region to region differences within global climate change scenarios.

It is difficult, if not impossible, to predict the amount of greenhouse gases that will be emitted in the future. The IPCC, the principal organisation assessing, synthesising and reporting on climate change literature, have developed four major emission scenarios (Box 1.1).

Economic Emphasis

Global Integration

Regional Emphasis

A1 storyline	A2 storyline
World: market-oriented **Economy:** fastest per capita growth **Population:** 2050 peak, then decline Governance: strong regional interactions; income convergence **Technology:** three scenario groups: **A1FI:** fossil intensive **A1T:** non-fossil energy sources **A1B:** balanced across all sources	**World:** differentiated **Economy:** regionally oriented; lowest per capita growth **Population:** continuously increasing **Governance:** self-reliance with preservation of local identities **Technology:** slowest and most fragmented development
B1 storyline	B2 storyline
World: convergent **Economy:** service and information based; lower growth than A1 **Population:** same as A1 **Governance:** global solutions to economic, social and environmental sustainability **Technology:** clean and resource-efficient	**World:** local solutions **Economy:** intermediate growth **Population:** continuously increasing at lower rate than A2 **Governance:** local and regional solutions to environmental protection and social equity **Technology:** more rapid than A2; less rapid, more diverse than A1/B1

Environmental Emphasis

Box 1.1 Summary characteristics of the four IPCC SRES emissions scenarios (from Carter et al. 2007)

Projections of climate change vary among models. For the purpose of the Forest Vulnerability Assessment project, it was determined that the working groups would use a single set of climate change projections. The “worst case” A1FI emissions scenario was chosen because current emission trends and climate observations closely track this scenario (Allison et al. 2009). Climate modelling was carried out using the SimCLIM modelling software (Warrick 2009).

To provide the present day baseline, the SimCLIM Model uses observed monthly-mean values of precipitation and mean, maximum and minimum temperature derived from the 1961-1990 baseline period (source: Australian Bureau of Meteorology), interpolated to a 0.25 lat/long grid. For future projections, it includes spatial patterns of change for these same variables from general circulation models (GCMs). In order to capture the four areas of uncertainty already discussed, there are three points within the SimCLIM model where different ranges of data can be selected to capture different levels of uncertainty. They are:

- **Climate sensitivity** which determines the *magnitude* of global warming in response to a given change in greenhouse gas concentrations.
- **Greenhouse gas emissions** which determine the *rate* of change of greenhouse gas concentrations and associated radiative forcing (capturing uncertainties 2 and 3 from the Steffen et al., 2009, list – see above).
- **Spatial patterns of change from general circulation models (GCMs)** which determine the *regional differences* in changes in temperature, precipitation and other climate variables.
- For this project the following specifications were applied for all projections:
    - Climate sensitivity – **high**
    - Emission scenario – **A1FI** (highest future emissions)
    - General circulation model – **the median value of an ensemble of 21 equally weighted GCMs**

Two time horizons were selected for the project, 2030 and 2070, to provide a mid- and long-term scenario in each case. Projections were made for annual rainfall, seasonal rainfall (all seasons for the southern half of Australia and wet and dry seasons for northern Australia), February maximum temperatures, days over 35ºC and days over 40ºC and frost days (days with minimums less than 0ºC).

A full description of the SimCLIM methods and a complete set of mapped projections is provided in both Work Package 1 (Wood et al. 2011) and the FVA Synthesis Report (Boulter et al. 2011)

1.6 Projected changes in climate factors

Under current climate change projections there is a high certainty that across Australia temperatures are likely to rise in response to global increases in CO_2 (CSIRO and Bureau of Meteorology 2007; IPCC 2007; and Wood et al. 2011). Annual rainfall patterns and moisture availability are likely to change, but a general trend of increases or decreases is less clear and is mainly dependent on location.

The key climate-related changes that will most likely have an effect on forest system functioning in Australia are summarised below.

Atmospheric CO_2 concentration: The atmospheric CO_2 concentration is currently 380 ppm; estimates for the year 2099 range from 600 ppm under a low-emission scenario, up to 1100 ppm under a high-emission scenario (Sitch et al. 2008).

Temperature: Maximum and minimum temperatures are projected to increase in all regions and seasons. By 2030, increases of approximately 1ºC are projected, with the greatest increases occurring in inland Australia. By 2070, increases of as much as 4ºC could occur.

Extreme hot days: Increases in the number of extreme hot days are expected. By 2070, large areas of interior Australia in particular would be facing average daytime temperatures in February in excess of 39ºC.

Snow and frost: Duration and occurrence will likely decrease across Australia.

Precipitation: There is considerable uncertainty around future trends. Current best estimates of annual precipitation change indicate possible increases or little change in the far north and decreases of 2% to 5% elsewhere. There could also be changes in seasonality. In Northern Australia, projections indicate that the wet season will get wetter and the dry season drier. In southern Australia, widespread decreases in rainfall are likely to occur during winter and spring. The west and southern coasts are likely to show decreases in rainfall in all seasons.

Storms: More severe and/or frequent storms are projected, including an increased occurrence of damaging hail and windstorms. Rainfall intensity is also likely to increase, which may lead to more flooding.

Potential evapotranspiration: Annual potential evapotranspiration is currently projected to increase across Australia. Best estimate projections reported by CSIRO (2007) are for an increase in potential evaporation of 6% in the south and west, and 10% in the north and east, under the A1FI scenario by 2070. However, new research demonstrating non-stationarity in other climate variables affecting the process of evaporation, particularly wind speed (see Roderick and Farquhar, 2004, McVicar et al., 2008, Donohue et al., 2010) suggests that these projections need to be re-modelled using all the forcing meteorological variables (net radiation, vapor pressure, wind speed and air temperature).

Droughts: With decreasing rainfall, increasing potential evapotranspiration and higher temperatures, drought occurrence is projected to increase over most areas, but particularly in southwest Australia.

1.7 Structure of this report

In this report, our aim has been to review the primary literature on evidence of impacts of climate change on Australian forests. There have been several previous excellent reviews of climate change impacts on Australian forests (Battaglia et al. 2009; Booth and Jovanovic 2005 Nitschke and Hickey 2007; Pinkard et al. 2009; Stokes and Howden 2010) as well as reports on climate change impacts on natural heritage and biodiversity (Australian National University 2009; Dunlop and Brown 2008; Hughes 2003; Steffen et al. 2009). However, for this report, we aimed at an independent and updated evaluation of the current state of scientific knowledge. Therefore, we have deliberately not repeated conclusions drawn by previous reviews. Instead, we have focused on drawing evidence from the primary literature, including grey literature. Relevant literature was identified by bibliographic searches and in consultation with experts across Australia. Over one hundred scientific experts working in this field were invited to contribute information to this report; responses were received from well over thirty scientists.

The impacts of climate change on forest functioning and ecosystem services are complex (Figure 1.1). Change in CO_2 concentration, temperature and rainfall, impact on plant processes such as growth, transpiration, and phenology, which in turn impact on vegetation function and properties, such as productivity, canopy structure and community composition. The occurrence of other stresses on forests, such as fire, pests, pathogens and weeds, are affected by these changes in vegetation properties whilst also responding directly to climate change. The overall impact on vegetation and the ecosystem services provided depends on the outcome of these many interacting influences.

This report is structured as follows. First, we introduce the types of scientific evidence available; this section gives a critique of the evidence and indicates the level of confidence that can be attached to different pieces of evidence (Chapter 2). Second, we review the scientific evidence relating to each of the individual topics highlighted in *italics* in Figure 1.3 (Chapters 3 - 11). We consider ways of integrating this scientific knowledge to draw conclusions about the overall impact on forest ecosystem services (Chapters 12 - 14). Finally, we provide conclusions and recommendations to improve the underpinning science (Chapter 15).

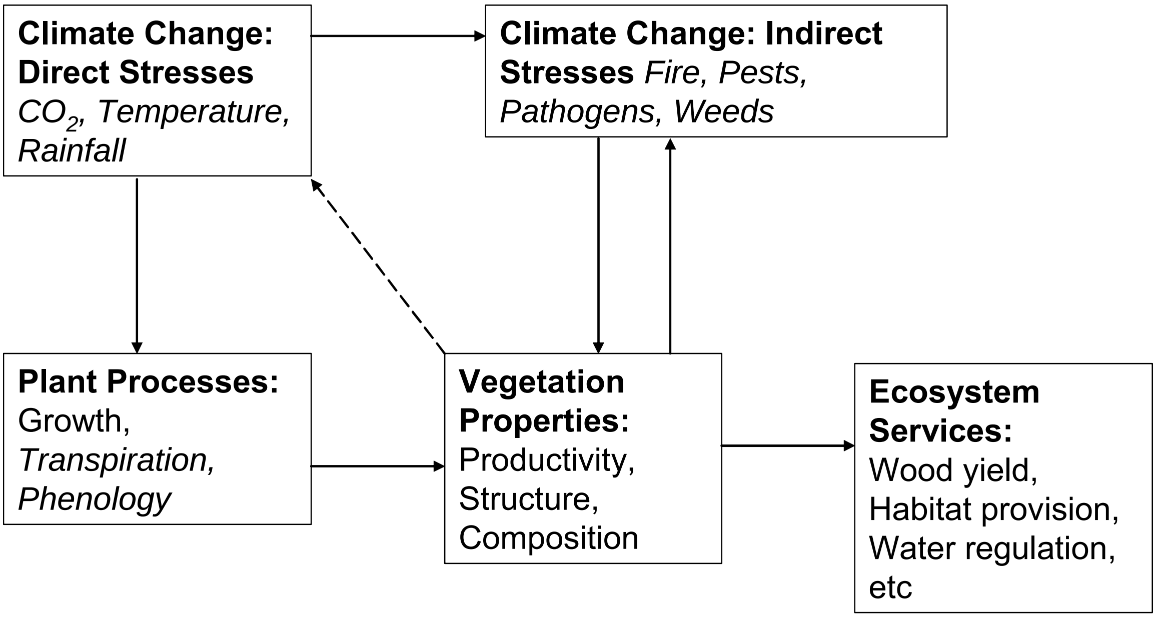

Figure 1.3 Conceptual structure of the report. Topics highlighted in *italics* are addressed separately in Chapters 3 - 11. The integration of individual effects is considered in Chapters 12 - 14.

2. Primer: Types of Scientific Evidence

The aim of this section is to provide some important background on the types of scientific evidence used to draw conclusions about climate impacts on forest carbon and water cycles. We provide a critical comparison of the different methodologies used. This section provides a basis for evaluating the certainty of the conclusions of different types of study.

An essential first point to make is that responses of vegetation to environmental change depend greatly on scale. The responses are determined by a range of plant and ecosystem processes that operate on widely different time and spatial scales (Medlyn and McMurtrie 2005). The range of scales involved is shown in Figure 2.1.

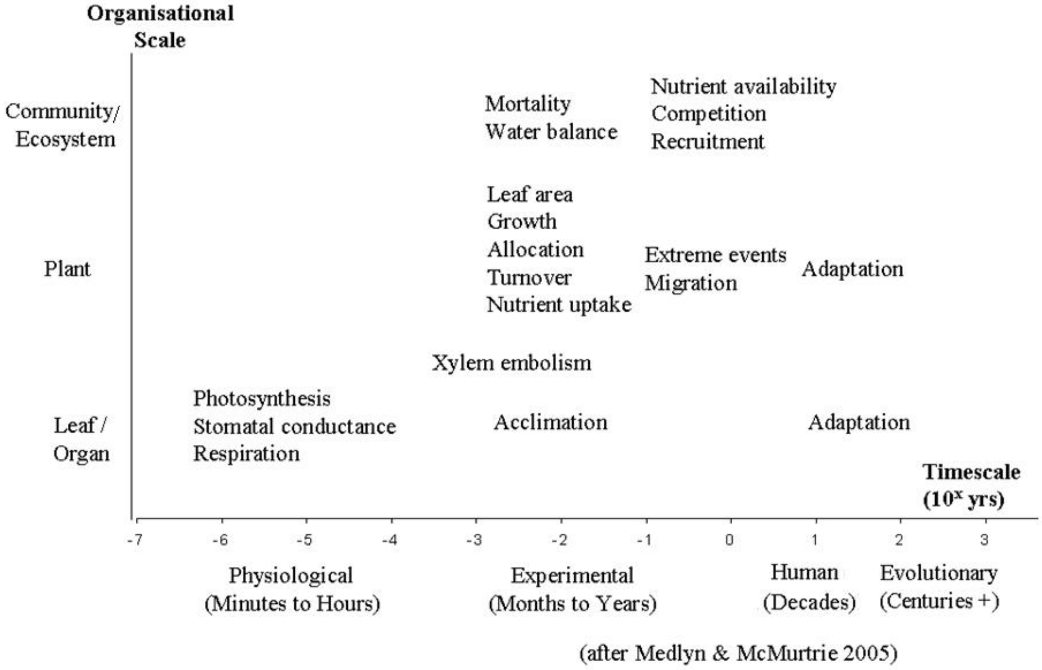

Figure 2.1 Different organizational scales and timescales influencing plant processes.

In Figure 2.1, we classify processes according to four timescales. Processes occurring at the ‘physiological’ timescale adjust to environmental change within minutes to hours. These changes are readily measured:

- Feedbacks through plant growth, water and nutrient cycles occur more slowly, on the scale of months to years. We denote this timescale the ‘experimental’ timescale, because it is feasible to conduct manipulative experiments measuring these processes.

- The intermediate timescale, decades, we denote the “human timescale”, since it represents the timescale of most concern to human society. Unfortunately, this timescale is also the most intractable to study.
- Processes that can be of importance on this timescale include rare events, such as extreme droughts, fires or storms; processes of generational change such as recruitment, establishment and competition; and processes with a long response time, such as soil nutrient cycling.
- The longest timescale, centuries and beyond, may be regarded as the “evolutionary timescale”, during which adaptation to new environments is possible. It is possible to study processes occurring on this timescale by observing responses to naturally occurring climate gradients.

Responses occurring on longer timescales are overlaid on process responses at shorter timescales, making it difficult to unravel different mechanisms. We now discuss the types of scientific evidence available, and how they can be used to inform our understanding of vegetation responses to climate change on this human timescale.

2.1 Manipulative experiments

This type of experiment generally ranges from days to years; some experiments with elevated [CO_2] have run for up to 17 years (e.g. Kimball et al. 2007). In this type of experiment, plants are grown under different environmental conditions. For example, plants may be grown at current and elevated CO_2 levels; a range of temperatures; with different watering treatments; or a combination of these factors. These experiments are useful because they allow us to directly study how plant function is affected by a change in a given environmental factor. This type of experiment is most easily carried out with individual seedlings or small trees growing in pots in glasshouses. The responses measured tell us about plant function but cannot be directly extrapolated to mature plants growing in the field.

Some high CO_2 experiments have been carried out under field conditions. For example, open-top chambers or whole-tree chambers have been constructed around trees growing in field soils. These experiments more closely mimic field conditions, but must still use relatively young trees. Again, these experiments are useful in identifying mechanisms, but responses may be different for older, mature trees.

There have been some free-air manipulative studies on CO_2 enrichment. In Australia, so far, there have been two Free Air CO_2 Enrichment (FACE) experiments in grasslands in tropical savanna (Stokes et al. 2005) and Tasmania (Hovenden et al. 2006). A new FACE experiment is to be established in mature woodland in western Sydney. Internationally, there have been five major FACE experiments with forest vegetation, including three in closed-canopy forests

(Norby et al. 2005; Asshoff et al. 2006). These data are invaluable in understanding forest ecosystem responses to rising CO_2.

Most experimental manipulation studies on temperature responses have been on seedlings or saplings to date, due to the difficulties in conducting large scale temperature experiments. A number of increased temperature studies have recently started in the USA on *in situ* forest trees, but there have been no such studies to date with forest species in Australia.

With respect to water availability, there have been several field-based irrigation (water addition) manipulations with forest trees, including several Australian studies (e.g. Leuning et al. 1991; Raison and Myers 1992). Experimental drought (water withholding) studies have been applied internationally, and facilities to run this type of experiment are under construction in Australia (rain-out shelters, University of Western Sydney).

Manipulative experiments provide much fundamental information about the processes and mechanisms by which forests respond to changes in environmental conditions. Such studies do, however, have disadvantages, in that they are relatively short-term, capturing only the effects on processes with fast timescales (Figure 2.1), and largely focus on experimentally tractable young plants. Also, studies can generally only manipulate one or two factors at a time, whereas climate change consists of a number of environmental variables changing simultaneously.

2.2 Observational studies

We use the term “observational studies” to describe a range of different types of studies that utilise natural environmental variation in climate to examine climate impacts on vegetation, such as:

- Diurnal and seasonal variation in weather, e.g. plant responses to seasonal drought.
- Responses to long-term trends in climate, e.g. decadal oscillations in rainfall.
- Spatial variability in climate, e.g. spatial gradients in rainfall
- “Common garden” studies where species originating from different climate zones are grown together, to examine adaptive differences among species.

The chief advantage of these types of study is that they use mature vegetation growing in the field. However, there are also disadvantages. A number of factors may be co-varying, such as rainfall and soil nutrient availability, or recovery from disturbance and it may be difficult to separate the influence of these covariates. Natural environmental variation may not mimic likely climate changes: for example, it is unclear how we can use responses to seasonal drought to predict responses to a long-term reduction in rainfall.

Furthermore, many observational studies pertain to the long-term ‘evolutionary’ timescale, rather than the ‘human’ timescale. For example, if observed differences in rainforest productivity along temperature gradients reflect long-term adaptation to environment, such differences ought not to be used to infer responses of rainforests to rising temperatures over several decades.

2.3 Ecophysiological models

These are computer models that are based on a mechanistic understanding of plant function. Typically they include a representation of how CO_2, temperature and water availability affect plant production on a day-to-day basis. Forest growth rates can be predicted for a given climate, species and soil type. Models can be run to predict productivity of a given species in a given location; for example, to predict productivity of a *Pinus radiata* plantation. Models also exist to predict the type of vegetation (savanna, rainforest, etc.) existing at a given location, as well as its productivity. Such models are called dynamic vegetation models because they allow vegetation type to change dynamically.

Ecophysiological models attempt to integrate the knowledge gained from other types of studies and use it to predict responses of vegetation to climate in new locations. They are probably the best source of information about likely future climate effects on vegetation on the human timescale. However, they are only as good as the inputs used. In evaluating the outcomes from these models, it is important to examine:
What climate scenarios were used? Climate simulations for Australia vary considerably in predicted changes in rainfall, with different GCMs predicting quite different changes in rainfall. Because drought is a major driver of productivity, the assumed change in rainfall is particularly important.
What assumptions were used about responses to climatic factors? For example, is rising CO_2 taken into account, and in what way? Are the assumptions consistent with current best understanding of mechanisms? What uncertainty is there?

2.4 Bioclimatic modelling

Bioclimatic modelling uses the current geographical distributions of species and/or ecosystems and relates them to the local climate, including temperature and rainfall of those locations. The climatic envelope that each species exists in, the ‘realised niche’, is calculated. Then using climate scenarios, the regions that each species will occur in may be modelled for a different climate. This approach can be used for any taxon; applications of this approach to insects and fauna can be found in the sections on pests and biodiversity. This type of modelling does not directly predict carbon or water cycling, but can suggest regions where productivity of a given species will be good or poor.

There are several caveats attached to this type of modelling. The most important is that the model shows the “realised niche”, i.e. the climate where the species is currently found. This may differ from the “fundamental niche”, or the climate where the species can actually grow. Thus, although a given species is not found at, say, a mean annual temperature of 27 degrees, that does not necessarily mean that it could not grow at that temperature. There are many examples of Australian forest species that can be grown successfully in climatic conditions beyond their native ranges (Paton 1980; Booth and Jovanovic 2005).

Another caveat is that bioclimatic models cannot account for effects of rising CO_2, which may alter the drought tolerance of species. There are also issues related to the provenance of species. For example, while *Eucalyptus tereticornis* may have presence records all along the east coast of Australia, indicating a thermally tolerant species, this species range may include several different provenances with different climatic requirements. If this is the case, individuals may be more sensitive to climate than indicated by bioclimatic modelling.

Another limitation of the method is that it is usually based on long-term climatic average data, whereas species distributions may be determined by extreme events, such as deep frosts or severe droughts. Other caveats to this approach are discussed in detail by Yates et al. (2010). Despite these caveats, the method can be used to identify species that are particularly vulnerable to climate change. Such species should be the focus of more detailed studies.

Individual Factors – Direct Climate Stresses

3. Rising atmospheric CO_2 concentration

3.1 Introduction

Atmospheric CO_2 was 280 ppm pre-industrially and is now approximately 380 ppm. It continues to increase rapidly, by 1.7 – 1.9 ppm per annum (Canadell et al. 2007). The level reached later this century will depend on emissions trajectories and the strength of ocean and terrestrial sinks. Estimates for atmospheric CO_2 in the year 2099 range from 600 ppm under a low-emission scenario, up to 1100 ppm under a high-emission scenario (Sitch et al. 2008).

Rising atmospheric CO_2 is largely beneficial for plants. In the short-term, increasing CO_2 increases plant photosynthesis in all woody species. Typically, an increase from 380 to 550 ppm increases unstressed leaf photosynthesis by about 50% (Medlyn et al. 1999). This increase in photosynthesis has the potential to yield significant increases in plant productivity and carbon storage in both above- and below-ground biomass and in soil. Additionally, increasing CO_2 generally reduces stomatal conductance, which determines the rate of water lost by the plant (Medlyn et al. 2001). This reduction in the rate of water loss could be beneficial in water-limited systems by delaying the onset of drought. However, these potential benefits may not be realised, because of feedbacks that occur at the whole-plant and ecosystem scale.

First, above-ground productivity may not be increased if plants use the extra photosynthate to build below-ground tissues (roots) rather than stems or leaves (e.g. Norby et al. 2002). In this case, soil carbon storage may still increase, but there is no increase in harvestable mass. Also, some experiments find that the stimulation of photosynthesis by elevated CO_2 does not persist, that is, there is down-regulation of photosynthesis (e.g. McMurtrie et al. 2009). Down-regulation is caused in some cases by low sink strength – such as in slow-growing plants – and in other cases by low nutrient availability (Medlyn et al. 1999). Reductions in water use may lead to increased runoff and drainage, rather than being used to support plant growth.

3.2 Effects on productivity

There is clear evidence from the international literature that rising CO_2 can increase forest productivity, with an average 23% increase in total productivity found in the first years of elevated CO_2 exposure in four forest FACE experiments (Norby et al. 2005). However, in one FACE experiment with plantation sweetgum, the initially high CO_2 effect on net primary productivity (~30%) decreased over time to just 7%. This decrease has been ascribed to increasing nitrogen limitation as the forest ages (Norby RJ et al., in review.) In other experiments, changes in the pattern of allocation of carbon mean that the CO_2 response of above-ground production is considerably less than the response of total production. In one FACE experiment in a mature mixed deciduous forest, there was no increase in above-ground productivity with elevated CO_2 despite a large increase in photosynthetic rate (Körner et al. 2005). In another FACE experiment with plantation loblolly pine, there was an interaction between the CO_2 response of production and fertilization, with larger responses of above-ground woody biomass in fertilized plots (Oren et al. 2001). Thus, although rising CO_2 has the potential to increase above-ground production in forests, it does not always do so.

In Australia, long-term experiments with CO_2 enrichment have been conducted on saplings of the sub-alpine species *Eucalyptus pauciflora* , the temperate species *E. tereticornis* and *E. saligna,* and the tropical species *E. tetrodonta*, *E. miniata*, *Maranthes corymbosa,* and *Mangifera indica*. Summary results are shown in Table 3.1.

Table 3.1: Growth response of Australian woody species to elevated CO_2. Data come from manipulative experiments where plants grown at ambient C_a (340 – 380 ppm) are contrasted with plants grown at enriched C_a (600 – 700 ppm).

Species	Growth response	Experiment details	Reference
E. tereticornis	n.s. (well-watered) +100% (droughted)	Seedlings grown in 50L pots for 23 weeks in glasshouses	Atwell et al. 2007
E. tetrodonta *E. miniata*	+150% n.s.	Seedlings grown in ventilated tents for 32 weeks	Duff et al. 1994
E. pauciflora	+50%	Seedlings grown in open top chambers early winter to late spring	Roden et al. 1999
E.pauciflora	No change (sheltered) Negative effect (exposed)	Seedlings overwintered (Mar – Nov) in open top chambers	Barker et al. 2005
E. grandis	n.s. (unfertilised) +80% (fertilised)	Seedlings grown in large controlled-environment chambers in 80L drums for 14 months	Diogo 2002 MSc thesis, Univ. Witwatersrand, S. Africa
E. saligna *E. sideroxylon*	+45% +75%	Seedlings grown in 7L pots for 150 d in glasshouses	Ghannoum et al. 2009
E. saligna	Negative effect	Saplings grown for two years in whole tree chambers	Hawkesbury Forest Experiment (McMurtrie et al. 2009)
Maranthes corymbosa	+60%	Seedlings grown in ventilated tents	Berryman et al. 1993
Mangifera indica	+60%	Seedlings grown in the ground in ventilated tents for 80 weeks	Goodfellow et al. 1997a,b

As can be seen in Table 3.1, there is considerable variation in growth responses among experiments. Several of these experiments demonstrated strongly positive growth responses to elevated CO_2. Thus, Australian tree species also have the potential for production to increase with rising CO_2. However, as with the overseas literature, there are also a number of experiments where no response in above-ground production is seen.

There has been debate as to whether some species might be intrinsically more responsive to elevated CO_2 than others. This debate is ongoing, but we note that the table above shows no pattern in species differences, which suggests that environmental conditions, rather than species differences, are more likely to account for different responses across experiments. For example, growth of *E. saligna* was increased at elevated CO_2 in a glasshouse experiment (Ghannoum et al. 2009) but decreased at elevated CO_2 in the whole-tree chamber experiment. Differences in soil nutrient availability in the two experiments may explain the difference in responses (D. Tissue, D. Ellsworth, pers. comm.). In the closely related species *E. grandis*, there was no growth response in unfertilised trees but a strong growth response in fertilised trees (Diogo 2002). Thus, in the Hawkesbury Forest whole-tree chamber experiment, the primary hypothesis is that nutrient availability restricted the response.

Overall, we can conclude that there is likely to be an interaction between the CO_2 response of productivity, and soil fertility. Above-ground growth productivity increases are likely only in the most fertile sites. As fertility declines, production may still increase, but is likely to be diverted belowground. In this case, soil carbon storage may still increase. At infertile sites, there is not likely to be any increase in production. It is not yet possible to define thresholds for these different responses.

3.3 Interactions with water availability

The interaction between rising CO_2 and water availability is quite different than that with nutrient availability. At high CO_2, water use efficiency (carbon gain per unit water transpired) is increased consistently across experiments. It therefore seems logical that plants growing at high CO_2 should be less stressed during drought, and that productivity gains due to elevated CO_2 (eCO_2) should be higher in dry systems. These interactions between atmospheric CO_2 and drought are enshrined in most process-based models and could be expected to have significant effects on woody biomass in water-limited Australian environments. However, although these effects have been found in some grassland systems (Morgan et al. 2004), they have rarely been demonstrated experimentally in forest tree species. In studies of potted trees, Centritto et al. (1999a,b; 2002) did not find a CO_2 × drought interaction in cherry and peach seedlings, in part because increased leaf area under eCO_2 compensated for lower water use per unit leaf area. Similarly, field-based open-top chamber and FACE studies on tree species have failed to demonstrate that the eCO_2 effect is enhanced during drought conditions (Schäfer et al. 2002; Hymus et al. 2003; Gunderson et al. 2002; McCarthy et al. 2010). One exception is the experiment by Atwell et al. (2007), where growth was enhanced more for *E. tereticornis* when grown with limited water availability. At the Hawkesbury Forest Experiment, it was found that although whole-tree water use declined at elevated CO_2, trees growing at high CO_2 still became drought-stressed when water was withheld, because eCO_2 trees were smaller and had shallower rooting depths (McMurtrie et al. 2009).

It is not yet known why experiments with trees largely fail to show the anticipated interaction between elevated CO_2 and water availability. However, this interaction is of crucial importance for Australian ecosystems (see also section on hydrology, below). Further research aimed at quantifying the CO_2 response of forest canopies under water-limited conditions is therefore a high priority.

3.4 Interactions with rising temperature

Australian research has also highlighted the interaction between elevated CO_2 and leaf temperatures. A consequence of reduced stomatal conductance at elevated CO_2 is that leaf temperatures are increased, due to reduced transpirational cooling. This change in leaf temperature has implications for both frost and heat damage. In the study on *E. pauciflora* by Barker et al. (2005), higher leaf temperatures under elevated CO_2 reduced the frost hardiness of leaves, and therefore increased frost damage. Woldendorp et al. (2008) used a simulation model to examine the consequences for *E. pauciflora* populations. An existing 'frost impact' model was adapted to include (1) the impact of elevated CO_2 on frost hardiness and (2) the temperature gradient between the ground during a frost and the screen height. The IPCC scenario A2, the most pessimistic scenario, and CSIRO C-CAM Global Circulation Model were used to predict future climates. Temperatures below 0 °C were predicted to occur less frequently, while the coldest temperatures (< -8 °C) were almost as common in the future as in the current climate. Delayed acclimation due to either warming or elevated CO_2, which in turn reduces stomatal conductance leading to warming, combined with an early frost, may make *E. pauciflora* more vulnerable to more frost damage and higher mortality than occur in current conditions (Woldendorp et al. 2008). The model was species specific, calibrated with only data from *E. pauciflora* and future research is suggested to include other sub-alpine species.

It is unclear whether rising CO_2 will alleviate or worsen high temperature stress. There are two alternative hypotheses: that reduced stomatal conductance at elevated CO_2 could cause an increase in leaf temperature, exacerbating heat stress, or that suppression of photorespiration at elevated CO_2 could ameliorate heat stress (Wang et al. 2008). The relatively scant literature on this subject is inconclusive. Both positive and negative interactions have been found, which may be a result of differing methodologies and different species responses (Wang et al. 2008). In the only work on Australian species, Roden and Ball (1996a,b) examined effects of elevated CO_2 on two *Eucalyptus* species grown in heat-stressed conditions (45°C). They found that there was increased photoinhibition in the high-CO_2 grown plants, suggesting that impacts of heat stress would be worse under elevated CO_2. However, this study used only small seedlings (to 8 weeks). With extreme high temperatures predicted to rise significantly, quantifying the interaction of elevated CO_2 with heat stress in the field is an important research priority.

3.5 Interactions with pests

We note that growth at elevated CO_2 affects the nitrogen content and pest palatability of leaves. Changes in leaf chemistry may have significant implications for foliage palatability and herbivore defense. For example, a study of *E. cladocalyx* seedlings grown at two N and CO_2 concentrations demonstrated that the proportion of N allocated to prunasin (a cynaogenic nitrogen based metabolite) increased significantly under the elevated CO_2, despite a decreasing pool of N in these plants (Gleadow et al. 1998). These changes could potentially lead to reduced pest damage as leaf palatability decreases. This interaction is discussed in more detail in Chapters on Insect Pests and Biodiversity.

3.6 Effects of atmospheric CO_2 on vegetation distribution

Rising atmospheric CO_2 could potentially drive changes in community composition, if different plant functional types respond differentially. Several different arguments along these lines can be found in the literature. For example, Berry and Roderick (2002) classified species into three groups according to leaf type: “Turgor” (T) leaves, which are deciduous or raingreen; “Mesic” (M) leaves are broadleaf evergreen and dominate in regions of high resources; and “Schlerophyll” (S) leaves are long-lived and dominate in areas of low nutrient availability. They argue that rising C_a increases plant water use efficiency, favouring “M” leaves, but also drives relative decreases in nutrient availability, which would favour “S” leaves. Therefore, they argue that the frequency of “T” leaf types should decrease. Specifically, closed forests and schlerophyllous woodlands should expand, and ephemeral herbaceous communities should contract.

Another hypothesis is that the balance between C_3 plants (largely trees and temperate grasses) and C_4 plants (largely tropical grasses) will change. Rising CO_2 increases photosynthesis more in C_3 plants than it does in C_4 plants, and therefore dominance of C_3 plants should increase.

To date, there is limited evidence from manipulative experiments to support changes in community composition with rising CO_2. A meta-analysis of effects of elevated CO_2 on biomass production of C_3 and C_4 grasses found little difference between the functional groups (Wand et al. 1999). Morgan et al. (2004) reviewed results from open-top chamber and FACE experiments on grasslands and found no predictable pattern in effects on community composition. Changes in species composition were identified in five of seven experiments, but these changes favoured different functional groups in each experiment, with some experiments finding a shift in favour of C_3 species (Polley et al. 2003) but others finding an increase in dominance of C_4 species (Owensby et al. 1999). In Australia, in the Tasmanian FACE experiment, rising CO_2 was found to negatively impact on production of the major C_3 grass species, favouring the C_4 species (Williams et al. 2007).

The general lack of evidence for shifts in community composition is in part because the temporal and spatial scales on which such changes occur are larger than is feasible for manipulative CO_2 experiments. In particular, the impacts on species composition of woody species are too long-term to be examined in manipulative experiments. There is just one experiment demonstrating an increase in cover (from 1 to 4%) of a small woody C_3 sub-shrub in a mixed C_3-C_4 grassland at high CO_2 (Morgan et al. 2007). In summary, hypothesized effects of rising CO_2 on community composition are extremely difficult to test in experimental manipulations, but data obtained so far do not consistently confirm the major hypotheses.

3.7 Conclusions: Rising atmospheric CO_2 concentration

Although Australian forest species are physiologically capable of strong positive growth responses to rising CO_2, evidence is mounting that limited nutrient availability will restrict these responses. In moderately infertile sites, carbon uptake is enhanced by rising CO_2, but stem growth does not increase proportionately. In very infertile sites, there may be complete downregulation of photosynthesis, resulting in no increase in carbon uptake.

Rising CO_2 also affects plant water use. Across a wide range of experiments with forest tree species, there are consistent increases in plant water use efficiency at elevated CO_2. However, it is unclear how this change in water use efficiency will manifest in Australian ecosystems. Forest LAI and productivity may increase, or runoff and water yield may increase. Further large scale experiments are urgently needed to determine which of these outcomes is most likely.

4. Temperature

4.1 Introduction

Current estimates for mean temperature increase across Australia range from 0.6 to 1.5 °C by 2030 and 1 to 5 °C by 2070. The lower estimates correspond to low emissions scenarios and the higher estimates to high emissions scenarios; if the current emissions path is followed, then temperature increases are likely to be at the upper end of these brackets, with warming of 2.2 to 5 °C by 2070.

Rising temperature will impact differently on different ecosystems. Growth responses to temperature are always peaked; that is, there is an optimum temperature for growth (Figure 4.1). Rising temperature will affect plants differently according to whether they are currently above or below optimum temperature. Ecosystems where growth is limited by cold temperatures, such as eucalypt plantations in Tasmania, can be expected to have increased productivity with rising temperature, whereas ecosystems that are at or above optimum temperature will be negatively affected.

Predicting the response to rising temperature for a given plant species or ecosystem is complex, for two major reasons. Firstly, temperature affects nearly all biological and chemical processes, meaning that there are many mechanisms by which changes in temperature impact on plant growth and ecosystem function, and the overall effect is given by the interaction of the individual responses. Secondly, most processes show acclimation to temperature. For example, the optimum temperature of photosynthesis changes depending on the temperature at which the plant is grown (Slatyer and Morrow 1977). Therefore, it is not possible to predict long-term responses to rising temperature based on short-term measurements of temperature responses. The long-term temperature response depends on the degree of acclimation that the species is capable of, which is considerably more difficult to establish.

This section discusses the impacts of temperature on plant and soil processes, including photosynthesis, respiration, and soil decomposition. We then consider the implications for growth and carbon sequestration.

4.2 Temperature effects on Photosynthesis

Photosynthesis has a peaked response to temperature (similar to Fig. 4.1), being reduced by both low and high temperatures. In many species, the temperature response shows a broad peak. For example, Hill et al. (1988) showed that photosynthetic rates were at least 80% of maximum over a range of 9 - 14 °C in eight rainforest species. Most plantation species similarly have a broad range of optimum temperatures (Battaglia et al. 2009).

The optimum temperature for photosynthesis differs among species depending on the region of origin. For example, Hill et al. (1988) measured the temperature response of photosynthesis of seedlings of eight temperate rainforest species from Tasmania and mainland Australia grown for 12 to 18 months. Species restricted to northern temperate rainforests had substantially higher optimum temperatures for photosynthesis than the southern species. Similarly, Cunningham and Read (2002) found that optimum temperature for photosynthesis was higher in tropical rainforest species than temperate rainforest species. Such differences have also been found within species. Different provenances of *Eucalyptus pauciflora* were found to have photosynthetic temperature optima that were negatively correlated with elevation of the region of origin (Slatyer 1977). These studies demonstrate that the temperature dependence of photosynthesis adapts to the climate of the region of origin.

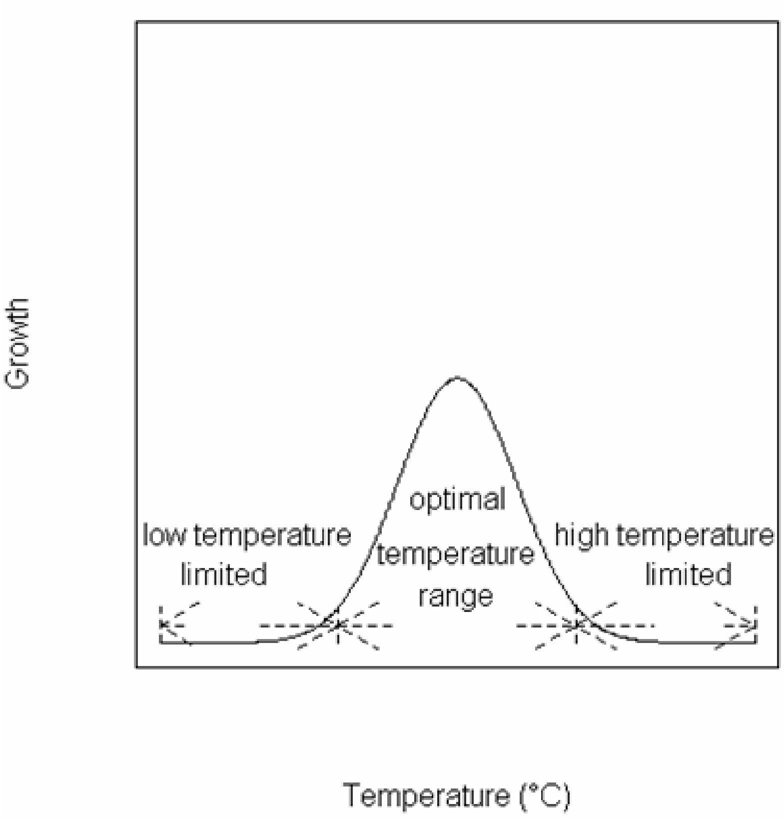

Figure 4.1 Idealised diagram of the impact of temperature on plant growth. When temperatures are above or below the optimal range, growth will be temperature limited. Within the optimal temperature range, high growth rates may be achieved (assuming nutrients and water are available). The optimal temperature range is likely to vary with location and species provenance: for example, it is likely to be markedly different for alpine compared to semi-arid species.

Most species also demonstrate acclimation of the photosynthetic temperature response. For a given species or provenance, the optimum temperature increases with growth temperature. This acclimation response has been demonstrated in a range of eucalypt species (e.g. Ferrar et al. 1989) and rainforest species (Cunningham and Read 2002). However, the change in the optimum temperature is generally less than the change in growth temperature. The capacity for acclimation can be estimated by comparing the change in the optimum temperature with the change in growth temperature. Cunningham and Read (2002) found that tropical rainforest species had higher acclimation capacity than temperate rainforest species; the optimum temperature changed by 0.5 °C per degree change in growth temperature in a tropical rainforest species but only 0.1 °C per degree change in growth temperature in a temperate rainforest species. The growth temperatures used in this study, however, did not go above the growth temperatures experienced by the tropical species in their natural habitat, so we cannot be sure if the tropical species can acclimate to higher temperatures.

In general, however, we can conclude that because of the broad temperature peak for photosynthesis, and the acclimation potential of most species, increases in temperature in the range of 1 - 3° are unlikely to directly reduce photosynthesis (Körner 2006).

4.3 Temperature effects on respiration and the whole-plant carbon balance

The amount of carbon available for plant growth is given by the difference between photosynthetic uptake and respiratory loss. In the short-term, plant respiration increases near-exponentially with temperature. If there is no acclimation of respiration rates, plants can potentially respire themselves to death as temperatures rise. Such a response has been observed in some alpine species (Larigauderie and Korner 1995). However, for most species, respiration rates acclimate to growth temperature, such that the long-term response to rising temperature is weaker than the short-term response (Atkin and Tjoelker 2003).

It has been proposed that respiration rates, in the long term, depend on substrate (carbon) availability rather than temperature, and therefore that respiration rates should correlate with photosynthetic rates rather than temperature (e.g. Gifford 1995, Dewar et al. 1999). Experimental studies show, for example, that shading of leaves to reduce photosynthesis is swiftly followed by a drop in respiration rates (Whitehead et al. 2004). Many forest growth models (e.g. 3PG, Landsberg and Waring 1997) model plant carbon uptake by assuming that the ratio of respiration to photosynthesis (R:P ratio) remains constant with rising temperature. De Lucia et al. (2007) compared estimates of the R:P ratio across forest ecosystems and found that the ratio changed with stand age but did not differ among biomes. This study suggests that the respiration : photosynthesis balance of different forest types is adapted to climate (DeLucia et al. 2007).

However, there is some evidence to suggest that, for a given plant species, respiration does not fully acclimate to changes in climate. For example, Atkin et al. (2007) calculated the R:P ratio for *Plantago* species grown at different temperatures and found that the ratio was constant for plants grown at 13° and 20°C, but increased at higher growth temperatures (27°C). Thus, rising temperatures can reduce net carbon uptake and therefore plant production, through direct effects on plant metabolism.

4.4 Frost and extreme cold

Extreme temperatures can reduce productivity, cause leaf necrosis, or cause plant mortality, depending on species sensitivity to extremes. Frost has a major impact on growth of many species, and reduced frost impacts on productivity are expected to result from warming under climate change. For example, Battaglia et al. (2009) predict increased productivity for *Eucalyptus* plantations in Tasmania due to fewer frost events.

Counterintuitively, some studies have found that rising temperatures lead to increasing frost damage due to reduced frost hardiness. For example, eucalypts are known to 'harden at temperatures just below 4 °C (Harwood 1980; Paton 1980), and frosts of -5 to -6 °C may severely damage or kill seedlings of many eucalypt species if they are not frost acclimated (Harwood 1981). In contrast, if seedlings are frost acclimated, they may survive temperatures below -12 °C (Harwood 1981). Recent evidence suggests that eucalypts may be more susceptible to frost under elevated CO_2 because leaf temperatures rise when stomata close under elevated CO_2, reducing frost hardiness (Barker et al. 2005; Loveys et al. 2006).
A reduction in the number of frost events will also have significant biodiversity implications, as frost-intolerant species may invade regions from which they had previously been excluded. For example, cold induced photo-inhibition has been reported to limit the regeneration of *E. pauciflora* at the tree line in south-eastern Australia (Ball et al. 1991). The distribution of juveniles was reported to be correlated with the occurrence and severity of cold-induced photo-inhibition. A reduction in the number of frost events is likely to allow upwards expansion in the range of *E. pauciflora*, as has been observed by Wearne and Morgan (2001). Similarly, *E. delegatensis* and *E. dives*, normally excluded from higher elevations due to better frost

tolerance by *E. pauciflora*, may also expand their ranges into areas previously dominated by *E. pauciflora* (Bell and Williams 1997).

4.5 Heat stress

At the other end of the spectrum, extremely high temperatures, in the range 45 – 60 °C, can also cause leaf necrosis or plant mortality. Heat stress could become a real threat to Australian ecosystems, particularly given evidence from climate models that extreme high temperatures could increase by double the increase in average maximum temperatures, giving predicted rises of 5 to 8°C across southern Australia (Pitman and Perkins 2008). Increases of this size have the potential to push ecosystems over upper temperature thresholds.

The temperature thresholds for leaf damage vary among species (Larcher 2001). In desert arid or semi-arid ecosystems, vegetation is undamaged by frequent temperatures over 45 °C (Jiang and Zhu 2001), whereas similar temperatures would severely damage leaves of temperate deciduous trees. Also, there is an interaction with drought because transpiration cannot be used to cool leaves when water availability is limited. Leaf temperatures are therefore more likely to reach extreme values in dry periods.

Remarkably little is known about upper temperature thresholds of Australian species. In an early paper, the heat resistance of leaves of *Eucalyptus camaldulensis* varied from 47 to 50 °C, and was not related to the mean maximum temperature of the hottest month at the seed source (Karschon and Pinchas 1971). Cunningham and Read (2006) tested upper temperature tolerances of temperate and tropical Australian rainforest species by heating sampled leaves in water baths. They found that significant visible leaf damage occurred at temperatures ranging from 48 to 55°C, and that threshold temperature increased with average maximum temperature of the hottest month. Yan-Shih Lin (University of Western Sydney) is currently using chlorophyll fluorescence to estimate *in situ* temperature tolerances of a range of *Eucalyptus* species and thus far has found that the critical temperatures are relatively low, below 50°C. (Y. Lin, Pers. Comm.).

In southwestern Australia, a heat wave (> 45 °C over two days) resulted in extensive mortality and leaf damage in a sclerophyllous mallee-heathland (Groom et al. 2004). Principal components analysis of leaf traits of the 40 heat-damaged and 14 undamaged co-occurring species showed that undamaged species had, on average, 61% thicker leaves, and were more exposed to wind, sun and bare soil. Differences between damaged and undamaged trees were attributed to preconditioning to more exposed habitats by the undamaged leaves (Groom et al. 2004).

Pot studies also demonstrate that preconditioning (defined here as increasing the temperature at which a leaf is grown) increases tolerance of high temperatures. For example, *E. macrohyncha* and *E. rossii* leaves grown under ambient temperatures and ambient CO_2, which were then exposed to high temperatures showed increased levels of photoprotective pigments when compared to leaves which developed under high temperatures (Roden and Ball 1996b). This result suggests that trees may be more tolerant to gradual increases in temperature rather than step changes.

The limited evidence available so far thus indicates upper temperature thresholds in the range of 45 to 55°C for Australian species. Extreme maximum temperatures in the southern States are already in the range of 45 to 50°C; increases in these upper temperatures of 5 to 8°C would clearly have the potential to push species over these thresholds. There is a real need to quantify these thresholds for a range of Australian species, both using physiological studies and field monitoring of forest health following heatwave events.

4.6 Soil decomposition and nutrient availability

Rising temperature also has a significant effect on soil processes, with consequences for productivity and ecosystem carbon storage. Soil is the largest terrestrial carbon store (Livesley et al. 2009), and global warming is likely to increase the decomposition of soil organic carbon (Lehmann et al. 2008) and thereby deplete carbon stocks. As temperature increases, soil microbial activity increases, increasing the rate of decomposition of soil organic matter. It is generally accepted that rising temperature will result in a loss of stored carbon via this mechanism (Kirschbaum 2000). However, increased temperatures can also accelerate N mineralization and stimulate plant growth (Simioni et al. 2009). Soil warming experiments in North American forests show that nutrient mineralisation is enhanced by rising soil temperature, and that the resulting increase in soil nutrient availability can drive an increase in plant growth. A meta-analysis of the impact of warming by 0.3 to 6.0 °C on soil processes across a range of sites in the northern hemisphere reported that soil respiration increased by 20%, net N mineralisation increased by 46% and productivity by 19% (Rustad et al. 2001). However, it is uncertain whether these northern hemisphere responses will be similar for Australian forests, as there have been no studies of soil warming effects on Australian forest ecosystems. Simulations of temperature impacts on ecosystem carbon sequestration suggest that enhanced plant growth can outweigh loss of soil carbon in some circumstances, leading to a net increase in total ecosystem carbon storage with rising temperature (Medlyn et al. 2000).

4.7 Impacts on wood density

Increased growth temperatures have been related to increases in wood density in the past and plant biomass accumulation typically increases with increasing temperatures before declining at supra-optimal temperatures (Thomas et al. 2004; Thomas et al. 2007). To test how wood density of eucalypts varies with growth temperature, seedlings of *E. camaldulensis* were grown in growth chambers for 9 weeks, (Thomas et al. 2004) and *E. grandis* seedlings grown at high temperatures for 19 weeks at temperatures from 10 to 35 °C. Wood density was increased in both species, with an increase of 20% in wood density in *E. grandis* (Thomas et al. 2007). Temperature optima for maximum growth (biomass accumulation, stem volume, leaf area ~ 25 °C) differed from the temperature for maximum wood density (~31 °C). These studies suggest that wood density may increase as temperature increases, but studies on large trees are needed to confirm this observation in seedlings.

4.8 Overall impacts of rising temperature on growth

Many studies have attempted to predict plant responses to rising temperature based on the responses of metabolic processes, photosynthesis and respiration. However, this approach is problematic (Körner 2006). Because of acclimation, and temperature dependence of other growth processes, temperature dependences of photosynthesis and growth can be quite different. For example, optimum temperatures for light-saturated photosynthesis of Australian rainforest species range from 18°C in cool-temperate species up to 27°C in tropical species (Cunningham and Read 2002). In contrast, the optimal temperature for growth of cool-temperate species was 28°C while for tropical species the optimal growth temperature was above 30°C (Cunningham and Read 2003). Thus, impacts of rising temperatures on plant growth may be better estimated by examining whole-plant responses rather than responses of individual processes.

Paton (1980) studied growth responses to temperature in a range of *Eucalyptus* species. He found that, for a range of species, there were adverse effects of high temperature on growth. Negative growth impacts occurred for several species at day/night growth temperatures of 33 / 28°C.

Paton’s (1980) conclusions are worth quoting in full:

> “Any predictions of temperature responses in the field thus appear restricted to poor frost hardening as occurs generally in tropical species, and to adverse effects of high temperature. Provided that these temperature limitations do not apply, the potential

> for vigorous growth in several species over a wide range of temperatures appears to be largely independent of any differences in their temperature optima. This kind of versatility helps explain how some *Eucalyptus* species thrive under a range of climatic conditions that Pryor (1976) finds is much wider than their natural distributions suggest."

That is, impacts of temperature on growth are largely due to effects of extremes, and rising temperature should not impact greatly on growth unless impacted by these extremes. This finding concurs with our survey of temperature effects on individual processes. However, the question of why many *Eucalyptus* species have very narrow climatic distributions remains unanswered (see section on Bioclimatic Modelling, below).

Other ways to study temperature impacts on plant growth include gradient studies and dendrochronology (Körner 2006). Such studies also indicate the importance of temperature extremes. Battaglia et al. (1998) compared leaf area index of *Eucalyptus globulus* and *E. nitens* plantations across southern Australia and found a strong relationship with mean annual temperature (MAT). Reflecting the difference in frost tolerance between the two species, leaf area index (LAI) of *E. globulus* was reduced below MAT of 10 °C and that of *E. nitens* below MAT of 8 °C. It would be of interest to investigate productivity across wider temperature gradients, such as the latitudinal gradient occupied by Australian rainforests. Differences in ecosystem productivity along this gradient have not been quantified to date, but could shed considerable light on the temperature effects on growth.

Dendrochronological studies of eucalypts are problematic owing to methodological issues, so this approach has not been widely applied to the genus (Brookhouse 2006). However, these limitations are being overcome. Recent work on *E. pauciflora* demonstrates a strong dependence of ring width on springtime maximum temperature at the highest elevations (Brookhouse and Bi 2009). In trees growing at lower elevations, where cold temperatures are not so extreme, ring width was more strongly correlated with summer and autumn rainfall. This observation appears to confirm the importance of temperature extremes in determining temperature responses.

4.9 Conclusions: Temperature

- Photosynthesis and respiration are dependent on temperature, but in most plants both processes have the capacity to acclimate to growth temperature. The response of plant growth to temperature may therefore be quite different from the response of net photosynthesis.

- Despite relatively narrow natural climatic distributions, experimental manipulations suggest that many Australian species thrive at a wide range of temperatures.
- Extremes of temperature are suggested to be more important in determining distributions than mean temperatures. Frost tolerance is a major limiting factor. Reduced incidence of frost under climate change may enable range expansions of some species. However, warmer temperatures can also increase frost damage, if frost hardiness fails to develop.
- Extreme high temperatures are predicted to increase more than average maximum temperatures. Heat stress has the potential to negatively affect performance of a wide range of species, and further research quantifying the effects of extreme high temperatures on plant growth is required.
- There are several interactions between rising temperature and moisture availability. One important effect is that rising temperatures could increase potential evapotranspiration, reducing water availability. This interaction is discussed in the next section.

5. Water availability

5.1 Introduction

Australia’s water limited environment means that the scarcity of water resources is a major concern for forest managers. Forests dominate the hydrological balance of many of Australia’s main urban water catchments (Macar et al. 2006). In particular, transpiration has a significant influence on the volume of water available for catchments downstream. Drought has incurred an enormous cost to Australia over recent decades, with the droughts of 1982-83, 1991-95 and 2002-03 costing $A3 billion, $A5 billion and $A 10 billion respectively (Hodgkinson and Garner 2008).

Potential impacts of climate change on water availability include changing rainfall patterns, increased frequency of drought, and higher evaporative demand (CSIRO 2007). A decrease in rainfall is ‘likely’, that is, more than 67% probability of decrease, in south-eastern and Western Australia, with decreases strongest in winter-spring. Any increases in rainfall (nowhere ‘likely’) are most possible in the north and east in summer and autumn (“wet season”). Local changes may vary significantly (CSIRO 2007). There is likelihood of more frequent drought (as compared to current climate) over most of Australia, particularly in the south-west. The seasonality of rainfall is also projected to change, with decreases in winter and spring particularly in the south-west. In summer and autumn decreases are predicted to be smaller, and slight increases predicted for eastern Australia.

Additionally, as temperatures increase, potential evaporation rates could increase, leading to increased evaporative demand. Many ecophysiological models (e.g. Battaglia et al. 2009) assume such an increase in evaporative demand. Best estimate projections reported by CSIRO (2007) were for an increase in potential evaporation of 6% in the south and west, and 10% in the north and east, under the A1FI scenario by 2070. While the values from the CSIRO (2007) report were then “best-practice” projections, there is considerable new research demonstrating non-stationarity in other climate variables affecting the process of evaporation, particularly wind speed (Roderick et al. 2007; Rayner 2007, McVicar et al. 2008; Donohue et al. 2010; Johnson and Sharma 2010). This research suggests that these projections need to be re-performed as a matter of priority using a formulation of potential evapotranspiration (PET) that explicitly uses all the forcing meteorological variables (net radiation, vapor pressure, wind speed and air temperature).

On balance, however, the changes in rainfall and evaporation are likely to reduce water availability and add pressure on water allocation systems (DAFF 2006), leading to increased conflict over Australian water resources. Climate change will alter the dynamics of surface and groundwater, in addition to changing plant requirements for water. The impact of climate change on forests and changing rainfall in particular will depend on two factors; first, the final degree of change, and second, the resilience of the ecosystem in question (Warman and Moles 2009).

In this section we first discuss the general physiological impacts of moisture availability and drought on leaf area and productivity. Experiments on the impact of drought are conducted using pot or glasshouse studies, observational studies of drought on *in situ* trees and seedlings in forests, or transect studies along rainfall gradients. Evidence of interactions between water availability and productivity, growth and leaf area based on these different types of experiments is reviewed. Thresholds which must be exceeded before mortality results from drought are then described. Australian studies describing the impact of drought on mortality, community structure, soil processes and interactions between CO_2 and drought are presented, followed by caveats and conclusions.

5.2 Degrees of drought and impacts on production

The definition of ‘drought’ varies across continents and experiments depending on whether the research perspective is hydrological, meteorological, physiological or agricultural. Droughts can range in length from several days in a glasshouse experiment, through to the multi-year droughts experienced in Australia. Droughts may occur as infrequent extreme events, for example the 50% reduction in annual rainfall across Europe in 2003 (Ciais et al. 2005), or as regular seasonal droughts, for example savannas which receive monsoons (Hutley et al. 2001). Impacts of drought on productivity and mortality will clearly depend on the length and intensity of the ‘drought’.

There is a cascade of impacts on plants which result from drought, as both the drought intensity and duration increase. In short-term (several days) or moderate levels of drought, plants control water use by reducing stomatal conductance. In the medium term (weeks or months) leaf area is reduced, and biomass allocation patterns are altered, with a shift towards higher root:shoot ratios. During the longer-term (months or years) or high levels of drought intensity, xylem embolism occurs, leaf shedding takes place and finally death occurs. If drought becomes prolonged, regeneration of seedlings is likely to be reduced.

Timing of precipitation will also influence mortality and productivity, as high growth rates are unlikely to be maintained in regions where precipitation is erratic. Some species, for example, *E. globulus*, are adapted to short periods of drought stress, although prolonged periods of drought stress lead to mortality (Mendham et al. 2005). Importantly, forests also become more prone to damage from fire and pests after periods of drought (Kliejunas et al. 2008;

Pinkard et al. 2009) leading to either reductions in productivity or mortality. Trees and communities are likely to recover from short term drought, whereas long-term and intense drought can lead to insect damage and severe fires which may ultimately alter forest composition. These issues are further addressed in sections on pests and fire.

5.3 Relationships between water availability, leaf area and productivity

Arguably, decreasing water availability is one of the greatest concerns for forest productivity in the future, especially considering that when water stressed, forests are highly susceptible to pests, disease, fire and drought. Water availability is not determined by climatic conditions alone: other factors that influence water availability include soil depth, topography, aspect, and soil texture and structure (Battaglia and Williams 1996; Mendham et al. 2005). Therefore estimates of the impacts of decreasing rainfall on productivity need to consider soil type and other influences on water availability. For example, it is likely that sites with high soil water holding capacity will show more resistance to decreasing rainfall, than sites with low water holding capacity.

Water availability has a strong influence on leaf area index (LAI, which is calculated as m^2 leaf area m^{-2} ground area). In turn, LAI is strongly and positively correlated with forest productivity. Both field data and remote sensing studies have reported an increase in LAI or tree cover (Fensham et al 2009) with increasing rainfall across a number of sites throughout Australia and overseas (Ladd et al. 2009; Pekin et al. 2009). Conversely, the impact of decreasing water availability leading to reductions in forest growth (Keith et al. 2009; Myers B. et al. 1996; Stoneman et al. 1997) and leaf area (Battaglia et al. 1998; Pook et al. 1997) is well known. There is considerable research describing the influence of water availability on leaf area index and productivity in Australian forests, from a range of experimental methods, forest types and regions. The chief methods of investigating impacts of water availability on forest LAI and productivity include 1) manipulative experiments; 2) observations during naturally occurring droughts; and 3) observations across naturally occurring gradients in rainfall or depth to groundwater.

5.3.1 Manipulative experiments

There have been many glasshouse-based studies of drought impacts on productivity, which consistently demonstrate that reduced stomatal conductance and leaf area at low water availability lead to reduced productivity (e.g. Battaglia and Williams 1996, Austin et al. 2009). However, responses to drought vary significantly among species. For example, different hybrid clones of *Eucalyptus grandis* (*E. grandis x urophylla,* GU and *E. grandis x camaldulensis,* GC) gave different growth patterns in response to drought. The GU clone ceased growth under drought conditions but responded rapidly when water became available. GC grew more slowly on more days of the year than the GU, over a 3.5 year study (Drew et al. 2009). Similarly, two different eucalypt seedlings, *E. obliqua* and *E. tenuiramis* gave different growth responses (linear or with a threshold) to a gradient in soil water availability, imposed by different soil depths (Battaglia and Williams 1996). The height increment response to soil water was complex. At the shallow-soil end of the gradient, growth increment of both species was low but not significantly different. At the mid region (0.30 to 0.45 g g^{-1}; -0.05 to -3.0 MPa) height increment of *E. tenuiramis* was significantly greater, and at the deep soil end of the gradient the height increment of *E. obliqua* exceeded that of *E. tenuiramis*. At the deep end of the gradient, *E. obliqua* plants had a greater leaf area than *E. tenuiramis.*

Rates of recovery following drought depend on the severity of the drought. In a pot study on four woody angiosperm species which were subjected to mild or severe drought, transpiration and leaf hydraulic conductance were strongly related to the severity of drought imposed (Blackman et al. 2009).

It is important to note that many of the manipulative studies on the impacts of water availability have been made with young plants, seedlings or saplings rather than mature forest stands. Both tree growth and evapotranspiration are known to vary as trees age (Kirschbaum 2005; Vertessy et al. 2001). Consequently it is difficult to estimate the impacts of water availability on forest growth directly from seedling or pot studies.

5.3.2 Naturally occurring droughts

Much can be learnt by monitoring forest health during naturally occurring extreme events. A classic series of papers by Pook (1985, 1986) reports on the effects of the severe droughts of 1980 and 1982 on a forest dominated by *Eucalyptus maculata* at Kioloa on the south coast of NSW. Impacts on leaf area and shedding were markedly different between the two drought years, due to the different timing of rainfall (Pook 1985; Pook 1986). In 1980, LAI was reduced from 4.3 to 0.8 due to massive leaf shedding which occurred in response to the drought, whereas in 1982 this leaf shedding was not repeated. Although the rainfall deficiency and duration of drought were similar in both years, the ‘effective’ rainfall which fell in winter-spring when evaporation was reduced, was lower in 1980 than 1982. It is noteworthy that the temperatures in the latter half of 1980 were also higher, contributing to higher evaporative demand than in 1982. In 1982 when soil moisture reached critically low levels, a sufficient amount of rainfall allowed a modest recharge of soil water and averted water stress in trees.

In contrast, in 1980 soil moisture was depleted during much of the study period. Thus, the timing of rainfall during two drought years had a marked impact on leaf area.

A long-running eddy flux study in a native *Eucalyptus delegatensis* forest at Tumbarumba in the Snowy Mountains has similarly provided insights into effects of drought on forest carbon exchange. In this study, net ecosystem exchange of carbon has been monitored since 2001 (Leuning et al. 2005). During this period, two drought years have occurred. Net ecosystem carbon uptake, which was strongly positive in wet years, was reduced below zero during the first drought year but unaffected in the second drought year (van Gorsel, pers. Comm.) The reduction in carbon uptake during the first drought year has been ascribed to pest damage rather than direct water stress (Kirschbaum et al. 2007). This study demonstrates the potential for relatively mild drought to impact significantly on forest productivity due to pest interactions.

Observational studies also show that different species have different performance under drought. A plantation study comparing water relations of *E. nitens* and *E. globulus* found that pressure-volume curves and leaf water potential data indicated that *E. globulus* had greater drought tolerance than *E. nitens* (White et al. 1996). The implication is that reduced water availability can drive important changes in community structure, as drought impacts favour species that can tolerate drought stress. As a consequence, severe drought can have rapid, widespread and long-lasting impacts on the vegetation composition of a landscape (Hanson and Weltzin 2000).

5.3.3 Gradient studies

Natural gradients in rainfall can also be used to assess effects of water availability on LAI and productivity. However, it is important to bear in mind that other factors may also vary along the gradient, confounding such studies: in addition to mean annual rainfall, herbivory, fire and climate variability are interrelated factors which influence the tree cover of a site (Lehmann et al. 2009).

A number of studies across rainfall gradients within Australia and internationally have demonstrated that LAI or Plant Area Index (the sum of the stem area index and the leaf area index) (Scholes et al. 2004) increases to a maximum value as rainfall or water availability increases (Ellis and Hatton 2008; Ladd et al. 2009; Specht and Specht 1999). For example, the North Australian Tropical Transect comprises three sites across a gradient in mean annual rainfall from 600 to 1200 mm (Eamus et al. 2000; Hutley et al. 2001; O'Grady et al. 2000). LAI increases as rainfall increases across this rainfall gradient, and differences are higher in the wet season (Hutley et al. 2001).

A study in south-west Western Australia examined jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) stands along an aridity gradient with variable fire histories (Pekin et al. 2009). Stem density, basal area, stand biomass, sapwood area, leaf area and litterfall were measured. Leaf area (and standing biomass) was lower at more arid sites, while sapwood area was unaffected, suggesting these stands respond to decreased water availability by lowering leaf area relative to sapwood area (Pekin et al. 2009).

However, another study in south-west Western Australia, this time on *E. globulus* plantations across a gradient in mean annual rainfall from 600 to 1420 mm, showed that although carbon isotope discrimination and basal area were strongly positively correlated with water availability, LAI was only weakly correlated with basal area (Macfarlane et al. 2004). The authors concluded that canopy conductance is a more important determinant of growth than LAI in water-limited (but fertilized) *E. globulus* plantations (Macfarlane et al. 2004). These findings are in contrast to a study which reported that LAI in fertilized *E. globulus* plantations across southern Australia increases from 3 to 6 as water stress decreases (Battaglia et al. 1998).

The depth to groundwater also clearly influences LAI and productivity (Benyon and Doody 2004). A study in south-western Australia quantified the impact of water availability on sites with comparable species and site conditions. *E. kochii* trees that had shallow access to groundwater had three times higher LAI (3.2 m^2 m^{-2}) than trees over deep groundwater (1.0 m^2 m^{-2}) (Carter and White 2009). Similarly, a comparison of biomass on two west Australian sites with the same climatic conditions showed that a restored mine site, with higher soil water and nutrient availability than the control site, had higher biomass. This was indicated by 20-25% thicker leaves, 30-70% greater leaf area, 10-30% greater leaf area to sapwood area ratios on the restored site (Bleby et al. 2009).

Wood density also may increase as water availability decreases (O'Grady et al. 2009; Pickup et al. 2005; Wright et al. 2006). A series of drought risk trials on *E. globulus* in Western Australia across a rainfall gradient (Mendham et al. 2005) reported that wood density was 20% higher at a low rainfall site (Annual rainfall of 600 mm) compared with a high rainfall site (Annual rainfall of 1000 mm).

5.3.4 Summary

Thus, the mechanisms by which decreasing water availability affects productivity are well understood, and have been quantified for some of the more important forestry species, such as *Eucalyptus globulus*. However, it is clear that different species respond differently to water availability. We need better quantification of growth and productivity responses to declining water availability, particularly for native forest species. Because species respond differently to water availability, it is likely that community composition will be altered as water availability changes, with important implications for biodiversity. Research that groups species into different hydraulic functional types based on water use strategies and growth responses may assist with water management (following Mitchell et al. 2008). Such research can be used in models predicting drought impacts on forest species, which are of vital importance for managing water and carbon of Australia’s native forests under climate change.

5.4 Drought and mortality

5.4.1 Introduction

As discussed in the previous section, droughts may cause reductions in forest productivity. For forest managers, however, the more important risk from drought is that of mortality, which threatens forest viability. The risk of drought mortality under climate change urgently needs to be quantified. However, we have little information on mortality to base the assessment of such risks. In fact, even the causes of drought mortality are still not fully understood (Adams et al. 2009a; Adams et al. 2009b; Sala 2009). Drought could cause mortality through several alternative mechanisms, including hydraulic failure (stems can no longer transport water) and carbon starvation (insufficient photosynthesis because stomata are closed) (McDowell et al. 2008). It is not yet clear which of these mechanisms is the more important. Drought stress can also predispose trees to pests and diseases, which may be the ultimate cause of mortality.

Mortality within and across a species is typically highest in more arid locations, such as sun facing aspects, well drained soils or ridgetops (McDowell et al. 2008). Drought-associated tree mortality appears to particularly affect trees at either end of the size spectrum; that is, seedlings and tall trees (McDowell et al. 2008). Seedlings are particularly susceptible to drought due to shallow roots (Nitschke and Hickey 2007). For example, in a seedling establishment study in northern Australia, higher soil temperatures in a savanna compared with a nearby rainforest caused reduced soil water availability and reduced seedling survival in the savanna (Bowman 1993).

Drought-induced mortality has implications for ecosystem function, land-surface interactions and ecosystem services. Overstorey mortality reduces photosynthesis, potentially causing ecosystems to become a CO_2 source for a time. Understorey mortality may increase growth within the overstorey, and successional pathways may change. Reductions in leaf area impact solar radiation reaching the ground, influencing water evaporation, transpiration and

soil processes such as nutrient cycling, mychorrhizal activity and erosion. The consequences of these changes on subsurface hydrology remain untested (McDowell et al. 2008).
Episodic severe droughts can completely reverse long-term trends in ecosystem production and biomass. For example, in northern Australia, a net increase in tree cover was observed over fifty years and was ascribed to above-average rainfall over this period. However, this trend was completely negated by tree mortality during a severe drought (Fensham et al. 2009). Thus, predictions of long-term ecosystem dynamics need to consider the impacts of drought-induced mortality.

Despite knowledge that drought leads to mortality in Australian eucalypts (Battaglia et al. 2009; Fensham and Fairfax 2007; Rice et al. 2004), the physiological mechanisms causing drought mortality remain poorly understood, and thresholds for drought mortality are poorly quantified. Therefore, our ability to predict when regional-scale plant stress will exceed a threshold that results in widespread mortality is lacking, yet this ability is fundamentally needed to assess potential climate-change impacts (McDowell et al. 2008). There is an urgent need to better understand the impact of drought on plant function and particularly on the physiological mechanisms which underlie plant responses during and in recovery from water stress (Blackman et al. 2009).
Observational studies suggest that there are differences among species in susceptibility to drought. For example, a severe drought in 1992-94 in a eucalypt woodland in north Queensland resulted in tree mortality regardless of grazing intensity (Fensham 1998a; Fensham 1998b). The study found that 27% of all tree species (not individual trees) were killed as a result of the drought. Mortality ranged from 4% for *Corymbia dallachiana* to 29% for the dominant species *Eucalyptus xanthoclada* although the differences were not statistically significant.

Differences among species in susceptibility to drought could drive shifts in community composition. There have been several recent advances in identifying physiological differences among species that give rise to differences in drought tolerance. Some eucalypts use solutes, especially quercitol (Merchant et al. 2007) as a kind of ‘safety net’ under conditions of extreme drought, that may assist the overall drought tolerance of these species and enable them to avoid mortality. Many studies give evidence of the potential importance of these compounds (Arndt et al. 2008; Merchant et al. 2009; Merchant et al. 2006a; Merchant et al. 2006b). These species use the solutes to aid adjustment of water potential to tolerate the effects of drought. However, we currently lack an understanding of the relative importance of this mechanism compared to other physiological mechanisms involved in maintenance of leaf water potential under drought conditions. It is unclear if eucalypts mainly employ osmotic adjustment (net adjustment of solutes) or elastic adjustment (adjustment of cell wall flexibility) in response to drought, and which of these strategies is more effective under increased drought conditions (Callister et al. 2008).

It is also known that species differ in their ability to maintain leaf water potential: species can be classified as isohydric, in which case leaf water potential is maintained above a minimum threshold, anisohydric, in which case leaf water potential is not controlled, or seasonally isohydrodynamic, in which case the gradient between leaf and soil water potential is maintained constant (Franks et al. 2007). It is not known, however, whether different physiological responses to drought among species can be used to infer differences in drought tolerance in the field. Field studies investigating differences in mortality among species during extended droughts in savannas suggest that relative rooting depth is a major determinant of drought tolerance (Rice et al. 2004, Fensham and Fairfax 2007). Research linking physiological studies with ecological observations of drought tolerance is needed in order to establish a scientific basis for identifying differences in drought susceptibility among species.

5.4.2 Estimates of drought risk thresholds

A few studies have quantified the threshold that must be exceeded before mortality occurs, in terms of drought intensity and duration, in eucalypt plantations (Mendham et al. 2005) and forests (Pook 1985; Pook 1986). It is likely that this threshold differs across ecosystems, and differs for species within ecosystems (Battaglia et al. 2009).

A plantation study defined drought thresholds beyond which growth declined, using pre-dawn leaf water potential measurements (White et al. 1996). Growth, conductance and assimilation of *E. nitens* and *E. globulus* decreased when pre-dawn leaf water potential fell below ~ -0.5 MPa (White et al. 1996). Mendham et al. (2005) conducted a study on the risk of mortality due to drought in south-western Australian plantations, and defined thresholds for mortality risk as follows. Moderate drought was defined as occurring when one or more months during the peak LAI period (age 3 to 6 years old) had predicted pre-dawn leaf water potential less than -3 MPa and mean maximum air temperatures higher than 30 °C (Mendham et al. 2005). Severe drought was defined as one or more months during the critical period with predicted pre-dawn water potentials less than -3.2 MPa and mean maximum air temperatures higher than 35 °C (Mendham et al. 2005).

In a *Eucalyptus maculata* forest in Kioloa, NSW, severe drought risk was quantified. Foliage retained normal appearance above pre-dawn leaf water potential of -3 MPa but became dull and obviously wilted in the range of -3 to -5 MPa, and was severely wilted and turned brown (dead) below -5 MPa (Pook 1986). As mentioned above, mortality resulting from decreased water availability was also linked with increased temperatures in the comparison of two drought years. It is likely that the effect of high temperature in these studies is actually a response to higher vapour pressure deficit.

With few exceptions, (notably mangroves) stomata of plants grown under natural conditions begin to limit transpiration and assimilation as leaf water potential falls below -1.5 MPa, with 60% closure occurring close to -2 MPa (Brodribb 2009). Under optimal conditions whole-plant conductance (K_{plant}) determines maximum stomatal conductance, but as soil dries, soil water potential becomes the dominant controller of stomatal aperture. At some point during the drought the pipes which constitute the xylem pathway collapse and they become non-functional. This process limits the recovery of plants from drought and determines the point at which leaves are shed (Brodribb 2009).

Recent studies have demonstrated that the vulnerability of stem and leaf xylem to cavitation sets a quantitative limit to the drought tolerance of evergreen conifers (Brodribb and Cochard 2009) and angiosperms (Resco et al. 2009). Vulnerability to cavitation is therefore an important factor in terms of predicting distributional limits for native plants and predicting the conditions which are likely to result in death during drought (Brodribb 2009).

More questions remain to be answered regarding plant responses to water stress. For example, what determines the difference between dead and surviving trees? Additionally, at what point do the surviving trees experience observable reductions in photosynthesis due to water stress? A comparison of fluorescence and leaf water potential was conducted on *E. camaldulensis* stands which had varying degrees of forest health, which was estimated using percentage live basal area, plant area index and crown vigour. Results showed that although a stand may show visual signs of extremely poor condition, the few living trees may not show measurable levels of water or photosynthetic stress, as defined by measurements of leaf water potential or fluorescence (Cunningham et al. 2007). Thus, further research is required to assess the physiological mechanisms employed by Australian trees that enhance drought resistance and drought tolerance.

Several studies demonstrate that risks to plantations from drought stress can be minimized by managing stocking density of stands. Horner et al. (2009) showed that drought mortality of *Eucalyptus camaldulensis* plantations in Victoria was high in high density stands, whereas low density stands were relatively unaffected by drought. CSIRO studies on *Eucalyptus globulus* plantations in Western Australia have shown similar results (Mendham et al. 2005).

5.5 Conclusions: Water Availability

The impact of drought on plantations and native forests will differ depending on species, provenance and site conditions. Also, impacts of drought on forests will depend on the intensity and duration of drought, and the seasonality and timing of rainfall events, as well as interactions with fire and pests.

There is a cascade of responses depending on drought severity: forest trees are likely to recover from slight drought, productivity may decline for moderate drought, whereas if drought is prolonged and severe, mortality may result.

A range of options are available to plantation managers to avoid drought risk. These include: selecting more drought tolerant species or provenances; selecting sites in areas with higher or more certain rainfall; reducing leaf area and therefore drought risk through thinning or reducing fertilizer use. Such management techniques allow plantation managers to balance profit from timber production against drought risk.

There have been several recent advances in understanding of the physiological mechanisms underlying drought tolerance. However, it is unclear whether physiological differences among species correspond with ecological observations of drought tolerance in the field. There is a real need for research that bridges these different scales: we need to quantify drought tolerance in the field, particularly for native forest species, and link it with understanding derived from physiological research.

Implications: In order to prevent mortality of plantations, leaf area may be managed by manipulating stocking and soil fertility, as well as careful site and species selection, keeping in mind possible future reductions in water availability in some regions (Battaglia et al. 2009; Mendham et al. 2005). Native forests may also be managed for productivity, by altering grazing, fire regimes, patch size and the volume of wood gathered. Finally, forest managers may need to balance the trade-off between high productivity and risk of mortality in water limited regions, keeping in mind that reduced water availability may decrease LAI, therefore mitigating potential decreases in stream flow.

Individual Factors – Plant Processes

6. Vegetation Water Use

The impact of climate change on water resources is of fundamental importance for Australia, the driest inhabited continent. Vegetation water use is a major factor in determining runoff to streams and recharge to groundwater. In this section, we review current knowledge of the role of forests in determining hydrological responses to climate change.

6.1 Impact of rising CO_2 on water relations

A key point is that rising atmospheric CO_2 concentration has a direct effect on plant water use. A meta-analysis of stomatal conductance of forest trees grown under elevated CO_2 found an average reduction of 21%, with larger decreases in angiosperms than gymnosperms (Medlyn et al. 2001). This reduction in stomatal conductance has the potential to reduce canopy transpiration, or to increase soil moisture for a period (Leuzinger and Körner 2007; Onoda et al. 2009). However, it is unclear how these reductions in stomatal conductance will play out at ecosystem scale. Water savings from reduced stomatal conductance could drive an increase in ecosystem LAI, resulting in increased productivity but unchanged water use (Field et al. 1995; Wullschleger et al. 2002). Increasing LAI could also impact on hydrology by increasing the amount of leaf litter, leading to increased retention of soil moisture (Schäfer et al. 2002).

Data from FACE studies in closed-canopy forests have not resolved this issue. At the Duke FACE experiment, stomatal conductance of *Pinus taeda* was not reduced by growth at elevated CO_2 (Ellsworth 1999), which is typical for coniferous species (Medlyn et al. 2001). At the Oak Ridge and Swiss Canopy Crane FACE experiments , stomatal conductance was reduced and LAI did not increase, leading to reduced transpiration and increased soil moisture at elevated CO_2 (Leuzinger and Körner 2007; McMurtrie et al. 2009). However, ambient peak LAI in both these experiments was very high, of the order of 5 $m^2\ m^{-2}$, indicating that water availability was not limiting to growth at either experiment (Calfapietra et al. 2010). Thus, none of these experiments is directly relevant to the water-limited broadleaf forests dominating Australia.

Australian research on elevated CO_2 has reported some decreases in transpiration and stomatal and hydraulic conductance (Eamus et al. 1995), but not in all experiments (Table 6.1). In an early unreplicated study using a large clear plastic tent and weighing lysimeter in a

12 year old regenerating eucalypt forest, Wong and Dunin (1987) found lower transpiration on a day when the trees were exposed to doubled CO_2, compared to a day at ambient CO_2, even after correction for differences in VPD between the two days. In tropical savannas, *Maranthes corymbosa* which were exposed to elevated CO_2 showed reductions in stomatal conductance of 10 to 30%, and stomatal acclimation did not occur (Goodfellow et al. 1997a). Saplings of *Mangifera indica* were exposed to elevated CO_2 for 28 months and stomatal conductance and density was reduced (Goodfellow et al. 1997b). Eamus et al. (1995) found significant reductions in whole plant conductivity under elevated CO_2 for two tropical Australian tree species. *Eucalyptus tereticornis* plants grown under elevated CO_2 and drought treatments showed no significant effect of elevated CO_2 or water supply on Huber values of trees experiencing 18 weeks of treatment, whereas 23-week old trees under elevated CO_2 and drought showed significantly lower Huber values (sapwood area:leaf area) ($P < 0.05$) (Atwell et al. 2007). Although the plants subject to elevated CO_2 had larger canopies, the CO_2 also improved the day time water status of the leaves of droughted trees. The effect of elevated CO_2 lead to a highly significant reduction in hydraulic conductance (defined as 'potential axial flow rate', see Atwell et al. 2007).

At the Hawkesbury Forest Experiment, carbon and water fluxes were measured on 12 *Eucalyptus saligna* trees in whole tree chambers under ambient and elevated CO_2, and high and low water treatments. Results showed that under elevated CO_2 stomatal conductance decreased, the rate of water use was lower, and water use efficiency increased.

Table 6.1: The impact of elevated CO_2 on water relations in Australian woody vegetation. Data come from manipulative experiments where plants grown at ambient CO_2 (340 – 380 ppm) are contrasted with plants grown at enriched CO_2 (600 – 700 ppm).

Species	Stomatal conductance	Transpiration	Hydraulic conductance	Experiment details	Reference
E. macrorhyncha *E. rossii*	30% reduction in well watered plants	n/a n/a			Roden and Ball (1996a)
E. pauciflora	45% reduction. No change in stomatal density.	n/a n/a		Seedlings overwintered (Mar – Nov) in open top chambers	Barker et al. (2005)
Mangifera indica	Reduced due to declines in both stomatal density and aperture	n/a n/a		Seedlings grown in the ground in ventilated tents for 28 months	Goodfellow et al. (1997a & b)
E. saligna	30% reduction	Negative effect	n/a	Saplings grown for two years in whole tree chambers	McMurtrie et al. (2009)

Species	Stomatal conductance	Transpiration	Hydraulic conductance	Experiment details	Reference
E. tetradonta *M. corymbosa*	48% reduction 53% reduction	36% reduction 53% reduction	78% reduction 72% reduction	Seedlings grown in ventilated tents	Eamus et al. 1995
E. saligna, *E. sideroxylon*	No effect			Seedlings grown in 7L pots for 150 d in glasshouses	Ghannoum et al. (2009)
E. tetradonta *M. corymbosa*	g_s reduced for saplings grown and measured in CO_2 for both species	n/a n/a		Seedlings grown in ventilated tents	Berryman et al. (1994)
E. maculata *E. globoidea* *A. longiflora*	n/a Red	uced by 30%	n/a	12 year old regenerating forest, unreplicated, one day	Wong and Dunin (1987)
E. pauciflora	n/a n/a		Four-fold higher below-ground hydraulic conductance	Seedlings grown in OTCs and glasshouses	Atwell et al. (2009)
E. tereticornis	n/a	n/a	‘capacity for water transport was increased’	Seedlings grown in 50L pots for 23 weeks	Atwell et al. (2007)

Thus, experiments consistently show that stomatal conductance of Australian species is reduced by growth at elevated CO_2, leading to short-term reductions in transpiration. However, it is unclear whether reductions in transpiration will be maintained in the long-term, or whether additional soil moisture will support enhanced productivity. Ecosystem-scale studies, such as the EucFACE experiment to be established in *Eucalyptus* woodland at University of Western Sydney, are urgently needed to resolve this question.

A further point is that the influence of CO_2 on transpiration varies with vapour pressure deficit (VPD), with larger effects on stomatal conductance and sapflow under low VPD conditions (Cech et al. 2003; Will and Teskey 11997; Wang et al. 2005). A similar result has been observed at the Hawkesbury Forest Experiment. The effect of rising CO_2 on transpiration is thus likely to be strongest in mesic environments where VPD is relatively low.

Implications: The impact of CO_2 on Australian forests will depend on nutrient and water availability of the site, as well as whether canopy closure has been reached. Because the ‘water savings’ have been reported to increase in drought conditions, there is the potential that CO_2 may increase drought tolerance in some instances. These water savings are only likely to occur if productivity or leaf area does not increase and if temperatures and rainfall remain similar. Further large-scale research into interactions between CO_2 and water availability is a high priority for predicting dynamics of water use in Australian woody ecosystems.

6.2 Evidence of species differences in water use

There are clear species differences in rates of water use per unit leaf area and in drought tolerance (Austin et al. 2009). However, there is debate over whether whole stand water use differs with species (Hatton et al. 1998). Several studies now show that different species within a stand may use different strategies to achieve the same end, of using all available water. That is, co-occurring species may have different wood density, leaf area and sapwood area (Pekin et al. 2009) yet at stand level, generally appear to use all available rainfall (Hatton et al. 1998; O'Grady et al. 2009; Zeppel and Eamus 2008). Further research is needed to determine whether this ‘functional convergence’ is widespread, and if we can ignore the role of species-level diversity when estimating stand water use.

6.3 Impacts of altered precipitation and temperatures on the water balance

It is well known that increasing water availability leads to increased tree water use, up to a certain threshold, above which tree water use reaches a plateau (Eamus et al. 2006; Zhang et al. 1999). Conversely, the negative impact of drought on tree water use has been researched extensively (Eberbach and Burrows 2006; McJannet and Vertessy 2001; Veneklaas and Poot 2003; White et al. 1998; White et al. 1996; Whitehead and Beadle 2004; Zeppel 2006; Zeppel et al. 2008a; Zeppel et al. 2008b. Water availability at a site may be influenced by topography (Mitchell et al. 2008), depth to groundwater (Carter and White 2009; O'Grady et al. 2009; O'Grady et al. 2006) soil type and depth, (Battaglia et al. 2009) rooting depth (Mitchell et al. 2008), as well as precipitation (Zeppel et al. 2008b).

6.3.1 Tree water use in response to changes in rainfall

Impacts of changes in rainfall on tree water use depend strongly on the nature of the ecosystem, whether it is energy-limited or water-limited. In energy limited regions, such as the tropics of northern Australia, decreasing rainfall will not influence LAI or tree water use strongly. However, the large amounts of run-off, of the order of 6500 mm yr^{-1}, (McJannet et al. 2007a) which flow from some wet tropic sites make significant contributions to environmental flows and water balance of the region. Hence, although LAI and water use may not decrease, river flows are likely to be influenced by altered rainfall. As a result, although productivity may not decrease under reduced rainfall, the ratio of runoff to rainfall will.

Changes in rainfall generally have a dramatic impact on water use in water-limited systems. For example, a native forest stand dominated by *Eucalyptus crebra* and *Callitris glaucophylla* exhibited decreased annual stand water use (318 mm) in a drought year with reduced mean annual rainfall (522 mm, 51% of Mean Annual Rainfall, MAR), and 443 mm in a year with above average rainfall (1062 mm, 171% of MAR) (Zeppel et al. 2008b). Thus, stand water use increased by 39% when rainfall almost doubled.

6.3.2 Hydrology of tropical forests

Climate change is expected to have significant impacts on tropical montane cloud forests, that differ from effects on forests in other regions. It has been hypothesized that climate change could reduce cloud contact with forests by increasing the height of cloud formation and also increasing evapotranspiration (Still et al. 1999). In four to six different rainforest types in the Wet Tropics, cloud interception was a significant input of water at high altitudes (> 1000 m) reaching up to 66% (McJannet et al. 2007b), and over the 3.5 year study period varied between 7 and 30% of total water input (McJannet et al. 2007a). Upper montane cloud forests have a positive net water balance throughout the year and their exceptionally large annual run-off (approximately 6500 mm yr^{-1} at a site with rainfall of 7500 mm yr^{-1}) is a significant source of water for river flows (McJannet et al. 2007a). Interestingly, at all sites actual evaporation was greater than potential evaporation by between 2 and 53% on an annual basis, with the source of additional energy uncertain but likely to come from advection (McJannet et al. 2007a).

6.3.3 Forest hydrology after fire

The water balance of a forest changes dramatically after fire (Wood et al. 2008). Water use of the forest stand immediately after fire is very low, and runoff into downstream rivers and streams is high. Research from catchments dominated by mountain ash forests in Victoria shows that in the years and decades after fire, forest growth recovers and stand water use increases, leading to a level of runoff that can be significantly lower than before the fire event (Macar et al. 2006; Vertessy et al. 2001; Vertessy et al. 1998). In the centuries following, water use and runoff return to pre-fire levels. Recent work which incorporated understorey tree water use has provided new insights into the magnitude of water used by old-growth forests (Wood et al. 2008). Increases in the frequency and severity of fires, predicted under climate change, will lead to significant changes in forest water use and hydrology, as well as increased erosion and reduced water quality. However, the bulk of the evidence available on fire impacts on hydrology comes from research on species which regenerate from seed, and more research is needed from species which resprout after fire, as these may take a shorter time for tree water use to recover to pre-fire levels. In particular, there is little evidence from drier, open forests from other regions of southern Australia which would provide a quantitative framework to allow prediction of how changes in fire regime would impact on tree recovery and transpiration rates (Macar et al. 2006).

6.3.4 Groundwater dependent ecosystems

There are many groundwater dependent ecosystems in Australia (GDEs), some of which contain forests, including riparian GDEs (O'Grady et al. 2006). However, ecophysiological modelling does not take into account the presence of groundwater. As water availability increases in water limited regions, leaf area index increases, which may in turn lead to increased tree water use. Evidence suggests that the presence of groundwater (or shallow, compared with deep groundwater) increases tree water use and leaf area (Benyon and Doody, 2004), and also reduces water stress, demonstrated by comparisons of leaf water potential and stomatal conductance (Carter and White 2009).

A study on Mallee Eucalyptus in Western Australia reported that although summertime water use per unit sapwood area was 20-30% higher in trees over shallow groundwater compared with trees over deep groundwater, there was little difference in water use on a leaf area basis, because trees over shallow groundwater had a higher leaf area (Carter and White, 2009). Furthermore, stand water use was four times higher over shallow groundwater than that over deep groundwater (1230 mm yr^{-1} compared with 320 mm yr^{-1}) (Carter and White, 2009).

It is possible that the presence of groundwater may mitigate the impact of drought, (exacerbated by increasing temperatures and decreasing rainfall in some regions). During short term droughts, GDEs may be more resilient than forests which do not have access to groundwater. However during prolonged periods of drought, groundwater resources may become depleted and the differences between GDEs and non-GDEs may be reduced. Additionally, the impact of the extraction of groundwater for human use should be considered in forests in these areas (MacKay 2006). There remains a paucity of research on forests within GDEs and the impact of climate change on forests within GDEs needs to be addressed. Research being conducted by the National Centre for Groundwater Dependent Ecosystems has the potential to address this issue.

6.4 Modelling climate change impacts on water yields

Changing rainfall patterns in conjunction with increased temperatures may reduce water availability and increase pressure on water allocation systems in Australia, particularly the Murray-Darling Basin. Information on likely future water yields is critical for management of water resources in Australia. Therefore, much research work is currently attempting to model climate impacts on water resources including surface and groundwater. To date, most of these studies have employed rainfall-runoff type models (Chiew and McMahon 2002; Chiew et al. 2009; Preston and Jones 2006).

Chiew and McMahon (2002) used a hydrologic model along with ‘present’ climate data and greenhouse enhanced climate scenarios. Modelling results indicated that changes in rainfall are amplified in runoff. For example, in wet and temperate catchments, the percentage change in runoff was approximately twice the percentage change in rainfall. In ephemeral catchments with low runoff coefficients, the percentage change in runoff was up to four times the percentage change in rainfall.

Current research in this area is being conducted by CSIRO and collaborators within the framework of the ‘Sustainable Yields Projects’ which aim to provide robust, transparent and consistent information on current and future water yields (CSIRO 2007).The Murray-Darling Sustainable Yields and Northern Australia Sustainable Yields programs conducted extensive research programs which estimated water yields based on rainfall runoff models over large areas of Australia; Sustainable Yields projects for Tasmania and south-west Australia have recently been completed.

The Murray-Darling Sustainable Yields (MDSY) project summarised assessments of water yield from 18 regions that comprise the Murray-Darling Basin (MDB). The project is described as ‘a world-first for rigorous and detailed basin-scale assessment of the anticipated impacts of climate change, catchment development and increasing groundwater extraction on the availability and use of water resources’. Rainfall-runoff modelling and groundwater recharge modelling were included across the entire MDB. The project integrated all available data on streamflow and water use and estimates of evapotranspiration losses from satellite imagery. Results showed that total flow at the Murray mouth has reduced by 61%, and now ceases to flow 40% of the time compared to 1% of the time in the absence of water resource development. Impacts of climate change , (with assumptions of current development for farm dams and plantation forestry), suggest that future mean annual runoff in the MDB in ~2030 relative to ~1990 will be lower by 5 to 10% in the north-east and southern half, and by about 15% in the southernmost parts (Chiew et al. 2008). Plantations can significantly affect local runoff but the projections assessed for this project reported that the impact averaged over the entire basin was negligible (Chiew et al. 2008).The reductions likely in future water availability in southern Australia under climate change ‘require a significant planning response and potentially a change in the way water resources are managed’ (Chiew et al. 2009).

One concern that has been raised about these studies is that the relationship between vegetation water use and climate is assumed to be constant or ‘stationary’ (Milly et al. 2008). Changes in vegetation water use due to land use change (such as plantation establishment) are taken into account, but it is assumed that water use of forests in a given climate does not vary. As discussed above, major factors that can alter the relationship between climate and forest water use include rising CO_2, forest health, and fire frequency. However, we do not currently understand the relationship between these factors and vegetation water use well enough to incorporate them satisfactorily in water yield projections. We urgently need a better understanding of the impacts of these factors on vegetation water use in order to enable us to improve projections of future water yields and enable better management of water resources.

Implications: Modelling which directly accounts for vegetation properties is required to incorporate responses to CO_2, in addition to evaporative demand and rainfall. This will improve modelled outputs of hydrological processes and enable better management of water resources (cf. Peel 2009).

6.5 Conclusions – Vegetation Water Use

Elevated CO_2 has a significant effect on plant water relations, with reductions in stomatal conductance, transpiration and hydraulic conductance reported in Australian vegetation. Ecosystem-scale experiments are urgently needed to investigate the impacts of these changes on ecosystem leaf area index and water use.
Changes in rainfall and potential evapotranspiration also have an impact on plant water relations, although the magnitude of change will depend on species and site conditions. Forest hydrology after fire is well studied in trees which regenerate from seed, although research is needed on species which resprout after fire. When deciding whether afforestation is appropriate for a particular site, the implications of afforestation on the local or regional water balance should be considered, as well as the carbon sequestration. That is, the trade-off between water and carbon needs to be considered (Jackson et al. 2005).
Rising CO_2, changing rainfall, temperatures and fire will all have an influence on forest hydrology, with responses dependent on the degree of change in each climate variable. Some variables may increase vegetation water use (rising temperatures and VPD, early regeneration from fire) and others may decrease it (rising CO_2, decreasing rainfall).The overall direction and magnitude of change are currently unknown.
In addition to experiments addressing the impact of climate change on stand scale processes, modelling studies are required to address the many complex and interacting processes.

Improving process representations in ecophysiological models, and using these models to test the key drivers to evapotranspiration will provide further understanding.

Changes in the water balance of forest catchments have implications for populations and their water needs downstream. Understanding this issue is important, allowing adaptation and improved management of plantations, reserves and water resources. Additionally, when planting large regions (catchments) of forests for carbon sequestration, it is important to consider hydrological consequences.

7. Phenology

In this section of our review, we look at the evidence base for (i) how climate change factors will likely affect phenological events, and (ii) how these effects could flow-on to the forest ecosystem, with a specific focus on the vegetation and its interactions with key fauna species.

7.1 Introduction

Phenology is the study of how seasonal and interannual variations in climate and environmental conditions influence periodic plant and animal life cycle events. Examples of phenological events include the first emergence of butterflies in spring or the timing of leaf abscission in autumn (Walther et al. 2002). Changes in key phenological events have been used as early indicators of climate change (Rosenzweig et al. 2007). Temperature, moisture, and photoperiod are the three most important triggers for phenological events for both animals and plants. Of these three key phenological factors, temperature and moisture availability are most likely to be altered under the simulated climate change scenarios, with a high level of variability predicted depending on geographical region (CSIRO and Bureau of Meteorology 2007).

The main body of work to date on climate change affecting phenology has been conducted in the northern hemisphere focussing on the global trend of increasing temperatures. Globally, studies using long-term historic records have shown that temperature increases observed over long time scales affect the timing of phenological events in a range of ecosystems (e.g. Menzel et al. 2001; Menzel et al. 2006; Miller-Rushing and Primack 2008; Parmesan 2007; Parmesan and Yohe 2003; Studer et al. 2005). The most convincing evidence of phenological responses to climate change is seen in changes in the flowering and leaf-out times of temperate and arctic plants in Europe at the beginning of spring (Fitter and Fitter 2002; Menzel 2000; Menzel et al. 2001; Menzel and Fabian 1999; Menzel et al. 2006; Parmesan 2007; Primack and Miller-Rushing 2009). A Europe-wide phenological gardens project, using records of 23 plant species collected at 50 sites across Europe since 1959, showed a general increase in growing season. Plants showed earlier flowering and leaf-out times in spring and later leaf colouring and leaf fall in autumn, and these changes were found to be strongly correlated with temporal rises in temperature (Menzel 2000; Menzel et al. 2001; Menzel and Fabian 1999; Menzel et al. 2006; Primack and Miller-Rushing 2009). Additionally, a global review of the evidence of ecological responses to increasing temperatures showed a clear trend of phenological events occurring earlier in spring since the 1960’s (Walther et al. 2002). Further global assessments also show that spring phenological events are generally commencing earlier, primarily driven by rises in temperature (Parmesan 2006; Parmesan

2007; Parmesan and Yohe 2003). These results show that the increases in temperature have a clear effect on phenology of native forest systems globally (Parmesan and Yohe 2003).

Variations in the effect of temperature rises on phenological events were found across regions and between species (Walther et al. 2002). This variations may have further impacts on ecosystem functioning (Hughes 2000; Hughes 2003) and key biotic interactions. For instance, if synchronisation with flower availability and pollinator emergence is disrupted, forest system functioning might equally be disrupted. The importance of understanding this possible mismatch of timing of phenological events between co-dependant species (e.g. plant and insect pollinator) has been highlighted in several reviews (e.g. Parmesan 2006; Walther et al. 2002). However, the impacts of phenological mismatches are still rarely explored. Some evidence for mismatches in pollination interactions have been found, however their demographic consequences are largely unknown (Hegland et al. 2009; Parmesan 2006). Globally, Hegland et al. (2009) found that phenological responses to temperature rises were generally similar between plants and insects. Furthermore, studies on multi-species plant-pollinator assemblages indicated that the observed structure of pollination networks that determine overall system functioning are likely to be robust against perturbations caused by climate warming (Dupont et al. 2009; Hegland et al. 2009; Williams and Adam 1994).

Altogether, the trends observed globally suggest that forest systems are likely to be affected by shifts in phenology due to climate change. To what extent these changes will impact on biodiversity and the actual functioning of these systems remains unclear. Furthermore, the current evidence is largely based on phenological studies conducted in the northern hemisphere. In the following section, we review and discuss the phenological studies that have been undertaken in Australia with specific reference to the Australian forest estate.

7.2 Research findings in Australia

In her review of the impact of climate change on Australian ecosystems, Hughes (2003) highlighted the fact that Australia lacks the long-term datasets and tradition of phenological monitoring that have allowed the detection of climate-change-related trends in the northern hemisphere. There is therefore very limited evidence on the possible effects of changes in climate on the phenology of species in Australia (Hughes 2003).

The most thorough study in Australia to date to look at phenological responses to climate change for native trees, related the commencement of flowering to temperature and rainfall over a period of 23 years (Keatley et al. 2002). This study was based on data collected in Maryborough, Victoria, southeast Australia, and looked at the flowering events of four Eucalypt species (*Eucalyptus leucoxylon, E. microcarpa, E. polyanthemos,* and *E. tricarpa*).

This study revealed that the best predictor for the commencement of flowering for all species was a combination of average daily temperature and total monthly rainfall (Keatley et al. 2002). This conclusion demonstrates that temperature is not the only driver for this phenological event, and highlighted the importance of rainfall as a trigger for phenological events in Australia. Furthermore, Keatley et al. (2002) also found that the species investigated responded differently to increases in temperature and rainfall. They found that *E. leucoxylon* and *E. tricarpa* would commence flowering later, where *E. polyanthemos* and *E. microcarpa* would show an earlier onset of flowering. This result indicates that, compared to temperate regions in the northern hemisphere, Australian tree species show a higher variability in terms of phenological response to the predicted changes in temperature and rainfall.

Williams et al. (1999) looked at the variation in flowering for 50 common species of trees (Eucalypt) and shrubs within a mesic savanna system near Darwin, northern Australia, over a period of 30 months. This system has a very low variability in daily average temperature year round, but has distinct wet and dry seasons. This variability led to the hypothesis that in this case the phenological events are likely to be primarily driven by the amount of rainfall. Williams et al. (1999) found that flowering events for both Eucalypt and shrub species were generally spread out over the year. A study by Boulter et al. (2006) found similar patterns. They looked at the flowering times of 1371 tree species found in herbaria records that were collected in the Wet Tropics bioregion of far northern Queensland, northeast Australia. As in the study are of Williams et al. (1999), this system is characterised by very low variability in daily average temperature year round, so phenological events are likely to be mainly driven by the seasonality in the amount of rainfall. They also found a relatively even spread of flowering events across species and the year, and that seasonal flowering events were generally correlated with temperature and rainfall based on altitude and latitude. Together these studies indicated that for these forested systems the predicted changes of phenological events are likely to be primarily rainfall driven. However, it is unknown how projected changes in rainfall (and temperature) will alter the timing of flowering of individual species in these particular systems. It is however likely that each species will respond in a distinctive way, as shown by Keatley et al. (2002).

Further results of phenological studies on plants within the subalpine regions of southeast Australia found that rises in temperature resulted in different responses in the timing of flowering (Gallagher et al. 2009; Jarrad et al. 2008). Some species commenced flowering earlier where others did not show a response or flowered later (Gallagher et al. 2009; Jarrad et al. 2008). Additionally, variable flowering responses observed during three years of experimental warming showed that the phenological responses did not appear to be driving significant community-level changes (Jarrad et al. 2008), although the short-term nature of this experiment might have obscured any long-term changes. For low elevation temperate grasslands in Tasmania, experimental increases in CO_2 showed no effect on the flowering times of plants, where increased temperature did show a general effect of earlier flowering. However, this was variable between species and with the year of experimentation, possibly driven by the effects of differences in monthly rainfall (Hovenden et al. 2008). These studies seem to support the observations made for tree and shrub species that show the high level of variability in their phenological responses to changes in climate factors observed for Australian species and forest communities.

Pollination is an essential process in the maintenance of functional forest systems (Williams and Adam 1994). Phenological events both occur in plants and insects and it has been recognised that mismatches in timing driven by climate change can have a negative flow-on effect on plant-pollinator interactions (Parmesan 2006), possibly disrupting forest system functioning. Williams and Adam (1994) reviewed the available evidence of the importance of plant-pollinator interactions in maintaining forest system functioning for subtropical rainforests in Australia. They highlighted that based on the evidence of the year round resource availability of flowering plants and differences in flowering events within and between species, generalist plant-pollinator interactions are most likely to drive and maintain these systems. This pattern and process was found to be particularly applicable for tree and large shrub species occurring in these systems. For this type of system, it seemed that flowering events are opportunistic in nature triggered by favourable climatic conditions. Flowering and regeneration of species within the system therefore did not seem to be restricted to a certain time in the year, indicating that these tropical systems are likely to be resilient to the possible temporal phenological shifts driven by climate change. However, for all other forest systems in Australia this evidence is largely lacking.

The general spread of phenological events across the few systems that have been studied suggests that these systems might be robust to changes in phenology (driven by climate change) in terms of functioning. Pollination and the provision of food sources such as nectar and seeds for fauna seem to be a variable and year round process within forest systems. The relevance and importance of timing of phenological events negatively and/or positively influenced by climate change therefore seems to be less for the Australian scene compared to systems in the northern hemisphere.

7.3 Conclusions: Phenology

The lack of long-term phenological data has limited the number of studies that have looked at the possible impacts of climate change on phenological events in Australia. Of the few studies that have been conducted to date, all have been focussed on native forest systems. Plantation forests in Australia have not been studied in this respect. How the likely increase in temperature and changes in rainfall will influence the timing of phenological events, and how this will affect the associated biotic interactions operating within forest systems remains therefore largely unknown.

Within the limited amount of evidence that is available, however, there are indications that the direct effects of climate change on the phenology are likely to be less pronounced in Australia’s forested systems compared to the effects shown in the northern hemisphere. The predominantly evergreen forest systems in Australia seem less influenced by seasonality in this respect. Phenological events in Australian forests appear to be highly variable in timing. There appears to be a more opportunistic response to favourable climatic conditions that trigger for instance, flowering events. However, what favourable conditions trigger these events remains largely unclear for the majority of forest systems in Australia. They are most likely to depend on temperature and rainfall/moisture availability or a combination of the two; however, to date these relationships have hardly been studied.

An integrated framework for understanding plant community assembly needs to incorporate abiotic and biotic interactions, including plant–pollinator and other plant–animal interactions (Sargent and Ackerly 2008). The most likely biotic interaction linked to phenology that is thought to be affected by changes in climate factors is the plant-pollinator relationship. Shifts and changes in phenology will be most distinct in forested areas with higher altitude and latitude distributions. Mismatches in plant-pollinator relationships are most likely to occur there, possibly resulting in the decline of specialist plant and pollinator species. However, to date no substantial evidence-base has been collated on these responses in Australia. Furthermore, the multi-species plant-pollinator assemblages driven by generalist pollinators suggests that forest systems are generally resilient to shifts in phenological events induced by climate change. It is likely that some specialised plant-pollinator interactions will be affected by phenological mismatches resulting from climate change. However, if and how this will influence forest system functioning remains largely unknown.

Together, the forest systems in Australia seem to have persisted over time using an opportunistic approach towards reproduction and regeneration. For instance, several dominant eucalypt species were found to exhibit phenotypic plasticity, i.e. growing and flowering when conditions were favourable. Changes in the timing of phenological events driven by climate change are therefore believed to have a relative low impact on biodiversity and overall functioning of the forest system.

Individual Factors – Indirect Climate-Related Stresses

8. Fire

This section looks at the evidence describing how climate change will likely affect fire regimes within forest systems across Australia, and how this will have a flow-on effect on forest system functioning, focussing on key fire – vegetation and fauna interactions.

8.1 Introduction

Fire is an intrinsic phenomenon in most Australian landscapes (Bradstock et al. 2002; Burrows 2008; Jurskis 2005a; Williams et al. 2009). Native forest systems have evolved correspondingly, increasingly becoming resilient to fire. Species occurring in fire prone systems have adopted a variety of strategies that are designed to cope with fire events. For instance, a large group of woody species have the capacity to resprout after fire, including the majority of the native *Eucalyptus* species. Other species have developed reproductive strategies that are dependent on fire, such as many species within the *Banksia* genus.

The majority of the climatic changes projected to occur due to greenhouse gas emissions are positively related with fire occurrence (Howden and Gorman 1999). A general increase in fire risk is projected with higher temperatures, a reduction in rainfall, likely increases in evapotranspiration, and a higher frequency and severity of thunderstorms and drought periods (Steffen et al. 2009; Williams et al. 2009). Elevated CO_2 levels will potentially increase plant growth and productivity, resulting in more and drier fuel (e.g. dead wood and litter) becoming available over a longer period of time, which is likely to increase frequency and intensity of fires (Steffen et al. 2009; Williams et al. 2009). Such changes in fire regime can be expected to have a considerable flow-on effect on forest biodiversity and overall system functioning.

The main projected effects of climate change on current fire regimes are changes in frequency and/or intensity. Additionally, there are potential shifts in the timing (i.e. season) of fires, and the scale of the area affected by fire. For instance, fires might occur earlier or later during the year, because of possible changes in fire weather caused by extreme weather patterns, such as droughts providing more dry material for fuel, or thunderstorms causing ignition of these fuels. Furthermore, the area affected by fire might change due to increases in fuel causing more intense fires that have the potential to affect larger areas.

Modelling studies for south-eastern Australia indicate that, under projected hotter and drier climate conditions, the number of fire days and the severity of fires are likely to increase over time for the region as a whole (Hennessy et al. 2005; Lucas et al. 2007). This region is characterised by hot, dry summers and mild, wet winters with periodic droughts that occur as a part of natural interannual climate variability. Winter and spring rains allow vegetation to grow and develop rapidly, increasing the amount of available fuel, while dry summers and periodic droughts allow the fuel load to become available for ignition (Lucas et al. 2007). The projected changes in climate conditions are likely to influence these natural cycles, potentially hastening the build-up of fuel, consequently increasing the risk of fires occurring.

In the following section, we review and discuss the studies that investigated the impacts of fire on forest biodiversity and functioning with specific reference to the Australian forest estate. We summarise findings and evidence on: (i) what fire related factors (i.e. frequency, intensity, timing, scale) are most likely to have the greatest impact on forest system functioning, (ii) what systems are most likely to be affected by changes in fire regime driven by climate change, and (iii) what the best management options are for preserving biodiversity in fire prone forested systems.

8.2 Impacts of fire on forest biodiversity and functioning

In this review, we will focus on the direct impacts of the properties of fire itself. However, fires have been found to influence important secondary processes affecting forest biodiversity and system functioning. For instance, phenological events in forested systems (Williams et al. 1999) and mycorrhizal diversity and distribution (Anderson et al. 2007; Barrett et al. 2009; Robinson 2006; Shedley 2007; Tommerup et al. 2000), were found to be altered by fire occurrence. Fires were further found to enhance pest outbreaks (Carnegie 2008b; Wylie et al. 1999); the likelihood of pathogen attack (Barrett et al. 2009; Moore 2005; Shedley 2007); and weed invasions (Barrett et al. 2009; Bradstock et al. 2002; Fisher et al. 2009; Turner and Virtue 2009). These changes can act as a positive feedback, resulting in further increases in the likelihood of fire (Australian National University 2009; Setterfield et al. 2005; Williams et al. 2009). These studies demonstrate that fire is an important factor influencing forest biodiversity and functioning in multiple ways.

We recognise that many useful reviews have already been undertaken that have looked at the impacts of fire on the Australian landscape and biodiversity. In particular, the recent report by Williams et al. (2009) gives a comprehensive and up-to-date assessment of the likely interaction of fire regimes with climate change and the possible effects on biodiversity across Australia.

Intuitively, the species most sensitive to fire are those that are unable to escape from fire and can die as a consequence. Plant species that have been identified as being most sensitive to fire include those that can only use seed to regenerate (i.e. obligate seeders) and/or have limited dispersal ability like some key dominant *Eucalyptus* species in southwest Australia (Barrett et al. 2009; Bradstock et al. 2002). In contrast, species that have the capacity to resprout are generally resilient to damage by fire (Shedley 2007). The fauna species that have been identified as being most affected are species that live on the ground and/or have limited dispersal ability (e.g. Andersen et al. 2005; Barrett et al. 2009; Bradstock et al. 2002; Williams et al. 2009). In our review, we will therefore focus on the available evidence of fire affecting these particular species.

Forest systems are generally characterised and classified by their dominant tree and shrub species. Fire affects the structure and composition of these systems. If a forest system is not resilient to fire, the species composition and structure will change, with fire sensitive species generally disappearing from the system. When a fire regime in a forested area changes, for instance the frequency of fires occurring, the functioning of the system will change accordingly. In terms of preserving biodiversity, this is often considered as undesirable, where the forest systems will likely lose their fire sensitive species. An additional factor is that many fire sensitive species are endemic and confined to relatively small geographical areas in Australia, like many species in the southwest of Australia (Barrett et al. 2009). This makes changes in fire regime likely to have a large impact on the rate of extinction of these species.

The vegetation of forested systems provides habitat for many fauna species. This habitat is inevitably affected when a fire occurs. Fauna generally lose habitat when a fire occurs and will only return when the vegetation of the system has recovered. The role of fauna in forest systems is often downscaled, where the vegetation is generally thought to be driving the system. However, fauna should not be overlooked as drivers of system functioning (Williams et al. 2009). For example, the dominant vegetation might be resilient to fires occurring, however, if a key faunal disperser of the dominant tree species disappears from a system because of the effects of fire, the forest composition and systems functioning will ultimately change. Furthermore, pollinator insects like butterflies are key components that facilitate forest ecosystem functioning, by ensuring that flora dependant on insect pollination can successfully set seed (Sargent and Ackerly 2008; Williams and Adam 1994). After setting seeds, the role of dispersers becomes important. Many vertebrate species like birds and ground-dwelling mammals, and some invertebrate species like ants, play an important role in dispersing these seeds and determining if a seed will germinate.

Research on the effects of fire on birds found a general lack of studies on birds in the north of Australia, where the majority of studies was conducted in the southeast and southwest mainly in Western Australia and Victoria (Leidolf and Bissonette 2009). In the relatively few studies undertaken, forest birds generally responded negatively to increases in fire frequency, however the long term impacts of frequent low intensity fires (e.g. controlled burning) are largely unknown (Woinarski 1999). Fire intensity was also found to have a negative impact on the forest bird species, where high intensity wildfires were more damaging than low intensity fires (Woinarski 1999). Small mammal species were equally found to decline due to high frequency and high intensity fires (Wilson 1996). The scale and timing of fire were found to be equally important, with small-scale patchy fires being more favourable compared to large scale fires (e.g. in terms of recolonisation), and the timing of fires being important with respect to the breeding season (Wilson 1996).

In our review, we have considered both plant and fauna species as biotic drivers of forested systems that are likely to be affected when fire regimes change. For plants, we have focused on long-lived woody species including shrub and trees, and for fauna, on pollinator insects and seed dispersers including ants, mammals and birds.

We used the review on Australian forest systems provided by Bradstock et al. (2002) as a starting point, and focussed on adding studies since 2002. The review considers the dominant forest systems of the northern and southern part of Australia separately. Where there was a heavy focus on studies conducted in forest systems in either the southeast or the southwest, we further separated and evaluated these studies accordingly.

8.2.1 Northern Australia

Tropical savannah systems

Wooded tropical savannah systems in the northern half of Australia are characterised by an understorey of annual and perennial grasses and an overstorey of *Eucalyptus* species growing up to 20m in height, with less than 30% canopy cover. The climate of these systems is generally hot with distinct seasonal wet and dry periods and annual rainfall of 1250-1500 mm. Fires are extensive and frequent (Andersen et al. 2005), and are mainly fuelled by the understorey grasses. There is a high level of variability in fire frequency between regions. Fire frequency is higher in mesic savannah systems (once every 2 years) than in drier semi-arid savannas (once in every 4 years), mainly because of lower fuel availability and differences in land-use (Bradstock et al. 2002; Williams et al. 2009). Fires follow a consistent inter-annual and inter-seasonal pattern driven by distinct wet and dry periods. Fires mainly occur during the dry season, and early dry season fires are less intense and extensive compared to late dry season fires. Humans mainly light fires in these systems, and prescribed burning in the early dry-season is used extensively as a management tool to minimise the occurrence of more severe late dry-season fires (Bradstock et al. 2002).

The effect of fire on savannah biota varies. Because of the high fire frequency, species of savannah systems are generally resilient to fire (Andersen et al. 2005). Some important woody obligate seeder species that are fire-sensitive have been identified as declining in these systems, *Callitris* being the best example (Edwards and Russell-Smith 2009). However, the number of woody obligate seeder species in these systems is low (Bradstock et al. 2002; Williams et al. 2009). Fire impacts on pollinators are poorly known, however in general these species disperse readily and can recolonise post-burnt areas from adjacent unburned areas. The mammal population, including possible seed dispersers, has been identified as fire-sensitive in these systems (Andersen et al. 2005; Bradstock et al. 2002), whereas ants were found to be highly resilient to fire (Bradstock et al. 2002).

Although *Eucalyptus* and shrub species in these systems are generally able to resprout after death by fire, the high fire frequency is likely to adversely affect successful resprouting and regeneration from seed (Bradstock et al. 2002). High frequency in combination with high fire intensity in these systems appears to impact on some of the dominant woody plant species. Tree mortality of *Eucalyptus* and woody shrub species was found to be higher with intense late dry-season fires (Bradstock et al. 2002). Further studies in eucalypt-dominated savannah woodland in Arnhem Land, Northern Territory, northeast Australia, found that a higher frequency of fires decreased tree recruitment, and that more frequent late dry season fires increased tree mortality, particularly in lowland savannah systems. The timing (season) of the burns was also found to be important for recruitment of the dominant tree species (*Acacia,* Proteaceae and Myrtaceae (including *Eucalyptus*) species). The intensity of fires was found to be less important for recruitment, but was linked with higher mortality of obligate seeders compared to resprouting species (Prior et al. 2009). In the same region, high frequency, intense, large-scale, late dry season fires were further found to negatively affect the persistence of the obligate seeder tree species *Callitris intratropica* (Edwards and Russell-Smith 2009).

For small mammals living in these systems, a general declining trend over time in populations has been observed across northern Australia (Andersen et al. 2005). This decline is likely the result of observed increases in fire frequency, the intensity of fire, and larger areas being burned annually, resulting in less habitat being available and less opportunity to recolonise areas previously burnt. Seasonality might also have affected these trends, interfering with the reproduction cycle of mammal species. Likely declines of woody species and fauna therefore seem to be a result of a combination of increased fire frequency, intensity and scale, and the timing of fire occurrence.

The likelihood of fires occurring in this system has been predicted to increase as a result of climate change. Specifically, the relatively certain increases in CO_2 and temperature are projected to increase the number of extreme fire days. Changes in rainfall are less certain, but the current best projection of a minimal change in annual rainfall for the majority of northern Australia would mean that no significant decrease in fuel availability would occur. The fire frequency, intensity and total area burnt are therefore predicted to worsen in this region, with likely negative flow-on effects for woody species (particularly obligate seeders), small mammal populations (Williams et al. 2009), and overall system functioning.

In terms of sustainable management of these systems, annual burning of large areas was found to be unfavourable, mainly due to the apparent negative impact on seedling recruitment of eucalypt species (Bradstock et al. 2002). However, small scale, low intensity early dry-season prescribed burning does not appear to have an overall negative effect on savannah system function. Implementation of good monitoring protocols is however essential to evaluate the impact of changes to fire regimes on the species diversity of these systems (Williams et al. 2009).

Tropical forest systems

Tropical open forest systems are similar to the savannah systems described in the previous section, but have a canopy overstorey that is dominated by *Eucalyptus* and *Terminalia* species, with >30% of canopy cover (Williams et al. 2009). These forests occur in locations that are hot and seasonally wet or dry, with average annual rainfall of around 1500 mm. Grasses mainly fuel fires in these systems. The fire interval is similarly high, around once every 2-5 years. Where these systems co-occur with tropical savannah systems, the sensitivity of the dominant woody vegetation and fauna to fire frequency, intensity and total area burnt were found to be similar (Williams et al. 2009), although less research has been done specifically on these systems. The combination of increased CO_2 levels, higher temperature, and relatively small decreases in annual rainfall, is likely to result in a higher rate of fuel accumulation. Climate change is therefore predicted to increase the fire frequency, intensity and total area burnt in these systems also (Williams et al. 2009). To maintain the function and persistence of these systems, fire management needs to prevent this trend, potentially by adopting strategic fuel reduction burns as a management tool.

Tropical rainforest systems

Studies on the effects of fire on rainforest systems have been few. Fires in these systems are generally rare with long inter-fire intervals (less than once every 20 years), driven by the year-round wet conditions of these systems (annual rainfall >1750mm). The systems are characterised by a high variety of herbaceous and shrub species in the understorey, with a mid-storey and canopy of an equally high variety of (mainly non-eucalypt) tree species, with more than 70% cover. These systems are considered sensitive to fire, where they have evolved largely in the absence of fire. The effect of fire on the structure and floristic communities of rainforests across northern Australia has been studied based on historical palaeoecological records and direct observations (Bradstock et al. 2002). This study showed that the rainforest communities were mainly affected by fire at the margins with tropical savannah and forest type systems where fires occur more frequently. Sharp boundaries occur between savannah and rainforest vegetation, often characterised by a narrow transition phase with a distinct and unique biotope. The vegetation and related fauna in this transition phase were found to be susceptible to the impacts of fire (Bradstock et al. 2002).

The majority of Australian rainforest tree and shrub species are resprouters and can therefore readily regenerate after fires. However, because of their high fire sensitivity, existing plants are likely to be killed by fire. Rainforest vegetation was found to respond positively in areas where the frequency of savannah fires was low (less than once every 5 years), expanding into adjacent savannah vegetation in moist areas (Bradstock et al. 2002). The margin vegetation was further found to be generally resilient to frequent early dry season low-moderate intensity fires occurring in adjacent tropical forest and savannahs. However, frequent high intensity fires in the late dry-season were found to have a highly negative impact on rainforest margins, killing most vegetation and allowing savannah (grass) species to invade. On moist sites, successful recovery of the vegetation after intense fire was found to take up to 5 years on wet and up to 20 years on drier locations (Bradstock et al. 2002). A historic landscape-scale study in Arnhem Land, Northern Territory, found that rainforest systems were negatively influenced by high frequent, intense, large scale, late dry season fires (Edwards and Russell-Smith 2009). Evidence from studies in dry forest systems suggest that fauna assemblages are likely to be similarly affected by these processes, however, no specific studies were found for tropical rainforest systems in this respect. Declines in woody species and fauna therefore seem to be a result of a combination of increasing frequency, intensity, scale of fire and the timing when fires occur.

It is unclear whether fire frequency and intensity will increase in tropical rainforest systems. However, the likelihood of fire in tropical forest and savannah systems bordering tropical rainforests has been predicted to rise with the effects of climate change (see above). The fire frequency and total area burnt for savannah systems are therefore predicted to worsen for many areas in this region (Williams et al. 2009), with likely negative flow-on effects for woody species (particularly obligate seeders) and small mammal populations in the adjacent rainforest systems. Furthermore, drought could cause more intense fires, with more severe effects on tropical rainforest systems. To prevent negative effects of fire in the margin vegetation of tropical rainforests, the inter-fire interval and particularly the intensity of fires in adjacent tropical forest and savannah systems need to be kept low to allow the vegetation sufficient time to recover after fire.

Arid forest systems

Arid forest systems have a wide distribution across Australia. These systems are characterised by an understorey of grasses and herbs and are dominated by *Acacia* species with a canopy cover of less than 30%. Arid forests occur in dry areas with low annual rainfall (250-300mm). Fires in these systems are mainly fuelled by the understorey grasses and herbs. Fire events are infrequent, occurring once every 10-80 years (Williams et al. 2009). Fire regimes in this system follow rainfall patterns, where infrequent periods of high rainfall stimulate understorey plant growth and therefore fuel accumulation.

The impacts of fire frequency, intensity, timing and scale on these systems are generally unknown. No studies to date have looked specifically at the effects of fire related factors on arid forest function. Howeverm it has been suggested that increases in the spatial scale of fires are likely to have a negative effect on long-lived obligate seeders and mammal populations (Williams et al. 2009).

In these systems, temperature is projected to rise in combination with a relatively large reduction in rainfall. Fire weather is therefore likely to change, with a projected increase in the number of high/extreme fire weather days. However, fuel availability is likely to be the limiting factor. The speed of fuel accumulation is likely to decrease because of the high decrease in rainfall. Climate change factors *per se* are therefore unlikely to significantly change the fire regimes in these areas (Williams et al. 2009). However, to find the appropriate fire frequency in combination with intensity, timing and scale; knowledge needs to be gathered on the response of the key drivers of these systems. The fire management strategy of this system should be guided by these ecological responses in order to maintain system function.

8.2.2 Southern Australia

Temperate open forest systems

The temperate open forest systems (or Mediterranean woodland) in the southern half of Australia are characterised by an understorey of grasses, herbs and shrubs. The canopy is dominated by *Eucalyptus*, *Casuarina* and *Callitris* tree species, which are generally no taller than 30 metres, with a canopy cover of <30%. These forest systems are found in locations with seasonally wet/dry conditions, characterised by long hot dry summers and mild wet winters. Annual rainfall is relatively low, around 550-600 mm, limiting the growth of the vegetation. Fire occurrence is mainly driven by drought and is fuelled by both understorey grasses, and herbaceous and woody plant litter (Williams et al. 2009). Fires in these systems are mainly caused by lightning, with a fire frequency generally less than once every 10-20 years. These systems are largely thought to be well adapted to fire (Bradstock et al. 2002)

Nonetheless, fire has a significant impact on vegetation structure and composition (Bradstock et al. 2002). In these forest systems, regeneration of many plant species is enhanced following fire, but the importance of fire for overall system maintenance is not clear. In particular, fire frequency impacts on species that are killed by fire and/or are obligate seeders. Where fire frequency is less than the reproductive age of these species, they are likely to decline and disappear from the system. On the contrary, lack of fire has been found to have a negative impact on species dependant on fire for seed releasing and/or germination (Bradstock et al. 2002). Effects of timing and fire intensity are less well known. In general, timing of fire appears to be important for regeneration success, but responses were found to be variable across species, and correlated with annual variations in total rainfall. The effects of fire intensity on vegetation recruitment were equally found to be variable, however high intensity fires were generally found to result in higher adult tree mortality (Bradstock et al. 2002).

The impact of fire on fauna also is also poorly known in these systems. Generally however, increases in fire frequency are likely to permanently alter and diminish the available habitat for fire sensitive fauna, which will have a negative effect on the survival of these species (Bradstock et al. 2002). There is a particular lack of studies on inland grassy (i.e. rangeland) systems. Most work has been conducted in shrubby systems in the coastal areas in either the southeast or southwest of Australia (Bradstock et al. 2002).

Additionally, this particular forest system has been largely fragmented over time by human activities. The vegetation and fauna in fragments will respond differently to fires compared to large continuous tracts of forests. In particular, the scale of fires becomes more important. Unburnt areas are needed for fauna species to be able to recolonise burnt areas. If whole fragments are burnt, recolonisation of some species (i.e. fire sensitive obligate seeders and mammals) is unlikely to occur (Bradstock et al. 2002). Together this indicates that increases in fire frequency, intensity and scale are likely to have a negative impact on forest system functioning.

For this particular forest system, fires are important for overall system functioning. Climate change projections indicate that these systems will become hotter, have a higher evaporation and receive less rainfall. Combined with projected increases in drought periods, the number of extreme fire danger days is projected to increase (Williams et al. 2009). The available fuel for fires is likely to stay at similar levels for these systems. Together this indicates that climate change is likely to impact on the current fire regime, where the frequency, intensity and scale of fires are likely to increase, negatively impacting on system function.

In these systems, human intervention by reducing the fuel load through prescribed burning at strategic locations within the landscape is probably the only management option to prevent frequent, high intensity, and large spatial scale fires from occurring. Finding an appropriate fire management strategy will largely depend on the management objectives for each geographical location. Finding the right balance between public safety and biodiversity conservation objectives will be the main challenge in this respect.

Temperate closed forest systems

The temperate closed forest systems in the southern half of Australia are characterised by trees covering more than 30% with their canopy. These forest systems include (i) *Eucalyptus* dominated systems in areas with hot dry summers and mild winters with relatively low rainfall (e.g. Perth, southwest Australia, 800 mm) or high rainfall (e.g. Sydney Basin, southeast Australia, 1200 mm); (ii) areas with short hot summers and cold winters with high annual rainfall (e.g. Tasmania, 1200 mm); and (iii) temperate rainforest systems in the southeast of Australia with hot summers and mild winters with high annual rainfall (>1750 mm). The fire frequency across these systems generally decreases with increasing annual rainfall and lower mean annual temperature. The drier eucalypt-dominated systems are more adapted to fire and burn more frequently and with a higher intensity on a 5-25 year cycle, compared to the wetter forest systems (cycle >20 years). Fires across these systems are mainly fuelled by woody materials (Bradstock et al. 2002; Williams et al. 2009).

The dry eucalypt-dominated systems were generally found to be resilient to fire due to existing high fire frequency. However, regardless of the type of fire, a fire event was always found to have either a long- or short-term impact on the vegetation and fauna in these systems. These systems are sensitive to increases in the fire frequency where several of the dominant eucalypt tree species have been identified as obligate seeders. In particular, obligate seeders that do not develop a seed bank in the soil and hold their seeds in the canopy were found to be most prone to declines due to fire, particularly increased frequency of high intensity fires. A high fire frequency was further found to change the understorey structure of these forest systems, generally sustaining fewer species. High intensity fires were found to often kill adult trees, and high fire frequency was found to negatively affect the successful establishment of seeder species (Bradstock et al. 2002).

Furthermore, fire was found to affect key habitat components of important forest fauna. Frequent fires, by changing the forest undergrowth, had a negative effect on ground-dwelling fauna. The scale of fires was also found to be important for the survival of both obligate seeder species and fauna. Small patchy-scale fires are more favourable for recolonisation. Dispersal ability was found to be a key determinant of the ability of a species to recolonise and survive after a fire (Bradstock et al. 2002).

Most work on temperate forest systems has been conducted either in the southeast or southwest of Australia. More detailed examples, focussed on these areas, are therefore reviewed in the following sections.

Southwest Australia

The open eucalypt forest systems of southwest Australia are generally resilient to fire and drought, whereas non-eucalypt wooded systems are more sensitive (Pekin et al. 2009). The impact of fire on biodiversity and forest systems has been thoroughly reviewed for two partially overlapping regions in the southwest of Australia. Shedley (2007) provided a review of published and unpublished fire-related literature relevant to the Avon river basin and Barrett et al (2009) for the South Coast region. Both reports aimed at providing landscape managers and ecologists with a synthesis of information on the fire ecology and fire sensitivity of individual taxa and the system as a whole, to provide scientifically based fire management guidelines for improved biodiversity conservation.

Shedley (2007) specifically reviews the responses to fire for (i) plants, grouped by their regeneration strategy in response to fire being (a) geophytes, (b) ephemerals, (c) obligate seeders, (d) resprouters; (ii) animals, covering (a) mammals, (b) reptiles and frogs, (c) birds, and (d) invertebrates; and (iii) fungi. Barrett et al (2009) provides a review covering fire responses of obligate seeders, resprouters and fauna, in relation to fire interval (i.e. frequency), intensity, seasonality (i.e. timing of fires) and spatial variation (i.e. scale).

The woody species within forested systems most sensitive to fire were found to be obligate seeder species. Obligate seeder species storing their seed in the canopy (i.e. serotinous species) were found to be more sensitive than seeder species storing seeds in/on the ground. Species with the ability to resprout were found to be generally resilient to fire (Barrett et al. 2009; Shedley 2007). Responses to fire for individual woody species are further discussed in Barrett et al (2009).

The most fire-sensitive fauna species were found to be species living in fragmented habitat and/or having low dispersal ability. However, in general there is a poor understanding of population-level responses of fauna to different fire regimes (Barrett et al. 2009; Shedley 2007). The few studies on species-specific responses of threatened fauna species are listed in Barrett et al (2009).

Fire effects on plants

Increases in fire frequency were found to have a negative effect on obligate seeder shrub and *Eucalyptus* species. High frequency fire regimes (once every 1-3 years) were further found to negatively impact on seedling recruitment and resprouting of both obligate seeder and resprouter species like *Eucalyptus wandoo* (Barrett et al. 2009; Shedley 2007). Increases in the intensity of fires were found to have the most profound negative effect on obligate seeders. High intensity fires were found to kill these species. Mortality for resprouters was also found to increase with fire intensity. However, high intensity fires *per se* were not found to affect forest function, because many woody species are reliant on occasional high intensity fires, for instance to release their seed. The combination of increases in fire frequency *and* intensity was found to be the most damaging for forest systems (Barrett et al. 2009; Shedley 2007). For instance, a high intensity fire was found to kill some *Eucalyptus wandoo* trees and subsequent frequent fires negatively affected the epicormic regrowth (Shedley 2007). Therefore, giving woody species enough time to recover was found to be the key to guarantee the sustained functioning of these systems. The timing or season of fire occurrence was found to be important in terms of recovery, particularly for obligate seeder species. Autumn fires impacted less severely than spring fires on seedling establishment and survival rate of obligate seeders. However, spring fires favoured resprouter species, like Jarrah (*Eucalyptus marginata*) (Grant 2003), but this effect was found to be less pronounced (Shedley 2007). Drought after fire had a severe negative impact on plant recruitment and seedling establishment (Shedley 2007). Autumn fires before winter rains are therefore preferred, and careful timing of controlled fires is therefore essential. The impact of different spatial scales of fires on vegetation recovery has not been thoroughly researched. Intuitively, a large spatial scale fire is likely to negatively affect the recolonisation of species that need to have their seeds dispersed from adjacent habitat, particularly in a fragmented landscape. A fire regime with small-scale fires therefore seems most favourable for forest system function in the southwest.

Fire effects on fauna

The effects of fire on insect pollinator species and ants was found to be largely unknown and poorly researched (Barrett et al. 2009). Increasing fire frequency was found to negatively affect species dependent on understorey habitat within forest systems. These habitats were found to be destroyed by both low and high intensity fires, negatively affecting the amount of food, cover and breeding sites. Mammals and birds living in the understorey were negatively affected by increases in fire frequency, mainly because of reduced habitat availability due to slow recovery of the vegetation. The impact of fire on fauna was further found to be directly proportional to the scale and intensity of the fire, with large and intense fires having greater negative immediate and long-term impacts than low intensity, patchy fires. Both mammals and birds mainly living in the understorey were found to respond this way. For instance Honey possums (*Tarsipes rostratus*) were found to respond negatively to intense large scale fires, but tolerated low intensity patchy fires (Shedley 2007). This was mainly due to the slower recovery rate of the more damaged habitat and the slower recolonisation rate from adjacent habitat. Particularly for ground dwelling animals, the scale of fire was found to affect the rate of recolonisation, where large-scale fires as well as related increased levels of predation were found to decrease the rate of recovery of the affected population (Shedley 2007). Species with low dispersal ability were found to be particularly sensitive in this respect. The timing of fires was also found to have an impact on fauna. Where fires occurred during the breeding season, birds were found to be negatively affected (Shedley 2007). Thus the interplay between fire frequency, scale, intensity and timing in relation to the mobility of the animal, and possible increased levels of predation, were found to determine the recovery response to fire in forest systems of the southwest. Low frequency small-scale patchy fires not burning more than 30% of a specific habitat fragment each time were favourable in terms of sustaining viable fauna populations within the landscape (Shedley 2007).

For the southwest, both Shedley (2007) and Barrett et al. (2009) provide an overview of the available evidence indicating the level of fire sensitivity for the forest systems present. Eucalypt moort, mallet and mallee dominated systems were found to be most sensitive, containing a range of fire sensitive obligate seeder species, like *Callitris* and *Banksia*, bird (e.g. malleefowl), and mammal species. Revegetated (i.e. planted) sites were further found to be more sensitive to fire in terms of recovery than similar naturally established vegetation (Herath et al. 2009).

Climate change effects

The species-rich eucalypt-dominated forests of southwest Australia contain a wide range of species susceptible to increased fire frequencies and high intensity fires. An increased scale and timing of fire was also found to have a likely negative effect on system functioning. The most damaging scenario was recognised to be an increased frequency of high intensity large-scale fires following a prolonged period of drought. The climate change projections and historic trends for the southwest indicate rising temperatures, a continued decline in rainfall and prolonged periods of drought. These changes have the potential to affect future fire regimes, in the short term providing more dry woody fuels resulting in a likely shift towards more frequent, large-scale, intense fires (Williams et al. 2009). In the long term, fuel accumulation might decrease through a reduction in plant productivity (Williams et al. 2009). However, in general, more frequent large-scale fires reduce the ability of a system to recover. Systems including fire-sensitive species, such as *Eucalyptus brevistylis* and *Eucalyptus jacksonii*, which have relatively long recovery times until they first set seed, would be at risk with such a shift in fire regime (Barrett et al. 2009). Furthermore, the drying climate will increasingly allow fires to enter and affect riparian forests in wetlands and coastal fringes. These systems are particularly vulnerable because only small remnants exist, and harbour a broad range of specialized flora and fauna. Fire impacts are therefore more likely to cause extinction in these remnant populations (Shedley 2007), which therefore need to be protected.

Management considerations

Based on the available evidence for the fire sensitivity of forest systems in the southwest, both Shedley (2007) and Barrett et al. (2009) provided a specific set of fire management guidelines for each system. The effect of fire was found to differ for each forest system, based on the number of fire sensitive species present. Identifying the most important fire sensitive species and establishing the time to reproductive maturity is the key to determining the appropriate fire interval. As a rule of thumb, the minimum tolerable fire interval was estimated as twice the juvenile period of the slowest maturing species within a functioning forest system (Abbott and Burrows 2003; Burrows et al. 2008). In fire sensitive habitats, this has been increased to 3-4 times the juvenile period for fire sensitive species (N. Burrows, personal communication). The projected increase in fire risk due to climate change will challenge the management of these forest systems. To prevent changes in system function, an appropriate regime of controlled burning needs to be designed for each forest habitat system, which incorporates a variety of fire frequencies, intensities and scales over time. This approach should result in a forest system that represents a mosaic of habitat differing in time since last fire, which will increase the overall resilience of the systems.

Southeast Australia

Southeast Australia is characterised by a wide range of forest systems, including temperate open forest systems on wet/dry and warm locations; temperate closed forest systems across a range of relatively wet/dry, warm or wet, cool locations; temperate rainforests, alpine forest systems and mangroves. Of these systems, fire occurs most often in the wet/dry temperate open forest systems and occurs less often in colder, high altitude locations and/or high annual rainfall systems. Research on the effects of fire is therefore scarce for forest systems such as temperate rainforest and mangroves. In the following paragraphs, we have summarised the findings on fire impacts on specific forest systems that have been studied in the southeast.

Temperate forest systems

A study carried out on Lambert Peninsula in Ku-ring-gai Chase National Park on the northern outskirts of Sydney found that fire frequency is the main driver of system function in dry-sclerophyll open forest systems (Morrison et al. 1996). The floristic composition was significantly altered if low-intensity fuel reduction burns were adopted on a 2-4 year rotation for a specific area. In particular, the abundance of long-lived woody species was significantly reduced. For sustainable system functioning, the required fire interval was found to be at least 8 years to preserve the fire sensitive species within the system (Morrison et al. 1996). Fire frequency was also found to be a major factor in determining forest system function in the temperate sclerophyllous eucalypt dominated forest systems in the Sydney Basin (Williams et al. 2009). A range of plant and fauna species was found to be sensitive to increases in fire frequency. In particular, obligate seeders and mammals were found to be negatively affected in this respect (Williams et al. 2009). However, as found in other forest systems, ant diversity was not affected by 2-4 year rotation burning as found in a dry sclerophyll eucalypt forest system in the Eden Burning Study Area in southeast NSW (Andersen et al. 2009), indicating the high resilience of this group of species and their potential role in post-fire recovery of these systems. The scale and intensity of fires was also found to have a significant effect on the rate of recovery of these systems (Williams et al. 2009). The impact of high intensity fire on small mammal populations was shown in a similar dry eucalypt dominated forest system in the Nadgee Nature Reserve on the far south coast of New South Wales (Recher et al. 2009). A high intensity fire did not kill all the animals (dasyurids and native murid rodents) immediately, but led to the extinction of each species from the study site over 18 months (Recher et al. 2009). However, the species did recover over time due to the low frequency of fires occurring in this area (Recher et al. 2009). This again indicates the importance of an appropriate interval between fires to allow the mammal populations to recover in parallel with their habitat (i.e. vegetation).

Predictions for this geographical location are that frequency, scale and intensity of fires are likely to increase with the projected changes in climate, affecting the fire-sensitive species in these systems (Williams et al. 2009). There is (already) a conflict in this area between public safety and biodiversity values related to high frequency fuel reduction burns. The rapid fuel build-up in these systems (2-4 years) means that controlled burning needs to take place on a 4 year rotation. For biodiversity conservation, however, this rotation was found to be too frequent to allow the system to recover (Morrison et al. 1996). The projected changes in the fire regime driven by climate change will therefore make the sustainable management of these systems even more challenging, and an appropriate compromise needs to be found between public safety and biodiversity conservation.

Alpine and wet forest systems

Current fire frequencies in these systems are generally low, less than once every 15-20 years. These systems, like ash forests in the highlands in southeast Australia, are sensitive to increasing fire frequency. Two consecutive fires resulted in Mountain ash (*Eucalyptus regnans*) and Alpine ash (*Eucalypt delegatensis*) being eliminated from some areas of the Central Highlands of Victoria when burnt at a 13 year interval (Tolhurst and Flinn 1992). It was shown that Alpine ash (an obligate-seeder) needs at least ten years to start producing seeds. However, current climate change projections for this area indicate drier and warmer conditions. The productivity of these forests is further expected to rise with elevated CO_2 levels, increasing fuel accumulation. Thus, fire frequency is likely to increase. If fires become more frequent than once every 10-15 years, i.e. below the minimum regeneration time of ten years, there will likely be a decline of these systems (Williams et al. 2009).

In the year-round moist winter cold/wet – mild summer sclerophyll Messmate/Gum eucalypt forests within the Wombat State Forest, Victoria, high fire frequency was found to affect vegetation recovery (Department of Sustainability and Environment 2003; Tolhurst and Flinn 1992). This rare long-term study (14 year and ongoing under the umbrella of the Bushfire CRC) looking at the effects of multiple low intensity fires on the recovery of this forest system, revealed that specifically woody species mainly in the understorey were negatively affected. Four 3-4 year rotation spring burns caused shrubs, small trees and seedlings to decline over the 14 years of study. This decline was more severe with three consecutive 4-5 year rotation autumn burns. A regime of long rotation burns (6-7 years) was found to be less damaging for these species (Department of Sustainability and Environment 2003; Tolhurst and Flinn 1992). The species composition changed significantly over the study period as a result of this high frequency fire regime, therefore changing the systems functioning. Mature trees were also found to become increasingly more damaged with higher intensity burns (Department of Sustainability and Environment 2003; Tolhurst and Flinn 1992). The negative effects of high intensity vs. low intensity fires were also observed in the winter cold/wet - summer warm/dry eucalypt forest systems in the Cotter River Catchment, Australian Capital Territory (ACT) (Vivian et al. 2008). The dominant *Eucalyptus* species that were able to resprout were found to be damaged but not killed by high intensity fires. The high intensity fires did however kill the dominant obligate seeder species *Eucalyptus delegatensis*. Furthermore, *E delegatensis* was found to be unable to disperse into adjacent sites, indicating low dispersal ability. This study indicates that a higher frequency of high intensity fires (that are likely to occur more often under climate change) will likely have a negative effect on systems dominated by obligate seeder species.

In the Wombat State Forest, invertebrate populations including pollinator species like moths and butterflies were found to recover quickly within 1-3 years after fire (Collett 2003; Collett and Neumann 2003). For birds, the response was very species specific, mainly driven by the availability and recovery after fire of their preferred habitat. Bird species reliant on the understorey were mainly negatively affected in this respect. The effect on small, ground-dwelling mammals was found to be significant if areas were completely burnt. Long-term unburned sites were found to be essential for refuge and recovery of the populations (Department of Sustainability and Environment 2003; Tolhurst and Flinn 1992). Furthermore, spring burning was found to impact less than autumn burning, likely related to the timing of reproduction occurring in autumn (Department of Sustainability and Environment 2003; Tolhurst and Flinn 1992). Very little is known about the impacts of fire on large ground mammals (Tolhurst and Flinn 1992). Large burrowing mammals such as the wombat (*Vombatus ursinus*) probably escape the immediate fire in deep insulated burrows (Newsome et al. 1975), however whether or not these species will remain or persist will largely be determined by habitat recovery and food availability. Additionally, a high intensity fire was not found to instantly decrease mammal populations, but rather had a more long-term negative effect, due to less vegetation cover making these species more vulnerable to predation (Green and Sanecki 2006). Altogether, these studies indicate that frequency combined with timing and intensity of fires is important in determining the population recovery in these forest systems.

Systems with relatively wet conditions year-round generally have low fire frequency, for example wet temperate forest systems in Tasmania (Williams et al. 2009). However, climate change factors are likely to alter the fire regime for these systems. In particular, currently wet forest systems in the southern half of Australia are likely to be influenced by the projected lower annual rainfall, which will make these systems more fire-prone. The evidence indicates that such a change in regime would likely have an overall negative effect on the functioning of these systems. Preventing an increase in fire frequency in these systems will be challenging. Prescribed low intensity burning to reduce fuel load is the only option to prevent more severe fires occurring. Although system changes might be inevitable, preventing frequent large-scale high intensity fires will be an essential step in the conservation of these systems in the face of climate change.

8.3 Conclusions: Fire

The aim of this review was to gather the available evidence describing how climate change will likely affect fire regimes within forest systems across Australia, and the consequences for forest biodiversity and functioning. We focussed here on key fire – woody vegetation and fire – fauna interactions. In the following paragraphs we will summarise the findings of this review on: (i) what fire related factors (i.e. frequency, intensity, timing, scale) are most likely to have the greatest impact on forest system functioning, (ii) what systems are most likely to be affected by changes in fire regime driven by climate change, and (iii) what the best management options are for preserving biodiversity in fire prone forested systems.

Fire plays a pivotal role in the Australian landscape and many plant species and communities have adapted to fire over time. However, many forest systems were identified as containing fire-sensitive species. The woody species identified as being most sensitive to fire were species that can only regenerate using seed (i.e. obligate seeders) and that have low dispersal ability. The faunal species most influenced by fires were species with low dispersal ability that live on the forest floor and understorey shrub layer. Flying pollinator species were found to quickly recover after fire, where potential ground-dwelling seed dispersers (with the exception of ant species) such as small mammals were found to be more sensitive to fire. These species were found to be impacted at various degrees by the frequency, intensity, scale and timing of fires. (1) Increases in fire frequency were found to have a general negative effect. (2) High intensity fires were found to have a more negative effect than low intensity fires. (3) Large-scale fires were found to have a more negative effect compared to small-scale fires, and (4) the timing of fires was found to have a variable effect on fire sensitive species depending on their timing and strategy of reproduction. The most damaging changes in fire regime on forest system functioning were found to be increases in fire frequency. The strongest empirical evidence indicates that an increase in fire frequency has an overall negative impact on species persistence and diversity. An increase in the frequency of fires will change current forest systems by altering species composition towards dominance of fire tolerant species (e.g. resprouters), whereas fire sensitive species (e.g. obligate seeders) are likely to decline. If the frequency of high intensity fires increases, this process is likely to be accelerated.

Climate change projections are positively correlated with an increase in fire frequency. Generally, the potential for increased fire occurrence is larger in areas where rainfall reduction and/or long droughts are predicted under climate change. The main impact of these climate changes will be that fuel for fire will be more readily available for longer periods of the year, making ignition more likely. Under these conditions the frequency and intensity of fires is likely to go up. Based on the projections of relatively small changes in rainfall, the impacts of climate change on fire regimes in northern Australia are predicted to be less than in the southern half of the country. The systems most likely to suffer an increased frequency of fires are the dry temperate forest systems found in the southeast and southwest of Australia. It is however largely unclear how the projected changes in climate will affect the build up of fuel in forest systems (Williams et al. 2009). Fuel availability will largely determine how fire regimes will change with the projected changes in climate. Interactions between climate, vegetation and fire need to be addressed in future research, in particular long-term monitoring of net primary production and quantitative modelling of fire influences on vegetation dynamics.

Management implications

Although it is largely unclear how climate change will influence fire regimes in different forest systems, in general the changing climate is predicted to increase the likelihood of fires occurring. This change in fire regime is of increasing concern in terms of sustainable management of native and plantation forest systems (Howden and Gorman 1999). It is therefore clear that fire will become an even more critical management issue for the protection of forests systems and their biodiversity as well as public health and safety across Australia.

Prescribed burning has been widely adopted as a management strategy for native and plantation forests. This strategy aims to limit the build-up of fuel, thus limiting the likelihood of wildfires occurring, but also to protect and conserve biodiversity and other environmental values. However, for many forested systems in Australia, a great deal of uncertainty still remains around the optimum fire regime for any particular forest type. Therefore, prescribed burning needs to be implemented with caution.

The challenge is to find the optimal mix of fire regimes and characteristics of individual fires to maximise biodiversity conservation, which will be different for each forest system and geographical location. The choice of an appropriate frequency, intensity, scale and timing can best be informed by knowledge of the biology of key species that represent particular forest systems. This could be fauna species that are important in facilitating dispersal or woody species (e.g. the dominant tree species) within forest systems. Identifying these key species and determining their fire sensitivity will help guide these management choices. In many forest systems, these species still need to be identified and this will be a key challenge for future research.

To estimate the appropriate fire frequency for a certain system the following guideline can be applied based on the woody species present. The minimum tolerable fire interval should be twice the longest juvenile period of species at risk of fire-related decline (i.e. fire sensitive species) (Abbott and Burrows 2003; Burrows et al. 2008). In fire sensitive habitats like rainforest systems, it has further been suggested to further increase this interval by 3-4 times the juvenile period of fire sensitive woody species (N. Burrows, personal communication). It was further found that it is important to leave some areas unburnt, (i) to provide wildlife refuge habitat, (ii) to protect fire sensitive plants that need a long fire interval to mature, and (iii) to facilitate regeneration and recovery of burnt areas through dispersal. To maximise biodiversity conservation at the landscape scale it is therefore recommended that a mosaic of either natural or controlled fires are applied that represent a range of fire frequencies, intensities, scales and timing to maintain the resilience and ensure the recovery of the forest systems.

Research coordinated by the Bushfire Cooperative Research Centres (CRC) into the impacts of fire on forest systems and landscape functioning is ongoing. In Australia, the majority of fire studies have been *ad hoc* with few long-term studies conducted. It is, however, clear that long-term studies are required for different forest ecosystems throughout Australia to adequately assess the impacts of fire frequency, intensity, scale and season of burn on forest system functioning. These gaps in knowledge need to be addressed to assure an effective and adaptive fire management strategy that can cope with the potential shifts in fire regimes driven by climate change in the forest systems across Australia.

9. Insect Pests

This section of the review looks at the probable responses of insect pest species and their plant hosts to the projected changes in climate, and how these changes will affect the likelihood of pest outbreaks within forest system across Australia.

9.1 Introduction

Insects are important drivers within forest ecosystems. Some species provide important ecosystem services like pollination, but many other insect species impact on forest vegetation through herbivory. When insect species have a significant negative impact on the development of forest systems, they are generally considered as pest species. Many abiotic and biotic factors influence the development of insect pest species that occur in and impact on forest ecosystems. For instance, temperature is the main regulator of the life cycle process of herbivorous insect species, plant chemistry of the host species influences their growth rate, and the presence of natural enemies affects their potential numbers, to name only a few. These factors and interactions will determine the likelihood and/or severity of a pest outbreak and consequently their effect on forest biodiversity and system functioning. The climate factors that are projected to change are likely to influence these factors and interactions in multiple ways. The potential impacts of climate change on these factors and interactions have been comprehensively summarised in various previous papers and reports globally (Bale et al. 2002; Bidart-Bouzat and Imeh-Nathaniel 2008; Deutsch et al. 2008; Logan et al. 2003; Menéndez 2007; Moore and Allard 2008; Volney and Fleming 2000) and for Australia specifically (Old and Stone 2005; Pinkard et al. 2009).

The projected changes in climate will have a direct impact on the development of insect pest species, and will also influence the likelihood and/or severity of outbreaks indirectly by affecting the susceptibility of their plant hosts (Old and Stone 2005). The direction of projected climate change is generally thought to increase the emergence of insect pest species within forest systems. On the other hand, the projected increases in CO_2 possibly will have a negative effect on the development of insect pests through the lesser palatability of and/or higher concentrations of defence chemicals within their plant hosts (e.g. Gleadow et al. 2009; Gleadow et al. 1998; Johns and Hughes 2002; Stiling and Cornelissen 2007). The projected increase in temperature has been found to be favourable for the development of typical insect pest species (e.g. Currano et al. 2008; Old and Stone 2005; Pinkard et al. 2009). The main effect of projected rises in temperature are that the life cycle of these species will speed up, making them able to develop and reproduce more quickly. Furthermore, the projected changes in rainfall and disturbances like droughts, storms and fire potentially increase the stress levels in trees making them more susceptible to pest attacks (Moore and Allard 2008), where chemical defence mechanisms of stressed trees generally function less well compared to healthy trees. For instance, in areas where rainfall is projected to decrease and droughts are more likely to occur, drought stress of the vegetation could result in increased frequency of pest outbreaks (Moore and Allard 2008).

9.2 Pests of plantation and native forest systems

9.2.1 Introduction

Most of the work to date on insect pest species has been performed on species affecting plantation forests. The effects of insect pests in monocultures have been found to be more severe than in multispecies native forests. Generally, insect pest species have been predicted to have an increased negative impact on plantation forest and possibly on native forest system functioning across Australia with predicted increases in temperature, variations in rainfall, and higher frequencies of extreme weather events such as droughts, storms and fires (Howden and Gorman 1999; Old and Stone 2005; Pinkard et al. 2009).

We recognise that many previous review studies have been undertaken. Therefore, we have specifically focused our work on reviewing the available literature on a selection of (key) pest species and species groups. These species (groups) were identified in consultation with scientists and stakeholder across Australia, and were highlighted as potentially becoming an increasing problem under the projected changes in climate.

For these species (groups), we aimed to (1) estimate their responses to projected changes in climate and (2) their future effect on the forest systems across Australia. We specifically looked at the direct responses of insect pests to the projected increases in temperature and rainfall, and at the evidence showing the impacts of changing climate factors on plant host susceptibility to pest attack.

9.2.2 Paropsine Chrysomelid Beetles (Coleoptera: Chrysomelidae)

Chrysomelid leaf beetles are common pests of eucalypt species that occur in native forests and plantations throughout Australia (Abbott 1993; Bashford 1993; Elliott et al. 1998; Neumann 1993; Old and Stone 2005; Plant Health Australia 2001; Stone 1993). Most Chrysomelid beetle species feed on eucalypts and other Myrtaceae (de Little 1979). Native forests have been found to be relatively unaffected by Chrysomelid beetles, where they occur naturally in sustainable populations. However, little work has been undertaken looking at the effects of this species group in native forest systems. They mainly cause damage in even aged young plantation stands, and are major pests in all Australian states where eucalypts are grown commercially (de Little 1989; Old and Stone 2005). In the dry tropics, *Chrysophtharta* impacts were found most severe on trees less than three years of age (Griffiths et al. 2004).

Most Chrysomelid species reported as pests of eucalypts in Australia are of the genera *Chrysophtharta* and *Paropsis*, where *Chrysophtharta cloelia* and *Paropsis atomaria* have been identified as two of the major pest species (Nahrung 2006; Nahrung et al. 2008). Species in this group defoliate new leaves and shoots of eucalypts, both as adults and larvae (dos Anjos et al. 2002). All ages of eucalypts are attacked but young trees are preferred. Damage is particularly severe on young trees, substantially reducing growth and in extreme cases, causing death. Heavy defoliation may cause up to 90% loss in height increment per year. Severe Chrysomelid damage also causes lateral shoots to develop, resulting in poor form.

Biological characteristics of *Chrysophtharta* species include high fecundity and adult longevity, resulting in the production of large numbers of offspring (Nahrung 2004). The insect pests have a one-year life cycle, with peaks of egg and larval activity over a short time interval (de Little 1983; Nahrung and Allen 2004; Ramsden and Elek 1998). The speed of development for this species group was found to be positively influenced by higher temperatures. For instance, for *Chrysophtharta* (or *Paropsisterna*) *agricola* development of egg, larval, prepupal and pupal stages were found to be faster at higher temperatures (24.2/17.2^{o}C compared to 17.3/12.5^{o}C day/night) in *Eucalyptus nitens* plantations (Ramsden and Elek 1998). This same effect was found for *Chrysophtharta bimaculata* where the increases in temperature positively influenced the development process, likely increasing the number of potential life cycles per growing season (Pinkard et al. 2009).

Indirect responses of the host species, for example higher C:N ratios in response to elevated CO_2, were found to have a possible negative influence on the development of this species group (Gleadow et al. 1998; Pinkard et al. 2009). Further studies in *Eucalyptus dunnii* plantations found that stands that suffered drought stress showed an increased amount of damage caused by Chrysomelid species (Whyte et al. in press). Stress in *E. dunnii* stands caused by flooding was also found to make the host tree more susceptible to attack and damage by Chrysomelid species (Old and Stone 2005; Stone 2001; Stone and Bacon 1994; Stone and Birk 2001). New foliage on stressed or damaged eucalypts was found to be smaller, thinner and more susceptible to herbivory (Landsberg 1990; Old and Stone 2005; Thomson et al. 2001).

Paropsine Chrysomelid Beetles are likely to aggravate under climate change, because these species were found to respond positively to increases in temperature and host susceptibility caused by climate change induced stress. Increasing temperatures were found to have a positive effect on the development of this species group, potentially speeding-up the life cycles resulting in more generations developing per year. Stress events driven by climate variability such as droughts, were found to increase the susceptibility and level of damage caused to host trees by this pest species group. Together with increases in the plantation estate, the geographic distribution of this species group is likely to expand (Nahrung 2004; Nahrung and Allen 2004), and the incidence of damage is likely to increase. The effects of this species group on native forests systems is however largely unknown. More resources should be allocated towards research, monitoring and management of this pest species group to prevent severe outbreaks from happening in the future.

9.2.3 *Phoracantha* spp. (Coleoptera: Cerambycidae)

There are 40 species in the genus *Phoracantha* (Longicorn beetles) and these are mainly associated with *Eucalyptus* spp. (Plant Health Australia 2001; Wang 1995). These species can be found in all forested environments across Australia (Plant Health Australia 2001). Longicorn beetles are widespread and have been identified as serious pests in eucalypt plantations in Queensland and northern New South Wales (Lawson 2003; Lawson et al. 2002). In Queensland, three species of *Phoracantha* have been identified as important pests in native forests and plantations, namely *P. solida* (two-hole borer), *P. acanthocera* (bullseye borer) and *P. mastersi* (ringbarking longicorn) (Lawson 2003).

In general, the life cycle of longicorn beetles is driven by temperature, where high temperatures favour the rate of development. Female beetles are attracted/can sense stressed trees or freshly cut wood where they lay eggs in groups under loose bark. Well watered or hydrated trees are rarely attacked, though it does occur. Longicorn larvae bore into the cambium, initially feeding on the phloem and later tunnel into the heartwood to pupate. Their damage leads to declines in wood quality, through the physical damage caused by the larvae and via wood staining and wood rot caused by associated pathogens. In addition, larval feeding can result in the detachment of bark from the tree, exposing large areas of sapwood to fungal infection (from Lawson 2003).

The increases in temperature are likely to have a positive effect on the reproductive cycle of this species group. Under the current climate change predictions, stress events like storms and droughts are likely to increase across Australia, which would make plant hosts of longicorn beetles more susceptible to attack. Together these effects are likely to mean the impacts of this pest group will increase in both native and plantation forests dominated by eucalypt species under the projected changes in climate.

9.2.4 *Ips grandicollis* (Coleoptera: Curculionidae)

Ips grandicollis (five-spined bark beetle) is an emerging exotic pest of plantation pine in Australia. It was first found in 1943 in the Wirrabara Forest in South Australia (Forestry SA 2008). It was separately introduced into WA in the 1950s (Elliott et al. 1998). It crossed state boundaries moving east in the early 1980s, and can now be found in *Pinus* plantations across NSW, QLD, SA, VIC, WA (Plant Health Australia 2001). It is considered a tree-killing pest in *P. elliottii, P. pinaster, P. radiata and P. taeda* stands and is causing increasing concern in southwest Victoria (Forests Commission Victoria 1982), New South Wales and Queensland (Wylie et al. 1999).

Adults form breeding galleries mainly in the phloem-cambial region inside or just underneath the bark of a host tree, where after hatching the larvae feed on the bark and wood of the tree (EPPO/CABI 1996). *I. grandicollis* has a high reproductive capacity that is primarily driven by temperature. Under ideal conditions (warm to hot) *I. grandicollis* can produce up to four generations between spring and autumn (EPPO/CABI 1996; Forests Commission Victoria 1982). The species is able to kill trees through a combination of breeding and/or feeding activities (EPPO/CABI 1996; Forests Commission Victoria 1982) and introducing fungi like *Ophiostoma ips* and *Ceratocystis ips* (Zhou et al. 2007). It further was found to be the vector of several nematodes and mites (Stone and Simpson 1990), like *Bursaphelenchus hunanensis* (Smith et al. 2008) and pine pitch canker (*Fusarium circinatum*) that also contribute to damaging and killing off trees. Although *I. grandicollis* is considered to be a secondary cause of decline (i.e. mainly attacks already stressed trees), it is thought that its damaging impact, also as a spreading agent of other damaging pests and pathogens will increase. The species has been increasingly found to attack stressed trees (e.g. drought, lightning, physical damage, fire). Compounds released by stressed trees attract the species. Where these stressed trees occur, healthy undamaged trees are also attacked during severe breeding and feeding outbreaks (Forests Commission Victoria 1982). Recently, in several state forests near Tumut and Tumbarumba in NSW, populations of *I. grandicollis* surged, causing large-scale tree mortality of drought-stressed 8-30 year old pine trees (Carnegie 2008a). Because this introduced species has such high potential for causing damage, as found globally and recently in NSW, more resources should be allocated towards research, monitoring and management of this emerging pest species in Australia (I Dumbrell pers comm).

The projected increase in temperature is likely to increase the rate of development of *I. grandicollis*. Milder (warmer) temperatures, particularly during spring and autumn, will allow the beetles to breed for longer (Carnegie 2008a), potentially increasing the number of generations that can be produced. Furthermore, the projected increases in extreme weather events such as droughts and storms and the likelihood of fire could increase the number of stressed trees. These conditions will increase the susceptibility of the host species to pest attack, attracting the attention of *I. grandicollis* increasing the likelihood of severe outbreak. For instance, it is likely that in areas such as southwest Australia and the southern tablelands of NSW where summer and winter temperatures are predicted to increase and extreme droughts are more likely to occur, the number of outbreaks will increase (A Carnegie pers comm). Therefore, together with increased breeding cycles, it is likely that more stress in the pine hosts will increase the incidence and severity of *I. grandicollis* associated deaths in softwood plantations in Australia. Therefore, monitoring and control programs developed overseas need to be implemented to prevent significant damage in the future.

9.2.5 *Sirex noctilio* (Hymenoptera: Siricidae)

The woodwasp *Sirex noctilio* has a wide host range, but is primarily a pest of pine species (Talbot 1977). In particular, *Pinus radiata* has been found to be highly susceptible to *S. noctilio* attack and induced mortality (Talbot 1977). Stands are most susceptible up to the age of 20-25 years (Carnegie et al. 2005; Madden 1975). *Sirex* have been found able to cause large scale mortality in even aged pine stands across Australia when uncontrolled (Talbot 1977). The wasp is a vector (i.e. spreading agent) of the symbiotic fungus that causes the ultimate mortality of the tree. Adult females use their ovipositor to drill holes in the tree in which they lay their eggs together with fungal spores of *Amylostereum areolatum* and mucus. The mucus acts as a drying agent of the wood tissue providing the right conditions for the fungus to grow and spread through the host tree (King 1966)). The host tree dies as the fungus spreads through the tree, further aided by the feeding larvae of *S. noctilio*.

The wasp is native to North Africa and Europe and was introduced into Australia in the 1950s from Europe via New Zealand (Talbot 1977). It is now an established pest of *Radiata* pine throughout Tasmania, Victoria, SA, ACT and NSW (Old and Stone 2005; Plant Health Australia 2001). In 2009, it was detected for the first time in southern Queensland, but has not been found in the northern subtropical regions (A Carnegie pers comm). Western Australia remains the only pine-growing state free of the wasp at this moment in time (Dumbrell 2009).

The species generally has a one-year life cycle, however, the speed of development is largely determined by the climatic conditions affecting the growth of the symbiotic fungus *Amylostereum areolatum*, which is the primary food source of the larvae stages of *Sirex* *noctilio* (Madden 1981). Adults are generally found to be present from late November to April, and most numerous in February-March (King 1966)). However, the life cycle has been found to be prolonged under unfavourable climate conditions affecting fungus growth. It has been shown that the development of the fungus within the trees is slowed under wet and cool conditions. Warm and dry conditions result in a more rapid growth of the fungus, resulting in a more rapid development of the egg and emergence of the larvae of *S. noctilio* (Madden 1981). Egg development was further found to be stimulated by elevated CO_2 levels (Madden 1981). Growth of the larvae was further determined by food availability, which is driven by favourable climate conditions for fungal growth and the amount of nitrogen provided by the fungus extracted from the tree (Madden 1981). The rate of development was slowed under wetter and cooler conditions in this respect. Furthermore, females were found to be attracted to stressed, sick or suppressed trees (King 1966); Talbot 1977), favouring these individuals for ovipositing their eggs.

The projected changes in climate are likely to favour the development of the fungus *Amylostereum areolatum*, which would speed up the development of the juvenile life stages of *Sirex noctilio*. Particularly in areas where temperatures will increase and rainfall will decrease, faster development and more life cycles per year are possible. Additionally, areas where droughts, storms and fires are more likely to occur, resulting in a large number of stressed trees, will become more vulnerable to *S. noctilio* attack. Furthermore, under the current climate change projections, *Sirex* is predicted to spread and become established in all areas where pine plantations exist across Australia (Carnegie et al. 2006). It is therefore highly relevant to continue the monitoring and control program through the National Sirex Coordinating Committee (NSCC) across Australia to prevent significant outbreaks and damage in the future (Carnegie and Bashford in press; NSCC 2002).

9.2.6 Psyllid species (Psylloidea: Hemiptera)

Psyllids or jumping plant lice are tiny sap sucking insects affecting the foliage of native Australian plant species including *Eucalyptus* spp. They are widespread across Australia (Plant Health Australia 2001). Some psyllid species have been observed to damage and in severe cases kill native eucalypt species (Pinkard et al. 2009). In response to increases in temperature, the number of life cycles increases, up to 4 times per year. Some emerging species of warm temperate eucalypt plantations were also recognised as likely to shift their home range southward (Pinkard et al. 2009). In some cases this species group was also found to favour trees grown under elevated CO_2 conditions (Wardell-Johnson et al. 2005). Furthermore, stressed trees were found to be targeted more frequently by this group of species (Wardell-Johnson et al. 2005). Together, these responses indicate that this species group will increasingly become a factor impacting on native and plantation forests dominated by eucalypt species under the projected changes in climate.

9.2.7 *Mnesampela privata* (Lepidoptera: Geometridae)

Mnesampela privata (Autumn gum moth) is a serious and frequently occurring pest of eucalypt plantations throughout southern Australia (Abbott 1993; de Little et al. 2008; McQuillan 1985). It has been found in NSW, SA, TAS, WA (Plant Health Australia 2001). The immature stages (i.e. caterpillars) cause damage, mainly to newly flushed leaves of young eucalypt trees. The host range of *M. privata* comprises many Eucalyptus species (Elliott and Bashford 1978; Lukacs 1999; Neumann and Collett 1997) including *E. nitens* and *E. globulus*. *M. privata* is a sporadic ‘gradient’ outbreak species (Steinbauer 2002) that, if left unchecked, is capable of completely stripping whole trees of foliage (Lukacs 1999). Defoliation caused by *M. privata* larvae can result in poor tree form, reduced growth rates (Abbott 1993) and in severe cases tree mortality (>50% defoliation, for several years) (Elliott and Bashford 1978; Farrow et al. 1994). Early identification and treatment of emerging outbreaks can prevent major damage from happening. The development of this species responds positively to increased temperatures, so increases in the number of life cycles per year under current climate change projections are likely to occur. However, because young leaves are preferred, areas where droughts will occur more often are likely to become less susceptible for outbreaks of this species.

9.3 Conclusions: Pests

In this section, we looked at several key pest species and groups, with the aim of estimating (1) their responses to projected changes in climate and (2) their future effect on the forest systems across Australia. We specifically looked at the direct responses of insect pests to the projected increases in temperature and rainfall, and at the evidence showing the impacts of changing climate factors on plant host susceptibility to pest attack.

All species that were reviewed showed positive responses to the climate factors that are projected to change, in terms of their development and/or in relation to their hosts. In general, it was found that insect pest species are likely to have a more negative impact on plantation forest and possibly on native forest system functioning across Australia as a result of the predicted increases in temperature. Only very limited evidence was found regarding how increases or decreases in rainfall affect the development of insect species (Moore and Allard 2008) and the flow-on effects on forest system functioning. Furthermore, relatively little information was found on native host or pest responses related to elevated CO_2, especially for the Australian scene (Pinkard et al. 2009). The effect of the projected changes in climate on plant host susceptibility, through increases in the level of stress, was found to generally increase the likelihood of pest outbreaks.

The projected increase in temperature was found to be generally favourable for the development of typical insect pest species (all species reviewed). The life cycles of these species were found to speed up, making them able to develop more quickly in response to food/habitat availability. Additionally, stressed trees (e.g. through prolonged droughts) were found to be more susceptible to pest attacks. Chemical defence mechanisms of stressed trees function less well than those of healthy trees. Furthermore, the ability of pest insects (e.g. *Ips grandicollis, Sirex noctili* and *Phoracantha* spp.) to identify/sense stressed trees consequently resulted in stressed trees being more likely to be attacked by pest species than healthy ones.

There is very little known about the impacts of insect pest species on native forest systems in Australia. In the limited studies undertaken, insect pest species were not found to have a significant negative impact on native forest systems. It is however unknown how the changes in climate will affect and possibly aggravate the effects of insect pests on biodiversity and native forest system functioning. For instance, species currently not found to be a problem in native forest and/or plantations could become more damaging and develop as pests with the projected changes in climate. This knowledge gap needs to be addressed in future research. Most of the work on the effects of insect pest species to date has been on species affecting plantation forest species. The effects of insect pests in monocultures of trees are generally found to be more severe compared to multispecies native forests. Modelling predictions show a general increase in potential areas affected (i.e. range expansion) by insect pest species, mainly driven by increases in temperature. Overall, however, the interactions between host and pests related to the changes in climate are still poorly understood and this limits our capacity to predict with certainty the future effects of pests on Australia’s woodland and forest systems (Pinkard et al. 2009).

To counter possible negative effects, adaptation can focus on making forest stands more resilient to climate related stress and/or eradication of the pest species. For example, appropriate thinning regimes can reduce the level of drought stress, to some extent (Pinkard et al. 2009). For some species, effective eradication programmes are already in place (e.g. for *Sirex noctilio*), but still need to be developed for new and emerging pest species. Additionally, plantation managers have the option of planting a mix of more drought/pest tolerant tree species. However, continuous monitoring within forest systems will be critical to guarantee a timely response to emerging outbreaks and identification of new insect pest species. Further development and wider accessibility of the Australian Plant Pest Database

(APPD) (Plant Health Australia 2001) would be highly favourable as a national information resource for forest managers and practitioners.

10. Pathogens

This section of the review looks at the probable responses of pathogens and their plant hosts to the projected changes in climate, and how this will affect their spread and overall impact on forest systems across Australia.

10.1 Introduction

Pathogens are important biological agents that affect forest ecosystem function. In forests, they cause disease in plant hosts, and consequently can significantly influence the forest dynamics. A range of abiotic and biotic factors influence the development of pathogen species. For example, ambient temperature is the main regulator of the life cycle process of many pathogens; water and wind play important roles in the dispersal of spores; and various insects, functioning as vectors, contribute to the spread of pathogens. These factors determine the development potential and rate of spread of pathogens and consequently their effect on forest biodiversity and function. The climate factors that are projected to change are likely to influence biotic interactions in multiple ways. The potential impacts of climate change on these factors and interactions have been comprehensively summarised in various previous papers and reports globally (Dale et al. 2001; Desprez-Loustau et al. 2006; Garrett et al. 2006; Harvell et al. 2002; Kliejunas et al. 2008; Moore and Allard 2008) and for Australia specifically (Howden and Gorman 1999; Old and Stone 2005; Pinkard et al. 2009).

The projected changes in climate will have a direct impact on the development of pathogen species, and also influence the likelihood and/or severity of outbreaks indirectly by affecting the susceptibility of their plant hosts (Moore and Allard 2008; Old and Stone 2005). The reviews mentioned above all indicate that the climate factors that are projected to change will have a variable effect on pathogen development. The change in host susceptibility also varies according to the level of stress resulting from climate change. For the majority of pathogens and their hosts, the response to shifts in climate and the consequent impact on forest systems was found to be difficult to predict because of a general lack of knowledge (e.g. Garrett et al. 2006; Kliejunas et al. 2008; Moore and Allard 2008; Pinkard et al. 2009). For example, within key parts of their life cycle, pathogens are generally dependent on relatively moist conditions. Thus, in areas where less rainfall is predicted, pathogen prevalence could decrease. However, this effect might be balanced by higher susceptibility of trees to infection, for instance, due to drought stress. The net effect of such interactions is largely unknown for the majority of species. It was therefore highlighted that interactions between individual host-pathogen complexes need to be studied in more detail if we are to gauge the impact of climate change on pathogens and consequent effects on biodiversity and forest system function (Garrett et al. 2006; Kliejunas et al. 2008; Moore and Allard 2008; Pinkard et al. 2009).

10.2 Pathogens of plantation and native forest systems

10.2.1 Introduction

The predicted increases in temperature, variations in rainfall and higher frequency of extreme weather events such as droughts, storms and fires will have an impact on pathogen-host interactions and consequently affect plantation forest and native forest system functioning across Australia (Old and Stone 2005; Pinkard et al. 2009). We recognise that many previous review studies have been undertaken. Therefore, we have specifically focused our work on reviewing the available literature on a selection of well-known pathogen species and species groups. These species (groups) were identified in consultation with scientists and stakeholders across Australia. The selected species were specifically highlighted as having the potential to become an increasing problem under the projected changes in climate.

For these species (groups), we aimed to (1) estimate their responses to projected changes in climate and (2) their future effect on the forest systems across Australia. We specifically looked at the direct responses of pathogens to the projected increases in temperature and changes in rainfall, and at the evidence showing the impacts of changing climate factors on plant host susceptibility in terms of infection rate/probability.

10.2.2 *Phytophthora cinnamomi* (Pythiales: Pythiaceae)

Phytophthora cinnamomi is a non-native pathogen (Cahill et al. 2008). It has a very broad range of plant hosts and in Australia it has affected and altered the species composition and biodiversity within many natural ecosystems (Shearer et al. 2004), including woodland and open forest systems (Weste 2003). *P. cinnamomi* was found to be a lesser problem in plantation forests (Old and Stone 2005). The species is found in all states of Australia (Old and Stone 2005; Plant Health Australia 2001), but has had the most significant impact in Western Australia, Victoria and Tasmania where it has caused major dieback and declines in biodiversity in areas with pristine native vegetation (Pinkard et al. 2009). *P. cinnamomi* has therefore been identified as a Key Threatening Process in the Commonwealth Environmental protection and Biodiversity Act, 1999.

P. cinnamomi is a soil-borne pathogen that mainly negatively affects the root system of plant and tree species. It causes premature cell death in the fine root system, in most cases causing death of the infected host (Grant and Byrt 1984; Weste and Cahill 1982). Aboveground symptoms are often most obvious following dry conditions during summer when plants may be water stressed. Plants that are not able to replace damaged roots fast enough suffer increased water stress and die. Once plants are infected, disease progression can only be slowed not stopped (Cahill et al. 2008). Depending on the health status of the plant and environmental conditions, death in plants may either occur rapidly, or the plant may decline (dieback) over many years (Cahill et al. 2008).

P. cinnamomi spreads through water, soil or plant material, and development and dispersal are favoured by warm moist or wet conditions. The reproductive body (chlamydospores) can survive for many years within dead roots of plants and soil (Weste and Vithanage 1978) and will germinate to produce sporangia under warm and wet conditions. Zoospores are the main propagules responsible for spread and cause the majority of infections within host plants (Weste and Cahill 1982). Zoospores predominantly infect plants via their roots, and on occasions via stems. Sporangia may be dispersed locally by rain splash, wind-driven rain, irrigation or ground water, soil and soil litter. Zoospores may also be carried in moving water across large distances. However, autonomous spread by root-to root contact also occurs. Therefore, once a site is infested, the pathogen is able to continue to spread and kill host plants even when environmental conditions are not conducive for sporangial production and zoospore release. Furthermore, humans, acting as dispersers of zoospores, have been recognised as the cause of the most significant, rapid and large-scale spread of *P. cinnamomi* in Australian landscapes (O'Gara et al. 2005).

Temperature plays an important role in growth (Hüberli et al. 2001; Shepherd and Pratt 1974), reproduction (Zentmyer et al. 1979), survival and pathogenesis (Shearer and Tippett 1989) of this species. In the laboratory, the optimal temperature range for zoospore production was found to be 18-22 °C, but zoospores were still produced at 30 °C (Halsall and Williams 1984). At 6-10 °C, infectivity of zoospores to roots of *E. pilularis* and *E. maculata* seedlings was restricted, however the pathogen survived (Halsall and Williams 1984). Soil temperatures are likely to increase under climate change favouring the development of *P. cinnamomi*. Infection probability will likely increase in areas where annual average soil temperatures are currently below 15 °C, which is recognised as the lower infection threshold for *P. cinnamomi* (Podger and Brown 1989). Thus, increasing temperatures due to climate change may result in new disease outbreaks in current cool areas presently unaffected by *P. cinnamomi*, especially placing vegetation at higher altitude at greater risk. For instance, high altitude areas of Tasmania previously too cold for the pathogen are likely to become more conducive to the pathogen (Pinkard et al. 2009). Furthermore, Brasier and Scott (1994) predicted that the activity of *P. cinnamomi* would increase in severity in southern Australia based on a +3^{o}C increase in temperature. However, this will be largely dependant on the effects of the predicted shift in rainfall.

It has been found that wet conditions are favoured by this pathogen, with water availability regulating the severity of outbreak events (McDougall 1996; Shearer and Tippett 1989; Weste 2003). Plants suffering water stress were less susceptible to invasion by *P. cinnamomi* than well watered plants (Smith and Marks 1982; Tippett et al. 1987; Tippett and Hill 1983). If rainfall decreases, development and spread of zoospores would therefore likely be retarded. In particular, if annual rainfall drops below 400-600 mm (Cahill et al. 2008), infection rate and spread will likely decrease. For instance, it is predicted that in south-west WA, coastal SA and western Victoria rainfall could decrease up to 25% by 2070. Such a drying trend would likely have a negative effect on *P. cinnamomi* development and host susceptibility (Shearer et al. 2009). A further reduction of prolonged wet spells and heavy rainfall days is also predicted to reduce the rate of spread and occurrence of mass collapse events in the south of Australia (Shearer et al. 2009).

In areas where rainfall will increase, the development and spread of zoospores will likely be positively affected. Particularly in areas where annual rainfall will rise above 400-600 mm (Cahill et al. 2008), infection rate and spread will likely increase. Warm wet summers were found to favour *P. cinnamomi* infection (Tregonning and Fagg 1985). Seasonal changes such as wetter summers, or more frequent extreme summer rainfall events, which will also be warmer, are therefore likely to increase the severity of the pathogen as long as these wetter events are sufficiently long enough to allow the pathogen to produce zoospores and infect host plants. Increased extreme summer rainfall events will also allow for more runoff in turn leading to greater spread and dispersal of the pathogen.

Climate change will influence the epidemiology of *P. cinnamomi* in a number of different ways, which will be difficult to predict. Furthermore, climate stress – pathogen susceptibility responses for the different plant hosts are largely unknown. For instance, currently we know very little about *P. cinnamomi* in the northern areas of Australia. This makes it difficult to make predictions about the possible changes, demonstrating the urgent need to better understand the distribution and impact of *P. cinnamomi* in northern Australia (K McDougall pers comm). For example, increased evaporation and higher temperatures will cause physiological changes in the pathogen and host plants, and their interactions. Furthermore, more extreme rainfall events could lead to more runoff and pathogen dispersal (Cahill et al. 2008), increasing the infection rate and spread of the disease. However, this needs to be investigated on a case-by-case basis because it is likely to differ among host species. Despite these uncertainties of the effect of climate change, rainfall is likely to be the driver of future impacts of *P. cinnamomi* on the native vegetation in Australia. Where the amount of rainfall is likely to decline, as in southern Australia, the overall impact of *P. cinnamomi* may decrease.

Where rainfall is predicted to increase, as in the Northern Territory and western Queensland, forests could become more susceptible to *P. cinnamomi* outbreaks, with negative consequences for biodiversity.

10.2.3 Foliar pathogens

Fungal pathogens affecting plant foliage are common and widespread across Australia (Old and Stone 2005; Pinkard et al. 2009; Plant Health Australia 2001). This pathogen group includes a wide range of species, such as *Mycosphaerella cryptica*, *Aulographina eucalypti*, *Kirramyces epicoccoides*, which are found primarily on foliage; *Quambalaria eucalypti and Q. pitereka*, which affect leaves and shoots; and *Botryosphaeria* spp. which affect leaves, shoots and stems (Carnegie 2007a; Carnegie 2007b; Old and Davison 2000; Stone et al. 1998; Yuan 1999). Most foliar pathogen species are native to Australia and occur naturally in native vegetation. Foliar pathogens were found to cause damage in both native forest systems and plantations. However, damage, mainly in the form of poor tree form, was found to be most pronounced in plantations and negatively affects their yield. Research to date has therefore focussed on plantation systems (Old and Stone 2005).

Plantations located adjacent to native woodland and forests are most likely to be affected by foliar pathogens (Carnegie 2007b). However, the majority of species were found to be largely harmless, with only a handful causing significant damage (Carnegie 2007a). In surveys performed in NSW, foliar and shoot fungi were the most commonly damaging (Carnegie 2007b). For instance, infection by *Quambalaria pitereka* commonly results in the repeated destruction of the growing tips, causing poor tree form and, in severe cases, death (Pegg et al. 2009). *Quambalaria pitereka* has been found in NSW, NT, QLD, VIC, WA (Plant Health Australia 2001) and is widespread in *Corymbia* plantations and native forests. For instance, *Quambalaria* shoot blight (*Q. pitereka*) was found to affect spotted gum (*Corymbia citriodora* and *C. maculata*) plantations in eastern Australia (Pegg et al. 2009). Surveys conducted to evaluate the impact of *Quambalaria* shoot blight have shown that the disease is present in all spotted gum plantations and on a range of *Corymbia* species and hybrids in subtropical and tropical regions surveyed in eastern Australia, also causing significant damage in northern NSW (Carnegie 2007a). The foliar pathogen *K. epicoccoides* (occurring in ACT, NSW, QLD (Plant Health Australia 2001)) was further found to cause severe damage to *Eucalyptus grandis* and *E. camaldulensis* plantations, and *Kirramyces eucalypti* occurring in ACT, NSW, TAS, VIC (Plant Health Australia 2001) caused severe damage in two *E. nitens* plantations in NSW (Carnegie 2007a).

This negative impact of this group of pathogens is predicted to increase with the projected increases in temperature, largely in areas where rainfall is likely to increase (Old and Stone

2005; Pinkard et al. 2009). In areas that become drier, impacts are projected to lessen (Old and Stone 2005; Pinkard et al. 2009). In the following sections, we consider likely responses of two major pathogen groups to projected changes in climate, based on their physiological response.

Mycosphaerella spp. (Capnodiales: Mycosphaerellaceae)

Mycosphaerella (and/or *Teratosphaeria*) species are fungi that are pathogens of native eucalypt forests and plantations. Many of the *Mycosphaerella* species described and studied in Australia have originated from surveys of plantations and have not been investigated in native forests. Disease symptoms are more obvious and significant in even aged plantations compared to multispecies native systems. When introduced to susceptible, even aged (exotic) plantations, they were found to have a significant impact on yield (Carnegie et al. 2007). *Mycosphaerella* species have been associated with defoliation events in native eucalypt forests and plantations in Tasmania (Milgate et al. 2005; Milgate et al. 2001; Park and Keane 1984; Yuan 1999), Victoria (Carnegie and Ades 2003; Carnegie et al. 1994; Park and Keane 1984), NSW (Carnegie 2007b) and WA (Abbott et al. 1993; Barber et al. 2008; Carnegie et al. 1997; Maxwell et al. 2003). They have been found in all states of Australia (Plant Health Australia 2001).

There are over 60 species of *Mycosphaerella* known from eucalypts, and they are associated with a disease complex called *Mycosphaerella* leaf disease (MLD) (Silva et al. 2009). *Mycosphaerella* leaf disease causes loss in photosynthetic area through leaf spotting, shoot blight, and defoliation (Pinkard and Mohammed 2006). It can lead to poor tree form, reduced growth and occasionally death. MLD was found to cause most damage in young eucalypt plantations, causing significant defoliation of juvenile foliage in trees up to three years of age (Barber et al. 2008; Carnegie et al. 1997).

Warm wet summers characterised by periods of high rainfall, relative humidity (>95%) and prolonged leaf wetness (>24 hours) and the presence of susceptible young flush leaves are favourable for disease spread and development of *Mycosphaerella* spp. (Old and Stone 2005; Pinkard et al. 2009). Spores of this species group are dispersed by water splash and long distances by wind, and optimal infection levels were found to occur after 5 to 7 days of leaf wetness between 15 to 20 °C (Park 1988; Park and Keane 1982), with no spores being released at <10 °C or >30 °C (Cheah and Hartill 2007).

Rising temperature is thought to positively influence MLD development. However, rainfall is likely to be the main driver for the possible increase in incidence and impact of MLD on native and plantation forests (Moore and Allard 2008). Where annual rainfall is predicted to increase, as in some areas in the north of Australia, MLD incidence is likely to increase. However, in areas where rainfall is likely to decrease and summer temperatures are likely to rise above 30 °C, MLD incidence is likely to decline, possibly lessening the impact of this disease in the southwest and southeast of Australia.

Pinkard et al (2009) used the process-oriented climatic niche model CLIMEX to project the current and future potential distributions of MLD for southeast Australia and Tasmania, based on predicted changes in temperature and rainfall. Their projections showed an increasing impact across Tasmania because sites at higher altitude are likely to become more suitable with the projected rise in temperature combined with similar high/increasing levels of rainfall. The southeast of Australia showed a retraction to higher altitudes mainly driven by reduced rainfall at low altitudes and rises in temperatures combined with similar high/increasing levels of rainfall (Pinkard et al. 2009). They further predicted that the impact of MLD on *Eucalyptus globulus* plantations would significantly increase with the predicted changes in climate within this region (Pinkard et al. 2009), suggesting that the effects of defoliating pests on plantation productivity should not be ignored when considering future management of forest plantations.

Dothistroma septosporum/septospora or Mycosphaerella pini (Incertae sedis: Mycosphaerellaceae)

One of the most extensively studied foliar diseases in pine plantations is needle blight caused by the fungus *Dothistroma septosporum/septospora* or *Mycosphaerella pini* (Watt et al. 2009). *D. septospora* was introduced into Australia and New Zealand in the 1970's (Groenewald et al. 2007) and is now reported in ACT, NSW, QLD, TAS and VIC, mainly occurring in southeast Australia (Plant Health Australia 2001). It is considered one of the most severe and significant diseases of pine species (Watt et al. 2009). Infected trees drop their needles prematurely, and repeated defoliation events can significantly retard growth and eventually cause death of host trees (FAO 2009; Stone et al. 2003). *D. septospora* has a very wide host range within *Pinus* (Woods et al. 2005). Of the important Australian softwood plantation species, *P. radiata* and *P. caribaea* are highly susceptible, *P. pinaster* moderately susceptible and *P. elliottii* slightly susceptible to *Dothistroma* needle blight (Watt et al. 2009). The incidence and spread of *Dothistroma* needle blight is influenced by climatic conditions, site topography and stand structure, with the potential to rapidly reach epidemic outbreaks (Stone et al. 2003).

D. septospora is a primary pathogen that invades and kills host tissue. Spores germinate on needle surfaces during wet weather and produce fruiting bodies within the needles containing virulent spores that are dispersed mainly via rain-splash or wind (FAO 2009). Diseased nursery stock can further be responsible for long-distance transport of the pathogen (FAO 2009). Spores can be released and cause infections at any time when there is wet weather and temperatures are above 5°C. Generally, warm and wet periods are favoured for the development, dispersal and infection rate of this species (Old and Stone 2005).

Increasing temperature is thought to positively increase *Dothistroma* needle blight development. However, rainfall is likely to be the main driver for the possible increase in incidence and impact in pine plantation forests (Moore and Allard 2008). The importance of rainfall was also indicated by Watt et al (2009), who showed, using the CLIMEX model for Australia, that climatically suitable areas were confined to the moist periphery of the country. Outbreak events were further found to coincide with prolonged periods and increased frequency of (warm) rain events allowing for the rapid spread and increased rates of infection (Moore and Allard 2008; Woods et al. 2005). Where annual rainfall is predicted to increase, *Dothistroma* needle blight incidence is likely to increase. However, for the majority of areas where pine plantations are present (southern half of Australia) the amount of rainfall is projected to decrease, and the effects of *Dothistroma* needle blight incidence could therefore also decrease.

10.2.4 Canker-causing fungi

Canker-causing fungi have a wide host range and affect both native vegetation and pine species. These species have a wide distribution and occur naturally in woodland and forest systems across Australia (Plant Health Australia 2001). In particular, fungi from the genera *Botryosphaeria* and *Diplodia* have been found to cause damage to native eucalypts, but also pines, often causing the most significant damage in plantation systems (Old and Stone 2005). Canker fungi generally colonize plant tissue through wounds, growth cracks and leaf scars (FAO 2009). When a host is infected, the fungus causes death of sapwood cells (i.e. phloem) causing dieback of branches. When infecting the base of a tree, the fungus can cause death, particularly in young trees (FAO 2009; Old et al. 2003). These fungi can rapidly spread under favourable climatic conditions. Spores can be dispersed in a variety of ways including wind, rain splash and insect vectors (FAO 2009; Old and Stone 2005).

Canker fungi commonly live as endophytes (i.e. in symbiosis) within their hosts and generally do not cause significant damage. However, when hosts are stressed this group of fungi can switch from asymptomatic endophytes to pathogens (FAO 2009; Old et al. 1990; Slippers and Wingfield 2007; Zhonghua et al. 2001), causing significant damage to their hosts. For instance, *Botryosphaeria* fungi were found to cause disease and significant damage in native and plantation forests in eastern Australia (Old and Davison 2000; Old et al. 1990; Slippers et al. 2004) and Western Australia (Burgess et al. 2005; Burgess et al. 2006; Davison and Tay 1983; Shearer et al. 1987), likely caused by increased abiotic stress of the hosts. It has been shown that *Botryosphaeria ribis* found in ACT, NSW, QLD, VIC and WA (Plant Health

Australia 2001) have a higher ability to affect drought-stressed trees (Rayachhetry et al. 1996). Further research showed that canker-causing fungi like *Botryosphaeria* spp. and *Diplodia* spp. caused increasing and significant damage in stressed stands in WA (Wills 2007), NSW (Carnegie 2007a) and Tasmania (SoE Tasmania 2009) related to extended periods of drought and high temperatures (Carnegie 2007a; Wills 2007).

For their development, increasing temperatures were found to be favoured for this species group (Old and Stone 2005; Pinkard et al. 2009). However, reduction in rainfall was found to have the strongest impact on the severity of outbreaks and damage caused by canker fungi (Old and Stone 2005; Pinkard et al. 2009). In areas where annual rainfall is likely to decrease and extreme weather events such as droughts and storms are more likely to occur, the stress levels of trees are likely to increase. Higher stress levels increase the likelihood of hosts being infected and suffering damage from canker fungi. These fungi have a broad host range and are found in all states of Australia (Plant Health Australia 2001) and therefore pose a significant threat to plantations and native forest ecosystems. In particular, woodland and forest systems in areas predicted to have decreasing rainfall and more frequent extreme weather events, such as the southeast and southwest of Australia, are likely to become increasingly affected by canker causing pathogens. Adaptive management is needed to reduce water stress within stands to counter these negative climate change effects.

10.2.5 *Armillaria* spp. (Agaricales: Marasmiaceae)

Armillaria species are soil-borne pathogenic fungi primarily infecting the root system of a wide range of hosts in native hardwood and conifer forests and plantations throughout the world (Hood et al. 1991; Kile et al. 1991). In Australia, *Armillaria* species have been recorded in all states and are widespread within native woodland and forest systems mainly affecting *Eucalyptus* spp. (Old and Stone 2005; Pinkard et al. 2009; Plant Health Australia 2001). *Armillaria* species are native to forest ecosystems, however, they can cause wood decay, growth reduction and even mortality, particularly in trees stressed by other environmental factors. Most *Armillaria* spp. are secondary pests, and therefore can only infest trees when weakened e.g. by drought stress. Infection of host trees occurs through the bark of roots or wounds on the trunk from where the fungus enters the sapwood and cambial region of the tree (FAO 2009). After infection, *Armillaria* spp. spread throughout the tree and, depending on environmental conditions, over time host trees will start showing symptoms like leaf drop, dieback of twigs, branches and main stems, causing stunted growth and in severe cases death of the host tree (FAO 2009; Old et al. 2003). This process can, however, take several years depending on the health status of the infected tree. Dispersal can take place by wind, through spores from mushrooms, through the spread of rhizomorphs (i.e. fungal filaments) in the soil and movement of infected plants, trees and soil by humans (FAO 2009).

Several species of *Armillaria* occur in southeast Australia (Kile and Watling 1983), but not all are pathogenic (Robinson 2003). *Armillaria* spp. outbreaks have occurred in mature eucalypt stands on high quality sites in central Victoria and south-west Western Australia (Jurskis 2005b; Kile 2000). Of the known *Armillaria* species, *Armillaria luteobubalina* has been found to be the most damaging, with a broad host range within *Eucalyptus* and *Corymbia* spp. in Australasia (Kile 2000). *A. luteobubalina* is found in ACT, NSW, QLD, SA, TAS, VIC and WA (Plant Health Australia 2001) and acts as a primary pathogen mainly spreading by root to root contact (Robinson 2003). In Western Australia, it has been found as a common and damaging pathogen in *Eucalyptus diversicolor* (karri), *Eucalyptus marginata* (jarrah) and *Eucalyptus wandoo* dominated woodland and forest systems (Kile 1983; Pearce et al. 1986; Robinson 2003; Shearer 1994; Shearer et al. 1997; Shearer and Tippett 1988). *A. luteobubalina* further has been found to kill off rare and endangered species like *Banksia brownii, B. occidentalis,* and *B. verticillata* (Shearer et al. 1997). Furthermore, in the northeast of Tasmania, *Armillaria hinnulea*, which has also been found in NSW and VIC (Plant Health Australia 2001), was found to cause decline in *E. regnans* and *E. nitans* forests (SoE Tasmania 2009).

Increases in temperature are likely to have a positive effect on the development of *Armillaria* spp. particularly in the cooler regions in Australia (Old and Stone 2005; Pinkard et al. 2009). Development of *Armillaria* spp. was found to take place between 10-31 °C with general optimum temperatures for development of 20-22 °C (Pinkard et al. 2009). In areas where temperatures are currently unfavourable (i.e. too low), the effect of *Armillaria* spp. on woodlands and forests might therefore become more pronounced with the projected rises in temperature. Further research suggests that decreases in rainfall are likely to increase the infection rate of *Armillaria* spp., although direct evidence is lacking (Pinkard et al. 2009). *Armillaria* spp. need moisture during their development, therefore prolonged periods of drought will negatively affect their survival (Kile 2000; Pinkard et al. 2009). The positive effects of reductions in rainfall on *Armillaria* spp. development and infection rate have been mainly attributed to the stress level of its host. The stress level of trees, related to water availability, was found to be a main driver for susceptibility to *Armillaria* spp. infection. Periodic drought stress events were found to positively influence infection rate (Kile 2000). However, controlled experiments testing the effect of drought stress on tree susceptibility to *Armillaria* spp. did not show clear trends (Desprez-Loustau et al. 2006). Furthermore, in WA, disease extension in *Eucalyptus wandoo* was not correlated with yearly rainfall on calcareous sands of Holocene dune systems (Shearer et al. 1997). Additionally, *Armillaria* related dieback in southern Tasmanian regrowth was not related to stand density, and was actually worsened by thinning and fertilisation (Jurskis and Turner 2002; Wardlaw 1999).

The incidence of drought stress within stands is likely to increase in areas where droughts are projected to become more frequent, such as the southeast and southwest of Australia. In areas where periodic drought events are more likely to increase, *Armillaria* spp. infections are likely to become more prevalent. There are many uncertainties on how the combined changes in climate will affect the potential impact of *Armillaria* spp. on forest systems, which need to be addressed in future research. It is however clear that *Armillaria* spp. will continue to be a problem in forest systems and have the potential to aggravate under current climate change projections.

10.3 Conclusions: Pathogens

In this section, we looked at several key pathogens aiming to estimate: (1) their responses to projected changes in climate and (2) their future effect on forest systems across Australia. We specifically looked at the direct responses of pathogens to the projected increases in temperature and changes in rainfall, and at the evidence showing the impacts of changing climate factors on plant host susceptibility in terms of infection probability and rate.

Compared to insect pests, pathogens showed more variability in their responses and potential future effect on forest systems in relation to the projected changes in climate. Pinkard et al. (2009) concluded that in general, leaf diseases, shoot blights and some root pathogens will be favoured by warmer wetter conditions, and cankers and some root pathogens are likely to be favoured by warmer temperatures and periodic drought. The pathogen species that were reviewed in the current study, generally showed positive responses in their development related to the projected increases in temperature. These pathogen species are therefore likely to continue and possibly have an increased negative impact on biodiversity and plantation/native forest functioning across Australia with predicted increases in temperature. However, compared to temperature, changes in rainfall were considered to be a stronger driver for pathogen development, spread and infection rate. Responses to increases or decreases in rainfall were found to be less clear and varied between the species reviewed. Changes in rainfall are important for the epidemiology of pathogens: for example, moisture is needed for the dispersal of spores for some pathogens. However, only very limited evidence was found on how increases or decreases in rainfall affect the development of pathogen species (Moore and Allard 2008).

Although the effects of changes in rainfall are unclear, prolonged droughts are likely to increase infection, because stressed trees are generally more susceptible to pathogen infection. For instance, canker fungi are more able to infect drought-stressed trees than healthy trees, because chemical defence mechanisms of stressed trees are likely to function less well. This interaction indicates the complexity and difficulty of predicting the likely impacts of climate change on pathogen development and host susceptibility. Such interactions are little studied and need to be addressed in future research (Harvell et al. 2002). Furthermore, little information is available on native host and pathogen responses to elevated CO_2 (Garrett et al. 2006), especially for Australian forests (Pinkard et al. 2009).

Apart from the negative impacts of the introduced pathogen *Phytophthora cinnamomi*, there is very little known about the impacts of pathogen species on biodiversity and native forest function. In the limited studies undertaken, native pathogen species were not found to have a significant negative impact on native forest systems. It is however largely unknown whether changes in climate will aggravate the effects of pathogens on biodiversity and native forest function. For instance, species currently not found to be a problem in native forests and/or plantations could become pathogenetic and more damaging with the projected changes in climate. This knowledge gap needs to be addressed in future research. Most of the work on the effects of pathogen species to date has been on species affecting plantation forest species. The effects of pathogens in monocultures of trees are generally found to be more severe compared to multispecies native forests. For some pathogen species, modelling predictions showed a general increase in potential areas affected (i.e. range expansion), mainly driven by increases in temperature. Overall however, the interactions between host and pathogens related to the changes in climate are still poorly understood and this limits our capacity to predict the future effects of pathogens in Australia's woodland and forest systems (Pinkard et al. 2009).

To counter possible negative climate change effects, forest stands can be made more resilient. It has been shown that appropriate thinning regimes can reduce the level of drought stress to some extent (Pinkard et al. 2009). Additionally, plantation managers have the option of planting a mix of more drought/pest tolerant tree species. Eradication of pathogens once established in most cases seems difficult if not impossible. Focus should therefore be on prevention of their spread (Desprez-Loustau et al. 2006), as well as prevention of the introduction of new species such as *Phytophthora ramorum*. The consensus is that very little can be done to prevent the spread and infection of fungal pathogens that disperse by air. For soil borne pathogens, preventing the spread by humans should be the focus. Continuous monitoring of forests for emerging infestations, identification of the pathogen responsible, and setting up appropriate quarantine protocols should be the main courses of action. Development and wider accessibility of the Australian Plant Pest Database (APPD) (Plant Health Australia 2001) will further be highly favourable as a national information resource for forest managers and practitioners.

11. Invasive weeds

This section of the review looks at responses of invasive weeds to the projected changes in climate, and how this will affect the likelihood of their spread and overall impact within forest system across Australia.

11.1 Introduction

Invasive weeds are plant species that are considered to have a negative or adverse effect on biotic communities within the landscape. Invasive weeds have generally been introduced and have spread outside their intended geographical area, negatively affecting surrounding ecosystems and their biodiversity (e.g. Steffen et al. 2009). Invasive weed species are typically characterised by fast growth, short juvenile periods, high dispersal ability, high adaptability to different environments and high tolerance to changes in environmental conditions (e.g. climate) (Kriticos et al. 2010).

For Australia, a range of useful resources are available on weed species that affect agricultural and native vegetation (e.g. Parsons and Cuthbertson 2001; Thorp and Wilson 1998 onwards). One very useful free online resource, the 'Weeds Australia database' (Thorp and Wilson 1998 onwards), lists information for all recognised current (i.e. established) and potential (i.e. alert or sleeper) weed species, giving details on origin, morphology, dispersal strategy, distribution (e.g. maps) and links to other information sources. This web facility aims to bring all relevant information together on the current state of knowledge for all known weedy species in Australia. Based on the level of invasiveness, impacts, potential for spread, and socioeconomic and environmental values, a shortlist of twenty established invasive weed species were identified as having a significant adverse effect on Australia's agricultural and native vegetation (Thorp and Lynch 2000; Thorp and Wilson 1998 onwards; WoNS 2009). These so called 'Weeds of National Significance' (WoNS) have been actively monitored over time and rigorous management plans have been designed and implemented to stop and/or minimise their impacts on the natural environment (WoNS 2009). Further weeds that have been recognised as having a (potential) significant impact on the environment (i.e. alert and sleeper weeds) are continuously being reviewed and related management plans are being developed (WoNS 2009).

Alert and sleeper weeds are plants not currently posing problems but which could become serious problems and expensive to eradicate or control (Kriticos et al. 2010). They are believed to have not yet reached their potential to form large and widespread populations in Australia, despite being naturalised for some years. They have the potential to become significant problems as invasive weeds due to changes in environmental conditions driven by climate change (Scott et al. 2008). For instance, changes in the frequency of extreme weather events, such as fires or cyclones, are thought to have a potential triggering effect for these species to become invasive (Scott et al. 2008). Further changes in land or water management are also thought to potentially result in these species reaching a critical threshold leading to their increased negative impact on plantation and native forest systems (Australian Weeds Strategy 2006).

In forests, invasive weeds cause considerable changes in species composition and consequently have a significant influence on biodiversity and the dynamics and functioning of these systems (Gleadow and Ashton 1981; Kriticos et al. 2010; Scott et al. 2008; Steffen et al. 2009). Abiotic and biotic factors influence the development of invasive weed species that affect forest ecosystems in various ways. For instance, temperature extremes are an important factor determining the suitability for weed species to occur, as is annual rainfall (Kriticos et al. 2010; Scott et al. 2008; Steel et al. 2008). Wind, insect and other animals play an important role in weed dispersal, and the occurrence of disturbances such as storms can play a role in determining dispersal success (Steel et al. 2008). These factors and interactions will determine the development potential and rate of spread of weed species and consequently their effect on forest biodiversity and function across Australia.

The climate factors that are projected to change are likely to influence these factors and interactions in multiple ways. In Australia, the projected increase in temperature and decrease in rainfall will potentially allow weed species currently restricted to the tropical north, to invade and/or extend their range towards the south (Kriticos et al. 2010; Scott et al. 2008). Furthermore, temperate weed species currently present in the southern half of Australia might retreat towards the south coast and higher altitudes, while summer growing species might become more prevalent in the southern regions, consequently affecting new areas (Kriticos et al. 2010; Scott et al. 2008). Under the current climate change projections, disturbances are also likely to become more prevalent, potentially enabling weeds to further invade and establish in new areas (Steel et al. 2008).

11.2 Invasive weeds of plantation and native forest systems

11.2.1 Introduction

The predicted increases in temperature, variations in rainfall and increased frequency of extreme weather events such as droughts, storms and fires will have an impact on the development and spread of invasive weeds and consequently have a flow-on effect on plantation and native forest function across Australia. Weeds are opportunistic and able to adapt to a wide range of environmental conditions. Consequently, weeds do not generally limit themselves to one land-use and many will affect, to a greater or lesser degree, the biodiversity of native forests and plantations. For instance, grassy weed species like gamba grass (*Andropogon gayanus*) encroaching on tropical savannah systems in the north, and buffel grass (*Cenchrus ciliaris*) invading arid forest systems in central Australia, have been recognised as having a considerable impact on fire regimes and biodiversity within these systems (Steffen et al. 2009; Williams et al. 2009). Furthermore, during plantation establishment or in disturbed forests, high light levels and the relatively high water and nutrient availability might favour weed establishment (Balandier et al. 2006). Under these circumstances, fast-growing herbaceous and woody weed species can capture resources at the expense of plantation trees and native vegetation, negatively influencing the biodiversity, regeneration and functioning of the system.

A number of Weeds of National Significance (WoNS) impinge on forests, woodlands and plantations, including *Asparagus asparagoides* spp. (bridal creeper); *Rubus fruticosus* L. (blackberry); *Ulex europaeus* (gorse); *Acacia nilotica* (prickly acacia); and *Cryptostegia grandiflora* (rubber vine). Increasing temperatures are likely to enable tropical and sub-tropical WoNS species, like *Acacia nilotica* and *Cryptostegia grandiflora*, to expand their current distribution and invade areas where they currently cannot reproduce (Kriticos et al. 2010; Kriticos et al. 2003a; Kriticos et al. 2003b). Furthermore, improved water use efficiency as a result of elevated CO_2, may enable some species, such as *C. grandiflora*, to invade drier sites (Kriticos et al. 2003a). However, the possible impacts of many (potential) invasive weed species on forest biota and system functioning is largely unknown. To date little work has been undertaken on measuring the direct effects of changes in climate on the distribution and vigour of weed species, mainly because of a general lack of detailed knowledge of specific climate requirements for individual species (Kriticos et al. 2010; Scott et al. 2008; Steel et al. 2008). In this section, we therefore have highlighted likely responses and issues related to climate change effects on invasive weeds in Australia. We specifically looked at model predictions of future distributions of weeds under climate change, and we present two case studies demonstrating the complex interactions related to climate change effects on weed responses.

11.2.2 Modelling predictions

To predict the potential impact of climate change on invasive weed species, the majority of studies conducted in Australia have used a variety of bioclimatic modelling techniques to predict future distributions. In bioclimatic modelling, the current geographical distribution of a species is related to climatic variables, primarily temperature and rainfall, to enable projections of current and future potential distributions; see Chapter 2 for more detail. Bioclimatic modelling approaches have been used extensively to predict the changes in the distribution and range of invasive weeds under different climate change scenarios.

For instance, blackberry (*Rubus* spp.) (WoNS) occurs in humid and subhumid temperate regions mainly in areas with fertile soils and an annual rainfall greater than 750mm. Blackberry invades native forests like wet and dry sclerophyll forest, warm temperate rainforest and cool temperate rainforest (Parsons and Cuthbertson 2001) and plantations. It is a significant management problem in native forests and plantations, particularly influencing sapling establishment success after disturbance (J. Scott *personal communication*). The most widespread species in Australia has been identified as *Rubus anglocandicans* (Evans and Weber 2003). Bioclimatic modelling has shown that in the short-term, conditions across a large part of southeast Australia will remain suitable for *R. anglocandicans*. However, based on the predicted reduction in annual rainfall for the southeast and southwest of Australia, the area suited for establishment and growth is likely to decline (Kriticos et al. 2010; Steel et al. 2008). Although the climatically suitable area for weeds including *Rubus* spp. and *Cytisus scoparius* (scotch broom) is predicted to contract (Potter et al. 2009; Scott et al. 2008), without active management further spread is still likely and a considerable threat for forest biodiversity.

Scott et al. (2008) used the CLIMEX model to predict the future potential distribution for 41 alert and sleeper weeds across Australia. The CLIMEX model is an eco-physiologically based mechanistic model (i.e. refined bioclimatic model) that was developed specifically to deal with modelling potential distributions and climatic suitability for invasive species (Kriticos et al. 2010). The model was parameterised with climate change projections and estimates for plant temperature (min/max) and rainfall (i.e. moisture) requirements, based on the known biology of the species. Under the predicted general warmer and drier conditions, they found that climate suitability shifted for all modelled weeds from the north to the south. Generally, sleeper weeds were found likely to expand their range. Of the species modelled, the woody species *Acacia karroo* and *Retama raetam* were identified as having a high potential for causing problems in the future (Scott et al. 2008), potentially impacting on forest biodiversity and functioning. The southeast, and to a lesser extent the southwest of Australia were found likely to face a ~20% increase in weed species threat, where the north potentially will have less weed impacts depending on the introduction of new emerging weed species. Kriticos et al. (2010) used the same model with more detailed climate change scenarios for a range of weed species currently occurring and with a potential to establish in South Australia. For the 13 species modelled, the simulations predicted slight reductions in climate suitability and a general range shift towards the coast for species encroaching on native and plantation forests. However, high altitude areas were predicted to become more likely to be invaded, and introduction of new species from neighbouring states were indicated as becoming more likely (Kriticos et al. 2010).

Steel et al. (2008) similarly used a bioclimatic modelling approach for the southeast of Australia (i.e. Victoria). In their study, changes in climate suitability were modelled using known distribution data for 20 weed species in combination with their known climate requirements. The climate projections used were a general increase in minimum and maximum temperatures (summer more than winter) and a general decrease in rainfall (mainly in spring). Disturbances and land-use were not included in the models. The species selection was limited to those that had sufficient distribution data within Australia. Presence only data was used, assuming potential distribution was reached and so no emerging species were included.

Suitable climatic conditions were found likely to decrease for a number of weeds that currently pose a risk to native forests and plantations including: *Billardiera heterophylla* (blue-bell creeper); *Cotoneaster glaucophyllus* (Cotoneaster); *Leycesteria formosa* (Himalayan honeysuckle); and *Rubus fruticosus* L. agg. (blackberry) (Steel et al. 2008). Although this study indicates that their potential distributions could become smaller under climate change, they are still considered to pose an invasion risk to large parts of the state. Species identified in this study as having an increased risk to impact on native forests and plantations were *Asparagus aethiopicus* (basket asparagus) a weed also found in south-east Queensland and coastal New South Wales; *Bidens pilosa* (cobbler’s pegs), a summer annual and weed of field and plantation crops which has become established in all mainland states in Australia; and *Heliotropium amplexicaule* (blue heliotrope), a perennial herb which is a weed of cultivated land, pastures and forests (Steel et al. 2008).

To date there is a general lack of detailed information on the climatic requirements of weeds, particularly alert and sleeper weeds (Scott et al. 2008). This information is essential for parameterisation of bioclimatic models and generating accurate model predictions. Furthermore, it needs to be noted that bioclimatic models have various limitations (cf Chapter 2 and Chapter 14). For instance, soil characteristics and physical barriers within the landscape are important in determining the distribution of weeds, but are generally not considered in bioclimatic models (Kriticos et al. 2010; Scott et al. 2008; Steel et al. 2008). Furthermore, climate change is predicted to lead to more extreme weather events which could determine the limits of a species’ distribution, however, to date these events have not been considered in bioclimatic modelling (Scott et al. 2008). Therefore, increased scientific rigour needs to be incorporated into this kind of modelling to make more accurate predictions of potential weed distribution.

11.2.3 Two forms of bridal creeper (*Asparagus asparagoides*)

Bridal creeper (*Asparagus asparagoides*) is a Weed of National Significance (WoNS) that biologically is relatively well understood (Thorp and Wilson 1998 onwards). It was introduced from South Africa for ornamental and horticultural purposes, and since has become invasive in temperate southern Australia. Bridal creeper is now widely distributed across diverse ecosystems throughout the southern half of Australia and currently found in southern WA, SA, Vic and parts of NSW, Qld, and Tasmania (Thorp and Wilson 1998 onwards). It prefers shade or part-shade conditions and invades a range of native and plantation forest types including coastal vegetation, wet and dry sclerophyll forest, mallee shrubland and riparian vegetation. It is extremely competitive and its thick tuber mat limits the access of other plants to soil moisture, nutrients and seedling recruitment and is therefore considered a major threat to biodiversity in forest systems (Downey 2006; Thorp and Lynch 2000; Thorp and Wilson 1998 onwards).

Its effective reproductive techniques and dispersal mechanisms through birds and resprouting have made it difficult to control. However, after successful introduction of a biocontrol agent, the rust fungus *Puccinia myrsiphylli*, native vegetation on previously infested sites has been recovering and revegetation schemes have been implemented (Australian Weeds Strategy 2006; Kriticos et al. 2010; Turner et al. 2008; Turner et al. 2006). As with many biological control systems, the bridal creeper/ rust system works within a narrow window of optimum conditions. Climate change may disrupt the interactions between a biocontrol agent and their weed host, as was shown with elevated CO_2 and increased temperatures by Johns and Hughes (2002). This disruption could occur through alteration of the development of both weed and control agent, creating areas where the weed may no longer be adequately controlled (Johns and Hughes 2002; Kriticos et al. 2010). In the case of bridal creeper, the effectiveness of the control agent *Puccinia myrsiphylli* with the predicted changes in climate is currently unknown. This therefore needs to be tested and monitored over time to ascertain the future effectiveness of this biocontrol agent.

Another form of *A. asparagoides* referred to as Western Cape form (Kleinjan and Edwards 1999) was discovered near Adelaide and the SA/Victoria border (Coles et al. 2006), where it is still believed to be restricted (i.e. sleeper weed). The Western Cape form of bridal creeper is morphologically quite different from the widespread form of (common) bridal creeper (Coles and Willing 2006; Morin and Edwards 2006), but shows the potential for equally negative impacts on forest regrowth and biodiversity. The rust *P. myrsiphylli* does not infect the Western Cape form of bridal creeper (Coles and Willing 2006; Coles et al. 2006). Given that bridal creeper and the Western Cape form are found in similar areas, there are concerns that the latter will invade areas where populations of bridal creeper have been significantly reduced as a result of biological control (Coles and Willing 2006; Coles et al. 2006; Scott and

Batchelor 2006). Furthermore, the niches left vacant following successful control of bridal creeper, in the absence of restoration efforts (Turner et al. 2008; Turner and Virtue 2009), may facilitate such a substitution. This further indicates the complexity of the effects of changes in climate on biotic interactions and the difficulty to predict the responses of forest biota to these changes.

Under current climate conditions, CLIMEX modelling showed that the known form of bridal creeper has reached the limits of its potential distribution, except for potential spread to Southern Queensland and further within Tasmania (Scott and Batchelor 2006). For the Western Cape form of bridal creeper, modelling identified many areas, especially in WA and SA, which are currently suitable for invasion. However, confidence in the model is low as there is a lack of information on the conditions for growth of this form, especially in terms of temperature and moisture requirements (Scott and Batchelor 2006).

Model projections show that the area currently suitable for common bridal creeper will remain largely the same until 2080. The modelling suggests that the suitability will decrease slightly in many parts of temperate Australia (Kriticos et al. 2010), but that a potential increase in suitable areas is predicted for the extreme southwest corner of WA, the western half of Kangaroo Island, and in coastal Tasmania. Modelling also identified a potential range increase in highland areas of Victoria, NSW and Tasmania by 2080 (Kriticos et al. 2010). Although climate modelling of the distribution of common bridal creeper suggests a reduced threat of this weed under future climate scenarios, the effectiveness of the rust biocontrol should be closely monitored (Kriticos et al. 2010).

To date there has been no modelling of the Western Cape form of bridal creeper under future climate change scenarios. This sleeper weed requires close attention as *P. myrsiphylli* is ineffective against it. Furthermore, because of the scattered nature of the infestations in native bushland, complete control was found to be unfeasible (Coles and Willing 2006). It is therefore critical to gather more detailed information about its responses to variations in climate in order to undertake robust risk assessments of potential extent of this threat under climate change.

11.2.4 Weed invasion after disturbance

The typical weed characteristics of high adaptability and fast development are likely to enable weeds to take advantage of higher disturbance frequency under climate change (Steel et al. 2008). In native forests and plantations, disturbances such as storms, droughts and fires, provide the opportunity for weeds to invade and establish. One well-studied example of the response of weed species to disturbance is the invasion of tropical rainforest systems in north

Queensland following cyclone Larry in March 2006. Damage on the coastal lowlands and tablelands was extensive with some areas losing nearly 100% of their canopy (Metcalfe et al. 2007). Cyclone Larry caused large-scale removal of leaves exposing the understorey to high light levels, which provided perfect conditions for recruitment of light-demanding weed species (Metcalfe et al. 2007; Murphy et al. 2008a; Murphy et al. 2008b)

Murphy et al. (2008a; 2008b) studied the recruitment dynamics of weeds near El Arish in an area where damage was extensive. A year-long survey was conducted 12 months after the cyclone had hit. Affected areas were found to be rapidly invaded by non-native invasive weed species. Most of the herbaceous species were found to be rapidly declining over time and therefore unlikely to persist. However, one invasive shade-tolerant tree species was also found to have established, which was *Miconia calvescens.* This species has been recognised as a new and emerging weed in tropical rainforests (Csurhes 2008). *M. calvescens* is a small tree native to tropical Central and South America. It has many of the attributes of an effective weed particularly being shade-tolerant (Csurhes 2008). It has taken over large tracts of rainforest in French Polynesia and Hawaii where its rapid spread is associated with cyclone damage. Murphy et al (2008b) found that *Miconia* quickly colonises gaps in the rainforest created by cyclones, especially where debris is absent, but its shade-tolerance means recruitment can also occur under a closed rainforest canopy (Csurhes 2008).

The implication of the work by Murphy et al. (2008a; 2008b) is that severe cyclones also provide a greater window of opportunity for the more persistent and competitive exotic plants, such as *Miconia* and other invasive shrubs, to spread and establish consequently impacting on the diversity and forest system functioning. CLIMEX modelling of the potential distribution of *Miconia* under current climate conditions indicate that it has potential to establish itself in the top end of WA, NT and Qld. With climate change, there is high potential for this species to further expand its distribution into northern NSW (H Murphy and D Metcalfe pers comm).

The ecological roles of invasive species in rainforests and other forest systems following severe disturbance, such as cyclones, are generally poorly understood (Murphy et al 2008a). Long term monitoring is needed to determine the ability of *Miconia* and other woody weeds to persist and compete with shade-tolerant native species (Metcalfe et al. 2007; Murphy et al. 2008a; Murphy et al. 2008b; Turton and Dale 2007), and to what extent they impact on species diversity and forest system functioning.

11.3 Conclusions: Weeds

The predicted changes in climate factors are likely to make areas currently unaffected by invasive weeds more suitable over time. Modelling projections using a general rise in temperature and decrease in rainfall have indicated a future spatial boundary shift of weed species from the north to the south of Australia. However, direct evidence of the responses of weeds to these predicted changes in climate is generally lacking. Extreme weather events, like cyclones, floods and droughts, and disturbances like fire, have been shown to create opportunities for weeds to invade and establish in native forests and plantations. How climate change (i.e. extreme weather events, increasing temperatures, changing rainfall, elevated CO_2) will impact on weeds, their biological control agents, and their impact on overall forest system functioning is however still largely unknown. The responses of individual weed species to changes in climate therefore need to be studied in more detail to accurately gauge their future spread and impact on forest system functioning.

Although there has been a lack of work to date on weeds affecting native forests and plantations, every invasive (non-native) weed species will likely have an impact on the system it invades. Therefore, when a species is considered unwanted and/or non-native to the forest system, it should be managed appropriately through monitoring and eradication programs. Generally, because of the general high level of flexibility and adaptability of weeds to different environmental conditions, it is likely that their impact and adverse effects in native forest and plantations will continue under climate change. To date, the majority of research funding has been allocated to improve the management of the 20 recognised WoNS species (Thorp and Wilson 1998 onwards). With the predicted changes in climate, recognised alert and sleeper weeds, however, also warrant more research and attention. Good resources on weeds in Australia are available (e.g. the ‘Weeds Australia database’ (Thorp and Wilson 1998 onwards)) that can facilitate further knowledge transfer and dissemination of research findings. Continuous monitoring and management of known and emerging invasive weed species are needed to prevent their impact and spread particularly in currently unaffected forested areas.

Integration

As shown in the preceding sections, climate change is likely to affect forest ecosystem functioning through a wide range of processes and interactions. The vulnerability of forests to climate change depends on the net impact of these responses and feedbacks. However, because of the complexity and interacting nature of biological and ecological processes, it is very difficult to estimate what the net impacts of climate change will be (Dunlop and Brown 2008; Howden and Gorman 1999). In this section, we consider attempts to integrate these factors to arrive at an overall picture of forest vulnerability to climate change.

Chapter 12 uses biodiversity as an example to demonstrate the cascade of direct and indirect effects of climate change that are likely to impact on forest function. Evidence from natural systems can be used to demonstrate impacts of climate change in existing forests, and

Chapter 13 discusses this observational evidence. Quantitative modelling allows us to make predictions of future impacts of climate change based on observations. In Chapter 14 we review and compare predictions from different types of models.

12. Biodiversity

12.1 Cascading impacts on forest biodiversity

Several excellent reviews and reports have been published recently that provide overviews of the effects of climate change on the biodiversity of Australia (e.g. Australian National University 2009; Dunlop and Brown 2008; Howden et al. 2003; Steffen et al. 2009). Many of the effects of climate change on biotic interactions and biodiversity have been highlighted as affecting forest systems (Howden and Gorman 1999). The projected changes in climate have important indirect and potentially threatening effects on forest biodiversity, through changes in, for instance, fire regimes, phenological events, pest and pathogen outbreaks and weed invasions. These individual factors and their effect on forest biodiversity and functioning have been discussed in earlier sections of this report. In this section, we demonstrate how this range of factors combines to form a cascade of responses and feedbacks with an overall impact on biodiversity.

Firstly, consider the impacts of increasing atmospheric CO_2. As discussed in Chapter 3, increasing CO_2 is likely to stimulate forest growth, particularly in fertile regions. Further research suggests that elevated CO_2 may alter the primary and secondary chemistry of plants, which likely will have consequences for key biotic processes like plant-herbivore interactions (e.g. Gleadow et al. 2009; Gleadow et al. 1998; Howden and Gorman 1999). Several studies found that elevated CO_2 changed the concentrations of chemical compounds in leaf tissue of plants and trees, generally reducing leaf nitrogen content, increasing the C:N ratio and increasing phenolic content, which affected dependant folivores (Gleadow et al. 2009; Gleadow et al. 1998; Johns and Hughes 2002; Kanowski 2001; Stiling and Cornelissen 2007). For instance, Gleadow et al. (1998), Kanowski (2001) and Stirling and Cornelissen (2007) found that nitrogen content in leaves decreased with increased CO_2 levels, negatively affecting herbivore development and abundance. Johns and Hughes (2002) found that the combined effects of elevated CO_2 with increased temperatures were more pronounced than with elevated CO_2 alone. Increased ambient temperatures of 3°C combined with elevated CO_2 negatively affected the development of a leaf-miner, *Dialectica scalariella*, associated with the weed species *Echium plantagineum* (Paterson's Curse) more than did elevated CO_2 alone (Johns and Hughes 2002). This cascade of responses, from atmospheric composition, through plant response, to herbivore interactions, indicates the complexity of the effects of changes in climate on biotic interactions and the difficulty of predicting the responses of forest biota to these changes.

Similarly, temperature and rainfall play major roles in determining where individual species of plants and animals can live, grow and reproduce. The degree of resilience of the Australian flora and fauna to the predicted drier climate is likely to vary among species (Deutsch et al. 2008; Steffen et al. 2009). Predictions from bioclimatic modelling (see Chapter 14) indicate that in Queensland, tropical forests and individual species are highly sensitive to the range of climate changes that are expected through to 2070. Modelling predictions for highland rainforests in Queensland indicated that even with a 1°C in warming, tropical highland rainforest area might decline up to 50% by encroachment of lowland rainforest species (Hilbert et al. 2001). The predicted increases in average temperature may therefore result in the loss and large-scale fragmentation of highland rainforests and their associated unique biodiversity. Further bioclimatic modelling of rainforest fauna species showed that a 1-3.5°C increase in average temperatures is predicted to significantly decrease the bioclimatic range of endemic fauna species (Williams et al. 2003), drastically reducing the current habitat area of 30-50 endemic vertebrate species (Howden et al. 2003; Williams et al. 2003). Such declines in species diversity could result in further disruption of important biotic interactions such as pollination and dispersal, influencing forest regeneration and overall forest system functioning. For example, increased temperatures could change the rate of development in insect species. For highly specialized species, such a change might result in mismatches between their emergence and the availability of food sources, resulting in the possible decline of the species involved (see chapter on Phenology). On the other hand, insect pest species are also likely to display a higher rate of development, with negative consequences for their hosts (see chapter on Insect Pests).

Together these examples highlight the complexity of the effects of changes in climate on biotic interactions and the difficulty of predicting the responses of forest biota to these changes. Declines in overall biodiversity are however likely with the predicted changes in climate, which makes it even more important to understand these processes to enable the design of strategies for effective forest biodiversity conservation and adaptive management (Lindenmayer et al. 2006; Lindenmayer and Franklin 2002).

12.2 Case Study: Mycorrhizae

Mycorrhizal fungi are soil borne fungi that form symbiotic relationships with plants and trees (Brundrett 1991; Brundrett 2008). They provide nutrients to plants and trees primarily through the fine-root system and play a significant role in safeguarding plant and tree health and their development (Brundrett 1991; Brundrett 2008). Mycorrhizal fungi account for a major part of the biodiversity in forest systems (Lindenmayer and Franklin 2002). For instance, in WA and Tasmania the total number of macrofungal taxa were found to outnumber vascular plants four to one (Gardner and Malajczuk 1988; Hilton et al. 1989; Packham et al. 2002). The mycorrhizal fungi of Australia are further largely unique to the continent (Steffen et al. 2009). Together this makes mycorrhizal fungi an important focus group for biodiversity conservation.

The two main groups of mycorrhiza associated with forest systems in Australia are arbuscular mycorrhiza (AM), associated with both plants and trees and ectomycorrhiza (ECM), predominantly associated with plants in the understorey (Brundrett 1991; Brundrett 2008; Read et al. 2004). AM are common in undisturbed Australian native plant communities (Bellgard 1991; Brockoff and Allaway 1989; Brundrett and Abbott 1991; McGee 1989) and have been found in association with about 80% of all plant and tree species (Fester and Hause 2007). AM were further found to have a positive influence on the regrowth of plants in disturbed areas (Brockoff and Allaway 1989; Khan 1978; Miller 1979; Reeves et al. 1979), determining forest restoration success. ECM fungi are a dominant and important component of soil microbial communities in forest ecosystems. ECM fungi are regarded as key organisms in nutrient and carbon cycles in forest ecosystems (Anderson et al. 2007). They have been found responsible for a substantial component of forest soil carbon fluxes through the delivery of carbon to soils (Godbold et al. 2006; Hobbie 2006). Together with AM, ECM are therefore considered as strong drivers of forest ecosystem processes (Read et al. 2004).

The impact of climate change on mycorrhiza can be considerable, leading to possible declines in forest health and biodiversity. The impacts of elevated CO_2 have been extensively tested for AM fungi. Under controlled condition no differences were found in development and Phosphorous uptake of AM fungi under elevated CO_2 conditions, indicating no significance impact of the projected changes in CO_2 on this group of fungi (Gavito et al. 2003). However, in some instances increased temperatures were found to increase root colonisation and mycorrhizal hyphen production (Staddon et al. 2004). For example, Bunn et al. (2009) showed an increase in AM fungal structures both internal and external to the roots in response to elevated temperature. Furthermore, with increasing temperatures from 8-10^{o}C up, significantly more AM extra-radical hyphae were produced (Gavito et al. 2003; Heinemeyer and Fitter 2004), indicating a possible positive response to the predicted increases in temperature. However, the occurrence of different ECM species in Australia was found to be highly variable depending on annual rainfall and mean temperatures and other environmental factors (Claridge et al. 2009). Several researchers found significant relationships between air and/or soil moisture, temperature and ECM colonisation (Antibus and Linkins 1992; Blasius et al. 1989; Hacskaylo et al. 1965; Harvey et al. 1978; Ingleby et al. 1985; Parke et al. 1983; Rastin et al. 1990; Samson and Fortin 1986), however, responses were found to be highly site specific (Swaty et al. 1998). Furthermore, sensitivity of ECM to changes in temperature and soil moisture was found to lead to significant seasonal variation in colonisation (Swaty et al. 1998).

In some cases, mycorrhizae were found to help plant hosts recovering from abiotic stress events like droughts, highlighting the importance of their association with plants and trees in the face of a drying climate. Mycorrhizae were found to decrease the effects of drought in plants and trees (Boyle and Hellenbrand 1990; Davies et al. 1996), enhancing their drought tolerance (Davies et al. 1996), and help seedlings recover from water stress more quickly (Parke et al. 1983). However, responses to water stress of ECM fungi themselves have been mixed, with some researchers finding declines in ECM colonisation with moisture stress (Lansac et al. 1995; Nilsen et al. 1998; Read and Boyd 1986; Runion et al. 1997), while others observed a positive relationship (Davies et al. 1996; Gehring and Whitham 1994; Gehring and Whitham 1995; Swaty et al. 1998) or no significant association (Becker et al. 1987; Meier et al. 1990). The contradictory results may be due to differences in fungal taxa, difficulties quantifying the fungi and the highly variable water deficit conditions imposed. Studies measuring the effects of different soil water potentials, however, in general found reduction in growth and colonisation of mycorrhizal fungi with reduction in soil moisture availability (Becker et al. 1987; Coleman et al. 1989; Nilsen et al. 1998; Tommerup 1984), but again responses were highly site and species specific.

Together these examples highlight the complexity of the effects of changes in climate on the biotic interactions between mycorrhiza and plant hosts. Where the individual responses of mycorrhizal fungi on the various changing climate factors tested were found highly variable, influences of the likely changes in climate are difficult to estimate. It is however likely that the predicted changes in climate, like an increase in droughts, will cause shifts in plant/fungus symbiosis, influencing the composition and diversity in mycorrhizal communities. Furthermore, most of the results to date have been based on research conducted on coniferous tree species overseas, where hardly any work has been undertaken investigating these responses for native forest systems in Australia. There is therefore a high need for more research on the impacts of climate change on mycorrhiza and their role in sustaining forest biodiversity (Read et al. 2004), particularly for the highly divers systems of Australia.

12.3 Conclusions: Biodiversity

The previous examples all show the complexity of understanding and predicting the likely responses to changes in climate of forest biota within forested ecosystems. To date, research on the impacts of climate change on biodiversity in Australia has been limited to only a handful of studies (Steffen et al. 2009). The predicted responses are not based on direct proof, but largely based on our understanding of the fundamental principles that underlie species responses to changes in their environment (Steffen et al. 2009). The main reason for this lack of direct proof is the general lack of understanding of the complex biotic interactions that determine the diversity and composition of forest ecosystems in Australia. Not only understanding these interactions, but how the changes in climate will influence them are major challenges for future research and management.

It has been recognised that there is a high level of uncertainty in the likely responses of forest biodiversity to changes in climate (e.g. Steffen et al. 2009). This makes adaptive management for effective biodiversity conservation increasingly challenging (Lindenmayer and Franklin 2002). To facilitate the decision making process, Steffen et al. (2009) recommends to base decisions on fundamental responses to environmental change within and between biota, communities and ecosystems (i.e. across scales). In order to adapt and mitigate the impacts on biodiversity, monitoring the changes within forest systems will be key (Abbott and Le Maitre 2010). Future research could focus on identifying key indicator species representing a wider group of biota within forests systems (Hughes 2003). Monitoring their responses to the changes in climate can then help inform the implementation of appropriate conservation measures to preserve forest biodiversity.

13. Observational Evidence

In this section, we discuss evidence from natural ecosystems where climate factors are varying together. This evidence includes (1) observed changes in forest distribution or density over time; (2) paeleoecological records, such as tree rings and pollen cores. These studies all provide insight into ecosystem dynamics in response to a suite of interacting environmental factors.

Evidence from aerial photography and remotely sensed data demonstrates that the boundaries of Australian ecosystems are dynamic. Aerial photography has provided evidence of expansion of closed forests, with a 42% increase in total coverage in Australian monsoon tropics over five decades (Brook and Bowman 2006). This expansion of closed forests was attributed to the 'skillful use of fire by Aboriginal people in protecting isolated closed-forest patches'. However, the authors comment that other research suggests that replacing Aboriginal land management by European management is causing a contraction of closed forest. A second hypothesis for the expansion of closed forest is the recent increases in global CO_2 concentrations, which provide a competitive advantage for C_3 trees compared with C_4 grasses (Brook and Bowman 2006).

13.1 Observed changes in forest distribution and density

There is consistent evidence from remote sensing studies of large-scale changes in woody vegetation cover across Australia. However, there is much debate about the drivers of these changes. There is a long list of potential drivers that include changes in fire regimes, grazing, harvesting, soil disturbance, periods of high rainfall, climate change, and rising atmospheric CO_2.

Lunt et al. (2010) used information from Australia's National Carbon Accounting System to quantify changes in woody vegetation cover from 1989 to 2005 in native woodlands across Victoria. They found consistent increases of 5 to 9 % in woody cover in all ecosystems examined. They attribute this increase to significant changes in land management practices in Victoria in recent decades, such as livestock removal, reduced timber harvesting and reduced soil disturbance. They noted that the protracted drought in the last decade did not appear to have reduced woody cover, despite declining forest health observed in riverine woodlands (Cunningham et al. 2007, 2009).

An Australia-wide study examined remotely sensed vegetation cover, estimated from the AVHRR index of fPAR, or fraction of photosynthetically active radiation absorbed by vegetation. An analysis of trends in fPAR, precipitation, and pan evaporation from 1981 to 2006 showed a 21% increase in 'persistent' vegetation, which was interpreted as an increase in woody vegetation cover (Donohue et al. 2009). Vegetation was split into functional types, 'persistent' and 'recurrent'. Overall, there was a general background increase in persistent vegetation and a slight decrease in recurrent components (Donohue et al. 2009). Not surprisingly, total vegetation cover decreased in water-limited environments when water availability decreased. Unexpectedly, at around one-third of all water limited sites, despite negligible or negative trends in precipitation, total fPAR increased, due to increases in persistent vegetation (up to 36%) often at the expense of recurrent vegetation. The authors suggest that factors other than changes in precipitation are driving the observed increases in vegetation cover at these water limited sites. They found that the increase in persistent vegetation types compared to recurrent vegetation types was consistent with the effects of elevated CO_2 on vegetation hypothesised by Berry and Roderick (2002), but they also note that the attribution of the drivers of these vegetation changes requires further research.

More localized studies of vegetation change have made more progress in attributing causes for change. In northern Australia, research suggests that mesic and xeric savannas are responding differently to global change (Fensham et al. 2008). Dynamics of woody biomass in xeric (more arid, with mean annual rainfall < 900 mm) savannas appear to be driven by rainfall dynamics. Woody biomass increases in wetter periods: for example, a study of woody biomass from aerial photography of savannas of central Queensland found an increase in woody biomass over the second half of the 20th century, which was wetter than the first half (Fensham et al. 2005). However, multiple year droughts can exhaust soil moisture reserves in xeric savannas, causing widespread tree death, resulting in a crash in woody biomass (Fensham and Holman 1999, Fensham et al. 2008). Fensham et al. (2008) conclude that "drought-induced tree death seems to be an infrequent, but natural phenomenon in xeric savanna environments". The frequency of such multi-year droughts is likely to determine the accumulation of biomass in these environments.

In contrast, in more mesic savannas, rainfall is more reliable, and soil moisture reserves are rarely depleted (Bowman and Prior 2005). Observational studies from mesic savannas generally suggest that rainforest areas are expanding (e.g. Banfai and Bowman 2006, Brook and Bowman 2006) and that tree cover in savannas is increasing (e.g. Lehmann et al. 2008, 2009). Banfai and Bowman (2006) examined aerial photographs of Kakadu National Park over the period of 1964 to 2004 to quantify changes in the distribution of rainforest, which occurs as small (~ 5 ha) patches within a matrix of eucalypt savanna. They found that patches increased in size by ca 30% on average, over the period examined. Statistical analyses showed that fire and feral animal activity were poor predictors of expansion (Banfai et al. 2007; Banfai and Bowman 2007). The authors suggest that rising CO_2 and higher than average rainfall may be potential alternative explanations for the trend of rainforest expansion.

Similarly, Brook and Bowman (2006) used aerial photography to examine closed-forest patches at four locations in the southwest Gulf of Carpentaria, and found an average 42% increase in size of closed-forest patches over five decades. These authors found that changing from Aboriginal to European fire regimes was not a convincing explanation for the changes that they observed, and suggested that increased rainfall and rising CO_2 were more likely explanations.

Changes in percentage tree cover in mesic savanna in Kakadu National Park have also been examined using aerial photography from 1964 to 2004 over 50 sites spanning a rainfall gradient of 1200 to 1600 mm (Lehmann et al. 2009). Tree cover increased, on average, by ~5%, but this increase was highly variable. Tree cover was found to be positively related to prior tree cover and negatively correlated with fire activity. Across the rainfall gradient, greater variability in fire activity and inherently higher average tree cover at the wetter latitudes resulted in greater dynamism of tree cover compared with drier latitudes. Lehmann et al. (2009) concluded that variability in fire activity and mean annual rainfall were the most important drivers of savanna tree cover.

Similarly, aerial photographs from 1941 and 1994 showed that in Litchfield National Park forest cover increased from 5% to 10% of the study area, whereas the coverage of grassland decreased from 7% to 2%. In this study, the increase in forest cover was attributed to changes in landscape burning since the beginning of the study and a period of increased rainfall since the 1970s (Bowman et al. 2001).

In a different type of study, net carbon storage of a savanna 35 km from Darwin was measured using eddy covariance over the period 2001 to 2006 (Beringer et al. 2007). This site was burnt annually during the study, but despite losses of carbon during and following the fires, it was found that the site was a significant sink, storing 2 t C ha^{-1} yr^{-1}, in the form of increasing woody biomass and understorey shrub encroachment (Beringer et al. 2007). This study confirms the general finding of increasing woody biomass, but the driving mechanism is not known. Potential causes include rising CO_2 or recovery from disturbance (such as Cyclone Tracey, which occurred in 1975).

The eddy covariance approach has proved highly useful in quantifying net carbon storage by ecosystems on timescales ranging from hourly to decadal (Baldocchi 2008). In North America and Europe, use of this technique is widespread, enabling estimation of net ecosystem exchange on large regional scales (e.g. Xiao et al. 2008). In contrast, eddy covariance research in Australia is unfortunately sparse, with multi-annual data available from only two locations: Howard Springs, NT (Beringer et al. 2007) and Tumbarumba, NSW (Beringer et al. 2007; Hutley et al. 2005; Keith et al. 2009). From 2010, increasing numbers of flux towers will be established through the Terrestrial Ecosystem Research Network, providing much-needed data on carbon sequestration in Australian ecosystems.

In contrast to the studies demonstrating accumulating biomass, a study of woody vegetation cover in the Victoria River District, 350 km south of Darwin, found that cover increased at some sites and decreased at others, with an overall net effect of no change in woody cover (Sharp and Bowman 2004a,b). Because these changes varied so dramatically across the study sites, these authors concluded that the changes could not be due to landscape-wide processes such as climate change or altered fire regimes, but instead were the likely consequence of natural cycles of mortality and recovery in response to dry-season moisture stress.

In the mulga lands of central south Queensland, aerial photography was used to assess changes in vegetation density over the second half of the 20th century (Witt et al. 2009). Across the whole region, woody biomass increases were observed, but were small, averaging just 3.6%. The increases were slightly larger (~7%) in the more humid eastern part of the region, where mean annual rainfall > 450 mm. These changes were tentatively ascribed to long-term variation in rainfall, with extended droughts causing dieback and reduction of woody biomass as in the xeric savannas.

Observations from remote sensing and eddy covariance techniques are confirmed by data from permanent sample plots across Queensland (Burrows et al. 2002). Long-term monitoring of 57 sample plots in woodland across Queensland showed that these sites were accumulating, on average, 0.5 t C ha^{-1} yr^{-1} in above-ground biomass. The driver of this change remains unknown; Burrows et al. (2002) note that rising CO_2, changes in precipitation, fire regimes, and grazing patterns are all potential causes.

In summary, there appear to be small increases in woody biomass and tree cover across the north. In drier regions these increases are likely to be related to rainfall patterns and can be negated by severe drought. In wetter regions, the increases can be explained by fire activity in some cases, but in other cases distinct drivers could not be identified, leaving open the possibility that the changes are due to rising CO_2 and increased rainfall.

Moving south, there have been dramatic changes in vegetation, particularly in the south-east of the country, but changes in land use and land management are likely responsible for most of these changes (Lunt 2002, Lunt et al. 2010). It is therefore difficult, in general, to identify the “fingerprint” of climate change on vegetation communities in this part of the country.

Lunt et al. (2010) note that only one study has attributed increased woody vegetation cover to climate change in south-eastern Australia. This study (Wearne and Morgan 2001) found that

Eucalyptus pauciflora forest had encroached into sub-alpine grasslands in Victoria's high country, and attributed this movement to rising temperatures. However, the observed shift in tree-line (5m) was much less than expected from the warming that has already occurred (Green 2009). It is a common observation that alpine treelines are stable, and do not change to match changes in temperature isotherms (Grace et al. 2002). Green (2009) studied seedling establishment following wildfire in the Victorian Alps and found that treelines were very stable, despite removal of competing grass biomass. He suggests that there is little seed dispersal uphill, which limits the ability of seeds to establish above the existing tree-line.

13.2 Paleoecological studies

Paleoecological records, such as tree rings and pollen cores, can be used to infer climatic conditions, fire frequency, and vegetation community composition in the past, providing a long-term perspective on vegetation sensitivity to climate. We briefly discuss the Australian literature here. A thorough review of this literature was outside the scope of this work. However, it would clearly be insightful to integrate this literature with the research that has been discussed herein, and we strongly recommend this integration as a future research need.

In the extra-tropical northern hemisphere, tree ring records have been extensively used for climatic reconstruction over the last millennium (Briffa et al. 2004). As mentioned earlier, methodological issues have restricted the application of these techniques in Australia; however, these issues are gradually being overcome. Studies to date demonstrate that temperature limits growth only at cold extremes in Australia: in trees near the upper tree line in the Australian Alps (Brookhouse and Bi 2009) and in subalpine Huon pine in Tasmania (Cook et al. 2006). In other regions, water availability is more limiting to growth. Analysis from Western Australia has demonstrated that ring width of *Callitris columellaris* reflected variation in rainfall (Cullen and Grierson 2007; Cullen and Grierson 2009). These analyses suggest that chronology is most strongly related with rainfall over the autumn-winter period, and 350 year patterns of rainfall were described. Stable isotopes analysis of carbon (∆13C) and oxygen (∆18O) in tree rings of *Callitris columellaris* from the semi-arid Pilbara region of north-western Australia suggested an increase in stomatal control of photosynthesis in recent decades as rainfall has decreased by up to 30%. The authors suggest that stomatal control of photosynthesis of these trees may adjust to region-wide changes in climate, and that 'in a warmer, drier world, trees might adapt by increasing non-stomatal control of photosynthesis' (Cullen et al. 2008).

Longer-term paleological records, such as pollen cores, can also give insight into climate effects on structure and distribution of vegetation communities, although care is needed in the interpretation of these data because they represent equilibrium responses rather than dynamic responses to climatic change. In the northern hemisphere, past rapid warming events analogous to the warming predicted for this century have been used as a guide to likely vegetation change (e.g. Cole 2009). Such studies are hampered in Australia by the lack of any quantitative reconstruction of Holocene climates. It appears that temperature change was more muted in the southern Hemisphere than the northern Hemisphere, because the driving changes in insolation were weaker. Vegetation community changes were also more muted, and more closely related to changes in aridity than to temperature (Pickett et al. 2004). Quantifying past changes in aridity has proved problematic for Australia because of interactions among El Niño Southern Oscillation (ENSO), the Southern Annular Mode, and Asian monsoon influences on rainfall (Lynch et al. 2007). It appears that there is a general trend towards drier and/or more variable climates over the last 350,000 years, but the cause of this change is unclear (Kershaw et al. 2003). However, the changes in rainfall patterns may have differed between the north-west and south-eastern parts of the continent, depending on the strength of the monsoon influence (Lynch et al. 2007). A further problem with Australian pollen core records is the poor spatial coverage of the continent, with very few records from arid and semi-arid zones (Lynch et al. 2007, Pickett et al. 2004).

Given these data issues, there have been few attempts to use paleoecological data as a basis for predicting vegetation community response to 21st century climate change in Australia. Nonetheless, some relevant observations can be made.

Temperature sensitivity is clearly shown in alpine vegetation in Victoria and Tasmania. In Victoria, McKenzie (2002) showed that ca 18,000 years before present, when temperatures were 7 – 8 °C below present, many of the species now associated with the Victorian highlands were constrained to lowlands and much of the Central Highlands was treeless. As temperatures rose, alpine taxa were greatly reduced, and the treeline moved upslope. In Tasmania, pollen records indicate switches between rainforest dominance in warm interglacials, and dominance of grasslands and alpine vegetation during glacials (Hope et al. 2004). This responsiveness to temperature is consistent with our earlier discussion about the importance of temperature in frost-limited environments.

Elsewhere, moisture limitations appear more important in determining vegetation composition and structure (Hope et al. 2004, Pickett et al. 2004). This conclusion is also consistent with our earlier discussion that rising temperature is unlikely to strongly impact on vegetation not limited by frost. Pickett et al. (2004) comment that responses to precipitation regime largely appear to involve changes in vegetation structure such as spacing and height, as opposed to changes in species composition. They note that the forest and woodland biomes are dominated by genera such as *Eucalyptus* and *Acacia* that are tolerant of a wide range of conditions. Hope (1994) similarly makes the point that variable climates during the

Quaternary appears to have rewarded generalists such as the eucalypts, encouraging their dominance.

A third important point consistently emerging from the paleological record is the importance of fire in determining vegetation distribution (e.g. Lynch et al. 2007). Peaks in the charcoal record are generally associated with onset of ENSO conditions (Kershaw et al. 2003) and expansion of eucalypt woodland at the expense of rainforest (Hope et al. 2004). However, Lynch et al. (2007) note that the observational record requires considerable improvement in terms of quality, quantity and dating, if we wish to derive quantitative links between fire, vegetation and climate that could be used as a basis for prediction.

13.3 Conclusions: Observational studies

It is apparent that ecosystem boundaries are changing, although the causes of these changes are uncertain and the influences of CO_2, temperature, rainfall, previous disturbance, grazing and fire regimes are difficult to separate.

- In mesic savanna regions, it appears that rainforest is expanding and tree cover in eucalypt woodlands in increasing.
- In xeric savanna regions, woody biomass appears to be controlled by mortality during severe drought events.
- In the southern states, woody biomass is generally increasing, but anthropogenic disturbance through grazing, changes to fire regimes, and other aspects of management, is so large that a climate change signal is difficult to detect.

Paleoecological data demonstrate the importance of temperature in controlling vegetation distribution in frost-limited environments but not elsewhere. These data confirm the importance of fire in determining vegetation distribution. They also demonstrate strong sensitivity of Australian vegetation to moisture availability, but suggest that the largest responses are through changes in structure rather than species composition.

There is a real need to integrate data from the different types of studies: a high research priority is to draw together results from ecophysiological, observational, and paleological studies in a consistent framework.

14. Modelling Studies

With so many interacting factors potentially affecting forest function in future, our only real tool to integrate these factors and gauge future vulnerability is quantitative models. In this section we describe attempts to predict likely impacts of climate change on the “human timescale” using modelling. There are two major approaches to modelling climate impacts, the mechanism-based ecophysiological modelling and the statistically-based bioclimatic modelling. These methods are described in Chapter 2; in this chapter we discuss results from the two types of modelling.

14.1 Ecophysiological modelling

Some preliminary work was undertaken by Kirschbaum (1998) using a comprehensive ecosystem model (CENW) incorporating carbon, energy, water, and nutrient cycles. The model had been comprehensively tested with data from a fertilisation and irrigation experiment with *Pinus radiata* (Kirschbaum 1999). It was parameterised for a generic forest and used to estimate the sensitivity of forest NPP to doubled CO_2 and an increase in temperature of 3°C. The study suggested that NPP of southern forests would increase, because they are currently below optimum temperature, but NPP of northern forests could decrease as temperatures became supra-optimal. Outcomes were also sensitive to rainfall. Total forest NPP for the continent was predicted to increase by 11% with a doubling of CO_2 and a 3 °C increase in temperature. If rainfall was assumed to increase by 20%, this increased to 21% stimulation, whereas if rainfall was assumed to decrease by 20%, NPP was predicted to decline by 7%. Overall, Kirschbaum (1998) concluded that rising CO_2 should in general compensate for deleterious effects of rising temperature on productivity, but that there might be more severe impacts on individual species and specific regions.

This study was preliminary, with the potential to be improved by inclusion of more experimental data on different species types and their responses to climate; better information on soils and nutrient limitations to growth; and further testing of modelled CO_2 responses.

A thorough study of climate impacts on plantation productivity has recently been completed (Battaglia et al. 2009). This study used a model that has been developed specifically to simulate growth of *Eucalyptus* plantations. It incorporates results from several significant experimental field manipulations and has been thoroughly tested against plantation growth records across the plantation estate. For this study, the same model was parameterised and tested for five additional major plantation species. It was used to predict impacts of changing climate on productivity in six major plantation regions of Australia, using two alternative climate scenarios: a mid-range and an extreme hot-dry scenario.

The key results from this report were as follows:

- Predicted plantation production changes varied across sites depending on site attributes such as fertility and the relationship between current site climate and species optima.
- In some regions, particularly cool and moist regions, production is likely to increase, particularly if potential gains from rising CO_2 are realised. These regions included:
    - *E. globulus, E. nitens, P. radiata* in Tasmania
    - mid to lower northern regions of the hybrid pine estate
    - *P. radiata, E. globulus* in East Gippsland and higher altitude parts of central and NE Victoria
- In other regions, production is likely to decrease unless there is a significant benefit from rising CO_2 or adaptation options put in place. These regions included:
    - *Pinus radiata* plantations in southern NSW and possibly the western edge of the southern and central estates
    - The eastern and northern extents of the WA *E. globulus* and *P. radiata* estates.

This report may be regarded as state-of-the-art, but nonetheless flags several key uncertainties, in particular:

- The effect of elevated CO_2 was unknown. The authors used the alternative assumptions of either no down-regulation of photosynthesis or full down-regulation of photosynthesis. The use of these alternative assumptions allows the range of uncertainty to be quantified. A key area for future research is to synthesise CO_2 experiments appropriately to narrow this uncertainty. In particular, data from the recent Hawkesbury Forest Experiment has now become available (McMurtrie et al. 2009). This experiment found no positive effect of elevated CO_2 on production (see Chapter 3). Compared with these results, the positive CO_2 effects incorporated into the CABALA model are high, indicating that the model may overestimate future production.
- The model does not simulate mortality. Thus, during drought, production is reduced, but is assumed to recover following sufficient rain. The omission of mortality means that production estimates are likely to be optimistic. The authors attempted to quantify drought risk by calculating the number of high-risk days (above a given temperature and leaf water potential threshold). Better quantification of this threshold was flagged as a vitally important research gap.
- Indirect effects of climate change, including changes in pest distribution, host-pest dynamics, and changes in fire frequency and severity, are not incorporated in the

modelling. These effects are likely to be important, and again, are likely to reduce actual production below that predicted by the model.

Both ecophysiological modelling (Battaglia et al. 2009) and bioclimatic modelling (Booth and Jovanovic 2005, see below) flag plantations in south-west Western Australia as those most likely to be adversely affected by climate change due to severe reductions in precipitation. Ecophysiological modelling has been used to study this region in detail. Simioni et al. (2008) examined productivity of *Pinus radiata* plantations in this region using the CENW model. The model was first evaluated over seven sites and gave reasonable estimates of basal area and soil moisture at the six sites where water tables were not supplying additional water to the forest (Simioni et al. 2008). Under IPCC scenario A2, stem wood production and Net Ecosystem Productivity (NEP) were predicted to decrease strongly. These results were explained by the trade-off between the positive effect of CO_2 and the negative effect of rising temperatures and decreased rainfall (Simioni et al. 2009). The wettest site was least affected and the driest site was most affected by climate change. Because changes in ecosystem respiration lagged behind changes in plant growth, and because respiration was affected by increased temperatures, NEP was more negatively affected than stem wood production. Realistic predictions of forest production and carbon sequestration require modelling tools that (1) describe feedbacks between environmental variables, plant physiology and soil organic matter decomposition, (2) include a range of climate scenarios, and (3) simulations which account for gradual changes in climate to account for transient effects.

In a separate modelling study conducted in south-west Western Australia, the trade-off between productivity and drought in *E. globulus* plantations was examined (Mendham et al. 2005). Stocking rates to minimise the risk of drought death at each of seven regions with different soil depths were estimated. This report showed that drought risk needs to be managed in high productivity *E. globulus* plantations, however there are several management strategies available to reduce this risk, including site selection, stocking density and reducing the amount of nutrient application (Mendham et al. 2005).

A further study of climate impacts on Australian production forests is underway at the Bureau of Rural Sciences but was not due be completed in time for this report. That study will estimate impacts of climate change on productivity of given forest types across key forest regions in Australia, but will not attempt to model changes in the distribution of forest types. Assessments of climate impacts on forest productivity in other countries commonly take into account changes in species distribution (Fuhrer et al. 2006; Iversen et al. 2008; Kellomaki et al. 2008; Lexer et al. 2002). However, such models do not currently simulate the distribution of vegetation within Australia well, reflecting our poor understanding of the factors controlling vegetation distribution on this continent (e.g. see presentation by Stephen Roxburgh:http://www.globalcarbonproject.org/global/pdf/2Roxburgh.pdf). Developing models that can successfully simulate vegetation dynamics in Australia should be regarded as a major research priority.

14.2 Bioclimatic modelling

In Australia, most projections of the impacts of climate change on species and communities have involved the use of bioclimatic models to predict changes in geographic range. These models are correlative, and relate the occurrence of a species or forest type to climate or biogeography. For reasons outlined below, these studies should be regarded as indicative, rather than definitive. That is, they can indicate species that are vulnerable to climate change because they only occur in a narrow climatic range. However, the climate is likely to be not the only limiting factor to distribution, and therefore species may be more tolerant than indicated by this type of analysis. Ideally, species indicated as vulnerable by this type of analysis should be the subject of more detailed ecophysiological study.

Notable studies of bioclimatic modelling for Australian tree species include the following. Hughes et al (1996) identified climatic ranges of 819 species of *Eucalyptus.* Half of these species had ranges of mean annual temperature of less than 3 °C and one-quarter had ranges of less than 1 °C (Figure 14.1). The authors conclude that "if even a moderate proportion of present day boundaries actually reflect thermal or rainfall tolerances, substantial changes of the tree flora of Australia may be expected" (Hughes et al. 1996). This is the study that led Hennessey et al. (2007) in the IPCC report to conclude that Australian forests would be vulnerable to changes in mean temperature of greater than 2 °C.

Hilbert et al. (2001) used an artificial neural network model to predict changes in the distribution of tropical rainforest types in Queensland. They found that the climatic range of most rainforest types was small and concluded that several forest types would be highly stressed by a 1 °C warming and most were sensitive to any change in rainfall (Hilbert et al. 2001).

Hughes (2003) reports on a CSIRO study by Pouliquen-Young and Newman (2000) which conducted a bioclimatic analysis for 92 species of the endemic genus *Dryandra* and 27 *Acacia* species, found in the goldfields region of Western Australia. This study found that both genera had very narrow climatic distributions, with high vulnerability to warming: 66% of the *Dryandra,* and 100% of the *Acacia* species bioclimatic profiles disappeared completely under a 2°C warming, and 59% of *Acacia* species bioclimatic profiles disappeared under a 1°C warming. This study was rather unfortunately interpreted in the media as saying that 100% of *Acacia* species in Western Australia were at risk from climate change, when it examined only a very small number of existing species (27 out of 450 to 500) (Booth 2007). The conclusions of this study are also subject to the critique that species moving out of their climatic range will not necessarily go extinct: forestry trials around the world have demonstrated that many acacias and eucalypts are able to survive in different temperature environments from their native ranges (Booth et al. 1988). For example, *Acacia mearnsii* is only found in regions with mean annual temperatures below 17.5 °C but has successfully been grown in plantations up to about 23 °C overseas, possibly due to reduced competition with other species (Booth 2007).

A study on the Victorian Central Highlands used bioclimatic modelling, combined with a semi-mechanistic species distribution model, to identify the vulnerability of the regeneration niche of forest species to climate change (Nitschke and Hickey 2007). Results showed narrow climatic breadths of the species studied. They concluded that an increase in mean annual temperature of 1.4 °C and a decline in precipitation by 5 % would be sufficient to cause a significant contraction in 20 species regeneration niches and significant changes in the size and location of species potential ranges.

Most examples of bioclimatic modelling do not incorporate migration, however one notable study examined migration of 100 *Banksia* species modelled at a rate of 5 km per decade (Fitzpatrick et al. 2008). Similar to other bioclimatic studies, narrow distribution ranges were also found for these species. The range of two-thirds of the species were projected to decline. Species losses were driven primarily by changes in current precipitation regimes, with the greatest losses of species projected to occur in a transition zone between wet coastal areas and interior arid regions, which are projected to become more arid in the future. The author's conclude, “Because the ranges of most species tended to collapse in all climate scenarios, we found that climate change impacts on flora of south-west Western Australia may be large, even under optimistic assumptions regarding migration abilities” (Fitzpatrick et al. 2008). These results suggest that biodiversity in south-west Western Australia may largely depend on the degree to which this biodiversity hotspot experiences increased drought and in the ability of species to tolerate decreases in precipitation.

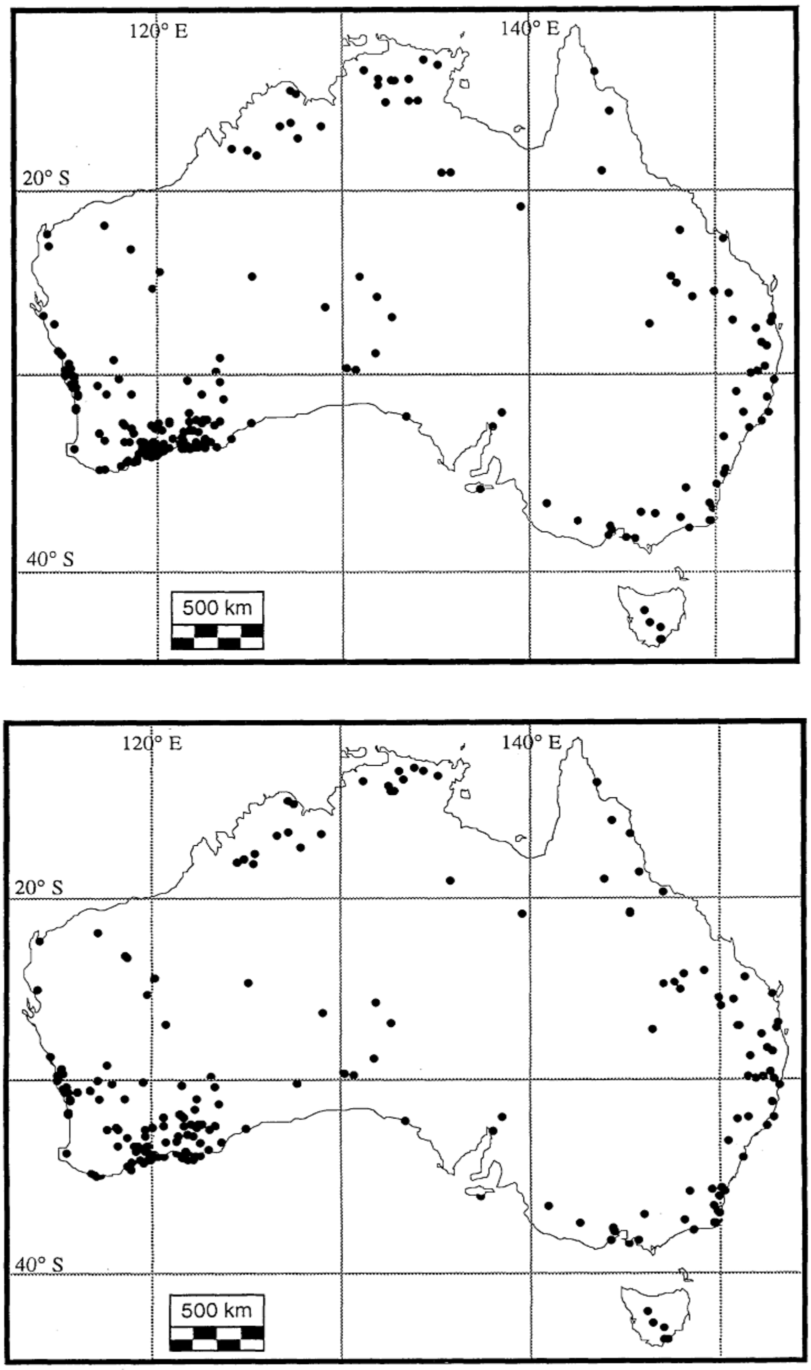

Figure 14.1 (a) Distribution of *Eucalyptus* species with mean annual temperature ranges <1°C (n = 210 species). Location shown is the midpoint of the species range. (b) Distribution of *Eucalyptus* species with mean annual rainfall range less than 1.2 (highest annual rainfall:lowest) (n = 192 species). Location shown is the midpoint of the species range (courtesy Hughes et al. 1996).

The previous studies focused on native forests and their responses to climatic change. Booth and Jovanovich (2005) applied a similar methodology to plantation species, and simulated climatic regions suitable for growth of Australian tree species in current and future climates.

They updated their climate distribution descriptions with reports from overseas trials, in particular from Africa (Booth et al. 1988) so their climatic limitations may better reflect fundamental niches. They found marked changes in several species distributions by 2070, although some modelled distributions did not change greatly. Booth and Jovanovich (2005) suggested that species which are commercially important (*E. globulus)* and/or particularly vulnerable to climate change are worthy of further analyses. Booth and Jovanovich (2005) propose that *E. diversicolor* (Karri) would warrant a detailed analysis as it grows in a relatively limited area, and they suggest *E. pilularis, E. dunnii, C. maculata* and *P. pinaster* are also worthy of futher analysis. However, in general, the sensitivity to climate found in this study seems to be less than the sensitivity to climate reported by Hughes et al. (1996) for eucalypts, which may be a result of incorporating data from overseas trials into the climate distributions.

Bioclimatic modelling of native forests indicates a high sensitivity to climate change. However, methods used in bioclimatic modelling have been criticized, and current research is focusing on methods of improving predictive modelling for plant species. Austin (2007) discusses sources of uncertainty and provides a critical approach and suggestions for new approaches for modelling species distributions. Error and uncertainty which result from Digital Elevation Models (DEMs) include geographic location, slope, rock type, aspect, in addition to derived measures such as mean annual rainfall, temperature, ‘topographic wetness index’ and radiation index. A cause for concern is that some variables which are prone to DEM error, especially topographic wetness index and topographic position, are both the strongest predictors for some species (Van Niel and Austin 2007). Austin (2007) gives a list of 9 ‘rules of thumb’ which should be applied when predictive species modelling is used, including investigating whether relationships are curvilinear, stating the explicit theory being tested or assumed, investigation of model residuals, and using more than one statistical model.

The role of biotic processes such as competition and predation are rarely incorporated into modelling the realised niche. This means application of the results to changed conditions is questionable and changes in trophic interactions may be critical for predicting responses to climate change. Leathwick and Austin (2001) improved the fit of General Additive Models by including tree density for the dominant tree genus *Nothofagus* in New Zealand. Interactions between density, mean annual temperature and water deficit further improved the models (Leathwick and Austin 2001).

Austin (2007) questions whether we have enough suitable ecophysiological knowledge to choose appropriate environmental variables for bioclimatic modelling. Plant responses to nutrients are hyperbolic, where species abundances increase to a maximum level. Evaluation of niche models should incorporate a test of whether the shape of the response to an environmental predictor is consistent with ecological theory. For example, rainfall has a direct effect on plants, although it is a ‘distal variable’, whereas the ‘proximal variable’ would be the water availability at the root hair. Therefore water balance models are useful to determine the relationship between rainfall and water availability. Austin (2007) argues that progressive incorporation of more direct and proximal predictors using water balance models rather than variables such as slope and aspect significantly improve regression models describing the niche of eucalypt species.

There have been some recent studies examining why species distribution models (such as General Additive Models, as well as novel methods such as machine learning methods) perform differently (Elith and Graham 2009) and suggestions for improved predictions (Elith et al. 2006). Over 226 species from 6 regions of the world were modelled using 16 different methods, using presence-only data to fit the models and presence-absence data to evaluate the predictions. The success of different models varied markedly for different regions, and species which are judged to be specialists had more realistic predictions than generalists (Elith et al. 2006). Community models were regarded to be promising for rare species as the additional information provided by the wider ecological community may help inform modelled relationships. The authors note that although projection of modelled relationships is becoming popular, the strong performance of a particular model in the present climate does not guarantee similar performance under different climates, especially where this requires predictions outside the range of environments on which the original model was based (Elith and Graham 2009; Elith et al. 2006). It is crucial to understand how the algorithm performs when projected into novel environmental conditions which differ from the training data which was supplied. That is, we need to ensure that the way algorithms extrapolate are appropriate from ecological and ecophysiological perspectives.

Thus, new and better methods of bioclimatic-type modelling are in development. However, they have not yet been widely employed to predict vegetation distribution changes in Australia in the future.

14.3 Comparing modelling studies

A striking observation from this review is that bioclimatic modelling tends to show that Australian tree species will be highly vulnerable to climate change, whereas, with the exception of south-west Western Australia, ecophysiological modelling tends to show relatively minor or even positive impacts of climate change on forest productivity.

For example, bioclimatic modelling demonstrates very narrow climatic niches for many Australian species, with ranges of < 1°C common, suggesting a strong vulnerability to temperature. Ecophysiological studies, on the other hand, indicate that many species grow vigorously at a wide range of temperatures.

Why do the different types of study draw such strikingly different conclusions? This question is quite fundamental to understanding vulnerability to climate change in Australian forests.

A) It is possible that bioclimatic models overstate species vulnerability to changes in climate, or omit key processes.

- Bioclimatic models simulate the realised niche, rather than fundamental niche, of species. It is possible that the current distributions of species are limited by factors other than climate, and climate sensitivity will therefore be less than estimated by bioclimatic models.
- Recent work shows that bioclimatic modelling should account for soil type, fine scale habitat diversity, phenotypic plasticity, and interactions between species, when determining climatic niches. These factors are not taken into account in most bioclimatic modelling studies.
- CO_2 impacts on plant growth and water use efficiency are shown to be important in ecophysiological modelling but cannot be incorporated into bioclimatic modelling.

B) It is possible that ecophysiological models omit key processes that affect responses to climate.

- The ecophysiological models reviewed here simulate the productivity of established vegetation, based on understanding of plant physiological responses to climate. Notably absent from these models are potential bottleneck factors and processes including regeneration, mortality, competition, pests and diseases, and interactions with wildfire. If climate change exacerbates these stressors and processes, climate impacts will be more severe than predicted by ecophysiological models.
- An interesting point is that bioclimatic models have been shown to perform better when calibrated with presence-absence data rather than presence-only data. Ecophysiological models, on the other hand, tend to be tested against productivity measurements of existing plantations; effectively, against presence-only data. Ecophysiological models ought also to be used to predict productivity for regions where plantations are known to fail. For example, Battaglia et al. (1998) included plantations which failed due to mortality caused by frost damage when evaluating a model of temperature effects. Without such testing, we cannot be confident that ecophysiological models capture adverse climate impacts.

C) It is possible that the two approaches are both correct because they are simulating climate change impacts on different things.

- It is possible that differences arise because the two approaches have been applied to different types of forest: bioclimatic models are applied largely to native forests and ecophysiological models largely to plantation forests. The possibility exists that native forests may be more vulnerable to climate change than plantation forests.

- Another explanation, suggested by Lesley Hughes (pers comm.), is that biodiversity may be more at risk than productivity. Bioclimatic modelling focuses on species existence, whereas ecophysiological modelling estimates ecosystem productivity. It is possible that ecosystem productivity will be maintained or increases under climate change even though biodiversity decreases due to species loss and replacement.

A clear and compelling research need is to integrate these two approaches. Although, as stated above, bioclimatic studies are only indicative of vulnerability, there do not appear to be any studies where species identified as vulnerable have been followed up with manipulative experiments testing the climate sensitivity of the species. Work of this type is clearly needed. Austin et al. (2009) move towards this integration, but their manipulative experiments were performed before their bioclimatic modelling and therefore, as they note, are not ideally targeted. Austin et al. (2009) state that their work "highlights the value of having a statistical model (description) of the realised environmental niches *prior to* developing hypotheses and experimental designs relevant to understanding the major determinants of species distributions." Thus, targeted manipulative experiments and observational studies directly addressing the climatic sensitivity identified by bioclimatic modelling are needed.

15. Conclusions

15.1 What do we know? The main threats posed by climate change

There are clearly many uncertainties involved in assessing forest vulnerability to climate change, including uncertainty over changes in the climate factors themselves, the ecosystem-scale responses, and interactions with other global change processes. What we do know about impacts of individual factors can be summarised as follows.

The most certain change is the global rise in atmospheric CO_2 concentration. This change has significant consequences for ecosystems; it may benefit productivity through enhanced photosynthesis and water use, although nutrient feedbacks may restrict this benefit. It may also drive shifts in species distributions, with largely negative consequences for biodiversity.

A related increase in temperature is also likely (Australian Academy of Science 2010), although the magnitude of this increase is as yet unknown. Rising temperature has the potential to increase productivity in cool and cold forests, but will also negatively impact on biodiversity, with cool-climate specialists being edged out. In warmer ecosystems, rising temperatures could cause decreases in productivity, and combined with lower rainfall cause more severe droughts.

Reductions in water availability and increased drought frequency are of major concern for many forest systems and pose a significant threat to most aspects of ecosystem functioning.

In contrast, the limited evidence on the direct effects of climate change on phenology suggests that flowering and reproduction of forest systems in Australia is relatively robust under climatic variability.

Fire occurrence was identified as a factor positively influenced by temperature rise and most other projected climate change variables. However, fire occurrence was found to be highly location specific, and dependent on the ability of the vegetation to build up a critical fuel load. Fire will stay an important stressor, affecting native and plantation forests, and under the projected changes in climate is most likely to increase in frequency and severity in dry temperate forest systems found in the southeast and southwest of Australia.

Insect pest species were generally found positively influenced by temperature rise. Pest outbreaks can therefore be considered as an important stressor of native and plantation forest that will likely increase under the projected changes in climate.

Pathogens and invasive weeds are likely to continue to have an impact on forest systems, but the available direct evidence indicates no general strong positive influence of temperature rise on these stressors. However, the responses were found to be highly species dependent. Based on climate suitability there is a likely range shift for most species, however, in general the overall impact of these stressors on native and plantation forests is unlikely to worsen with the projected changes in climate.

15.2 What don't we know? Major research priorities

There are very significant gaps in our knowledge. At this point we do not have credible predictions for impacts of climate change for most of the Australian forest estate, and we are not yet in a position to make such predictions. The major research gaps can be classified into four key areas as follows:

(1) Climate projections. Water availability has been shown to be the key environmental factor structuring Australian forests and woodlands, but there are major uncertainties surrounding future projections of water availability. In particular:

- Climate models currently disagree on rainfall projections for many parts of the country.
- It is commonly assumed that evapotranspiration will increase with rising temperature, but this assumption is called into question by recent research. There is a real need for better projections of evapotranspiration.
- It is also generally assumed that interannual rainfall patterns will remain unchanged in the future. However, infrequent, severe multi-year droughts have been shown to play a major role in shaping Australian woodlands. We need better projections of drought frequency.

(2) Ecosystem scale data. Researchers around the world use ecosystem scale data sets to develop and test ideas about controls on forest productivity. These data include long-term forest monitoring, eddy covariance data, long-term ecological research (LTER) sites, phenological records, ecosystem-scale manipulations, and paleological records. The availability of data for Australian forests lags well behind other countries in each of these categories. Such data are a fundamental requirement for scientific research into forest vulnerability to environmental factors. We critically need better measurements and monitoring of current and past forest processes if we are to project into the future.

(3) Process understanding. There are significant gaps in our understanding of major response processes. Some clearly defined problems can be identified, for example:

- Effects of rising atmospheric CO_2 concentration on productivity and water use of Australian forests is a major source of uncertainty. Ecosystem-scale CO_2 enrichment experiments in Australian woody systems are urgently needed to resolve this uncertainty.
- Effects of long-term drought on ecosystem processes, particularly mortality. Drought mortality is one of the major risks to production forests, but we have a poor understanding of the processes causing mortality and thresholds beyond which it is likely to occur. Studies identifying these thresholds for different forest types are an important priority.

There are also more fundamental questions. We found that there was a real mismatch between predictions of vulnerability coming from bioclimatic and ecophysiological models. Bioclimatic models, based on observed climatic niches, found that many Australian species have narrow ranges and concluded they are very vulnerable to climate change. On the other hand, ecophysiological models, based on mechanistic understanding of climate impacts on plant processes, predicted widespread increases in forest production. The difference between these two approaches reflects the fact that we do not understand, at a very fundamental level, what limits species distributions. We need basic ecological and ecophysiological research, targeted at apparent climatic limits identified by bioclimatic models, to better understand how climate limits species distributions.

(4) Research integration and modelling. Overall, we found that research was very fragmented, with many individual research groups doing very fine work, but few attempts to integrate across different strands of research, or to scale up from existing research to make quantitative projections for climate impacts on native Australian forests and woodlands. To achieve such projections would require that the wide range of research surveyed in this review be synthesized in a modelling framework. We strongly recommend the development of a dynamic vegetation model for Australia that could be used as a quantitative framework to draw together the large body of research discussed herein and make informed projections for the future.

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