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IMPROVING THE QUANTITATIVE LINKAGE BETWEEN ECOLOGICAL PROCESSES AND HYDROLOGIC DYNAMICS IN THE HIGH COUNTRY OF SOUTH-EAST AUSTRALIA

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy
in the Faculty of Agriculture and Environment at The University of Sydney

Mana Gharun
August 2013
Declaration

This thesis is submitted to the University of Sydney in fulfilment of the requirements for the Doctor of Philosophy.

The work presented in this thesis is, to the best of my knowledge and belief, original except as acknowledged in the text. I hereby declare that I have not submitted this material, either in full or in part, for a degree at this or any other institution. Credit for certain material is due to:

Chapter 4: Data during July-November 2009 were collected as part of my Masters’ degree and were extended in measurements and analysis for this thesis.

 Mana Gharun

August 2013
Thesis Summary

High country catchments in south-east Australia rank perhaps as the most important of all ecosystems in terms of water supply in Australia. A large proportion of the water supply to millions of people is sourced from mountainous catchments, forested with mixed-species native eucalypts, where stream flow is strongly leveraged to tree water use given that most of the incoming rainfall is returned to the atmosphere via transpiration.

So far, understanding of tree water use in response to the environment, topography and forest disturbance have focused on wetter mesic eucalypt forests (Mountain Ash and Alpine Ash, known as ‘ash-type’), that are largely confined to Victoria and Tasmania. We have little knowledge of the patterns and drivers, or base-level estimates of tree water use, for the millions of hectares of mixed species eucalypt forests.

In the context of climate change, rising temperature and increasing frequency of high intensity bushfires, an improved understanding of how plant structure and physiology control water use is necessary for assessing the consequences of climate change on the terrestrial water cycle. Such information is valuable in guiding hydrological models that are relied upon by those who manage the large water basins and catchments in south-east Australia.

In this thesis, water relations of high country catchments were studied at the leaf, tree, stand and catchment scale, using a range of measurements and modelling frameworks. A large proportion of the analyses in this study rely on sap flow measurements collected using the Heat Ratio Method (HRM). HRM probes inserted into the hydro-active sapwood combined with species-specific estimates of total sapwood area were used to derive rates of tree and stand transpiration.

This thesis linked variations in plant water use to aspects of stomatal structure, and found those species growing on less water-limited parts of the catchment to display more conservative, lower-risk strategies in their physiology and leaf structure, compared to drought tolerant species growing on a range of elevations and aspects. Eucalypt water use in the high country was largely governed by the atmospheric environment, mainly vapour pressure deficit and radiation, compared to soil moisture and wind speed, with species-specific sensitivity to atmospheric drought that were supported by species distribution patterns within the landscape.
In addition to water relations in response to soil and atmospheric drought, it appeared that in case of disturbance by bushfires, rates of water use in resprouting mixed-species forests, is similar to those for adjacent unburnt forests three years after the fire. These results strongly contrast post-fire patterns of water use in seeder (ash-type) eucalypt forests, and are consistent with catchment-scale observations that show no significant change in water yield, three years after bushfires in catchments forested with mixed-species eucalypts. This clear difference between resprouters and seeders corresponds to slower sap flow in resprouting trees and a comparatively limited increase in sapwood area index and a decrease in total leaf area of the resprouting forests.

In terms of predicting forest water use, this thesis shows that biological representation of transpiration in SPA (a process based soil-plant-atmosphere model) is adequately representative of the real world conditions for eucalypt forests, with leaf area index being the most important predictor of water use. SPA has proved to provide a valuable tool for a range of purposes including predicting the hydrology of mixed-species forests.

At the catchment scale, biological constraints of transpiration were included to describe variations in stream flow within a conceptual framework, and based on empirical data and theory. The results inform hydrological modelling with improved understanding of how evapotranspiration affects catchment water yield, which is of paramount importance in ecosystems where transpiration is a major part of the evapotranspiration flux.

In order to find a generic tool that is able to predict tree water use for a range of eucalypts, a model was developed using data-driven techniques, which predicts sap flux from potential radiation and atmospheric demand. Subsequently, this model was used to upscale tree sap flux across the catchment and to visualize variations in rates of sap flux with topography.

Directly from the investigations carried out here, there are opportunities for further work in terms of addressing shortcomings that were only highlighted in the thesis, and for answering a number of important questions that remain open. For example measurements of sap flow and soil moisture in this study were not sufficient for identification and quantification of water sources used by plants. Stable isotopes in combination with sap flow information can make a powerful tool to determine sources of water used by trees.

Overall, investigations carried out in this thesis provide the base for better integrating of plant physiology and ecology with catchment hydrology in order to improve management
practices, in south-east Australia. The thesis directly contributes knowledge that advances both the basic understanding of the scientific community while at the same time is beneficial to those managers working with water issues in the face of a changing climate.
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During my PhD I visited the Institute for Hydrology in Freiburg (IHF), Germany. I appreciate the feedback offered by Professor Markus Weiler and am thankful to the members and the staff of IHF, especially Drs Klemens Rosin and Andreas Hartmann, who made my visit an enjoyable and scientifically profitable experience.

The University of Sydney has provided me with an inviting and comfortable environment to work in, and I am especially grateful to the staff of the Faculty of Agriculture and Environment, in particular Prue Winkler, the Badham library and the Australian Centre for Microscopy and Microanalysis (ACMM). I would also like to thank people at
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Finally I am grateful to my family, especially Max, my loving husband and best friend, who remained interested in my research and offered ideas and encouragement. Without his support during the most difficult parts, this journey would have not been completed with joy.
To Max
Thesis Presentation

This thesis is formatted as a series of published/submitted papers. Within each chapter, reference is made to the papers as part of the scientific literature. In order to facilitate cross-referencing between chapters of this thesis, the corresponding chapter number has been annotated to each citation as an abbreviated prefix in superscript font. For example, the material in Ch.3 (Gharun et al. 2013) can also be found in Chapter 3.

The status of the papers is as follows:

Chapter 2 is in preparation for submission to Plant, Cell and Environment. Full citation:


Chapter 3 was published in Forest Ecology and Management. Full citation:


Chapter 4 was published in the Journal of Hydrology. Full citation:


Chapter 5 is in press with Journal of Hydrology. Full citation:

Gharun, M., Vervoort, R.W., Turnbull, T.L., Adams, M.A., Testing how the coupling of vegetation to atmospheric processes and soil water availability affects catchment water yield: A case study from south-east Australia.

Chapter 6 is in preparation for submission to Agricultural and Forest Meteorology. Full citation:
Gharun, M., Turnbull, T.L., Henry, J.D., Adams, M.A., Model of tree sap flux for high country forests of south-east Australia.

Appendix A was published in Forest Ecology and Management. Full citation:

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Appendix C has been submitted to Journal of Hydro-Environment Research. Full citation:
Gharun, M., Azmi, M., Adams, M.A., Modelling rainfall-runoff relationship of a mixed-species forested catchment in Australia, following the 2003 bushfires.
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1 General Introduction

A large proportion of the supply of water to agriculture, cities and the environment in south-east Australia is sourced from mountainous catchments dominated by mixed-species forests of *Eucalyptus* (L’Herit.). Notwithstanding several generally true assertions about the significance of leaf area, rainfall and vapour pressure deficit (e.g. Watson et al. 1999, Whitehead and Beadle 2004), there is poor knowledge of the factors controlling forest water use and catchment water yield (the amount of water leaving the catchment as stream flow) in response to soil, climate, topography and forest disturbance in the area. In similar fashion, there is a clear need for long-term quantitative data to test ideas and hypotheses concerning that control (Adams et al. 2013; Attiwill and Adams 2008). These deficiencies provided the impetus for this thesis.

Because of the limited understanding of forests of this type, this thesis conducts a comprehensive investigation of the ecological processes and their hydrological impacts in mixed-species eucalypt forests at varying scale, from individual leaf scale to tree, stand, and ultimately catchment scale. As fire is a frequent and significant occurrence in the eucalypt forests of south-east Australia, its impact on stand water use is specifically addressed. Finally, a range of modeling approaches are tested for simulating these processes at varying scales, and improvements to modeling the linkage between ecophysiology and hydrology of the catchment are proposed.

The remainder of this chapter provides a brief background on forests and water in the high country, followed by a description of the study areas and the research questions and thesis outline.

1.1 Background and motivation

High country catchments (defined here as regions above 750 m altitude, Figure 1.1) are invaluable sources of fresh water to millions of people in south-east Australia (Langford 1976; Vertessy et al. 1997).

Mixed-species eucalypts, are the dominating forest cover in these landscapes (more than 79% in the state of Victoria, Figure 1.2), even so most studies investigating impact on forest hydrology of stand age (Dunn and Connor 1993; Haydon et al. 1997; Vertessy et al.
stand structure (Jayasuriya et al. 1993; Vertessy et al. 1995), soil and litter (McJannet et al. 1996), night time transpiration (Buckley et al. 2011), tree morphology and anatomy (England and Attiwill 2006, 2007; Petit et al. 2010), climate (Pfautsch et al. 2010), summer drought (Pfautsch and Adams 2012), and impact of bushfires on water yield (Brookhouse et al. 2013; Buckley et al. 2012b; Kuczera 1987; Langford 1976) have been confined to wetter eucalypt forest types, especially Mountain Ash (Eucalyptus regnans F. Muell.) and Alpine Ash (E. delegatensis R.T. Baker), due to their dominance of catchments for the City of Melbourne. By contrast we have little knowledge of the patterns and drivers of tree water use or base-level quantification of tree water use, for the millions of hectares of mixed species eucalypt forest (Attiwill and Adams 2008).

Figure 1.1. High country catchments are invaluable sources of fresh water to millions of people in south-east Australia.

Eucalyptus regnans and E. delegatensis forests, known locally as ‘ash-type’ eucalypt forests, are composed of tall single species (even-aged), while mixed-species eucalypt forest (MSEF) are often a composite of three or four different eucalypt species, and are often multi-aged in structure (Figure 1.3). Topographic, geological and climatic variations across forested catchments in south-east Australia are accompanied by variation in dominance by tree species. Mixed-species eucalypt overstorey often comprises combinations of peppermints (e.g. E. radiata Sieber ex DC., E. dives Schauer), stringybarks (e.g. E. obliqua L’Hér., E. macrorhyncha F.Muell. ex Benth., E. baxteri
(Benth.) Maiden & Blakely ex J.M.Black) and boxes (e.g. E. goniocalyx F.Muell. ex Miq., E. polyanthemos Schauer), growing on a range of sites including sites with poor soils and relatively dry climates that are prone to frequent bushfires. These forests typically grow on soils that are duplex in structure with high proportions of sand or rock throughout soil profiles, and clearly differ in structure and function to adjacent mono-specific wet sclerophyll eucalypts forests of ash, that grow on deep, well-structures soils (Lacey and Grayson 1998).

In mixed-species forests, water balance at the stand level is clearly dependent on the varying responses of forest functional types to changing climate and disturbance patterns. Water balance and thus yield at the catchment scale represents an aggregation of responses at the stand scale.

Due to large differences in structure and functions, ash and mixed-species forests are widely expected to be hydrologically different. To this date, Australian research in native mixed-eucalypt forests is particularly lacking in the areas of:

- Response of forest water use to the environment (Mitchell et al. 2012),
- Effects of fire on water use of mixed-species forested catchments (Attiwill and Adams 2008).

Figure 1.2. Mixed-species forests (marked with light green colour) comprise more than 79% of the forest cover in the state of Victoria (Image from the state of Victoria Department for Sustainability and Environment, 2011).
Figure 1.3. Schematic view of a) an even-aged ash-type forest with dense vigorous re-growth among dead overstorey and b) multi-aged structure of a mixed-species forest with resprouting trees, three years after the fire.

1.2 Impacts of forests on the water balance

Forests are sources of freshwater and efficiently cycle nutrients and chemicals and decrease the sediment exported, thus reducing pollutants such as phosphorus and some heavy metals, leading to high quality water being discharged from forested watersheds (FAO, 2003).

Vegetation, soil and atmosphere interact through several processes that determine the water balance of the catchment. Water reaching the earth surface is either lost to atmosphere by the evapotranspiration process, starts flowing as runoff or adds to surface or underground water storages. Evapotranspiration includes all processes involving the phase change from liquid or solid (snow) to vapour, and is partitioned between evaporation from all surfaces (water, land, vegetation), and transpiration by vegetation.
Evapotranspiration, which is the major flux in forested catchments (Zhang et al. 1999), is clearly related to radiation balance and temperature. Energy inputs in the form of radiation drive the phase change in forested catchments. Where there is sufficient water available, evapotranspiration is limited by energy (Budyko 1958; 1974). Water availability within most forested landscapes in south-east Australia is at least partly determined by sub-surface hydraulic and hydrological characteristics such as transmissivity, water table depth, and up-gradient catchment area, that are in return related to climatic factors such as rainfall, temperature, radiation and humidity, which vary spatially responding to factors such as elevation and topographic position (Whiteman 2000).

It is obvious that precipitation and runoff are related at large spatial scales; regions with lower precipitation have lower runoff. However seasonal patterns of runoff are frequently not closely related to precipitation due to the seasonality of evapotranspiration (Dingman 2002). Understanding forest water relations facilitates understanding of variations in evapotranspiration and how forests impact other components of the water balance, such as streamflow. It is known that forest transpiration directly influences catchment stream flow, partially explaining variations in the seasonal (Hewlett 1982) and even (more recently investigated) diurnal fluctuations of water yield (Graham et al. 2012; Gribovszki et al. 2010).

Forest function and structure influence water balance at stand and even catchment scale, and are responsible for feedback effects to and from the atmosphere (Rodriguez-Iturbe and Porporato 2004). In forested catchments, forest structure (i.e. canopy cover and the amount of leaf area) plays an important role in water balance by controlling evaporation and amount of precipitation added to the soil after interception. Below ground, water balances are controlled by soil properties (e.g. hydraulic conductivity) that govern energy and water transport between soil layers, but also vegetation root properties (e.g. rates of root water uptake). Eucalypt spp. in particular can distribute deep roots that extract water from depths down to 6 m or more (Cohen et al. 1997; Le Maitre and Versfeld 1997; Sharma 1984). Hence, differing forest covers can produce different hydraulic conductivities and runoff generation properties compared to non-forested catchments (Burch et al. 1987).

Vegetation cover also directly affects energy balances within catchments. Rates of evaporation from forests depend on the amount of energy available. Net radiation, the balance between upward and downward fluxes of short and long wave radiation, is strongly controlled by surface albedo, that ranges from 0 to 1, and determines how much
shortwave radiation is reflected (light coloured, high albedo) or absorbed (dark coloured, low albedo, Goode and Palle 2007). Surface albedo changes with land cover type (e.g. forest cover versus grassland cover, Moore 1976). While the energy storage above the surface is controlled by storage of sensible and latent heat in the air, it also depends on the heat stored in the vegetation that in turn is determined by vegetation density and temperature.

In Australia, evapotranspiration by native eucalypt forests can reach up to 100% of rainfall (e.g. Bren and Hopmans 2007; Eamus et al. 2006) due to interception losses and water extraction from deep soil horizons (Sharma 1984). The process of transpiration, i.e. evaporation from within the leaves of plants, is the largest component of the evapotranspiration budget in forested catchments, internationally (Eagleson and Segarra 1985; Eamus et al. 2006; Moreira et al. 1997; Sala et al. 1992), and in south-east Australia (Mitchell et al. 2012). Understanding forest transpiration across spatial scales is therefore crucial for informing hydrological models and catchment managers.

So far, measurements of tree water use in the high country of south-east Australia have focused on ash-type species that are largely confined to Victoria and Tasmania (Buckley et al. 2011; Buckley et al. 2012b; Dunn and Connor 1993; Haydon et al. 1997; Moran and O’Shaughnessy 1984; Pfautsch and Adams 2012; Pfautsch et al. 2010; Vertessy et al. 1995; Vertessy et al. 1997), compared to one such study in mixed-species forests (Mitchell et al. 2012). Mixed species foothill forests comprise the largest proportion of the forest estate in south-east Australia (Attiwill 1994), yet are poorly understood hydrologically. Eucalypts are not different to other genera with respect to mechanisms and controls of water uptake from soil, which vary widely among species and sites. One of the main questions this thesis will be answering is the difference in canopy transpiration of different eucalypt species that dominate the high country of south-east Australia, followed by the environmental and physiological underpinnings that govern such processes.

1.2.1 *Environmental underpinnings*

Canopy transpiration is regulated by a number of biological and environmental variables that are expected to vary among sites and species. Environmental factors such as incident radiation, vapour pressure deficit, wind speed, and soil moisture availability affect transpiration (David et al. 2004; Ewers et al. 2009; Hernandez-Santana et al. 2008; Komatsu et al. 2006; Oren and Pataki 2001; Tang et al. 2006; Tognetti et al. 2005;
Wullschleger et al. 2000), at multiple temporal (Gazal et al. 2006; Oren and Pataki 2001) and spatial scales (Granier et al. 2000; Tromp-van Meerveld and McDonnell 2006).

More generally, soil and atmospheric conditions regulate water use in eucalypt forests. For example, water extraction from deep in soil profiles must be invoked to explain observed transpiration rates by some eucalypt species during drought periods (e.g. Leuning et al. 2005), or soil moisture within the top 35 cm in pine forests (Oren et al. 1998). In other cases, soil water in the upper soil profile has little influence on daily variations of transpiration of eucalypt (e.g. Zeppel et al. 2008; Buckley et al. 2012b), tropical (O’Brien et al. 2004) or hardwood forests of northern hemisphere (Bovard et al. 2005).

In contrast, there are clear and reasonably well-understood mechanisms that underpin relationships of atmospheric variables to forest water use (Dierick and Hölscher 2009; Oren and Pataki 2001). Climate variables such as radiation and vapour pressure deficit (VPD) explain a considerable proportion of variation in tree water use in a number of eucalypt forests, with accompanying diurnal and seasonal variations (O’Grady et al. 1999; Pfautsch et al. 2010; Yin et al. 2004; Zeppel et al. 2004). Air saturation deficit directly affects transpiration by establishing the vapour pressure gradient between the vapour-saturated leaf interior and the surrounding air, and radiation affects transpiration indirectly, through heating of the canopy and increasing the leaf-to-air pressure gradient.

The effect of changing atmospheric and soil water conditions on water use by high country mixed-species eucalypts, and the underlying physiological mechanisms is poorly documented (Attiwill and Adams 2008), and is investigated in chapters 2, 3 and 4. An improved understanding of how the environmental factors affect whole-tree water use in mixed-species ecosystems is necessary in assessing the consequences of climate change on the terrestrial water cycle.

This thesis also aims to improve the understanding of species-specific responses and coupling to atmospheric drought, which is the key element to improving hydrological models that are relied upon by those who manage the large water basins and catchments in south-east Australia (Murray Darling Basin Authority 2011). These models also need to be better informed in order to choose appropriate parameters and assumptions for simulating transpiration. For example, although it is widely assumed that stomata of woody species are tightly closed at night, night time transpiration has been reported as comprising up to 10% of daily total water use for eucalypts (Benyon 1999; Buckley et al. 2011; Pfautsch et
al. 2011; Phillips et al. 2010; Zeppel et al. 2010), and up to 25% around the world (Dawson et al. 2007; Donovan et al. 1999; Feild and Holbrook 2000; Oren et al. 1999). These observations bring into question the common assumption made by many hydrological models that night-time transpiration is negligible due to the controlling influence of solar radiation on overall transpiration. Contribution of night-time sap flow has not been examined in high country MSEF, while it can improve models that assume zero water loss by trees in the absence of radiation.

Forest transpiration is regulated by a composition of plant functional (e.g. stomatal regulation), and structural properties (e.g. the amount of leaf area and hydraulic properties). Some important biological variables that explain the variations in canopy transpiration include changes in transpiration with age, which is associated with hydraulic limitations of stomatal conductance (Delzon and Loustau 2005), or tree size (Dawson 1996), and regulation of transpiration by stomatal conductance (Collatz et al. 1991). For example, Dawson (1996) observed much larger rates of transpiration (per mm$^2$ leaf area) for bigger trees and lower rates for smaller trees within single stands, which they hypothesized to be related to the greater capacity of larger trees to hydraulically ‘lift’ water to surface soil layers. Hydraulic lift has not been confirmed for high country eucalypt forests, and larger trees do not always have faster rates of sap flow (e.g. in Jarrah forests of Western Australia, Macfarlane et al. 2010). Testing such information in MSEF has important implications for up-scaling tree water use to stand and landscape scale (Köstner et al. 2002).

1.2.2 Physiological underpinnings

At a smaller scale, leaves are the predominant site of gas exchange between a plant and its atmosphere, and their physiology and morphology adapt to maximise carbon gain whilst limiting water loss. Stomata thus play a key role in landscape carbon and water balance, since stomatal conductance - a physiological process - controls both photosynthesis and transpiration. Numerous models have been developed that link stomatal conductance to environmental conditions or to rates of net photosynthesis. An updated picture of stomatal conductance models, ranging from the purely empirical to fully process-based, along with their mechanistic or deterministic bases, is provided in the review by Damour et al. (2010). It is through understanding of stomatal control of transpiration that forest management can be used as a tool for managing water yield, i.e. by manipulating the transpiration and
evaporation components of the water cycle (Waggoner and Bravdo 1967). However, the interactions among plant water status, stomatal conductance, transpiration and soil and atmospheric factors are complex and non-linear (Buckley 2005; Mott 2009). Catchment-scale models of carbon and water fluxes across south-east Australia will need to reflect variation in structure and function of different eucalypt species, if they are to fully capture species effects on water balance and yield.

For example, one such variation is the species-specific response to drought and related adaptations to different climatic conditions that are present within a complex terrain and might explain species distribution across the landscape (Kolb and Stone 2000). Physiological differences among different eucalypts growing together in the same area are not unexpected and have been observed elsewhere (Sinclair 1980). These aspects however have not been investigated in the high country eucalypt forests. Comparative studies of water relations of co-occurring species improve understanding of complex patterns of species distribution and water balance in eucalypt-dominated catchments.

Stomatal anatomy plays an important role in regulating gas exchange (Franks and Beerling 2009; Lammertsma et al. 2011). Stomata size (Brown and Escombe 1900; Franks and Beerling 2009; Lammertsma et al. 2011; Royer 2001) and other anatomical features such as the extension of the cuticular ledge over the stomatal complex (Roth-Nebelsick et al. 2013) control species-specific variations in stomatal conductance. Studying such attributes can improve our understanding of the species-specific hydraulic strategies in response to their environment. For example in Mountain Ash forests (*Eucalyptus regnans*), England and Attiwill (2006) observed an increase in waxy occlusion of the stomatal antechamber with tree age, effectively a morphological adaptation for conserving water and reducing water stress risks with increasing age and height. While studies of tree water relations are numerous (Wullschleger et al. 1998), they have rarely linked plant water relations to aspects of stomata structure.

In addition to environmental and physiological underpinnings of water use, in the context of climate change and more frequent bushfires predicted for south-east Australia (Lucas et al. 2007), it is of critical importance for catchment managers to have experimental knowledge about the impact of bushfire on water use in mixed-species forests.
1.3 Fire impact on forest water use

Fire is a very common forest disturbance in Australia with large areas of forests burning every year. Over the period of 2002-2007, there have been intensive and extensive bushfires in south-east Australia, with several fires burning more than one million ha of forests (Attiwill and Adams 2008). Questions regarding forest hydrology after fire were first raised following the 1939 bushfires around Melbourne (Black Friday bushfires) where around 1.5 million ha were burnt (Ellis et al. 2004) and water yield declined by up to 50% of pre-fire stream flow (600 mm year$^{-1}$) – a reduction that lasted for decades (Kuczera 1985, 1987).

On the other hand, bushfires play an important role in the conservation and shaping of native eucalypt forests (Tolhurst 2003). Over millions of years, Australian vegetation has evolved to gain adaptive features in response to fire regimes (Atwell et al. 1999). Adaptation to fire is highly variable among eucalypt species and, accordingly, based on their fire responses, eucalypt species are divided into two main groups (Gill and Bradstock 1992):

- “Seeders” that die from fire and re-establish from germination of canopy-stored seeds,
- “Resprouters” that survive and regrow via sprouts from the base (lignotuber) or stem (epicormic).

Fires that are of sufficient intensity to destroy forest canopies also promote the sprouting of epicormic shoots from bud tissues located below the bark. Dominance of forests by such resprouting eucalypts is generally considered to be intimately associated with fire regimes. For example, more frequent fires of lower intensity in drier forests are associated with dominance of resprouters, while seeders are dominant in wetter forests where fires are less frequent but of much higher intensity. Regenerating via epicormic sprouts is the norm for eucalypts, as less than 10% of the more than 700 eucalypt taxa are obligate seeders (Nicolle 2006). Even so, the published literature on fire effects on hydrology of eucalypt forests is overwhelmingly focused on ash forests where seeders dominate (Brookhouse et al. 2013; Buckley et al. 2012b; Kuczera 1987; Langford 1976).

As noted above, water yield can be adversely affected by high intensity bushfires, but the yield response is widely predicted to be species-dependent and thus dependent on the type of forest burnt. Reliable knowledge about ecological responses of different forest types is
important for a secure management of water resources. Fire sensitive species (wet sclerophyll forests such as Mountain Ash and Alpine Ash) are easily killed by moderate to hot fires, and thus form young even-aged forests that regrew from seed. The impact of fires in these forests on catchment water yield is expected to be more pronounced and longer lasting (due to high density and leaf area of regenerating ash saplings, Watson et al. 1999), than in catchments dominated by fire resistant species (mixed-species forests) that survive fires, and develop into multi-aged forests.

Research from the Mountain Ash (*Eucalyptus regnans*) forests in high country of Victoria showed that although stream flow initially increases following removal of forest cover by wildfires, it declines significantly with the vigorous development of dense regrowth (Figure 1.3a). Forest regeneration can take 5-20 years and maturity is not reached until 100 or more years. Owing mostly to the very high initial density of saplings, the amount of leaf area per unit ground area is far greater in regrowth forests than in mature forests, leading to greater interception and transpiration losses (Kuczera 1987; Langford 1976). In these forests, minimum stream flow has been recorded at about age 27 years and stream flow only returns to pre-fire conditions after 150 years.

The impact of fire on water yield has been well researched and reviewed for catchment dominated by ash forests (Mountain Ash, Alpine Ash) due to the water catchments of the City of Melbourne being almost exclusively of this type. Far less is known about catchments dominated by MSEF, where vegetative growth after the fire (epicormic or lignotubers) is the norm (Attiwill and Adams 2008).

Catchment management, including guiding hydrological models, has thus often been based on conceptual understandings that are based on responses to fire by ash-type forests. Currently, management relies on generalizations based on the response of ash-type forests (e.g. Watson et al. 1999) where the landscape is transformed into mosaics of even-aged regenerating forest (Kuczera 1987; Langford 1976). With the exception of Alpine Ash forests (Buckley et al. 2012b), we know little of the dynamics of forest water use in the first few years after fire in seeder eucalypt forests, and almost nothing about fire effects for resprouting mixed-species forests. This thesis examines stand-level hydrology of mixed-species eucalypt forests is examined for the post-fire period in which they contain leaves of juvenile form growing on epicormic branches along the entire height of the tree.
1.4 Modelling framework

The ability to predict components of the water balance, both with reasonable accuracy and in response to changes in the environment, is essential for catchment management. Biophysical models that can successfully reproduce and predict water fluxes can replace costly and labour-intensive alternatives.

1.4.1 Process-based models of soil-plant-atmosphere continuum

One such model is the soil-plant-atmosphere (SPA) model of Williams (1996). The ‘Soil-Plant-Atmosphere Continuum’ is a key concept in studies of plant water use. Theoretically, an electric circuit analogy is often used to model physical controls on the movement of water into and through plants, and to the atmosphere (van den Honert 1948). In its simplest form, the pathway is described as a chain of resistances connected in series. The total hydraulic resistance, therefore, is the sum of the individual resistances along the pathway, including the aerodynamic boundary layer resistances associated with canopy elements, the boundary layer at the leaf surface, stomatal pores, through the xylem pathway of the plant, across root membranes to the soil, and through the soil (Bond et al. 2008).

SPA is a process-based model that simulates eco-hydrological processes between soil, plant and atmosphere including evapotranspiration, soil energy flux, and gross primary production. The model employs variable stomatal conductance, and carbon uptake is maximized within limitations of canopy water availability (Jones and Sutherland 1991). SPA employs well-tested theoretical representation of eco-physiological processes, such as the Farquhar model of leaf-level photosynthesis (Farquhar and Von Caemmerer 1982), and the Penman-Monteith equation (Monteith 1981) for determining leaf-level transpiration. The scale of parameterization (leaf level) and prediction (canopy level) allow for scaling up leaf-level processes to canopy and landscape scales.

Models similar to SPA can be used to test biological controls of transpiration within a scheme represented by the model, to understand the underlying processes within the soil-plant-atmosphere continuum. For example there is still considerable debate over the mechanisms behind the stomatal control of water flux (Buckley 2005; Bunce 1996; Jarvis and McNaughton 1986; Pieruschka et al. 2010). In the scheme within SPA, stomatal conductance optimizes daily carbon (C) gain per unit leaf nitrogen (N) within the limitations of the hydraulic system, minimizing the risk of cavitation and damage to the tree. It is not clear whether such underlying assumption of stomatal control of water loss
holds, and whether SPA can successfully reproduce water fluxes in every forest type, including eucalypt forests.

SPA has been tested in a number of forest types. These include: mixed deciduous (oak-maple) forest (Williams et al. 1996), boreal forest (Williams et al. 2000) and tropical rainforest (Williams et al. 2002). In Australia, Zeppel et al. (2008) validated the model for a eucalypt-dominated woodland. Owing to the great variability in species dominance and structure of eucalypt forests in Australia (Specht and Specht 1999), it remains unclear how much confidence can be attributed to predictions made using SPA or any other similar model in the majority of forests of south-east Australia. This thesis validates SPA for simulating canopy transpiration in a mature mixed-species forest.

1.4.2 Conceptual model of catchment hydrology

In forested watersheds, vegetation and topography exert large controls on runoff generation processes. Compared to topography, the vegetation biological response to the environment is less stable, and this adds complexity to the understanding of the overall watershed processes. Even though plant biological responses are well studied within soil-plant-atmosphere studies, most hydrological studies remain unconnected to the ecological characteristics that make the interplay between climate, soil and vegetation specific to the region (Rodriguez-Iturbe 2000).

Theoretically, evapotranspiration (ET) can be estimated via a suite of physical models, including those that can predict stomatal conductance as functions of water availability in the soil and atmosphere (Collatz et al. 1991; Damour et al. 2010; Gerosa et al. 2012). However, estimation of ET via such models requires extensive data inputs – data that are not readily available in many instances. As an alternative, ET is commonly represented, more conceptually, as a macroscopic function of available soil moisture determining the proportion of the potential evapotranspiration (Budyko 1958; 1974; Zhao et al. 2013). According to this general form, when soil moisture is limiting, evapotranspiration is only a proportion of the potential evapotranspiration (depending on the type of vegetation). When soil moisture is not limiting anymore, evapotranspiration reaches the potential value. Such a supply-limited function is based on long term patterns between climate, evapotranspiration and runoff, and does not include the demand-limiting impacts of vegetation on actual evapotranspiration. Based on the current representation, evapotranspiration rates during abundant soil moisture periods will be overestimated,
because of lack of any limitation on transpiration when soil moisture is abundant. Considering the key role of atmospheric demand on the water balance in eucalypt forests (O’Grady et al. 1999; Zeppel et al. 2004) due to the sparse and well-coupled canopies of eucalypts (Hutley et al. 2000; Mielke et al. 1999; Morris et al. 1998; Zeppel and Eamus 2008), this thesis tests through a conceptual framework, how vegetation coupling to atmospheric and soil moisture affects catchment water yield, during supply and demand-limited periods.

Transpiration has an important role on the water movement in the soil-plant-atmosphere continuum (Emanuel et al. 2007), and the heterogeneous impact of such control at the watershed scale remains poorly understood (Emanuel et al. 2010; Mitchell et al. 2012). Investigating such controls in high country eucalypt forests will have important implications for hydrological modelling and will improve understanding of how ET affects catchment water yield, which is of paramount importance in ecosystems where transpiration is a major part of the ET flux.

1.4.3 Data-driven model of tree sap flux

Determinants of tree water use are complex due to the non-linear underlying physical and biological processes. One general response in the literature is to greatly simplify these processes; the resulting models are then somewhat limited in their application. Empirical tools for particular forest types and species can be extended in their range of applications via models like SPA that use adjustable parameters.

There is a large number of experimental formulae for estimating tree water use. These include: 1) physically-based equations that describe the functions of the system and the physical laws that govern these processes (Chuang et al. 2006; Diaz-Espejo et al. 2012) - these equations require extensive input data which is seldom readily available at each location within a landscape; 2) empirically-based models that do not require extensive inputs, but which need local parameterization and are not usable for species other than those studied (Buckley et al. 2012a; Dierick and Hölscher 2009; Langensiepen et al. 2006). Researchers have also built simpler forms of empirical models that are based on VPD and Photosynthetically Active Radiation (specific to waveband ca. 400-700 nm of solar radiation). Even so, application of these simpler models across the landscape is still limited by the difficulty of parameter estimation (Dierick and Hölscher 2009; Dye and Olbrich 1993). Process-based models on the other hand are limited in their applicability for
catchment managers as parameterisation requires substantial input variables, which often require specialist equipment and are thus difficult to obtain.

In general, limitations of available predictive models across a range of fields have led to application of data-driven techniques that solve optimization problems and find structure among potential relationships. Some of the most applied methods of such ‘soft computing’ in the field of hydrology and water resources include Artificial Neural Networks (ANNs) and Genetic programming (GP). Their application has been encouraged by promising results for many prediction problems in hydrology (ASCE 2000).

For example, these methods have been successful in accurately estimating processes such as pan evaporation (Kişi et al. 2012; Terzi 2012), evapotranspiration (Aytek 2009; Cobaner 2011; Parasurman et al. 2007), reference evapotranspiration (Shiri et al. 2012), soil moisture estimation (Makkeasorn et al. 2006), precipitation (Kişi and Shiri 2011), ground water table depth fluctuations (Shiri and Kişi 2011), rainfall-runoff (Minns and Hall 1996; Savic et al. 1999; Whigham and Crapper 2001), suspended sediments in streams (Aytek and Kişi 2008), and risks in water supply (Babovic et al. 2001). Meijun et al. (2007) and Li et al. (2009) used Neural Networks to predict transpiration from poplar trees and transpiration from fruit trees, however their models requires in-situ measurements of at least three inputs, and lack a mathematical framework to describe underlying mechanisms.

This thesis tests application of Artificial Neural Networks and Genetic programming in Chapter 6 for modelling rates of tree sap flux for mixed-species eucalypt forests. To this date, there has been no attempt for modelling tree water use using genetic programming, and as such is worthy of investigation. The only attempt in Australian forests has been a study by Whitley et al. (2009) that used ANNs for a single site (a remnant forest in NSW) as a statistical benchmark for comparing different models of transpiration.

1.5 Area of study

This thesis is based on measurements at 15 different forest sites, within three main locations, Mount Beauty, Stanley and the Cotter catchment, within an area known as the Australian Alps in south-east Australia (Figure 1.4). The Australian Alps are the highest mountain range in Australia and are part of the Great Dividing Range, a series of mountains, hills and highlands that run about 3000 kilometres from northern Queensland into northern part of Victoria. The underlying bedrocks of the study areas are granite,
limestone, and shale. Soils are correspondingly variable (Johnson 2009). The area has a generally temperate climate (warm summer, cold winter) although the highest peaks and plateaus (> 1200 m a.s.l.) are snow-covered for around three months each year.

Sites that covered a range of species, topography, and disturbance were selected according to the objectives of individual studies. The Cotter catchment for example, was selected as it supplies water to the city of Canberra, is of high ecological significance, and provides a range of forest types (ash-type and MSEF). Further descriptions of each location are given within the respective chapters.

![Figure 1.4](image.png)

**Figure 1.4.** Location of three main study areas.

### 1.6 Objectives and thesis outline

In south-east Australia, impacts of climate change are likely to reduce water yield via changes in rainfall regimes (Chiew et al. 2009; Howe et al. 2005) and increase in atmospheric demand, via increase in mean annual temperature (Howe et al. 2005). An analysis on the sensitivity of runoff to a range of factors indicates that a 1 °C increase in average daily maximum temperature leads to around 4 percent decrease in stream flow (CSIRO 2012). However, additional feedbacks associated with plant functions are likely to modify this result and further research is necessary to test vegetation physiological
responses to the environment. In addition, high intensity bushfires are expected to become more frequent in south-east Australia (Lucas et al. 2007) and there is an urgency for more research in this area.

Throughout this thesis, daily and seasonal patterns of tree water use were measured using sap flow techniques, along with a suit of environmental and physiological measurements in several forests types across the high country of south-east Australia. Evapotranspiration can be measured through a variety of methods including closing the water balance at the land surface and separately measuring different components, or using Bowen ratio (Bowen 1926) techniques. Alternatively, sap flow sensors are low cost and allow measurement of transpiration at reasonable scales (stand level) and facilitate analysis of the transpiration process controlled by plant physiology, water fluxes and atmospheric drivers. Quantitative observations from forests provided the basis for assessing forest water use response to climate, soil, topography and bushfires.

Understanding the environmental and plant structural and physiological controls of forest water use is critical to being able to accurately assess and predict water yield in south-east Australia (e.g. Mitchell et al. 2012). The main objective in Chapter 2 “Within-catchment variation in regulation of water use by eucalypts, and the roles of stomatal anatomy and physiology” is to examine the central role of atmospheric drought in the physiological ecology of montane eucalypts. For this purpose, within a single catchment, leaf structural and physiological properties are measured and investigated as to how they relate to tree water use for several eucalypt species.

Due to large structural differences between seed-regenerating and re-sprouting eucalypt forests, it is hypothesized that bushfire has a contrasting effect on stand water use between mixed-species forests and ash-type forest. To examine this hypothesis, the effect of bushfires on tree and stand-level water use is examined in a resprouting MSEF, in Chapter 3 “Stand water use status in relation to fire in a mixed species eucalypt forest”, using a suite of tree water use and physiology, forest-stand structure, soil and micro-climate measurements.

In the context of resource management, models of vegetation processes are valuable tools (Eamus et al. 2006; Porporato et al. 2004), and are known as principal method for integration of small-scale process-level phenomena into a comprehensive description of forest or ecosystem function (Hanson et al. 2004); however there are relatively few models
that can successfully characterise the dynamics of soil-plant and atmosphere interactions in a range of forest types. In Chapter 4 a soil-plant-atmosphere model is tested for a mixed-species forest, for two main purposes:

- to validate sap flow simulation by one of the most widely and successfully applied models that resource managers would be able to use as a key tool; and
- to understand the relationship between tree water use and several biotic factors.

In Chapter 5 “Testing how the coupling of vegetation to atmospheric processes and soil water availability affects catchment water yield”, a theory, originated from empirical data collected in this thesis, is tested: that including the biophysical constraints of transpiration in the ET function can determine variations in stream flow at the catchment scale. Surfaces of temperature and air vapour pressure deficit over the catchment are inferred taking into account the topographic influence on the forcing variables, and are used also in mapping tree sap flow in the chapter that follows.

At larger spatial scales, topographic control of climatic factors and soil moisture may affect vegetation water use (Eagleson 1982), which is coupled with hydrological processes (Wigmosta et al. 1994) and that, in return, controls vegetation in favour of their structure and distribution within mountainous catchments (Daubenmire 1968, 1980). The main objective of Chapter 6 was to find a suitable data-driven model to simulate tree sap flux, combining in situ observations with high resolution climatic variables, in order to understand the variation in tree water use with topography, within a mountainous forested catchment.

The thesis ends with Chapter 7 that reviews the findings of the various individual studies and integrates them via a general discussion.
1.7 References


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2 Within-catchment variation in regulation of water use by eucalypts, and the roles of stomatal anatomy and physiology

Summary

In a single catchment sap flow was measured for four most common species of high-country south-east Australia, and leaf structural and physiological properties, and how they relate to tree water use were characterized for three of them: *Eucalyptus delegatensis* R. Baker, *E. pauciflora* Sieb. ex Spreng. and *E. radiata* Sieber ex DC. Sap flow was measured between May 2011 and May 2012, diurnal patterns in stomatal conductance, photosynthesis and leaf water potential were periodically measured, and stomatal anatomy was analyzed over four campaigns between January and May 2011.

A two-fold difference in stomatal conductance ($g_s$) was observed among species, yet $g_s$ was a poor indicator of tree water use, supporting suggestions that variations in water use among species depend on the scale of observations. *E. pauciflora* had the greatest $g_s$ (both measured and estimated from the stomatal characteristics), whilst *E. delegatensis* and *E. radiata* had greater rates of sap flow, instantaneous transpiration efficiency (ITE), and leaf area index (LAI) than *E. pauciflora*.

Among environmental variables, vapour pressure deficit (VPD) and photosynthetically active radiation ($Q$) were the strongest drivers of tree water use. Sap flow was impeded by reduced stomatal conductance at VPD > 1 kPa, even when soil water was not limiting. *E. radiata* was less sensitive than *E. delegatensis* and *E. pauciflora* to changes in VPD, indicating greater tolerance of atmospheric drought. The generalist species, *E. radiata*, which grows over a wide range of elevations and landscape positions, also has structural features (e.g. minimal cuticular ledge) that indicate a reduced structural capacity to minimise water loss. In contrast, the two species restricted to higher elevations, *E. pauciflora* and *E. delegatensis*, have physiological and structural features ($g_s$ driven by VPD, well-developed cuticular ledge) that help conserve water. In summary, both water relations and stomatal anatomy varied with species and corresponded well with their distinct distributions within the catchment. Catchment-scale models of carbon and water
fluxes will need to reflect such variation in structure and function, if they are to fully capture species effects on water balance and yield.

2.1 Introduction

In Australia, the high country forests of the south-east rank as perhaps the most important of all Australian ecosystems in terms of water supply. A large proportion of the water supply to millions of people in south-east Australia is sourced from these head catchments, dominated by a mix of native eucalypts (Langford 1976; Vertessy et al. 1997). Understanding environmental and plant structural and physiological controls of forest water use is critical to being able to accurately assess and predict water yield (e.g. Mitchell et al. 2012). Most predictive models rely on a number of biological and environmental variables that in turn depend on species and site, to estimate plant water use. Climatic variables and soil water can exert contrasting controls on vegetation water uptake. For example while soil moisture is observed to exert a stronger control in Amazonian rainforests (Fisher et al. 2008), climate variables such as radiation ($Q$) and vapour pressure deficit (VPD) have been used to explain most of the temporal variation in water use in eucalypt forests across diurnal and seasonal scales (Buckley et al. 2012; O’Grady et al. 1999; Pfautsch et al. 2010; Zeppel et al. 2004). Whether $Q$ or VPD is more important varies with forest type; Zeppel et al. (2004), for example, reported that radiation was the dominant driver of tree water use in remnant forests of eastern Australia, while Pfautsch et al. (2010) showed that maximum daily temperature was a useful proxy for atmospheric conditions and their influence on water use in Mountain Ash forests with sufficient soil moisture. Buckley et al. (2012) used long-term data to show that evaporative demand drove tree water use in mature and regrowth subalpine forests, regardless of soil moisture content.

In addition to environmental conditions, rates of tree water use (per unit sapwood or leaf area) depend on a range of biological variables such as hydraulic properties associated with tree size, age and stomatal regulation of transpiration. For example, Dawson (1996) observed much larger rates of transpiration (per mm$^2$ leaf area) from bigger trees and lower rates from smaller trees within single stands, which they hypothesized to be related to the greater capacity of larger trees to hydraulically ‘lift’ water to surface soil layers. Hydraulic lift has not been confirmed for high country eucalypt forests, and larger trees do
not always have faster rates of sap flow (e.g. in Jarrah forests of Western Australia, Macfarlane et al. 2010). At the leaf scale, regulation of transpiration by stomata is a complex mechanism that depends on a range of structural, physiological and environmental processes (Collatz et al. 1991; Damour et al. 2010). For eucalypts, the physical structure of stomata varies widely (e.g., England and Attiwill 2006), especially in features of significance to water conservation such as development of cuticular waxes.

Depending on their position within the landscape matrix, the capacity of individual species to regulate their water use potentially varies as a result of differences in temperature, radiation, soil moisture and water vapour deficit of the atmosphere (Whiteman 2000). Single catchment studies of the regulation of water use by multiple dominant tree species are rare but have benefits inasmuch as key environmental drivers (such as radiation, VPD, temperature) are often similar across the catchment, thereby facilitating comparisons between and among species. Such studies also offer benefits for hydrology inasmuch as distributions of dominant species within native forest catchments usually reflect environmental conditions yet individual species may exhibit contrasting relationships with environmental variables. Improved precision of hydrological modelling may require species-specific and landscape position-specific underlying relationships.

In this study sap flow was measured in four of the most common species (8 sites, 2 per species) within a single catchment in the high country of south-east Australia. The selected species represent distinct topographic and landform features within typical high country catchments: *E. pauciflora* is restricted to higher elevations where the diel minimum temperature is below zero for several months in winter, *E. delegatensis* grows on southern aspects and more protected slopes, while *E. radiata* and *E. dives* are generalists found on mostly lower elevations on all aspects and often grow as a co-dominant. Average minimum temperature in the coldest month (July) and annual net radiation are two environmental variables differentiating the occurrence of *E. pauciflora* and *E. delegatensis* (Moore et al. 1993).

Studies of sap flow and tree water relations are numerous (Wullschleger et al. 1998); however, they have rarely tested the impact of scale of analysis on the hydrologic responses of plants, nor linked plant water relations to aspects of stomata structure. One such study, by Wullschelger et al. (2002), observed that the responses to elevated CO$_2$ differed among leaf-level stomatal conductance, sap velocity and stand transpiration. In this study, a hypothesis was that variation in water use in high country eucalypt species...
depends on the spatial scale of observations (i.e. leaf versus whole tree). To test this hypothesis, three of the eight sites were selected and leaf water potential and gas exchange was measured. Variations in plant water use were also linked to aspects of stomatal structure for the first time. The particular species were selected because they grow on distinct sites within the forest, where variation in species composition among sites is largely a reflection of physiographic and edaphic differences, especially soil type and aspect (Pook et al. 1966; Thistlethwaite 1970; Woods and Raison 1983). Second hypothesis was that species whose distributions suggest a pattern of avoidance of soil drought are more sensitive toward atmospheric drought.

2.2 Methods

2.2.1 Study area

The Cotter Catchment, a part of the high country of south-east Australia, lies to the west of Canberra (lat 35.6 °S, long 148.8 °E). The forests of this catchment are part of the Namadgi National Park. Vegetation cover is native eucalypt forest. Snow gum (Eucalyptus pauciflora) forests dominate the highest elevations (> 1200 m a.s.l.), while southern aspects and protected slopes at 900-1200 m a.s.l. are often covered by tall-open forests of Alpine Ash (E. delegatensis). Lower slopes and elevations (500-900 m a.s.l.) and more exposed topographic locations are covered by mixed-species forests, where two or more species may dominate. The co-dominants include broad-leaved peppermint (E. dives), narrow-leaved peppermint (E. radiata), manna gum (E. viminalis), mountain gum (E. dalrympleana) and brown barrel (E. fastigata). The leguminous shrub Daviesia mimosoides may form a nearly continuous understory on exposed aspects and is usually replaced by Acacia dealbata in moist gullies within E. delegatensis forests (Woods and Raison 1983).

Sap flow measurements were made in eight 0.25-ha plots, each dominated by one species. A full description of the sites is given in Table 2.1. Three of the sites (one per species) were used to compare sap flow and physiological data (sites no. 1, 2 and 3) for E. delegatensis (1250 m a.s.l.), E. radiata (1100 m a.s.l.), and E. pauciflora (1650 m a.s.l.).

Winter fogs, frosts and snowfall frequently occur at higher elevations (> 1200 m a.s.l.) within the study catchment. In summer, weather is usually warm and often hot and dry
with periods of between 6 and 8 weeks with little rain and maximum temperatures > 30 °C (Moore et al. 1993). Mean maximum and minimum temperatures are 4 °C and -1 °C, respectively, in July (winter), and 24 °C and 10 °C in January (summer). With increasing elevation, average temperatures decline and minimum air temperatures are locally sensitive to topography. Overnight, hillslopes and ridges are often warmer than valleys where cold air collects (Australian Bureau of Meteorology). Mean annual rainfall across the whole catchment is approximately 1150 mm. Although snowfalls are common in winter, the soil never freezes (Woods and Raison 1983).

2.2.2 Sap flux and environmental measurements

At each plot individual tree diameter was measured and three trees were selected for sap flux measurements, considering the diameter distribution of the stand (Figure 2.1). Sap flux was measured using the Heat Ratio Method, HRM (Burgess et al. 2001). Each HRM set consists of two needles and a heater probe integrated with a microprocessor. Each needle contains two thermocouples (at different lengths along the needle, corresponding to different depths of sapwood). Sap flux is determined via the ratio of increase in sapwood temperature above and below a heater needle following a heat pulse, and is proportional to the heat pulse velocity ($V_h$ cm hr$^{-1}$):

\[
V_h = 3600 \frac{k}{x} \ln \left( \frac{v_1}{v_2} \right)
\]

(2.1)

Where $k$ is the thermal diffusivity (cm$^2$ s$^{-1}$) of fresh wood, $x$ (cm) is the distance between the heater and either of the probes, $v_1$ is the increase in temperature (°C) from the initial temperature at the downstream probe, and $v_2$ is the increase at the upstream probe. Thermal diffusivity was resolved using species-specific estimates of thermal conductivity, density and specific heat capacity of fresh sapwood (Burgess et al. 2001). Sapwood heat capacity was estimated from water content and fresh volume of sapwood cores that were measured immediately after coring, and dry weight of sapwood was measured after samples had been oven dried at 60 °C for 72 hours. To determine the zero-flow baseline, datasets from each site were screened for the periods in which VPD remained < 0.1 kPa for at least 24 hours. The mean heat velocity during the final 25% of the longest such period for each sensor was used as the zero flow reference for that sensor (see Buckley et al. 2011).
heat pulse velocities were corrected for wounding using a homogeneous third-order polynomial and assuming a wound diameter of 0.18 cm (Burgess et al. 2001):

\[ V_c = bV_h + cV_h^2 + dV_h^3 \]  

(2.2)

where \( V_c \) is the corrected heat pulse velocity and \( b, c \) and \( d \) are empirical coefficients \((b = 1.73, c = -0.0013, d = 0.0002)\). Sap flux, \( V_s \) (also called sap velocity, or sap flow per unit sapwood area; cm\(^3\) cm\(^{-2}\) hr\(^{-1}\)) was then computed by multiplying \( V_c \) by the ratio of the volumetric heat capacities of fresh wood and sap:

\[ V_s = V_c \frac{\rho_b(c_w + m_w) + \rho_s c_s}{\rho_c c_s} \]  

(2.3)

where \( \rho_b \) and \( \rho_s \) are the basic densities of fresh wood and sap, respectively (kg m\(^{-3}\)), \( c_w \) and \( c_s \) are the specific heat capacities of fresh wood and sap, respectively (J kg\(^{-1}\) K\(^{-1}\)) and \( m_c \) is the volumetric water content of sapwood (m\(^3\) m\(^{-3}\)) (Burgess et al. 2001). Finally whole tree sap flow \((F_s, \text{L day}^{-1})\) for each stem was computed as

\[ F_s = 0.024 \cdot S \cdot \langle V_s \rangle \]  

(2.4)

where \( \langle V_s \rangle \) is the mean of \( V_s \) in a given day, \( S \) is total sapwood area (cm\(^2\)) and 0.024 is a unit conversion ([L day\(^{-1}\)]/[cm\(^3\) hr\(^{-1}\)]). To calculate \( F_s \), \( V_s \) values were used based on \( V_h \) measurements in only the outer probes of each probe set, because only one tree out of nine in the study had enough sapwood depth (> 27.5 mm) for both inner and outer probes to collect measurements. Note that this assumes that outer probes were indicative of flow through the entire sapwood. Throughout the study both sap flux \((V_s)\) and whole-tree sap flow \((F_s)\) are compared.

To estimate the water conducting cross-sectional area of sapwood \((S)\), four cores were collected from four different azimuths around the circumference of the tree and sapwood-heartwood boundaries were identified by staining the cores with a 1% methyl orange solution (based on the orange-to-red colour change from sapwood to heartwood; Kutscha
The measured depths of sapwood and bark thickness (measured using a bark probe) were then combined with measured tree diameter to calculate sapwood area of each tree. Sapwood area for the entire plot was derived from the relationships between tree diameter and sapwood area given in Figure 2.2. Information about the trees selected for sap flux measurements is given in Table 2.2. Leaf area index (LAI) was measured in three campaigns during August 2010, November 2011 and January 2012, using cover photography and following the method of Macfarlane et al. (2007). Briefly, in this method images are converted to a binary image and LAI is derived from the proportion of pixels found in gaps and pixels with foliage. Image analysis was done in MATLAB (The MathWorks Inc., Natick, MA, 2011) using the script written by (Fuentes et al. 2008).

Air temperature ($T$, °C) and relative humidity (rH, %) were measured at 1 m above the forest ground at the centre of each plot. Sap flow and meteorological measurements were collected every 30 minutes. Vapour pressure deficit (VPD, kPa) was calculated from measurements of temperature and relative humidity (World Meteorological Organization, 2008):

$$ VPD = \left( 0.6112 \times e^{\frac{17.62 \times T}{243.12 + T}} \right) \times \left( 1 - \frac{rH}{100} \right) $$

(2.5)
Figure 2.1. Tree diameter distribution for the measurement plots. Dashed lines show the diameter group from which trees were selected for sap flow measurements.
Ratio of sap flow to vapour pressure deficit was used as proxy for canopy conductance following Buckley et al. (2012). This assumes that the air within the canopy was well mixed with the air outside the canopy, which is consistent with the relatively sparse canopies and low leaf area indices in our study area and in similar eucalypt forests (Zeppel 2013), and is further supported by numerous reports of quite low decoupling coefficients ($\Omega$, Jarvis and McNaughton 1986) in other eucalypt forests (Hutley et al. 2000; Mielke et al. 1999; Morris et al. 1998; Zeppel and Eamus 2008).

Photosynthetically active radiation ($Q$, waveband ca. 400-700 nm) was collected from a weather station (HOBO weather station, Micro DAQ Ltd. USA) at an open patch at 1200 m a.s.l., 23 km from the *E. delegatensis*, 6 km from the *E. radiata*, and 7.7 km from the *E. pauciflora* sites (sites no. 1, 2, 3 that were used for further water relations analysis). In addition, soil moisture was continuously measured at 2 depths (30 cm and 60 cm) at each plot. Volumetric soil moisture content was measured using standing wave soil moisture probes (MP406, ICT International Pty Ltd, Armidale, Australia). Sap flow was measured for one year; however, shorter time frames were used during which measurements of environmental variables were available for all species, where this was required for particular analyses. Due to large gaps in the data, environmental controls on sap flow were only analysed for and compared between *E. pauciflora* and *E. radiata*. These two species are also most distinct in structure and distribution. Sap flow and environmental variables were collected for 165 days for *E. pauciflora* and 360 days for *E. radiata* and were compared during a period of 53 days (16 March to 10 May 2012) where these data overlap.

In order to find the most influential environmental variables on tree water use at the daily and hourly scale, Generalized Additive Model (GAM) was used (mgcv package in R). GAM was selected since it is a non-parametric method suitable for identifying non-linear covariate effects in data that may not satisfy conditions of normality required for parametric tests (Guisan et al. 2002; Hastie and Tibshirani 1986; Yee and Mitchell 1991). The result of GAM was compared in terms of significance and relative importance of the environmental variables. The Akaike Information Criterion (AIC) was compared between a model that included all predictors and several other models, each of which excluded one predictor. The variables tested (continuous fixed factors) were vapour pressure deficit, photosynthetically active radiation and soil relative water content at 30 cm and 60 cm, and sampled trees as random factors.
2.2.3 Gas exchange measurements

Three trees were selected from each species for measurement of gas exchange and leaf water potential in situ within the canopy. Canopies of the trees were accessed using a hydraulic lift.

Rates of assimilation ($A$) and stomatal conductance ($g_s$) were measured with an infrared gas analyser (Li-Cor 6400, LiCor, Lincoln, NE, USA) equipped with an LED light source and the standard 2 × 3 cm leaf chamber. Irradiance, air moisture and leaf temperature were set close to ambient values and [CO$_2$] in the reference air stream was controlled to 380 ppm. Readings were taken once steady state was achieved. Total leaf stomatal conductance to water vapour ($g_s$) was also measured simultaneously on adaxial and abaxial surfaces with two diffusion porometers (Decagon SC-1, Decagon, Pullman, WA, USA). Since all the study species had amphistomatous isobilateral leaves, measurements of $g_s$ at each surface were averaged among leaves, and summed within each leaf for total leaf $g_s$. Immediately after stomatal conductance was measured, leaves were excised for immediate (i.e. less than 20 seconds between excision and measurement) measurement of leaf water potential ($\Psi_l$, MPa) using a portable pressure chamber (Model 1000 Pressure Chamber, PMS Instruments OR, USA). Hourly measurements were made over the daytime (0600 – 1800 hr) for one day per species in February and May 2011.

For the analysis of gas exchange measurements, since they were collected in different campaigns, comparisons among the species were limited to a time frame with similar light ($Q$ between 25-100 µmol m$^{-2}$ s$^{-1}$), temperature ($T$ between 10 – 15 °C) and humidity conditions (VPD between 0.5 – 1.0 kPa) among the sites.

2.2.4 Leaf anatomy

For each species, three leaves from three different branches were randomly selected to measure stomatal traits using scanning electron microscopy of the leaf surface. A subsample (about 5 mm × 5 mm) was cut from the middle third of each leaf and specimens were fixed in glutaraldehyde (2.5% aqueous) in 0.1 M phosphate buffer pH 6.9 and post-fixed in OsO$_4$ (1% aqueous). Fixing the samples with glutaraldehyde was undertaken in the field to minimize the effect on stomatal apertures. Specimens were dehydrated through an ethanol series, critical point dried and mounted on aluminium stubs using carbon tabs, and were sputter-coated with gold. Specimens were imaged in a Philips XL30 scanning...
electron microscope and images were analysed using ImageJ software (National Institute of Health, USA) for stomatal size and frequency.

Based on the original theory of Brown and Escombe (1900) and the developed equation of Franks and Beerling (2009) (Equation 2.6), potential maximum stomatal conductance ($g_{\text{max}}$) was estimated from measures of stomatal size and density:

$$g_{\text{max}} = \frac{d_w}{v_w} \cdot D \cdot a_{\text{max}} \left( l + \frac{\pi}{2} \sqrt{a_{\text{max}} / \pi} \right)$$

(2.6)

where $d_w$ is the diffusivity of water vapour in the air ($\text{m}^2 \text{s}^{-1}$), $v_w$ is the molar volume of air ($\text{m}^3 \text{mol}^{-1}$), $D$ is stomatal density, $a_{\text{max}}$ is the maximum area of the open stomatal pore (estimated from the pore length), and $l$ is the pore depth. Pore depth is assumed equal to guard-cell width per Franks and Beerling (2009).

### 2.3 Results

In general, environmental variables showed that *E. dives* sites had the driest soil and atmosphere, and *E. delegatensis* had the least dry atmosphere among all ($p < 0.05$, Table 2.1). Average soil moisture was greatest in *E. pauciflora* during the measurement period, and it also varied the least (fluctuated 2% compared to 12% at the other sites). Individual trees used on average 37.2 L day$^{-1}$ water for *E. delegatensis*, 16.7 L day$^{-1}$ for *E. radiata*, 14.3 L day$^{-1}$ for *E. dives*, and 6.0 L day$^{-1}$ for *E. pauciflora* (Table 2.2).
Table 2.1. Description of the sites within the Cotter catchment. Data are daily means for 27 October 2010 – 12 August 2011 (when environmental data overlap). Sites no. 1, 2 and 3 (underlined) are further selected for the analysis of tree and leaf level water use, and significant differences in environmental variables among the three sites are denoted with different letters (ANOVA, \( p < 0.05 \)). Soil classification is based on recent measurements by J. Henry (unpublished data).

<table>
<thead>
<tr>
<th>Species</th>
<th>( E. ) delegatensis</th>
<th>( E. ) radiata</th>
<th>( E. ) pauciflora</th>
<th>( E. ) delegatensis</th>
<th>( E. ) radiata</th>
<th>( E. ) pauciflora</th>
<th>( E. ) dives</th>
<th>( E. ) dives</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site no.</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1250</td>
<td>1100</td>
<td>1650</td>
<td>1493</td>
<td>1130</td>
<td>1496</td>
<td>1234</td>
<td>1138</td>
</tr>
<tr>
<td>Aspect (°)</td>
<td>227</td>
<td>315</td>
<td>81</td>
<td>165</td>
<td>227</td>
<td>155</td>
<td>310</td>
<td>48</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>15</td>
<td>5</td>
<td>57</td>
<td>26</td>
<td>47</td>
<td>13</td>
<td>18</td>
<td>21</td>
</tr>
<tr>
<td>Australian soil classification order</td>
<td>Dermosol</td>
<td>Kandosol</td>
<td>Dermosol</td>
<td>Kurosol</td>
<td>Rudosol</td>
<td>Kurosol</td>
<td>Dermosol</td>
<td>Dermosol</td>
</tr>
<tr>
<td>DBH range (cm)</td>
<td>23.5 - 86.5</td>
<td>10.5 - 74</td>
<td>10.1 - 65.6</td>
<td>11.9 – 103.5</td>
<td>10.1 - 81</td>
<td>11.2 – 77.3</td>
<td>12.5 - 61.8</td>
<td>16 - 77.5</td>
</tr>
<tr>
<td>Approximate mean height (m)</td>
<td>43</td>
<td>20</td>
<td>17</td>
<td>31</td>
<td>10</td>
<td>17</td>
<td>15</td>
<td>28</td>
</tr>
<tr>
<td>Mid 50% of DBH</td>
<td>52.5 – 64.4</td>
<td>25.8 - 45.7</td>
<td>18.6 – 27.5</td>
<td>27.9 – 48.2</td>
<td>15.7 - 33.1</td>
<td>19.1 - 31</td>
<td>21.8 - 37.3</td>
<td>28.6 – 48.5</td>
</tr>
<tr>
<td>Stand density (stem ha(^{-1}))</td>
<td>188</td>
<td>260</td>
<td>640</td>
<td>336</td>
<td>428</td>
<td>408</td>
<td>188</td>
<td>324</td>
</tr>
<tr>
<td>Basal area (m(^2) ha(^{-1}))</td>
<td>50.7</td>
<td>29.1</td>
<td>31.4</td>
<td>53.8</td>
<td>28.3</td>
<td>30.7</td>
<td>15.8</td>
<td>44.6</td>
</tr>
<tr>
<td>Leaf area index (m(^2) m(^{-2}))</td>
<td>1.30</td>
<td>1.02</td>
<td>0.93</td>
<td>1.13</td>
<td>1.02</td>
<td>1.12</td>
<td>0.75</td>
<td>1.00</td>
</tr>
<tr>
<td>Sapwood density (g cm(^{-3}))</td>
<td>0.520</td>
<td>0.496</td>
<td>0.578</td>
<td>0.526</td>
<td>0.481</td>
<td>0.560</td>
<td>0.506</td>
<td>0.515</td>
</tr>
<tr>
<td>Air temperature (°C)</td>
<td>7.4(^{\text{a}})</td>
<td>7.3(^{\text{a}})</td>
<td>5.2(^{\text{b}})</td>
<td>6.0</td>
<td>7.4</td>
<td>6.0</td>
<td>7.4</td>
<td>7.8</td>
</tr>
<tr>
<td>Relative humidity (%)</td>
<td>91.3(^{\text{a}})</td>
<td>85.3(^{\text{b}})</td>
<td>85.2(^{\text{c}})</td>
<td>80.2</td>
<td>86.7</td>
<td>80.2</td>
<td>83.7</td>
<td>83.8</td>
</tr>
<tr>
<td>Vapour pressure deficit (kPa)</td>
<td>0.13(^{\text{a}})</td>
<td>0.22(^{\text{b}})</td>
<td>0.17(^{\text{c}})</td>
<td>0.23</td>
<td>0.20</td>
<td>0.23</td>
<td>0.23</td>
<td>0.24</td>
</tr>
<tr>
<td>Soil moisture at 30 cm (%)</td>
<td>22.2(^{\text{a}})</td>
<td>20.1(^{\text{b}})</td>
<td>27.0(^{\text{c}})</td>
<td>23.4</td>
<td>21.5</td>
<td>23.4</td>
<td>13.3</td>
<td>19.1</td>
</tr>
<tr>
<td>Soil moisture at 60 cm (%)</td>
<td>16.6(^{\text{a}})</td>
<td>15.8(^{\text{a}})</td>
<td>22.2(^{\text{b}})</td>
<td>19.0</td>
<td>17.7</td>
<td>19.0</td>
<td>18.6</td>
<td>23.9</td>
</tr>
</tbody>
</table>
Figure 2.2. Relationship between stem diameter (DBH) and sapwood area. Lines are least-squares regressions, based on power functions ($Y = Y_0 X^b$) applied in similar studies (Meinzer et al. 2005; Oishi et al. 2010; Vertessy et al. 1995).

- **E. delegatensis (Site no. 1)**
  - $y = 0.003x^{2.72}$
  - $R^2 = 0.92$

- **E. delegatensis (Site no. 4)**
  - $y = 0.791x^{1.54}$
  - $R^2 = 0.81$

- **E. radiata (Site no. 2)**
  - $y = 1.488x^{1.54}$
  - $R^2 = 0.78$

- **E. radiata (Site no. 5)**
  - $y = 0.104x^{2.04}$
  - $R^2 = 0.82$

- **E. pauciflora (Site no. 3)**
  - $y = 2.279x^{1.11}$
  - $R^2 = 0.88$

- **E. pauciflora (Site no. 6)**
  - $y = 0.104x^{2.04}$
  - $R^2 = 0.82$

- **E. dives (Site no. 7)**
  - $y = 0.075x^{2.08}$
  - $R^2 = 0.98$

- **E. dives (Site no. 8)**
  - $y = 0.021x^{2.40}$
  - $R^2 = 0.64$
2.3.1  **Control of tree water use**

Total sap flow per tree is governed by two factors: sap flux (sap flow per unit functional sapwood area) and actual sapwood cross-sectional area. Linear regression analysis showed that tree water use increased significantly with increase in tree diameter \( (r^2 = 0.62) \) and height \( (r^2 = 0.45) \) (Figure 2.3). Cross-sectional sapwood area also increased in relation to tree diameter \( (r^2 = 0.81) \); hence, *E. delegatensis* trees had the greatest sap flow rates (Table 2.2). Tree diameter and height, however, were not strong predictors of sap flow \( (p > 0.05) \), which is consistent with other eucalypt forests in Australia (Macfarlane et al. 2010), but differs from other montane broad-leaved forests (Motzer et al. 2005).

Vapour pressure deficit at the forest floor reached up to 3.5 kPa across the species for the period of study, and maximum sum of \( Q \) received was 36 mol m\(^{-2}\) day\(^{-1}\). Among the three sites selected for further analysis, VPD varied between 0 and 0.8 kPa for the *E. delegatensis*, between 0 and 1.3 kPa for *E. pauciflora*, and between 0.02 and 0.84 kPa for *E. radiata*. Average daily sap velocity (mean ± se) was 4.98 ± 0.33 cm hr\(^{-1}\) for *E. delegatensis*, 3.53 ± 0.17 for *E. radiata*, and 2.34 ± 0.20 cm hr\(^{-1}\) for *E. pauciflora*, between May 2011 and February 2012.

Radiation and VPD are often found to be the most important controls of tree water use (Oren et al. 1999a; Pallardy and Kozlowski 1979; Zeppel et al. 2004). To distinguish the effect of co-varying \( Q \) and VPD on sap flow for *E. delegatensis*, *E. radiata*, *E. pauciflora*, and *E. dives*, sap velocity is plotted against VPD at two main classes of \( Q \) in Figure 2.4. During high radiation period \( (Q > 50 \, \mu \text{mol m}^{-2} \text{ s}^{-1}) \) tree water use increased linearly with increase in VPD, until under conditions of VPD > 1 kPa sap flow became limited and relatively insensitive to either \( Q \) or VPD (the asymptotic part of the relationship in Figure 2.4).
Table 2.2. Total daily tree water use ($F_s$), and maximum daily sap velocity ($V_{\text{max}}$) of water use for our study trees over the 181 days for which sap flow data overlap (May 2011-December 2011). Values in parentheses show standard error of the mean. DBH = stem diameter at breast height.

<table>
<thead>
<tr>
<th>Species</th>
<th>Site no.</th>
<th>Tree height (m)</th>
<th>DBH (cm)</th>
<th>Sapwood area (cm$^2$)</th>
<th>$F_s$ (L day$^{-1}$)</th>
<th>$V_{\text{max}}$ (cm hr$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. delegatensis</td>
<td>1</td>
<td>57.1</td>
<td>86.0</td>
<td>775</td>
<td>91.3 (3.0)</td>
<td>11.1 (0.3)</td>
</tr>
<tr>
<td>E. delegatensis</td>
<td>1</td>
<td>50.1</td>
<td>66.0</td>
<td>244</td>
<td>17.8 (0.6)</td>
<td>7.4 (0.2)</td>
</tr>
<tr>
<td>E. delegatensis</td>
<td>1</td>
<td>36.9</td>
<td>58.0</td>
<td>222</td>
<td>40.5 (1.5)</td>
<td>18.9 (0.5)</td>
</tr>
<tr>
<td>E. radiata</td>
<td>2</td>
<td>24.7</td>
<td>53.3</td>
<td>386</td>
<td>50.9 (0.9)</td>
<td>13.2 (0.3)</td>
</tr>
<tr>
<td>E. radiata</td>
<td>2</td>
<td>19.3</td>
<td>39.0</td>
<td>248</td>
<td>22.2 (0.6)</td>
<td>13.3 (0.4)</td>
</tr>
<tr>
<td>E. radiata</td>
<td>2</td>
<td>9.3</td>
<td>22.1</td>
<td>106</td>
<td>5.7 (0.1)</td>
<td>6.3 (0.1)</td>
</tr>
<tr>
<td>E. pauciflora</td>
<td>3</td>
<td>15.6</td>
<td>34.0</td>
<td>92</td>
<td>4.3 (0.2)</td>
<td>5.0 (0.2)</td>
</tr>
<tr>
<td>E. pauciflora</td>
<td>3</td>
<td>17.6</td>
<td>32.5</td>
<td>151</td>
<td>15.7 (0.7)</td>
<td>11.6 (0.4)</td>
</tr>
<tr>
<td>E. pauciflora</td>
<td>3</td>
<td>8.6</td>
<td>13.3</td>
<td>35</td>
<td>1.8 (0.1)</td>
<td>5.9 (0.2)</td>
</tr>
<tr>
<td>E. delegatensis</td>
<td>4</td>
<td>26.2</td>
<td>38.2</td>
<td>217</td>
<td>27.6 (1.5)</td>
<td>15 (0.7)</td>
</tr>
<tr>
<td>E. delegatensis</td>
<td>4</td>
<td>35.2</td>
<td>49.2</td>
<td>397</td>
<td>8.9 (0.5)</td>
<td>3.0 (0.1)</td>
</tr>
<tr>
<td>E. delegatensis</td>
<td>4</td>
<td>37.7</td>
<td>46.7</td>
<td>366</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>E. radiata</td>
<td>5</td>
<td>9.4</td>
<td>16.4</td>
<td>45</td>
<td>8.3 (0.2)</td>
<td>18.1 (0.3)</td>
</tr>
<tr>
<td>E. radiata</td>
<td>5</td>
<td>9.4</td>
<td>28.4</td>
<td>72</td>
<td>7.0 (0.2)</td>
<td>9.1 (0.1)</td>
</tr>
<tr>
<td>E. radiata</td>
<td>5</td>
<td>15.2</td>
<td>40.6</td>
<td>233</td>
<td>6.0 (0.3)</td>
<td>4.3 (0.1)</td>
</tr>
<tr>
<td>E. pauciflora</td>
<td>6</td>
<td>13.4</td>
<td>16.2</td>
<td>3</td>
<td>0.04 (0.0)</td>
<td>1.7 (0.1)</td>
</tr>
<tr>
<td>E. pauciflora</td>
<td>6</td>
<td>15.5</td>
<td>20.7</td>
<td>35</td>
<td>5.1 (0.2)</td>
<td>15.7 (0.5)</td>
</tr>
<tr>
<td>E. pauciflora</td>
<td>6</td>
<td>17.6</td>
<td>32.5</td>
<td>151</td>
<td>9.3 (0.4)</td>
<td>7.4 (0.3)</td>
</tr>
<tr>
<td>E. dives</td>
<td>7</td>
<td>8.1</td>
<td>15.2</td>
<td>17</td>
<td>2.8 (0.0)</td>
<td>19.2 (0.4)</td>
</tr>
<tr>
<td>E. dives</td>
<td>7</td>
<td>8.9</td>
<td>26.3</td>
<td>83</td>
<td>11.5 (0.3)</td>
<td>19.8 (0.5)</td>
</tr>
<tr>
<td>E. dives</td>
<td>7</td>
<td>17.1</td>
<td>46.2</td>
<td>219</td>
<td>34.4 (0.8)</td>
<td>19.1 (0.6)</td>
</tr>
<tr>
<td>E. dives</td>
<td>8</td>
<td>17.7</td>
<td>23.5</td>
<td>56</td>
<td>3.9 (0.1)</td>
<td>10.4 (0.3)</td>
</tr>
<tr>
<td>E. dives</td>
<td>8</td>
<td>37.4</td>
<td>63.2</td>
<td>350</td>
<td>17.5 (0.3)</td>
<td>6.6 (0.2)</td>
</tr>
<tr>
<td>E. dives</td>
<td>8</td>
<td>34.9</td>
<td>32.0</td>
<td>97</td>
<td>15.6 (0.4)</td>
<td>18.5 (0.3)</td>
</tr>
</tbody>
</table>
Figure 2.3. Average daily tree water use (May 2011- December 2012) as a function of tree diameter ($r^2 = 0.62$) and height ($r^2 = 0.45$). Data are pooled for all species.
Figure 2.4. Sap velocities in relation to vapour pressure deficit (VPD) for eight sites (four species) across the catchment. Symbols indicate different time of the day (night time is when $Q < 50 \text{ µmol m}^{-2} \text{s}^{-1}$ and normally between 1500 h and 0600). Data are between January-May 2012, due to failure in sensors at sites no. 1 and no. 8 during this period data is presented for six sites only. Regression functions between VPD and sap flow rates for the sites that were selected for further analysis are for \textit{E. radiata} (no. 2): $y = 0.73 \ln(x) + 3.59$, $r^2 = 0.42$ during night time and $y = 1.99 \ln(x) + 8.56$, $r^2 = 0.81$ during daytime, and for \textit{E. pauciflora} (no. 3) $y = 0.37 \ln(x) + 1.72$, $r^2 = 0.44$ night time and $y = 1.57 \ln(x) + 5.84$, $r^2 = 0.67$ during daytime.

Ratio of sap flux to vapour pressure deficit (a proxy for canopy conductance) for the three selected species, was significantly larger in \textit{E. delegatensis} than the other two species ($p <$
0.05). This ratio in *E. delegatensis* was 64% larger than that in *E. pauciflora*, and 68% larger than *E. radiata*, during a 107 day period, from April to August 2011. This is in contrast with observations at the leaf scale, where stomatal conductance in *E. pauciflora* is two-fold stomatal conductance of *E. radiata* (*p* < 0.05).

Rates of tree water use were linearly related to daily sum of $Q$ for all three selected species, although the strength of this relationship varied among species (Figure 2.5). Results of generalized additive modelling for determining the most important control on tree water use among vapour pressure deficit, total daily sum of $Q$ and soil relative water content at 30 cm and 60 cm, showed that soil moisture was not an important control for daily sap flow in either *E. pauciflora* or *E. radiata*, and that VPD and the daily sum of $Q$ were the most important variables for both species (Table 2.3). At the daily scale $Q$ had the greatest effect on tree water use for both species. For *E. pauciflora* VPD was the second most influential environmental factor on tree water use, but this influence was weaker in *E. radiata*. At a sub-daily basis, VPD was a better predictor of tree water use than $Q$, and soil moisture had a significant but marginal influence on both species (Table 2.3).

![Figure 2.5. Dashed line shows the linear relationship between total $Q$ received per day and sap velocity (*E. delegatensis* $r^2 = 0.65$, *E. radiata* $r^2 = 0.71$, *E. pauciflora* $r^2 = 0.78$) for 55 days in summer (from 5 February to 30 March 2012, *p* < 0.0001).]
The three selected species had generally sparse canopy structures (Table 2.1). A very coarse estimate of equivalent stand-level water use (mm day$^{-1}$) can be computed for each sampled tree as the product of average daily sap velocity, sapwood area and stand density. This leads to ranges of 0.13 – 0.54 mm day$^{-1}$ for *E. pauciflora*, 0.23 – 0.85 mm day$^{-1}$ for *E. radiata*, and 0.50 – 1.74 mm day$^{-1}$ for *E. delegatensis*, and averages among sampled trees of 0.33, 0.54 and 0.93 mm day$^{-1}$, respectively.

**Table 2.3.** Results of Generalized Additive Model (GAM) analysis on four environmental variables. The reduction in AIC and associated significance is given for each variable. Data belong to 53 days where environmental and sap flow data overlap, between March and May 2012. Data for *E. delegatensis* is missing during this period due to instruments malfunction.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Daily</th>
<th>Hourly</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Δ AIC</td>
<td>p</td>
</tr>
<tr>
<td>Q</td>
<td>-16.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>VPD</td>
<td>-23.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>rwc30</td>
<td>-21.8</td>
<td>n.s.</td>
</tr>
<tr>
<td>rwc60</td>
<td>1.9</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

**2.3.2 Leaf water relations**

Stomatal conductance was significantly greater ($p < 0.05$) in *E. pauciflora* than *E. radiata* but not significantly different from *E. delegatensis* (Figure 2.6a). *E. pauciflora* also had the lowest instantaneous transpiration efficiency (ITE, the ratio of photosynthesis to transpiration) compared to *E. radiata* and *E. delegatensis* both of which having a similar ITE (Figure 2.6b). Net photosynthesis rate was not significantly different among the species (Figure 2.6c).

Generally $g_s$ decreased with increasing VPD; with different sensitivity of stomata to VPD amongst species (Figure 2.7): standardized regression slopes ($\beta$) showed that $g_s$ is most sensitive to atmospheric VPD for *E. delegatensis* and *E. pauciflora*, and insensitive to VPD for *E. radiata* ($\beta = -0.07$, $p > 0.05$), compared to $\beta = -0.65$ and $\beta = -0.63$ in *E. delegatensis* and *E. pauciflora* respectively ($p < 0.05$ in both cases). These observations also concur with the theory of Oren et al. (1999b); that higher $g_s$ at low VPD (VPD =
1kPa) is an indicator of greater sensitivity to VPD (at VPD of 1 kPa, gs for *E. delegatensis*, *E. pauciflora* and *E. radiata* was 0.177, 0.261 and 0.125 mol m\(^{-2}\) s\(^{-1}\) respectively).

*Q* also significantly influenced *gs* (shown as the curvilinear relationship shown in Figure 2.7d). As *Q* increased in the presence of reduced VPD, increases in *gs* were primarily driven by radiation, and conversely, stomatal closure in the afternoon was induced by large VPD. A simple relationship was derived between stomatal conductance and both *Q* and VPD (pooled for the three species, *p* < 0.05):

\[
g_s = 0.203 \cdot e^{-0.027V_{PD}/Q} \tag{2.7}
\]

Stomatal conductance was negatively related to *ψ_1* in all three species (Figure 2.8), the three study species displayed different sensitivities however; *E. delegatensis* incurred reduced *gs* at leaf water potentials of -1.3 MPa, while *E. radiata* did not reduce *gs* until *ψ_1* reached -1.5 MPa (Figure 2.8).
Figure 2.6. a) Stomatal conductance ($g_s$), b) instantaneous transpiration efficiency (ITE), and c) net photosynthesis ($A$) for a time frame with similar light ($Q$ between 25-100 µmol m$^{-2}$ s$^{-1}$), temperature ($T$ between 10 – 15 °C) and humidity conditions (VPD between 0.5 – 1.0 kPa) among species. Error bars represent 95% confidence intervals.
2.3.3 Stomatal characteristics

Stomatal density was similar for all species (~164 mm\(^{-2}\), \(p > 0.05\)), but there was significant among-species variations in other stomatal characteristics, such as length of stomatal pore and the extent of the cuticular ledge over the stomatal complex. The extent of the cuticular ledge was so great in \(E.\) pauciflora and \(E.\) delegatensis that less than 10% of the pore-space remained uncovered, significantly greater than the 40% of exposed pore-space for stomata of...
Figure 2.8. VPD condition above the canopy, stomatal conductance and leaf water potential (ψl) measured at our three sites in February (a-c) and May (d-f) 2011. Each data point (in panels b,c,e,f) is mean ± se of mean among three trees on each of which three leaves were measured.

E. radiata leaves (Figure 2.9, Figure 2.10a). While stomatal pore length was smallest in E. radiata, this species also had the largest depth of the diffusion path (Figure 2.10b, c). Depth of the diffusion path, which is assumed to be equal to the guard cell width on the grounds that inflated guard cells are typically circular in cross-section (Franks and Beerling 2009; Lammertsma et al. 2011), and the stomatal pore length, are determining factors in controlling potential maximum stomatal conductance (g_max). Based on the original theory of Brown and Escombe (1900) and the developed equation of Franks and Beerling (2009)
(Equation 2.6), while assuming similar diffusivity of water vapour in the air \((0.257 \text{ cm}^2 \text{ s}^{-1})\) and molar volume of water \((22.414 \text{ mol}^{-1})\) for all species, \(g_{\text{max}}\) was estimated \(0.976 \text{ mol m}^{-2} \text{ s}^{-1}\) in average for \(E. \text{ pauciflora}\), \(0.844 \text{ mol m}^{-2} \text{ s}^{-1}\) for \(E. \text{ delegatensis}\), and \(0.678 \text{ mol m}^{-2} \text{ s}^{-1}\) for \(E. \text{ radiata}\). Potential \(g_{\text{max}}\) in \(E. \text{ pauciflora}\) was 45 % larger than \(E. \text{ radiata}\), and in \(E. \text{ delegatensis}\) was 24% larger than \(E. \text{ radiata}\) \((p < 0.05)\).

![Figure 2.9](image)

**Figure 2.9.** Scanning electron micrographs of stomatal complexes showing cuticular ledge over the stomatal antechamber for a) \(E. \text{ radiata}\), b) \(E. \text{ delegatensis}\), and c) \(E. \text{ pauciflora}\). Individual panel width is app. 5 μm.

### 2.4 Discussion

Sap flow, leaf physiology and stomatal features of the most dominant eucalypts within high-country catchments of south-east Australia was measured in this study. The three chosen species occupy different environments; \(E. \text{ pauciflora}\) grows at the highest elevations and experiences the greatest variation in temperature, \(E. \text{ delegatensis}\) grows on southern aspects and protected slopes, and \(E. \text{ radiata}\) is generalists found at the lowest elevation on all aspects. The results provide quantitative insights into the main processes controlling transpiration at leaf and tree scales for these distinct species. Water relations and stomatal anatomy varied largely among those species with distinct distributions within the landscape.
2.4.1 Environmental regulation of transpiration

In the high country, sap flow was largely governed by the atmospheric environment – mainly vapour pressure deficit and radiation (compared to soil moisture). Sap flow measurements from similar forests in Victoria observed no influence of wind speed on tree water use (Buckley et al. 2011; Ch.4, Gharun et al. 2013b). Although the effect of wind speed on tree water use might vary with site conditions (Phillips et al. 2010; Zeppel et al. 2010), the canopies of eucalypt forests are well coupled with the atmosphere (Hutley et al. 2000) and transpiration rates are closely coupled with the atmospheric VPD. Changes in the VPD and stomatal conductance therefore exert much stronger impact on transpiration (Jarvis and McNaughton 1986). Therefore, generally little effect of wind speed and consequently low influence of aerodynamic conductance on tree water use is expected in well-ventilated eucalypt canopies studied here.
Soil moisture within the top 60 cm of the soil was not an important control of daily sap flow in either *E. pauciflora*, *E. radiata* or *E. delegatensis* as previously investigated by Buckley et al. (2012). These findings question the general hypothesis that the top 35 cm of the soil provide most (more than 90%) of the water required for transpiration (Oren et al. 1998). The lack of a strong influence on tree sap flow from the moisture in the upper soil layers could relate to: 1) trees possibly not having experienced sufficient drought during the measurements period, although even in climates with seasonal drought soil moisture can be less influential compared to other environmental variables (Gebauer 2010), 2) trees might have a very conservative utilisation of soil water, which adjusts to drought via stomatal control of water loss, rather than via osmotic properties (Körner and Cochrane 1985), 3) extraction of water from deep soil layers that can enable eucalypt species to maintain transpiration even during dry periods (Leuning et al. 2005, Mitchell et al. 2012). The actual water available to trees for a given species primarily depends on the root density and distribution (Crombie et al. 1988, Callaway 1990) and Eucalyptus species are generally known to extend active roots below 7 m (Ashton 1975, Silberstein et al. 2001) that can be responsible for the bulk of the water uptake (Lai and Katul 2000).

Rates of sap flow did not relate to tree size for the montane eucalypt species. While these results are consistent with similar observations from Jarrah forests (*E. marginata*) in Western Australia (Macfarlane et al. 2010), or *E. sieberi* and *E. regnans* forests in south-east Australia (Roberts et al. 2001; Vertessy et al. 2001), they are in contrast with those observations from humid tropical forests (Horna et al. 2011; Meinzer et al. 2001) where tree diameter accounts for more than 90% variations in rates of sap flow (Meinzer et al. 2001). An important implication from these results is that the size-class approach for scaling individual tree water use to whole stand, where trees are divided into size classes and transpiration is weighted according to the number of trees in each class (Köstner et al. 2002), would not be a suitable upscaling approach for this type of forest.

Leaf level measurements (i.e. stomatal conductance and potential maximum stomatal conductance estimated from stomatal geometry) exhibited differential responses compared to canopy conductance (i.e. whole tree) supporting the hypothesis that hydrologic response of montane eucalypt species depends on the scale of observations. This study confirms that stomatal conductance does not necessarily predict sap flow, and question the validity of an approach in which sap flow rates are used as an approximation of plant hydraulic conductance.
Stomatal closure at high VPD is a feedback response exhibited by isohydric species to prevent excessive dehydration and physiological damage by maintaining leaf water potential above a minimum limit (Saliendra et al. 1995). In this sense, regulation of stomatal conductance by VPD indicates a species’ tolerance to atmospheric drought (Kolb and Stone 2000). Among the three species studied, the lack of relationship between $g_s$ and VPD in *E. radiata* (Figure 2.7c) indicates that this species had the greatest tolerance toward atmospheric water stress, which might explain its wider distribution across elevations, temperature gradients and site conditions. Conversely, *E. delegatensis* and *E. pauciflora* were more sensitive to atmospheric drought (Figure 2.7 a-b).

In addition to stomatal sensitivity toward VPD, *E. radiata* exhibited greater seasonal differences in midday leaf water potential (56% compared to 28% and 38% in the other two species, $p < 0.001$) (Figure 2.8c and f), indicating that this species is less isohydric than the other two species examined in this study (Franks et al. 2007).

Often a distinction between isohydric and anisohydric strategies is not clear, and species can exhibit both contrasting hydraulic behaviours (Domec and Johnson 2012; Franks et al. 2007; Zhang et al. 2012). In this study, the two species growing on sites with more soil moisture exhibited higher stomatal conductance (*E. delegatensis* and *E. pauciflora*) and this isohydric behaviour (Franks et al. 2007) allowed them to maintain similar leaf water potential (Figure 2.8c and f, $p > 0.05$), despite significant differences in the site conditions (Table 2.1, $p < 0.05$) (Fernandez et al. 2011).

Drought tolerance has a direct role in determining species distribution with respect to local and regional water availability (Engelbrecht et al. 2007). In Australia, Pook et al. (1966) and Morgan (2004) suggest occasional periods of severe summer-autumn drought as a contributory factor in distribution of dry sclerophyll species (e.g. *E. radiata*) within the study area. The less isohydric behaviour allows the *E. radiata* species to grow on drier sites with shallow rocky soil and tolerate drought better (McDowell 2011). The distribution of *E. delegatensis* suggests a pattern of avoidance of soil drought – it is strongly restricted to less water limited slopes and protected southern aspects (Adams 1995).

This view of *E. delegatensis* is also supported by the coarse estimates of equivalent plot-level water use for each species, which averaged 0.33, 0.54 and 0.93 mm day$^{-1}$ among trees for *E. pauciflora*, *E. radiata* and *E. delegatensis*, respectively. Whilst these estimates are strictly preliminary (reliable scaling would require measurements of sap flow across the
range of tree sizes for each species), the estimate for *E. delegatensis* is similar to values recently measured in mature plots of this species in Victoria (1.1 mm day$^{-1}$, App.A Buckley et al. 2012). The latter study also found that periodic soil droughts up to several weeks in duration did not strongly reduce diurnal water use in mature trees of this species, and this study shows strong diurnal regulation of water use by atmospheric drought. Together these results inform a growing understanding of the central role of atmospheric drought in the physiological ecology of montane eucalypts.

2.4.2 Physiological regulation of stomatal conductance and transpiration

The primary environmental factors controlling stomatal conductance in leaves of *E. delegatensis*, *E. radiata* and *E. pauciflora* are light and vapour pressure deficit. This conclusion is consistent with observations from other studies on *E. pauciflora* (Körner and Cochrane 1985) and other montane broad leaved forest trees (Motzer et al. 2005). VPD and radiation have generally opposite effects on stomatal conductance (Meinzer et al. 1995), which in this study was expressed as the curvilinear relationship given in Equation 2.7, a similar function as that proposed by Martin et al. (1997). In the eucalypt trees studied here, radiation controls stomatal aperture until VPD reaches a maximum threshold; a mechanism that limits water loss from the plant with a species-specific sensitivity to VPD.

Stomatal conductance was negatively related to leaf water potential in all three species, which is consistent with many other eucalypt trees (e.g. Körner and Cochrane 1985; Whittington and Sinclair 1988). The earlier closure of stomata in *E. delegatensis* (Figure 2.8) may be a result of hydraulic limitations of taller trees, because hydraulic resistance increases as trees grow taller and leaf stomata in trees with higher resistance close earlier in the day, to prevent any cavitation damage to the tree (Ryan and Yoder 1997; Yoder et al. 1994).

2.4.3 Structural regulation of stomatal conductance

Leaves are the predominant site of gas exchange between a plant and its atmosphere, and their physiology and morphology adapt to maximise carbon gain whilst limiting water loss. Stomatal anatomy plays a role in regulating gas exchange, because potential maximum $g_s$ is related to stomatal density and stomatal size (Franks and Beerling 2009; Lammertsma et al. 2011). Evidence suggests that leaves with small stomatal complexes have greater maximum $g_s$ for the same total stomatal pore area, because smaller stomata have a shorter diffusion path through the pore (Brown and Escombe 1900; Franks and Beerling 2009;
Lammertsma et al. 2011; Royer 2001). Results in this study are consistent with this prediction: *E. pauciflora* had the greatest measured $g_s$ and the largest potential maximum stomatal conductance as calculated from stomatal anatomy, and *E. radiata* had the smallest measured $g_s$ and the smallest potential maximum $g_s$ (cf. Figure 2.6a and Figure 2.10d).

Another stomatal anatomical feature, the extension of a cuticular ledge over the stomatal complex, may also limit maximum stomatal conductance (Roth-Nebelsick et al. 2013), and have been hypothesised to contribute to a form of hydraulic ‘risk management’ (England and Attiwill 2006). This study also supports this hypothesis; the generalist *E. radiata* displayed less conservative physiological (i.e. $g_s$ insensitive to VPD) and structural (i.e. minimal cuticular ledge) strategies for minimising leaf water loss. In contrast, *E. pauciflora* and *E. delegatensis* both displayed more conservative, lower-risk strategies ($g_s$ sensitive to VPD, well-developed cuticular ledge). *E. pauciflora* also possesses a thickened cuticle, which further prevents leaf desiccation (Körner and Cochrane 1985).

From an ecosystem point of view, this study suggests that under the scenario of severe drought, changes in VPD (e.g. due to increase in temperature) would have a different effect on the *E. delegatensis* or *E. pauciflora*, compared to *E. radiata* stands. The more isohydric behaviour of *E. delegatensis* and *E. pauciflora* might enable these species to maintain a more stable condition, with an advantage in terms of growth and carbon assimilation (Kumagai and Porporato 2012). Under optimal to moderate water availability, however, the less isohydric behaviour of *E. radiata* could be in favour of higher productivity (Kumagai and Porporato 2012; McDowell 2011; Sade et al. 2012) that supports its wider distribution; however, the soil moisture under which this species tends to lose its advantage and will not be able to recover from a stressful period needs to be determined as well.

One promising criterion to confirm drought tolerance among these eucalypt species would be to assess their xylem vulnerability to cavitation (Cochard et al. 2007; Maherali et al. 2004; Pockman and Sperry 2000; Tyree et al. 2003), especially because this criterion is predominantly associated with genotype, rather than environmental conditions (e.g. hydraulic conductivity depends mainly on the environmental conditions)(Abrantes et al. 2013; Willigen and Pammenter 1998).

While testing xylem vulnerability to cavitation was beyond the scope of this study, this aspect of plant regulation of water use deserves mentioning here. Eucalypts are generally less vulnerable to xylem embolism than many other tree species, in particular tropical
species (Prior and Eamus 2000; Tyree et al. 1998); however, there is no information for the majority of eucalypt species. Since drought-tolerant behaviour is associated with cavitation-resistant xylem and better adaptation to drier environments (Brodribb and Holbrook 2004; Clearwater and Clark 2003; Ewers et al. 2005; McDowell et al. 2008; Oren et al. 1999b) it is speculated that *E. radiata* trees have xylem that is less vulnerable to cavitation. This may enable this species to survive without the need for enhanced stomatal sensitivity to VPD, as seen in less drought-tolerant species, including the other two species examined in this study (Bush et al. 2008). Additional measurements in a wider range of site conditions are needed to confirm the generality of these results; however, they are supported by the patterns observed in the distribution of these species.

### 2.5 Conclusion

High country native eucalypt species grow at a range of altitudes where temperature, radiation and water vapour concentration differ widely. This study investigated tree water use and sensitivity to atmospheric drought among three key high-country eucalypt species, and linked water relations to aspects of stomatal physiology and structure. The primary environmental controls of water use at the leaf- and tree-level for *E. delegatensis*, *E. radiata* and *E. pauciflora* are light and vapour pressure deficit. The stomata of *E. radiata*, a generalist species that occupies a wide range of sites at moderate altitudes, were minimally sensitive to evaporative demand and had minimal cuticular ledges, with the result that water use in this species persisted during atmospheric drought. Conversely, the stomata of *E. delegatensis* and *E. pauciflora* – specialist species that occupy sun-sheltered slopes and exposed high-altitude sites, respectively – were more VPD-sensitive and had larger cuticular ledges, and as a result their water use declined during atmospheric drought. The greater tolerance of *E. radiata* to atmospheric drought may explain its wider distribution across elevations and temperature gradients, and in a variety of site conditions within the forest.
2.6 References


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3 Stand water use status in relation to fire in a mixed species eucalypt forest

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Summary

Previous research on seed-regenerating eucalypt species (e.g. ash-type eucalypts) posits that water use by regenerating forests increases quickly after fire and may exceed that of mature forests (by as much as 100%) for periods of many decades. This hypothesis has not been tested in forests dominated by re-sprouting eucalypts. This study examined the effect of fire on tree and stand-level water use in a resprouting mixed species eucalypt forests close to Stanley in north-east Victoria, Australia.

In general, rates of water use in regenerating mixed-species eucalypt forests three years after fire were very similar to those for adjacent unburnt mature forests (0.48 ± 0.14 in regenerating vs. 0.66 ± 0.17 mm day\(^{-1}\) in unburnt forest, mean ± 0.95 CIs). This clear difference between resprouters and seeders corresponds to: slower sap flow in resprouting trees; a comparatively limited increase in sapwood area index (22% compared to 70% in Alpine Ash forests); and a 20% decrease in total leaf area index after the fire. While the general climate differed little amongst study forests due to their close spatial proximity, vapour pressure deficit within unburnt was greater than regenerating forest and was the main control of tree water use, irrespective of species. Midday leaf water potential and measures of leaf physiology (except stomatal conductance) derived from gas-exchange measurements were similar between mature and resprouting trees, but the stomata of resprouting trees maintained a greater conductance to water vapour than mature leaves.

A few years after crown-removing fires, water use by resprouting mixed-species eucalypt forests was little different to nearby mature forests. These results strongly contrast post-fire patterns in water use for the seeder (ash-type) eucalypt forests.
3.1 Introduction

The mixed-species eucalypt forests of south-east Australia’s low-elevation foothills meet much of the water needs of rural communities within the Murray Darling Basin. These mixed-species forests are dominated by eucalypts that mostly regrow vegetatively after fire via sprouting from stems and large branches (epicormic buds). Fires that are of sufficient intensity to destroy forest canopies also promote the sprouting of epicormic shoots from bud tissues located below the bark. Dominance of forests by such resprouting eucalypts is generally considered to be intimately associated with fire regimes. For example, more frequent fires of lower intensity in drier forests are associated with dominance of resprouters, while seeders are dominant in wetter forests where fires are less frequent but of much higher intensity. Seeders are characterized by producing large numbers of long-lived seeds and high rates of seedling growth that benefit from the ash on the forest floor, which is rich in nutrients (Eamus et al. 2006). Regenerating via epicormic sprouts is the norm for eucalypts, as less than 10% of the more than 700 eucalypt taxa are obligate seeders (Nicolle 2006). Even so, the published literature on fire effects on hydrology of eucalypt forests is overwhelmingly focused on ash forests where seeders dominate.

Catchment management, including guiding hydrological models, has thus often been based on conceptual understandings that are based on responses to fire by ash-type forests. Currently, management relies on generalizations based on the response of ash-type forests (e.g. Watson et al. 1999) where the landscape is transformed into mosaics of even-aged regenerating forest (Kuczera 1987; Langford 1976). These conceptual (and empirical and mechanistic) models predict a reduction in yield that can persist for many decades (Dunn and Connor 1993; Vertessy et al. 1995; Vertessy et al. 1997; Vertessy et al. 2001). Recently, Buckley et al. (2012) showed that within seven years of a major bushfire in Alpine Ash (Eucalyptus delegatensis) forest, transpiration ($E_t$) had increased more than two-fold, suggesting a major reduction in water yield (consistent with the Kuczera-type response).

With the exception of Alpine Ash forests (Buckley et al. 2012), we know little of the dynamics of forest water use in the first few years after fire in seeder eucalypt forests and almost nothing about fire effects for resprouting mixed-species forests. Changes in $E_t$ following bushfires may be due to many factors, including the structure and density of forests. Stream flow from eucalypt-dominated catchments is strongly leveraged to tree
water use given that as much as 80% of incoming rainfall is returned to the atmosphere via \( E_t \) (Adams and Attiwill 2011) and small changes in \( E_t \) at the landscape scale result in large proportional changes in run-off. As recently highlighted by Roderick and Farquhar (2011) in their development of the utility of Budyko approaches to predicting water yield, there is a profound lack of a broadly based knowledge of the effects of fire on \( E_t \), especially in forests other than ash type where large areas were burnt by high intensity wildfires over the last decade (Attiwill and Adams 2013).

Past hydrological research in mixed-species eucalypt forests has focused on drought (Mitchell et al. 2012) and silvicultural regime (Cornish 1993; Cornish and Vertessy 2001; Lane and Mackay 2001) effects on catchment water yield. While the water yield effects of regeneration processes in mixed-species forests have not been documented, they seem unlikely to mirror those of ash-type forests. Trees that regenerate by seed tend to create even-aged forests whereas forests of trees that regenerate vegetatively are characteristically multi-aged (Attiwill 1994). This complex structure means that generalisations about stand water use based on ash-type forests cannot be applied with confidence. Further complications arise from the multiple eucalypt species that form the forest canopy, and the variation in soils upon which these forests grow.

At least eight species of peppermints (e.g. *Eucalyptus radiata*, *E. dives*), stringybarks (e.g. *E. obliqua*, *E. macrorhyncha*, *E. baxteri*) boxes (e.g. *E. goniocalyx*, *E. polyanthemos*) and gums (*E. mannifera*, *E. globulus*), each with its own structure and physiology, contribute to mature canopies in mixed species forests in south-eastern Australia. In contrast to adjacent ash-type forests that grow on deep, mostly homogenous and well-structured soils (Lacey and Grayson 1998), mixed-species eucalypt forests grow upon heterogeneous substrates of varying structure and moisture-holding capacities. Typical soils range from shallow duplex profiles, with high proportions of sand and rock that typify steep slopes and higher peaks, to weakly bleached yellowish gradational soils or friable reddish gradational soils that are found on low-elevation sites (Clutterbuck and McLennan 1978).

In the context of climate change, and increasing frequency of high intensity bushfires and longer fire seasons (Lucas et al. 2007), the effects of fire on water use by mixed-species forests, and consequently catchment water yield, are of increasing scientific interest. The effects on water yield for the first ten or so years post-fire have not been studied in detail. This study sought to address the serious lack of knowledge of the stand-level hydrology of mixed-species eucalypt forests for the post-fire period in which they contain leaves of
juvenile form growing on epicormic branches along the entire height of the tree. Study sites were located in north-east Victoria, Australia, in forest that was burnt in 2009. It was hypothesised that water use in the mixed-species forest would not increase significantly after fire.

3.2 Methods

3.2.1 Site description

The study area is located within the Stanley State Forest, approximately 10 km to the south of Beechworth in north-eastern Victoria (36° 25’ S, 146° 43’ E). Mean annual rainfall (1971-2000) is 1014 mm with 90 days rainfall > 1 mm (Australian Bureau of Meteorology). The geology of the area is characterized by Ordovician aged sediments with sandstone, shale and mudstone horizons within fractured bedrock (Hough 1981). Much of this forest was severely burnt in 2009 by the series of fires known collectively as the Black Saturday fires. These fires started on January 7th 2009 when temperatures reached > 46 °C and wind-speeds > 100 km h⁻¹. The fires were precipitated by an intense heat wave and almost two months of little or no rain (Pfautsch and Adams 2012).

The site studied here was dominated by at least five eucalypt species and is typical of the greater region’s dry sclerophyll, open forests. The composition of canopy species varies greatly depending on aspect (and exposure), soil depth and altitude. Consequently, patches (> 5 ha) were identified in both burnt and nearby unburnt stands where one of the three most common species (Eucalyptus radiata Sieber, E. dives Schauer, and E. mannifera Mudie) dominated the canopy. Three pairs of study plots (0.25 ha) were then selected within these patches (i.e. six plots in total) such that for each species, a pair of adjacent (within 500 m) plots in burnt or unburnt condition was available. Each 0.25 ha plot was selected such that the selected species was the only overstorey species present in the plot. In the burnt plots, the entire understorey and overstorey crown was consumed. In each plot sap flow of the overstorey (three trees of each species), climate, and soil moisture was measured, and a forest inventory was completed. A general description of the selected species is provided in Table 3.1.
3.2.2 Soil and meteorological measurements

Soil water content was measured every six hours within each plot using standing wave soil moisture sensors (MP406, ICT International Pty Ltd, Armidale, Australia) at depths of 5 cm, 20 cm and 50 cm (soil pits revealed a shallow soil profile of <1 m at all plots). Average soil moisture among all depths was used in comparisons.

Table 3.1. Characteristics of eucalypt species studied. Descriptions are from Costermans (1981) and Boland et al. (2006).

<table>
<thead>
<tr>
<th>Species</th>
<th>Climatic distribution</th>
<th>Growth</th>
<th>Annual rainfall (mm)</th>
<th>Species edaphic conditions</th>
<th>Fire response¹,²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eucalyptus radiata</td>
<td>Occur largely on tablelands, more on hill and mountain slopes and sheltered aspects, north east Victoria to NSW</td>
<td>Varies from bushy to tall, 10 – 50 m</td>
<td>650 - 1100</td>
<td>Wide range of soils derived from a range of shale and granite parent materials</td>
<td>Resprout from epicormic shoots</td>
</tr>
<tr>
<td>Eucalyptus dives</td>
<td>From edges of plains to foothills of mountain ranges, particularly on drier northern aspects</td>
<td>Medium size, 12-25 m</td>
<td>600 - 1100</td>
<td>Rock substrates, particularly metasedimentary types, commonly found on poor shallow and stony soils of low fertility</td>
<td>Resprout from epicormic shoots</td>
</tr>
<tr>
<td>Eucalyptus mannifera</td>
<td>Woodland species, common in NSW tableland regions and foothills of north east Victoria</td>
<td>Small or medium size, 6-25 m</td>
<td>600 - 1600</td>
<td>Skeletal soils of lateaux and hillslope of Triassic and Permian sandstone parent rock</td>
<td>Resprout from basal stem buds</td>
</tr>
</tbody>
</table>

² Fire biodiversity in the Australian Alps national parks, Workshop Proceedings, Albury 2005.

At each site, air temperature and relative humidity sensors were placed at the centre of the plot and 1 m above the forest ground, and data was measured on a half hourly basis. Vapour pressure deficit (VPD) was calculated from the measurements of relative humidity...
and temperature and as described in section 2.2.2 of this thesis. A weather station (HOBO weather station, Micro DAQ Ltd. USA) was installed in an open patch close to the sites where rainfall was measured.

3.2.3 Sap-flow measurements

Specifications of trees used for sap flow measurement in each plot are summarized in Table 3.2. Sap flow was measured following the Heat Ratio Method, HRM (Burgess et al. 2001). A complete description of the method is given in section 2.2.2. The measured depths of sapwood and bark thickness were combined with measured tree diameter to calculate sapwood area of each tree.

Three trees were selected at each site, a large, a medium and a small size selected from the diameter distribution of the plot, for sap flow measurements. Heater and sensor probes (ICT International Pty Ltd, Armidale, Australia) were inserted 35 mm deep into tree xylem at breast height (1.3 m). One probe set was used per tree and tree bark was removed at the drilling location. A steel drilling guide was used to ensure holes were drilled parallel along the plant stem-root axis, with both temperature sensor probes installed at a distance of 0.5 cm from the heater probe. Sensor probes were shielded from incident radiation to prevent any radiation influence on the HRM. To minimize bias due to azimuthal variation, probes were installed at the same azimuth (north) in all trees.

All measured trees had sapwood depth < 27.5 mm. Data were thus averaged for the outer thermocouples (at ~ 12.5 mm depth) to estimate sap velocity. Water use was calculated using the assumption that sap flow measured by outer thermocouples applies to all sapwood area in each tree. Diameter at breast height was measured for every tree (including any seedlings present in the understorey) and sapwood area was estimated for every stem, and the entire plot, from measured diameter at breast height using linear regressions for observations in sampled trees (Figure 3.1). Estimated overstorey transpiration (plot-level water use in mm day\(^{-1}\)) was obtained from the product of mean sap flux and total sapwood area divided by the plot ground area. Both sap flux and scaled transpiration were used for comparing mature and regrowth (resprouting) water use, since scaled up sap flow has larger uncertainties associated with the scaling process. Mean, plot-level water use was the average of the 187 days of overlapping records of overstorey transpiration.
Table 3.2 Specification of trees instrumented with sap flow sensors. Details are diameter at breast height (DBH, cm), bark and sapwood depth (mm), and mean sap flux ($V_s$, cm$^3$ cm$^{-2}$ hr$^{-1}$) during the period when data from all trees overlap (187 days). The entire sapwood area corresponds to the outer sensor as none of the trees have sapwood large enough (> 27.5 mm) for the inner sensors to collect measurements.

<table>
<thead>
<tr>
<th>Species</th>
<th>Fire group</th>
<th>DBH (cm)</th>
<th>Bark (mm)</th>
<th>Sapwood depth (mm)</th>
<th>$V_s$ (cm$^3$ cm$^{-2}$ hr$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. dives</em></td>
<td>regrowth</td>
<td>83.0</td>
<td>26.3</td>
<td>20.2</td>
<td>1.6</td>
</tr>
<tr>
<td><em>E. dives</em></td>
<td>regrowth</td>
<td>27.8</td>
<td>13.5</td>
<td>15.6</td>
<td>4.0</td>
</tr>
<tr>
<td><em>E. dives</em></td>
<td>regrowth</td>
<td>12.5</td>
<td>16</td>
<td>23.9</td>
<td>3.8</td>
</tr>
<tr>
<td><em>E. dives</em></td>
<td>mature</td>
<td>68.0</td>
<td>20.5</td>
<td>22.4</td>
<td>12.0</td>
</tr>
<tr>
<td><em>E. dives</em></td>
<td>mature</td>
<td>67.0</td>
<td>20</td>
<td>17.9</td>
<td>9.7</td>
</tr>
<tr>
<td><em>E. dives</em></td>
<td>mature</td>
<td>58.0</td>
<td>20.7</td>
<td>16.4</td>
<td>3.9</td>
</tr>
<tr>
<td><em>E. mannifera</em></td>
<td>regrowth</td>
<td>80.5</td>
<td>17.2</td>
<td>12.1</td>
<td>8.8</td>
</tr>
<tr>
<td><em>E. mannifera</em></td>
<td>regrowth</td>
<td>57.0</td>
<td>16.5</td>
<td>17.8</td>
<td>6.2</td>
</tr>
<tr>
<td><em>E. mannifera</em></td>
<td>regrowth</td>
<td>40.0</td>
<td>16.5</td>
<td>20.6</td>
<td>5.8</td>
</tr>
<tr>
<td><em>E. mannifera</em></td>
<td>mature</td>
<td>78.0</td>
<td>21</td>
<td>21.5</td>
<td>2.5</td>
</tr>
<tr>
<td><em>E. mannifera</em></td>
<td>mature</td>
<td>33.0</td>
<td>17.2</td>
<td>21.9</td>
<td>0.9</td>
</tr>
<tr>
<td><em>E. mannifera</em></td>
<td>mature</td>
<td>50.5</td>
<td>13</td>
<td>13.8</td>
<td>4.6</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td>regrowth</td>
<td>80.0</td>
<td>21</td>
<td>24.3</td>
<td>1.3</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td>regrowth</td>
<td>23.7</td>
<td>28</td>
<td>19.0</td>
<td>3.0</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td>regrowth</td>
<td>14.6</td>
<td>22.7</td>
<td>15.6</td>
<td>0.8</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td>mature</td>
<td>62.0</td>
<td>22</td>
<td>25.9</td>
<td>2.7</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td>mature</td>
<td>43.0</td>
<td>25.5</td>
<td>22.3</td>
<td>2.1</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td>mature</td>
<td>19.0</td>
<td>17.2</td>
<td>22.7</td>
<td>6.2</td>
</tr>
</tbody>
</table>

When using sap flow methods to measure tree water use, large systematic errors can arise from assuming uniform sap flow across sapwood depth (Nadezhdina et al. 2002). To account for radial and circumferential variations in sap flow, sap flow probes were installed in two additional trees at each site with probes installed at 90° intervals around
the stem. An additional 5th probe was installed between the two probes with the most similar sap flow measurements. These additional measurements were collected for at least one week, assuming that relative azimuthal and radial variations in sap flow did not change over time. The additional probe was moved 5 mm every 24 hours to capture measurements from the inner bands of sapwood. This design facilitated collecting sap velocity from 3 to 4 depths within the sapwood and at 4 different positions around the trunk. Between-tree, radial and azimuthal variations of sap flow were accounted for in calculating confidence intervals of the plot level sap flow. 95% confidence intervals (CIs) were computed for estimated values of plot water use as $\pm 1.96 \times$ [standard error for water use], where 1.96 is the normal quartile for $\alpha = 0.95$. The standard error for water use was calculated from the sum of relative variances for flux among sampled trees, azimuthal and radial variances of sap flow, and sapwood areas predicted from the regressions of sapwood vs. diameter at breast height.

To determine the ‘zero-flow’ baseline, datasets from each site were screened for the periods in which VPD remained < 0.1 kPa for at least 24 hours, and the mean heat velocity during the final 25% of the longest such period for each sensor was taken as zero for that sensor per Buckley et al. (2011). Sap flow measurements began in July 2011 every 30 minutes and continued until July 2012, for 370 days.

Overstorey leaf area index was measured as the average of at least 25 upward-looking digital images following the method of Macfarlane et al. (2007), as described in section 2.2.2, during three campaigns in March 2011, December 2011 and April 2012. In addition to leaf area index, both overstorey and understorey foliage cover was measured with cover photography and following the method of Macfarlane and Ogden (2011). Current method provides only foliage cover for the understorey. Leaf area index for the understorey was estimated from the foliage cover, using the relationship between foliage cover and LAI of the overstorey.

For this purpose, an area of 25 by 25 m was selected within each site and 36 upward looking cover images (for overstorey) and 35 downward facing images, Nadir (for understorey) were collected along transects 5 m apart. Images were taken from approximately 2 m above the ground after the camera was mounted on an extendible pole. Before each image the pole was levelled with a bubble level mounted on the base and a remote control was used to take the image. To estimate foliage cover, digital images were
analysed in MATLAB (Mathworks, Natick, Massachusetts, US) and using the Image Processing Toolbox following the method of Fuentes et al. (2008).

3.2.4 **Physiological measurements**

A range of physiological variables were measured for leaves from both regrowth and mature trees. Locations were selected within the forest where individuals of all three species were growing close to each other and canopies were accessible via a hydraulic platform. Three individuals of each species were selected and leaves in both lower and upper canopy were selected for physiological measurements.

Hourly measurements were made over a full day in March and April 2012. Rates of assimilation and stomatal conductance were measured with an infrared gas analyser (Li-Cor 6400, LiCor, Lincoln, NE, USA) equipped with an LED light source and the standard 2 × 3 cm leaf chamber. Irradiance, air moisture and leaf temperature were set at ambient and [CO₂], in the reference air stream was controlled to 380 ppm. Readings were taken once steady state was achieved. Total leaf stomatal conductance (gₛ, mmol m⁻² s⁻¹) was also measured simultaneously on adaxial and abaxial surfaces with two diffuse porometers (Decagon SC-1, Decagon, Pullman, WA, USA) because all the study species had amphistomatous isolateral leaves. Measurements of gₛ were averaged for each surface and added for total leaf gₛ. Immediately after stomatal conductance was measured, leaves were excised for immediate (i.e. less than 20 seconds between fall and measurement) measurement of leaf water potential using a portable pressure chamber (Model 1000 Pressure Chamber, PMS Instruments OR, USA).

3.2.5 **Response to light and [CO₂]**

Photosynthetic response to light and [CO₂] concentrations (A-Q, A–Cᵢ curves) was measured on light-saturated leaves *in situ* on 29th April to 1st May 2012, using a hydraulic platform. All measurements were taken at ambient relative humidity and temperature and air flow through the chamber was adjusted to 400 µmol s⁻¹. Rapid light response curves were derived from data collected at 2000, 1500, 1000, 500, 300, 150, 100, 50, 25 and 0 µmol m⁻² s⁻¹, leaves being left to equilibrate for 2 minutes at each light level, with [CO₂] in the reference air stream maintained at 380 ppm. Photosynthetic response to elevated [CO₂] was measured on light-saturated leaves at 1500 µmol m⁻² s⁻¹ quanta for 11 levels of [CO₂] between 2000 ppm and 50 ppm. Relative humidity and temperature remained at ambient, however for comparative purposes, biochemical parameters maximum
carboxylation rate of Rubisco ($V_{\text{cmax}}$) and maximum rate of photosynthetic electron transport ($J_{\text{max}}$), were adjusted to a standard leaf temperature of 25 °C using the model of Sharkey et al. (2007).

![Graphs showing the relationship between stem diameter (DBH) and sapwood area for different species and stages of growth.](image)

**Figure 3.1.** Relationship between stem diameter (DBH) and sapwood area. Lines are least-squares regressions, based on power functions ($Y = Y_0 X^b$) applied in similar studies (Meinzer et al. 2005; Vertessy et al. 1995).
3.2.6 **Statistical analysis**

Relationship and best-fit functions between climate variables and sap flow, tree diameter and sapwood area were derived using linear regression analysis. Significance levels were calculated at $p < 0.05$, and all analyses were performed with R 2.14.1 (R Development Core Team, 2011).

![Figure 3.2](image-url)

**Figure 3.2.** Comparison of average monthly air temperature (top panel) and monthly rainfall (lower panel) during the study period with the 30-year average (1971-2000). Measurements of rainfall started in September 2011.
3.3 Results

3.3.1 Climate and soil moisture

Air temperatures during the study period closely followed the thirty-year average for a nearby recording station (Bureau of Meteorology, Australia). Whilst rainfall during the study period was less overall than the thirty-year average, the temporal pattern included significant rainfall during summer months that are normally dry (Figure 3.2).

Mean air temperature during the study period was 13 °C and maximum monthly rainfall fell in March (130 mm). Average daily vapour pressure deficit (kPa) within the forest, calculated from measurements of air temperature and relative humidity, was significantly greater in unburnt stands ($p < 0.05$, $0.61 \pm 0.44$ vs. $0.42 \pm 0.36$ kPa in regrowth; mean ± sd). When averaged over measured depths, soil moisture was greater under regrowth forests – together these data suggest water availability was greater in the regrowth forests (Figure 3.3).

3.3.2 Sap flow measurements

Sap flow was measured for 370 days between July 2011 and July 2012, and 187 days (06 Jan 2012- 24 July 2012), when data were available from all of the sites simultaneously, were used to compare stand water use between mature and regrowth sites.

Figure 3.4 shows the basal area and the contribution of small trees (trees with DBH < 10 cm) to total basal area for the sites. Mean sap flux ($V_s$, cm$^3$ cm$^{-2}$ h$^{-1}$) was not significantly different in the resprouting trees ($p > 0.05$) with $0.48 \pm 0.14$ mm day$^{-1}$ stand level water use in regrowth and $0.66 \pm 0.17$ mm day$^{-1}$ in mature (means ± 0.95 CIs, Figure 3.5).

Uncertainties in estimated stand level water use could be attributed to: 1) differences in sap flux among sampled trees (between 12% and 23% of the total variance for regrowth, and between 22% and 29% for mature), 2) azimuthal variation (between 15% and 19% for regrowth, and between 21% and 27% for mature), 3) radial variation (between 12% to 30% for regrowth, and between 12% to 31% for mature), and 4) variations in sapwood area (between 42% and 44% for regrowth, and between 24% and 31% for mature). The variations in measured sap flow and estimated sapwood are comparable with those measured in seeder forests (Buckley et al. 2012).
Figure 3.3. Comparison of average daily volumetric soil water content (top panel) and daily VPD at regrowth and mature sites during January to July 2012.

3.3.3 Leaf area index

Measurements of overstorey LAI during different campaigns are recorded in Table 3.3. Understorey photography was undertaken in April 2012 and LAI for the understorey was inferred from the foliage cover (Figure 3.6), assuming that the relationship between LAI and foliage cover of the overstorey holds for the understorey too. Total LAI of the burnt plots averaged 20% less than that of unburnt plots, while SAI (ratio of total sapwood area to ground area) of burnt plots was some 22% greater (Table 3.4).
Table 3.3. Overstorey leaf area index (LAI) measured during three different campaigns.

<table>
<thead>
<tr>
<th>Date</th>
<th>E. dives</th>
<th>E. radiata</th>
<th>E. mannifera</th>
<th>E. dives</th>
<th>E. radiata</th>
<th>E. mannifera</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(regrowth)</td>
<td></td>
<td></td>
<td>(mature)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>March 2011</td>
<td>1.30</td>
<td>0.77</td>
<td>1.15</td>
<td>1.73</td>
<td>1.24</td>
<td>1.30</td>
</tr>
<tr>
<td>December 2011</td>
<td>1.22</td>
<td>1.14</td>
<td>1.22</td>
<td>1.35</td>
<td>1.23</td>
<td>1.31</td>
</tr>
<tr>
<td>April 2012</td>
<td>0.65</td>
<td>0.66</td>
<td>1.01</td>
<td>1.19</td>
<td>0.83</td>
<td>0.85</td>
</tr>
<tr>
<td>Mean</td>
<td>1.06</td>
<td>0.86</td>
<td>1.13</td>
<td>1.42</td>
<td>1.1</td>
<td>1.15</td>
</tr>
</tbody>
</table>

Figure 3.4. Basal area (m$^2$ ha$^{-1}$) and the contribution of trees with DBH < 10 cm to total basal area, for each site.
**Figure 3.5.** Plot level water use in mature and regrowth sites averaged for three species. Error bars are 95% confidence intervals.

**Figure 3.6.** Relationship \((y = ax + b)\) between leaf area index (LAI, \(m^2 \cdot m^{-2}\)) and fraction of foliage cover (FC) for the overstorey. Filled symbols refer to regrowth and empty symbols to mature of each species. Coefficient of determination \((r^2)\) of species-specific relationships was 0.96 ± 0.02.
Table 3.4. Total leaf area index (LAI, m² m⁻²), sapwood area index (SAI, m² m⁻²), and average sapwood density (ρ_sapwood, g cm⁻³) for mature and regrowth sites.

<table>
<thead>
<tr>
<th>Species</th>
<th>mature</th>
<th></th>
<th></th>
<th>regrowth</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LAI</td>
<td>SAI</td>
<td>ρ_sapwood</td>
<td>LAI</td>
<td>SAI</td>
<td>ρ_sapwood</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td>2.45</td>
<td>0.000359</td>
<td>0.505</td>
<td>1.34</td>
<td>0.000371</td>
<td>0.492</td>
</tr>
<tr>
<td><em>E. dives</em></td>
<td>1.68</td>
<td>0.000637</td>
<td>0.561</td>
<td>1.49</td>
<td>0.000860</td>
<td>0.460</td>
</tr>
<tr>
<td><em>E. mannifera</em></td>
<td>2.10</td>
<td>0.000423</td>
<td>0.538</td>
<td>2.19</td>
<td>0.000590</td>
<td>0.466</td>
</tr>
</tbody>
</table>

3.3.4 Effect of environmental factors on tree water use

VPD exerted strong control of water use in both mature and regrowth forests (Figure 3.7). Changes in VPD alone explained between 64% (for regrowth *E. dives*) and 89% (mature *E. mannifera*) of the variations in tree water use irrespective of recent fire history (burnt/unburnt). Overall, the VPD influence on sap flow was stronger for *E. mannifera* than for the other two species.

Results of a multiple linear regression analysis show significant influence of volumetric soil moisture on sap flux from regrowth and mature sites (*p < 0.0001*). However, as it is apparent from Figure 3.3, there lays a co-linearity between VPD and soil moisture content in the sense that soil moisture decreases during periods of high VPD and increases after the rainfall and during the cooler periods when VPD is lower. To test the influence of soil moisture on tree water use without the influence of VPD, the ratio of sap flow to VPD (a proxy for canopy conductance, per *App. A* Buckley et al. 2012) was used as an independent factor and soil moisture as the predictor. The relationship becomes significant however not strong (*r² = 0.02* for regrowth, and *r² = 0.09* for mature). When isolating the effect of soil moisture within the measured depths on tree water use, this influence becomes marginal.
3.3.5 Leaf water status

Diel leaf water potential varied between -0.38 and -1.2 (MPa) for *E. radiata*, -0.35 and -1.4 for *E. mannifera*, and -0.35 and -1.7 for *E. dives*. Although leaf water potential measured at midday did not vary between mature and regrowth leaves, maximum daily stomatal conductance was greater in regrowth. Stomatal conductance in general was related to leaf water potential and increased as leaf water potential decreased (more negative). While regrowth showed much greater diurnal variation in stomatal conductance for similar leaf water potential (Figure 3.8), the data suggest that of the two, stomatal conductance in mature trees is more sensitive to water potential.

Stomatal conductance was significantly greater in regrowth (330.73 ± 102.8 vs. 225.87 ± 31.8 in mature), but photosynthetic capacity did not differ significantly between leaves on regrowth and mature trees. Stomatal conductance was also greater during the afternoon in mature trees which is consistent with observations from mature Alpine Ash forests, whereas in regrowth, morning rates of stomatal conductance were greater. This was directly associated with lower leaf water potential for the regrowth in the morning (Figure 3.8).
Leaf stomatal conductance decreased exponentially with increasing atmospheric saturation deficit in both burnt and unburnt trees (Figure 3.9); a feed-forward mechanism that the stomata show to regulate water loss at high VPD surface (Jarvis and McNaughton 1986). Albeit, the critical VPD at which stomata start to shut was not achieved during this study as VPD measurements collected were consistently above a critical level.

**Figure 3.8.** Diurnal trends of stomatal conductance (top panels) and leaf water potential (lower panels) of mature and regrowth trees. Each data point is mean ± standard deviation of one tree per species, on which three leaves were measured. Labels on the x axis show time of the day.

### 3.3.6 Response of photosynthesis to light and CO₂

The response of photosynthesis to light and CO₂ did not differ significantly for mature and regrowth leaves (p > 0.05, data not shown). Maximum assimilation rate ($A_{\text{max}}$) was between 12 and 21 (µmol CO₂ m⁻² s⁻¹) for regrowth, and between 8 and 16 (µmol CO₂ m⁻² s⁻¹) for mature trees.
3.4 Discussion

Bushfire’s greatest effects on water yield from native eucalypt forests arise through their effects on evapotranspiration (ET), largely because this component of stand-level hydrological cycles represents the greatest return of water to the atmosphere (Mitchell et al. 2012). While many Australian studies have measured stand water use within native eucalypt forests, most lack information: 1) on water balance for the first three years immediately after fire, and 2) on resprouting trees and forests dominated by resprouters. There are presently no published studies comparing water use by regrowth and mature stands of resprouting eucalypt trees. This study, of three co-occurring eucalypt species under adjacent brunt and unburnt conditions, sought to quantify stand-level water use for 187 days and determine the important environmental drivers of water use for trees regenerating from fire via epicormic shoots.

3.4.1 Environmental control of canopy transpiration

Amongst the different potential environmental controls of forest water use, VPD was the most significant, clearly controlling canopy transpiration for both mature and resprouting *E. dives*, *E. radiata* and *E. mannifera*. These results are consistent with observations in other studies (Kumagai et al. 2007; Pataki and Oren 2003; Zeppel et al. 2004). Vapour...
pressure deficit had a greater influence on tree water use than radiation, soil moisture and wind speed. Soil moisture effects on canopy conductance were negligible, suggesting root water uptake is not limited to the top 50 cm of soil that routinely dries out during summer months. Whilst the strength of this relationship might change in a drier summer (Figure 3.3), these results and similar observations from Alpine Ash forests (App.Á Buckley et al. 2012) contrast the general hypothesis that the top 35 cm of the soil provide most (more than 90%) of the water needed for transpiration (Oren et al. 1998). Contributions of water from roots at greater depth to transpiration are likely to vary with site and species characteristics (e.g. with distribution of fine roots). For example, studies have shown that as stand density and inter-tree competition increase, trees deplete the water content of deeper layers of soil (Eastham and Rose 1988).

3.4.2 Pre and post fire canopy transpiration

The sap flow measurements showed that water use by resprouting, mixed-species forests was not greater than adjacent mature forests. In ash-type eucalypt forests, increases in stand-level water use after bushfire (regrowing from seed) are associated with: 1) a rapid increase in the sapwood area of the forest and 2) faster sap velocity in the regenerating seedlings and saplings. Here, an increase in sapwood area of 22% was measured in the studied mixed species forests, much less than the 70% increase in sapwood area that has been recorded in stands of Alpine Ash forests (e.g. App.Á Buckley et al. 2012). In further contrast to ash-type forests, it was observed that leaf area index in mixed species forests had declined three years after the fire, and sap velocity in resprouting trees was not significantly different from that in the mature trees.

Sap velocity measured in this study is within a similar range to other studies of native eucalypt forests. Some variation in sap velocity was observed amongst species: slower rates were recorded for E. mannifera than for either E. radiata or E. dives. Sap velocities were also less than most literature records for ash-type eucalypts (App.Á Buckley et al. 2012; Pfautsch et al. 2010; Zeppel 2013). On average, forest water use in the mixed species regrowth forests was three quarters of that of adjacent, mixed species mature stands (0.48 ± 0.14 mm day⁻¹ in regrowth vs. 0.66 ± 0.17 in mature) three years after the fire. These data are consistent with catchment-scale observations for mixed species forests that also showed no significant change in water yield three years after 2003 bushfires (White et al. 2006).
At the leaf level, greater stomatal conductance in the resprouting stands can be partially related to morphological differences of the leaves that lead to adult foliage being hydrologically more conservative compared to the young foliage. Some of these morphological factors include leaf waxiness, leaf size, leaf specific area (leaf area/leaf dry mass), and leaf thickness. Studies on changes in leaf morphology in eucalypt species show that for example cuticle thickness and leaf waxiness, including wax occlusion of the stomatal antechamber, increase significantly with age (England and Attiwill 2006). Preliminary measurements in our area of study also showed that waxy occlusion of the stomatal antechamber in the resprouting leaves increased after one year (T.L. Turnbull, personal communication, October 2011). Increasing the extension of the cuticular ledge and waxy occlusion with age in eucalypt leaves encloses the stomatal antechambers and is a ‘xeromorphic’ (or conservative) characteristic that reduces the uncontrolled water loss and increases the water use efficiency (England and Attiwill 2006; Jeffree et al. 1971).

3.4.3 Pre and post fire leaf area index

Knowledge of both water use per unit leaf area and forest LAI are critical when modelling forest water use (Watson et al. 1999; Zeppel 2013). Conventional photography-based methods for measuring LAI do not include the understorey. In addition to measuring canopy LAI, photographic techniques were used to quantify understorey foliage cover and estimate understorey LAI from the foliage cover. In this study, whilst leaves on regrowth trees lost 45% more water through their stomata the total LAI was 20% less in the regrowing forest, leading to little overall difference in plot-level water use and presumably total evapotranspiration. Resprouting mixed species forests exhibit a slower recovery of canopy leaf area (and a gradual reduction in ground and understorey leaf area) after fire, when compared to ash forests. For example, three years after fire in Mountain Ash forests, stem density approached 20000 stems ha\(^{-1}\)(Attiwill 1994). In the mixed species forests studied here, stem density in the same period did not increase beyond 4000 stem ha\(^{-1}\). In general it seems highly unlikely that foliage cover in regrowth stands would exceed pre-fire cover, within the first decade after fire. Rates of fire survival is generally higher in fire tolerant species; a most recent study that compared survival after high and intermediate fires in south-east Australia shows more than 90% survival in mixed-species eucalypts compared to close to zero survival in ash forests (Benyon and Lane 2013) which is then followed by a rapid recovery.
Observations in this study might extend to other tree genera that respond vegetatively to fire and are able to resprout after fire, such as forest trees in Chile (Armesto and Pickett 1985), in South Africa (Kruger et al. 1997), or in California (Hanson and North 2006).

3.4.4 Management implications

In the context of forest management in south-eastern Australia, this study demonstrates clearly the (lack of) effects of high intensity bushfire on overstorey water use. This, combined with measures of understorey leaf area leads to the conclusion that within three years of fire, water yield from such forests are likely to be similar to that pre-fire. More interesting questions remain around the hydrological role(s) of the understorey and ground layer vegetation and the effects of fire thereon. While it is concluded that surface soil moisture is at least partially protected by the regrowth after fire of shrubs and grasses, it seems likely that those components will again decline in leaf area as the resprouting canopy recovers. In effect, this is a restatement of Eagleson’s hypothesis (e.g. Hatton et al. 1997) – that leaf area is in equilibrium with the availability of water. The other types of fire of significance to management are the prescribed or fuel-reduction fires used to reduce fuel loads. These fires are managed to be of lower intensity and not affect the overstorey canopy. In general, however, they do remove the understorey and ground layer vegetation. Regrowth of these layers after such fires is highly variable and the subject of much contention as to their species composition. Irrespective, the hydrological benefits (in terms of water yield) of that regrowth are likely to persist irrespective of species composition.

In summary, this study suggests that fires impact on the hydrology of mixed species eucalypt forests is much less than on that of even-aged ash forests. In part, it must be recognized that the increase in water use by ash-type species after fire is at least partly due to there being more water available to use. The much poorer soil and climatic conditions that prevail over the mixed-species forest estate, and consequent greatly reduced water availability, are in no small part the drivers of the lack of fire effects for this large proportion of the Australian forest estate.

3.5 Conclusion

In Australia, research into the dynamics of forest water yield has focused on the effects of replacement by fire of mature eucalypt overstorey with dense stands of regenerating
seedlings and saplings; a situation that prevails after fire in ash-type forests. Studies of water use and yield from mixed-species forests are very limited. This study investigated the hydrological effects of fires in mixed-species forests, including regrowth from epicormic shoots. An initial increase in water yield due to loss of leaf area might be common across resprouter and seeder forests, but results in this study show that three years after a crown-replacing fire, water use by resprouting trees was not different from their mature counterparts. Canopy reestablishment is such that within three years, individual trees were again competing for nutrients, light, and water, and canopies closely resembled those of mature forests. A significant increase in sapwood area or LAI, that might lead to a consistent increase in stand water use, is unlikely for periods exceeding three years after a canopy-replacing fire.

These results provide empirical information about the effects of fires on the water use of mixed-species forests in south-east Australia. Such information is also valuable for using forest water use models and successful management of the south-east Australian mixed-species forests.
3.6 References


4 Validation of canopy transpiration in a mixed-species foothill eucalypt forest using a soil-plant-atmosphere model

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Summary

Studies of the hydrology of native eucalypt forests in south-east Australia have focused on ash-type eucalypt species that are largely confined to Victoria and Tasmania. Mixed species foothill forests comprise the largest proportion of the forest estate in south-east Australia, yet are poorly known hydrologically. The ability to predict forest transpiration, both with reasonable accuracy and in response to changes in the environment, is essential for catchment management.

A soil-plant-atmosphere model (SPA) was validated for 222 days in a mature, mixed species forest of north-east Victoria using measurements of overstorey transpiration (Eucalyptus radiata and E. goniocalyx) and site-specific climate and vegetation parameters. There was a stronger relationship between average daily transpiration ($0.71 \text{ mm day}^{-1}$) and daily minimum relative humidity ($R^2 = 0.71$), than between average daily transpiration and daily maximum temperature ($R^2 = 0.65$). Stand water use could be predicted best from vapour pressure deficit ($R^2 = 0.89$).

SPA successfully predicted stand transpiration ($R^2 = 0.85$) over a range of soil water and climatic conditions. A sensitivity analysis suggests that among the various required inputs, leaf area index (LAI) was the most important, and accurate estimates of LAI could significantly improve estimation of stand transpiration.

4.1 Introduction

Forested catchments in south-east Australia supply water to cities, agriculture and industry, and to millions of people. Water yield is largely governed by the loss to the atmosphere via plants (e.g. trees and other vegetation), of soil water and intercepted rainfall. At the scale of the Australian continent, almost 3 100 000 GL of the 3 200 000 - 3 900 000 GL water received annually as rainfall is lost by evapotranspiration (Eamus et al. 2006) and for some
parts of the native forest estate evapotranspiration accounts for all (100%) of the annual rainfall (e.g. Bren and Hopmans 2007).

In the State of Victoria in south-east Australia, almost 79% of the total forested area is dominated by mixed species eucalypt forest (Attiwill 1994). Even so, most studies investigating impacts on forest hydrology of stand age (Dunn and Connor 1993; Haydon et al. 1997; Vertessy et al. 2001), forest disturbance (Kuczera 1987; Langford 1976), climate (Pfautsch et al. 2010), and stand structure (Vertessy et al. 1995), have been confined to ash-type eucalypt forests due to their dominance of catchments for the City of Melbourne. By contrast we have little knowledge of the patterns and drivers of tree water use for the millions of hectares of mixed species eucalypt forest or base-level quantification of tree water use.

Topographic, geological and climatic variations across forested catchments in south-east Australia are accompanied by variation in dominance by tree species. Mixed species eucalypt forests are common in the foothills of the Great Dividing Range and the overstorey often comprises combinations of peppermints (e.g. *E. radiata*, *E. dives*), stringybarks (e.g. *E. obliqua*, *E. macrorhyncha*, *E. baxteri*) and boxes (e.g. *E. goniocalyx*, *E. polyanthemos*). These forests typically grow on soils that are duplex in structure with high proportions of sand or rock throughout soil profiles, and clearly differ hydrologically to adjacent wet ash-type forests of *E. regnans* and *E. delegatensis* that grow on deep, well-structures soils (Lacey and Grayson 1998).

Recently Mitchell et al. (2012) showed that at the catchment scale, overstorey transpiration ($E_c$) in mixed species eucalypt forests strongly influences water balance. They noted that such influence varies with forest structure that was in turn influenced by aspect and topography.

Canopy transpiration is regulated by a number of biological and environmental variables which are expected to vary among sites and species. Among environmental variables that underline variations in $E_c$, canopy transpiration is expected to depend mainly on temporal (Gazal et al. 2006; Oren and Pataki 2001) and spatial (Granier et al. 2000; Tromp-van Meerveld et al. 2006) variations in soil moisture and sensitivity to the combination of temperature and relative humidity in the air (Ewers et al. 2007) as reported by previous studies.
More generally, soil and atmospheric conditions regulate water use in eucalypt forests. For example, water extraction from deep in soil profiles must be invoked to explain observed transpiration rates by some eucalypt species during drought periods (e.g. Leuning et al. 2005). In other cases, eucalypt water use is insensitive to large changes in soil moisture content in the upper soil profile (e.g. Zeppel et al. 2008; Buckley et al. 2012). Eucalypts though are not different to other genera with respect to mechanisms and controls of water uptake from soils, which vary widely among species and sites. In contrast, there are clear and reasonably well-understood mechanisms that underpin relationships of atmospheric variables to forest water use (Dierick and Hölscher 2009; Oren and Pataki 2001), as discussed in Chapter 2.

Improved knowledge of the dynamics of water use by mixed species eucalypt forests is critical to improving the hydrological models that are relied upon by those who manage the large water basins and catchments in SE Australia (Murray Darling Basin Authority 2011). These models need also to be better informed in choosing appropriate parameters and assumptions for simulating transpiration. For example, night time transpiration has now been reported as comprising up to 10% of diel (24 h) water use for a range of eucalypt forests (Buckley et al. 2011; Pfautsch et al. 2011; Phillips et al. 2010; Zeppel et al. 2010), and up to 25% around the world (Dawson et al. 2007; Donovan et al. 1999; Feild and Holbrook 2000). These observations bring into question the common assumption made by many hydrological models that night-time transpiration is negligible due to the controlling influence of solar radiation on overall transpiration. In this study contribution of water loss during the night to total water use was explored in mixed species eucalypt forests. In addition, some important biological variables that explain the observed variations in canopy transpiration include changes in transpiration with age which is associated with hydraulic limitations of stomatal conductance (Delzon and Loustau 2005), or tree size (Dawson 1996), and regulation of transpiration by stomatal conductance as it is simulated by a range of physiological processes (Collatz et al. 1991).

In this study biological controls of transpiration were tested within a scheme as represented by a soil-plant-atmosphere model. In this scheme stomatal conductance optimizes daily carbon (C) gain per unit leaf nitrogen (N) within the limitations of the hydraulic system, minimizing the risk of cavitation and damage to the tree. Leaf-level photosynthesis is simulated by the Farquhar model (Farquhar and Von Caemmerer 1982) and the Penman-Monteith equation is used to determine transpiration.
Bio-hydrological models that can successfully reproduce and predict water fluxes can replace costly and labour-intensive alternatives; however applicability of such models is not assured for every forest type. One such model is the soil-plant-atmosphere (SPA) model of Williams et al. (1996). SPA is a process-based model that simulates eco-hydrological processes between soil, plant and atmosphere, including evapotranspiration, soil energy flux, and gross primary production. The model employs variable stomatal conductance, and carbon uptake is maximized within limitations of canopy water availability (Jones and Sutherland 1991). The scale of parameterization (leaf level) and prediction (canopy level) allow for scaling up leaf-level processes to canopy and landscape scales (Williams et al. 2001b). SPA has been tested in a number of forest types. These include: mixed deciduous (oak-maple) forest (Williams et al. 1996), boreal forest (Williams et al. 2000) and tropical rainforest (Williams et al. 2002). In Australia, Zeppel et al. (2008) validated the model for a eucalypt-dominated woodland. Owing to the great variability in species dominance and structure of eucalypt forests in Australia (Specht and Specht 1999), it remains unclear how much confidence can be attributed to predictions made using SPA or any other similar model in the majority of forests of south-east Australia. If SPA successfully predicts forest water use without intensive parameterization and input collection, it provides a valuable tool for a range of purposes.

The objective of this study was to directly measure overstorey (Eucalyptus radiata and E. goniocalyx) transpiration in a mature mixed species eucalypt forest in north-eastern Victoria, Australia, and ascertain which variables (e.g. soil moisture, atmospheric conditions, forest structure) could best explain patterns of transpiration by first parameterizing SPA and then testing its sensitivity to input variables.

4.2 Methods

4.2.1 Experimental site

The research site lies within a mixed-species forest in south-eastern Australia (36.745° S, 147.188° E), within 5 km of the township of Mount Beauty. The site is around 250 km north east of the City of Melbourne in the State of Victoria. Mean annual rainfall (1971 – 1994) in the general area of Mt Beauty is 1263 mm with 113 days of rainfall > 1 mm, and
25% of rainfall events in July and August (Bureau of Meteorology, as recorded 3.5 km north east of the site).

The forest is dominated by *Eucalyptus radiata* Sieber ex DC. (narrow-leaved peppermint) and *E. goniocalyx* Miq. (long-leaved box), however, as is typical of such forests, one species (*E. radiata* in this case) provides the bulk of leaf area and basal area (93% of the basal area and 88% of the stocking). Measured tree density was 264 stems ha$^{-1}$ and the stand had a total basal area of 30.3 m$^2$ ha$^{-1}$. The experimental period ran from July to November 2009 and February to May 2012.

### 4.2.2 Soil measurements

Soils were classified visually using Isbell (2002) and the Australian Soil Resource Information System (ASRIS), as a Chromosol with a strong contrast between A and B horizons. Soil depth was estimated at 1 m, beyond which lay decomposing bedrocks. The soil profile was duplex in structure, with a strong texture contrast between upper and lower soil horizons (Northcote 1979).

Five replicate soil samples from 10 cm, 50 cm, and 100 cm were collected using a 75 mm auger and transported to the lab in zip-locked plastic bags for particle analysis. Proportions of sand and clay were measured following methods of Allen (1989). Mineral and organic soil fractions were directly measured by loss on ignition at 550 °C for 5 hours in a muffle furnace (Allen 1989).

Soil water content was measured every six hours within the study site with standing wave soil moisture sensors (MP406, ICT International Pty Ltd, Armidale, Australia) at three depths of 5 cm, 15 cm and 30 cm.

### 4.2.3 Meteorological measurements

Micrometeorological variables i.e. air temperature, relative humidity (rH), rainfall, photosynthetically active radiation, and horizontal wind speed were recorded in an adjacent open area at 5 minute intervals throughout the 222 days of study (HOBO weather station, Micro DAQ Ltd. USA). Vapour pressure deficit, VPD (kPa) was calculated from relative humidity and air temperature as described in section 2.2.2.
4.2.4 Sap flow measurements

Sap flow was measured using the Heat Ratio Method, HRM (Burgess et al. 2001). Description of the technique and sapwood sampling are described in detail in section 2.2.2. Sap flow measurements provide estimates of the velocity of water moving in the stem per unit time. The conducting area through which water flows in the tree is required to calculate the water volume. Multiple cores were taken from different sides of each tree and sapwood-hardwood boundaries were identified by staining the cores with a 1% methyl orange solution. A colour change from orange to red is indicative of the change from sapwood to heartwood (Kutscha 1962). The depth of sapwood was then measured with a digital calliper. Bark thickness was measured at the coring points. Sapwood area of each tree was calculated using knowledge of tree diameter, bark thickness and sapwood depth. Sap flow measurements in half-hourly time steps were focused on *E. radiata* as this species accounted for 93% of the total basal area.

In order to account for variation in sap flow within the stand, diameter distribution of the forest stand was divided into six classes and one tree from each class was selected for sap flow measurements. Sensor probes (ICT International Pty Ltd, Armidale, Australia) were inserted 30 mm deep into tree xylem at breast height. One probe set was used per tree. A steel drilling guide was used to ensure holes were drilled parallel along the plant stem-root axis, as both probes had to be installed at a same distance (0.5 cm) from the heater probe. Sensor probes were shielded from incident radiation since ambient temperature can cause the pulse velocity to fluctuate. To minimize bias due to azimuthal variation, probes were installed at the same azimuth in all trees. Azimuthal variation in sap flow was accounted for by installing 5 additional probe sets at 60° azimuth steps in one of the trees. The azimuthal and between-tree variation in mean sap velocity were used to estimate statistical confidence interval for plot mean sap velocity. Specifications of trees used for sap flow measurement are summarized in Table 4.1.

Trees could not be fell or cut through stems to determine ‘zero-flow’ for probe calibration. Instead a baseline was determined and set on the basis of measured sap flow toward the end of numerous nights (e.g. between 0300 and 0500 h) when relative humidity was greater than 95%. Single point data gaps were replaced with linear interpolation of the adjacent points.
4.2.5  Forest canopy transpiration ($E_c$)

After measuring sap flow, water use by sampled trees was extrapolated to the stand level and to estimates of overstorey transpiration per unit area of land ($E_c$). Measurements of tree water use were scaled to stand water use via the product of mean sap velocity ($V_s$, mm hr$^{-1}$) and total sapwood area of the stand. It was not possible to core every tree and determine sapwood area. Since the relationship between tree diameter and sapwood area varies little in many relatively low productivity forests (Eamus et al. 2006), measurements of diameter of all trees in the stand for were used for calculating total sapwood area. A simple least squared error regression was built between diameter and sapwood area using measurement of sapwood and diameter of the six trees (Figure 4.1). This relationship was derived from measurements from $E.\ radiata$ trees but was used for estimating sapwood area of every tree within the 0.25 ha experimental plot, as this is the dominating species.

Slow rates of sap flow during night may still contribute a significant proportion of total transpiration and represent the sum of nocturnal stem refilling and canopy transpiration. To separate and interpret these two processes, a separate set of measurements (Goldstein et al. 1998) or analysis such as the mathematical technique proposed by Buckley et al. (2011) are required. In this study, investigations of this phenomenon were limited to quantifying mean sap flow between 2100 and 0500 h during the measurement period and assuming these flows to be due to transpiration.

Table 4.1. Specifications of $Eucalyptus\ radiata$ trees used for sap flow measurement. Diameter was measured at breast height over bark (DBH).

<table>
<thead>
<tr>
<th>Tree no.</th>
<th>DBH (cm)</th>
<th>Bark width (mm)</th>
<th>Sapwood depth (mm)</th>
<th>Sapwood area (cm$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>55.6</td>
<td>31</td>
<td>18</td>
<td>268</td>
</tr>
<tr>
<td>2</td>
<td>33.8</td>
<td>18</td>
<td>14</td>
<td>131</td>
</tr>
<tr>
<td>3</td>
<td>52.9</td>
<td>29</td>
<td>16</td>
<td>222</td>
</tr>
<tr>
<td>4</td>
<td>75.5</td>
<td>21</td>
<td>15</td>
<td>322</td>
</tr>
<tr>
<td>5</td>
<td>47.4</td>
<td>19</td>
<td>19</td>
<td>258</td>
</tr>
<tr>
<td>6</td>
<td>26.4</td>
<td>8</td>
<td>10</td>
<td>74</td>
</tr>
</tbody>
</table>
Figure 4.1. Relationship between stem diameter (DBH) and sapwood area of the plot ($p < 0.05$). Lines are least-squares regressions, based on power functions ($Y = Y_0X^b$) applied in similar studies (Meinzer et al. 2005; Oishi et al. 2010; Vertessy et al. 1995).

4.2.6 SPA inputs

The SPA model was parameterized and validated for a period of 222 days from July to November 2009 and February to May 2012. Diurnal variation in leaf water status and photosynthetic parameters were recorded in September 2009 and March 2012 on 2 single days. Measurements were made on mature, sunlit leaves that were cut from top, middle and lower canopy layers of three sample trees, between 15 and 20 m tall, using a hydraulic platform and immediately measured over the hours of 0500 to 1700 at 90-minute intervals. Water potential of excised leaves was measured using a pressure bomb (Portable Plant Water Status Console, ICT International). Stomatal conductance ($g_s$), instantaneous assimilation rate ($A_s$), and photosynthetic response to intercellular CO$_2$ (i.e. for maximum rates of carboxylation $V_{cmax}$ and electron transport $J_{max}$, Manter and Kerrigan 2004) were measured using a portable photosynthesis system (LiCor 6400, LiCor Biosciences, Lincoln, Nebraska, USA).

Leaf area index, LAI ($m^2 m^{-2}$) was measured with hemispherical photography, following the method of Macfarlane et al. (2007), using five separate campaigns on 18$^{th}$ of June, 7$^{th}$ of July, 1$^{st}$ of October 2009, 8$^{th}$ December 2011, and 28$^{th}$ April 2012. During each campaign, 25 upward-looking images were recorded for the canopy, using a Nikon Coolpix 5700 digital camera located at 1.3 m height. Images were processed with the WINPHOT image processing tool (ter Steege 1996) and LAI for each campaign was the average of the images. Measured LAI varied among the campaigns and therefore a linearly
interpolated LAI was used for the period of modelling (Figure 4.2). The observed decline in LAI in spring was consistent with observations from other eucalypt forests of south-east Australia (Pook 1984) or Jarrah forests in Western Australia (Silberstein et al. 2001).

Soil water potential was determined using a conventional method (Kavanagh et al. 2007; O’Grady et al. 2006) which assumes similar soil water potential to pre-dawn water potential of bagged leaves. For this purpose, samples of leaves were wrapped in aluminium foil and were tightly sealed from air and moisture in the atmosphere, the night before they were collected. Next day, before dawn, they were cut from the stem and their water potential was measured. A root biomass of 2690 g m$^{-2}$ was estimated following Snowdon et al. (2000).

Leaf area was measured using a portable area meter (LI-3000C, LiCor Biosciences, Lincoln, Nebraska, USA). Nitrogen concentration of 1.9% in *E. radiata* leaves (Foley and Hume 1987) was expressed as g of nitrogen per m$^{2}$ leaf and it was up scaled to g of nitrogen to m$^{2}$ ground area using the plot leaf area index, for model application. The model was tested assuming one single canopy and was not parameterized for separate layers. Canopy hydraulic conductance was taken from estimations for eucalypt trees in the literature (Zeppel et al. 2008).

Time series of measured meteorological variables and initial soil moisture content were the inputs to the model and canopy transpiration was the output of the model that we validated against direct measurements. Where parameters were not directly measured at the site, estimates from a literature review were used. A summary of input parameters is provided in Table 4.2.

### 4.2.7 Model performance and sensitivity analysis

Simulated canopy transpiration was compared to sap flow measurements for two separate periods in 2009 (127 days) and 2012 (95 days). Performance of the model during these periods was evaluated by comparing the means and range of predicted data, slope ($b$) and coefficient of determination ($R^{2}$) of a regression through the origin, root mean square error (RMSE), and the Nash and Sutcliffe (1970) coefficient of model efficiency (NSE).

Response of model outputs to changes in some of the parameters that other studies (Williams et al. 2001a, b) found the model sensitive to, were inspected using a systematic approach. In this approach each parameter was varied over a predefined reasonable range and corresponding model outputs were compared with a reference. For this purpose LAI,
root biomass, and leaf dimension were varied by between 0.5 to 3 times original value, each time with a 0.1 times interval.

4.3 Results

4.3.1 Soil moisture status

Average volumetric soil moisture throughout the experiment period was (mean ± sd) 0.15 (± 0.06) m³ m⁻³ at 5 cm, 0.25 (± 0.05) m³ m⁻³ at 15 cm, and 0.24 (± 0.05) m³ m⁻³ at 30 cm soil depth. The upper 5 cm of soil showed the largest variations in moisture content, especially during low rainfall periods (Figure 4.3a). The decline in soil moisture content during this period is reflected in water uptake by trees with an approximately 24 hour time lag (Figure 4.3b). However it cannot be confirmed if the water lost to transpiration is limited to the soil profile depth where soil moisture was measured.

Figure 4.2. Time series of leaf area index (LAI) measured during five separate campaigns on 18th of June, 7th of July, 1st of October 2009, 8th December 2011, and 28th April 2012.
Figure 4.3. a) Comparison of soil moisture content at 5, 15, 30 cm, and b) average daily canopy transpiration (solid line; left axis) and relative volumetric soil moisture content (%) at 5cm (right axis) during a low rainfall period in 2009.

4.3.2 Meteorological measurements

Rainfall during the period July – November 2009 was 416 mm, with lowest during October (98 mm) and highest received during August (133 mm) in 2009 (Figure 4.4). In 2012 total rainfall was 400 mm from February to May with highest rainfall in March (185 mm) and lowest in April (42 mm). The average daily temperature was 12.6 (± 5) with a minimum of
4 and a maximum of 24 °C. Average daily vapour pressure deficit during the study period was 0.5 (± 0.4) kPa with maximum of 1.9 kPa.

Meteorological data showed that maximum daily temperature during the study period varied between 33 °C and 5.6 °C, while the minimum daily temperature varied from 11.4 °C to -0.8 °C on cooler days.

4.3.3 Forest canopy transpiration ($E_c$)

Figure 4.4 displays patterns in average daily sap flow against episodes of rainfall during the study. On average, 11% of diel water use was attributable to night-time, between 2100 and 0500 h (Figure 4.5). Average canopy transpiration for the forest was 0.71 ± 0.2 mm day$^{-1}$ and 11% of the total basal area of the stand was conducting sapwood (3.64 m$^2$ ha$^{-1}$). There was an overall strong positive relationship between VPD and sap flow ($R^2 = 0.89$, $p < 0.05$).

4.3.4 Tree water use relation to environmental variables

Tree water use showed a strong relationship to minimum relative humidity ($R^2 = 0.71$), and this relationship was stronger than with variations in maximum air temperature ($R^2 = 0.65$). Wind speed on the other hand did not have a strong impact on tree water use. A large proportion of variations in daily tree water use can be explained by changes in the average daily vapour pressure deficit (Figure 4.6). Based on these observations a simple model of tree water use from atmospheric vapour pressure, for the corresponding forest type and when soil moisture is not limiting, is:

$$E_c = 0.37 \ln (VPD) + 1.09$$

(4.1)

Where $E_c$ is canopy transpiration (mm day$^{-1}$) and VPD is vapour pressure deficit (kPa). This relationship follows the commonly-observed relationship with VPD (Pataki and Oren 2003; Koecher et al. 2009), where canopy transpiration increases rapidly at low VPD and tends to saturate with increase in VPD. Sensitivity of forest transpiration to changes in VPD was more profound when soil moisture in the upper soil layer was abundant (Figure 4.7).
Figure 4.4. Time series of daily canopy transpiration (line) and total daily rainfall (bars) during the study period.
Figure 4.5. Measured canopy transpiration ($E_c$) during daytime and night time (2100 – 0500 hours) in 2009.

Figure 4.6. Relationship between canopy transpiration ($E_c$) and vapour pressure deficit (VPD) ($p < 0.0001$).
Figure 4.7. Response of daily canopy transpiration ($E_c$) to vapour pressure deficit (VPD) under high (more than 60% quantile, open circle) and low (less than 40% quantile, closed circle) soil moisture contents. Differences in $E_c$ between the two soil moisture groups are significant ($p < 0.001$).

4.3.5 Modelled and measured sap flow

Leaf water potential varied between -0.2 and -2.2 MPa from pre-dawn to the middle of a single measurement day, and values of leaf area index, measured during different surveys, varied between 0.8 and 1.3 m$^2$ m$^{-2}$.

Daily transpiration predicted by SPA was compared with field measurements for the study period. There was a strong linear relationship ($R^2 = 0.85$, $p < 0.05$) between modelled and measured transpiration (Figure 4.8). The slope of the relationship was close to one (1.1) with an intercept of 0.16. Both daily and seasonal fluctuations in water use predicted by SPA followed measured values closely (Figure 4.9).
**Table 4.2** Summary of SPA parameters

<table>
<thead>
<tr>
<th>Input parameter</th>
<th>Unit</th>
<th>Module</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum leaf water potential ($\psi_{\text{leaf}}$)</td>
<td>MPa</td>
<td>Vegetation</td>
<td>-2.2</td>
<td>Measured</td>
</tr>
<tr>
<td>RuBP carboxylation capacity ($V_{\text{cmax}}$)</td>
<td>$\mu$m g$^{-1}$ s$^{-1}$</td>
<td>Vegetation</td>
<td>110</td>
<td>Measured</td>
</tr>
<tr>
<td>Maximum electron transport rate ($J_{\text{max}}$)</td>
<td>$\mu$m g$^{-1}$ s$^{-1}$</td>
<td>Vegetation</td>
<td>155</td>
<td>Measured</td>
</tr>
<tr>
<td>Root resistivity</td>
<td>MPa s g mmol$^{-1}$</td>
<td>Vegetation</td>
<td>100</td>
<td>Zeppel et al. (2008)</td>
</tr>
<tr>
<td>Leaf N content</td>
<td>g N m$^{-2}$</td>
<td>Vegetation</td>
<td>2.5</td>
<td>Estimated</td>
</tr>
<tr>
<td>Leaf dimension</td>
<td>m</td>
<td>Vegetation</td>
<td>0.05</td>
<td>Measured</td>
</tr>
<tr>
<td>Stomatal efficiency</td>
<td>%</td>
<td>Vegetation</td>
<td>0.07</td>
<td>Williams et al. (1996)</td>
</tr>
<tr>
<td>Canopy capacitance</td>
<td>mmol MPa$^{-1}$ m$^{-2}$</td>
<td>Vegetation</td>
<td>8000</td>
<td>Williams et al. (1996)</td>
</tr>
<tr>
<td>Latitude</td>
<td>°</td>
<td>Vegetation</td>
<td>36</td>
<td>Measured</td>
</tr>
<tr>
<td>Root radius</td>
<td>m</td>
<td>Soil</td>
<td>0.00015</td>
<td>Tippett and O’Brien (1976)</td>
</tr>
<tr>
<td>Soil water potential</td>
<td>MPa</td>
<td>Soil</td>
<td>-0.05</td>
<td>Measured</td>
</tr>
<tr>
<td>Soil sand content in top 10 cm</td>
<td>%</td>
<td>Soil</td>
<td>67</td>
<td>Measured</td>
</tr>
<tr>
<td>Soil clay content in top 10 cm</td>
<td>%</td>
<td>Soil</td>
<td>30</td>
<td>Measured</td>
</tr>
<tr>
<td>Soil moisture content</td>
<td>%</td>
<td>Soil</td>
<td>Time series</td>
<td>Measured</td>
</tr>
<tr>
<td>Leaf area index (LAI)</td>
<td>m$^2$ m$^{-2}$</td>
<td>Phenology</td>
<td>0.8-1.3</td>
<td>Measured</td>
</tr>
<tr>
<td>Root biomass</td>
<td>g m$^{-2}$</td>
<td>Phenology</td>
<td>2690</td>
<td>Snowdon et al. (2000)</td>
</tr>
<tr>
<td>Rainfall</td>
<td>mm</td>
<td>Climate</td>
<td>Time series</td>
<td>Measured</td>
</tr>
<tr>
<td>Wind speed</td>
<td>m s$^{-1}$</td>
<td>Climate</td>
<td>Time series</td>
<td>Measured</td>
</tr>
<tr>
<td>Air temperature</td>
<td>°C</td>
<td>Climate</td>
<td>Time series</td>
<td>Measured</td>
</tr>
<tr>
<td>Photosynthetically active radiation ($Q$)</td>
<td>$\mu$m m$^{-2}$ s$^{-1}$</td>
<td>Climate</td>
<td>Time series</td>
<td>Measured</td>
</tr>
<tr>
<td>Vapour pressure deficit</td>
<td>kPa</td>
<td>Climate</td>
<td>Time series</td>
<td>Measured</td>
</tr>
</tbody>
</table>
Figure 4.8. Modelled versus measured sap flow (mm day\(^{-1}\)) over the study period (n = 222, \(R^2 = 0.85, p < 0.05\)). Dashed line indicates the 1:1 line.

4.3.6 Evaluation of model performance

Differences in the mean and range of simulated and measured transpiration were minimal and very similar during the two measurement periods (Table 4.3). The SPA model performed best during 2009. This can be attributed to measurement in 2009 of key input variables that were not re-measured in 2012 (e.g. minimum leaf water potential, root biomass, leaf nitrogen content). A summary of model evaluation is presented in Table 4.3. Results of the sensitivity analysis, as displayed in Figure 4.10, show that stand transpiration predictions were most sensitive to variations in LAI. A 50% decrease in stand LAI would result in a 60% decrease in stand water use.
Table 4.3. SPA simulation of daily canopy transpiration evaluated using root mean square error (RMSE), slope and coefficient of determination ($b$, $R^2$), and Nash-Sutcliffe coefficient (NSE) for two separate simulation period.

<table>
<thead>
<tr>
<th>Simulation period</th>
<th>$N$</th>
<th>Measured (mm day$^{-1}$)</th>
<th>Simulated (mm day$^{-1}$)</th>
<th>RMSE (mm day$^{-1}$)</th>
<th>$b$, $R^2$</th>
<th>NSE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean         Range</td>
<td>Mean         Range</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July-November 2009</td>
<td>127</td>
<td>0.64         0-1.23</td>
<td>0.55         0-1.25</td>
<td>0.023</td>
<td>1.1, 0.90</td>
<td>0.79</td>
</tr>
<tr>
<td>February-May 2012</td>
<td>95</td>
<td>0.79         0.01-1.4</td>
<td>0.76         0-1.4</td>
<td>0.038</td>
<td>1.14, 0.76</td>
<td>0.57</td>
</tr>
</tbody>
</table>

Figure 4.9. Canopy transpiration ($E_c$, mm day$^{-1}$) predicted with SPA and measured from sap flow during the study period (222 days in 2009 and 2012).
4.4 Discussion

In south-east Australia, the body of research focusing on transpiration from Mountain Ash forests (Connor et al. 1977; Dunn and Connor 1993; Jayasuriya et al. 1993; Vertessy et al. 1996; Vertessy et al. 1997; Vertessy et al. 2001) forms the basis of many recommendations for hydrological management of eucalypt forests in general (Watson et al. 1999), even though these forests comprise < 1% of the national forest estate by area. This study of patterns and drivers of tree water use in one of the most common, mixed-species forest types (that constitute ~ 20% of Australia’s native forest estate) included testing the predictive power of simple models that can operate in the absence of detailed data.

In extrapolating individual tree water use to whole stand water use, the relationship between tree diameter and tree sapwood area, which were strongly correlated, was used. This relationship is site- and species-specific and probably not readily transferable to other
In broad terms, rates of stand transpiration calculated in this study were comparable with previous studies of native forests elsewhere in Australia with similar climate (e.g. Buckley et al. 2011; Hutley et al. 2000; Mitchell et al. 2009; O’Grady et al. 1999; Pfautsch et al. 2010; Zeppel et al. 2004). However, the present study is one of the first to focus on mixed species eucalypt forest common to the foothills of south-east Australia.

In the context of rising temperatures and other changes in climate, it is important to test generalized controls of transpiration to avoid false over-generalization. Pfautsch et al. (2010) for example, found maximum air temperature was strongly related to transpiration in *E. regnans* forest growing ~100 km further south. The present study suggests maximum air temperature was less important than relative humidity (or VPD) to transpiration. Up to 90% of the variation in transpiration could be predicted on the basis of VPD alone. However other meteorological variables such as radiation influence this relationship, with this influence varying across time as the stomatal regulation of transpiration changes with season (Zeppel et el. 2004). The difference in climatic conditions between the sheltered, more humid *E. regnans* forests to the much more exposed, north-facing forest studied here, largely accounts for these differences in controls of water fluxes.

Tree water use did not cease at night for the study species, with up to 11% of diel transpiration taking place overnight. Measured rates of nocturnal transpiration for eucalypts forests (Benyon 1999; Buckley et al. 2011; Phillips et al. 2010; Zeppel et al. 2010) range up to 10% of daytime rates. Considering the measurement period, observations in this study show clearly that, night time water use is not limited to summer periods. Daily average transpiration and daily average atmospheric vapour pressure deficit were correlated in a similar manner to the observations of Pataki et al. (2000), Koecher et al. (2009) and Gazal et al. (2006) for northern hemisphere forests; transpiration increases with increasing VPD and saturates at maximum transpiration. For forests of the type studied here, it is reasonable to assume strong coupling of forest transpiration with the atmosphere, given their generally sparse, well-ventilated canopies (Hutley et al. 2000).

In terms of predicting forest water use, models that combined Penman-Monteith relationships (Monteith 1965) with one of the many empirical or process-based models of stomatal conductance, have been widely and successfully used (Granier and Loustau 1994; Leuning et al. 1991; Lhomme et al. 1998). While the underlying assumption of stomatal control of water loss holds, there is still considerable debate over the mechanisms behind
the control processes (Buckley 2005; Bunce 1996; Jarvis and McNaughton 1986; Pieruschka et al. 2010). While that debate should continue, hydrological predictions of forest water use in south-east Australian foothill forests will benefit greatly from models that express stomatal conductance as a function of soil and atmospheric variables (Damour et al. 2010).

Validations against direct measurements showed that the biological representation of transpiration in SPA is adequately representative of the real world conditions. Such models (e.g. SPA) should be able to represent plant responses to VPD under water-stressed conditions. The empirical relationship between transpiration and VPD shown here (e.g. Figure 4.6) provides obvious guidance to relative importance of climatic parameters. However there are obvious shortcomings with such empirical tools. First, derived coefficients are site-specific and thus limited in application. Secondly, the relationships are derived from observations of limited periods that may represent the full range of likely conditions, or may require provisions of seasonality of tree water use to the atmosphere (e.g. Zeppel et al. 2004). Under non-water –limiting conditions where monthly rainfall is substantially more than canopy transpiration, transpiration is driven by climate and soil moisture has an insignificant control. This study showed that as soil within the root zone dries out, atmospheric evaporative demand exerts less control over the canopy transpiration, and instead, coordination of soil water and plant water use becomes stronger (Figure 4.7).

4.4.1 SPA model

Empirical tools for particular forest types and species can be extended in range via models like SPA that use adjustable parameters. In this study, SPA provided a good estimate of stand water use despite limited soil information. SPA was validated for the full range of seasons. Zeppel et al. (2008) found that when tested over long periods of little or no rainfall, SPA required adjustment of rooting depth to bring predicted water use close to observed values. In the present study no adjustment to rooting depth was required and model outputs were always close to those measured in the field. Sensitivity analysis confirmed that leaf area index was the parameter most requiring accurate measurement for adequate model performance. In contrast to Williams et al. (2001a) who suggested that changes in root biomass could affect patterns of total latent energy, both this study and Zeppel et al. (2008) argue that sap flow is insensitive to changes in the amount of root
biomass. Overall, SPA successfully predicted tree water use in a mature, open, mixed-species eucalypt forest for all seasons.

4.5 Conclusion

Forest transpiration was measured in a foothill eucalypt forest in south-east Australia for 222 days. Data confirmed that stand water use was strongly atmospheric-driven, especially when soil moisture is abundant. A soil-plant-atmosphere model (SPA) was tested and the model successfully predicted stand daily transpiration over a range of seasons. Leaf area index was the most important input to the model. Further validation of SPA in Australian woodlands, including the effects of fire and drought, is encouraged.

Knowledge gained here about patterns and dynamics of water use for foothill forests of south-east Australia adds significantly to the ability to reliably predict the hydrology of mixed-species eucalypt forests. Such information is critical to catchment managers in south-east Australia.
4.6 References


includes a laminar boundary layer. Agricultural and Forest Meteorology, 54(2-4), 107-136.


Foley, W.J., Hume, I.D., 1987. Nitrogen requirements and urea metabolism in two arboreal marsupials, the Greater Glider (Petauroides volans) and the Brushtail Possum (Trichosurus vulpecula) fed Eucalyptus Foliage. Physiological Zoology, 60(2), 241-250.


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5 Testing how the coupling of vegetation to atmospheric processes and soil water availability affects catchment water yield

Summary

Evapotranspiration (ET) is a major component of the water balance in water-limited ecosystems in south-east Australia. Due to variations in land cover and topography it can be spatially variable, especially in the steeper catchments of the Australian Alps. In hydrological models, ET is most often simulated as mainly supply-limited, i.e. depending on the soil moisture availability. In reality, transpiration is also strongly controlled by the atmospheric demand during demand-limited periods. In this study, a simple conceptual rainfall-runoff model (HBV) was used to test the hypothesis that atmospheric constraints to transpiration, especially during conditions when soil moisture is not limiting, determine the variations in catchment water yield. This is tested by parsimoniously including demand limitations of transpiration in the macroscopic ET function.

A further hypothesis was that integrating spatial climate variable surfaces, derived using physiographic co-variables, rather than point (gauge) measurements improved the model performance. These hypotheses were tested using a model for a medium-sized catchment (148 km$^2$) in south-east Australia, under a forest cover composed of mostly native eucalypts.

Spatial surfaces of the model inputs (air temperature, rainfall, vapour pressure deficit and potential ET) were generated, taking into account the topographic influence of the forcing meteorological variables. Annual stream flow represented an average 23% of the water budget with average estimated daily potential ET varying between 7 mm d$^{-1}$ in summer and 0.39 mm d$^{-1}$ in winter. The largest spatial variability in the meteorological variables and potential ET was observed during winter.

Inclusion of atmospheric-induced limitations to transpiration into the ET sub model improves stream flow simulation in south-east Australia, especially during demand-limited periods. This was expected given that canopies of eucalypt forests are well-coupled to the atmosphere, meaning that changes in atmospheric demand have a large influence on
transpiration. In addition, aggregation of high resolution (30 m) surfaces of potential ET, temperature, and vapour pressure deficit, developed by including the influence of topography on the forcing variables, improves the model performance compared to point-based inputs.

5.1 Introduction

Evapotranspiration (ET) is a major flux of water and energy, and is closely linked to vegetation characteristics in forested catchments (Eagleson 1982; Rodriguez-Iturbe and Porporato 2004). In Australia, ET sometimes approaches 100% of incoming rainfall (Bren and Hopmans 2007; Eamus et al. 2006). Among different processes included in evapotranspiration (e.g. transpiration, soil and leaf evaporation, canopy interception) transpiration is the most important component, especially in forested catchments of south-east Australia (Mitchell et al. 2012). Understanding transpiration control is therefore crucial for water yield management in water supply catchments in this area.

Vegetation water use fundamentally depends on the amount of water stored in the soil that is available to plants (Fisher et al. 2008). This dependency is partly governed by plant responses to climatic conditions and water stress (Emanuel et al. 2010). As a result, actual rates of ET ($\text{ET}_a$) are less than potential rates ($\text{ET}_p$), due to the variable resistance of leaves to molecular diffusion of water to the atmosphere, imposed by stomata and other features of plant leaves (Dickinson et al. 1991).

The amount of water transpired can be divided into water transpired under stressed and water transpired under non-stressed conditions. In Australia, eucalypt forests cover the high country catchments of the south-east and have sparse and relatively well-ventilated canopies (Hutley et al. 2000), that are well coupled with the atmosphere (Jarvis and McNaughton 1986). During periods where soil moisture is abundant (no water stress), transpiration is limited by the plant demand for water, and regulation of water loss at the leaf level is strongly coupled to atmospheric demand. Once atmospheric demand reaches a certain level, stomata begin to close and this limits transpiration to a constant level (Chapter 2; Emanuel et al. 2010, Ch.3,4 Gharun et al. 2013a, b). In contrast, down-regulation of plant water use with increasing atmospheric demand when soils are dry can be negated in response to soil water deficit (Oishi et al. 2010). In other words, constraints on transpiration are not limited to dry seasons. In terms of hydrology, focus is generally on
how transpiration mediates stream flow during dry seasons (Barnard et al. 2010; Graham et al. 2012; Moore et al. 2011). However, during wet periods transpiration is more likely to involve the gravitational water that impacts the stream flow (Brooks et al. 2010).

The assessment of the plant physiological response to water stress is a very complex topic which potentially can be included in hydrological modelling based on a mechanistic framework (Porporato et al. 2001). A suite of physical models have been used to predict stomatal conductance as a function of water availability in the soil and atmosphere (Damour et al. 2010; Gerosa et al. 2012), and can be included in models of ET$_a$, such as in the Penman-Monteith equation (Monteith 1981), depending on the complexity of the hydrological model.

Estimation of ET$_a$ via such models requires extensive data inputs – data that are not readily available in many instances. As an alternative, ET$_a$ is commonly represented, more conceptually, as a macroscopic function where the available soil moisture determines the proportion of ET$_p$ (Budyko 1958, 1974), based on a soil moisture extraction function. Such a supply limiting function is based on long term patterns between climate, evapotranspiration and runoff, but does not include the demand-limiting impacts of vegetation on ET$_a$. Such macroscopic functions are common in many conceptual hydrological models, for example SIMHYD (Chiew et al. 2002), GR4J (Perrin et al. 2003), HBV (Seibert 1997), and IHACRES (Croke et al. 2006), that employ a range of soil moisture extraction function (Zhao et al. 2013), none of which however incorporate a demand-limitation.

Considering the key role of atmospheric demand in determining transpiration – for a high proportion of catchment area and every year - and the complexity of calculating ET$_a$, it was hypothesized that including a simple description of VPD in a standard, supply limited representation of ET$_a$ in hydrological models can improve stream flow simulation, and improve the understanding of how transpiration signals are transferred to the stream in forested catchments.

Lumped hydrological models often are given input data that are collected from a single weather station, or from the average of several stations. Since climate variables can largely be influenced by the terrain (Raupach and Finnigan 1997, Moore et al. 1993), a hypothesis was tested that when climate variables are aggregated over the space, a better representation of the actual distribution of the climate across the terrain is provided,
because sparse weather stations, even if numerous and spread across the terrain, are unlikely to represent the actual distribution of the climate variable. A lumped model (discussed later) is used to test this effect on stream flow simulation.

Numerous methods exist to interpolate and aggregate forcing variables across landscapes (e.g. deterministic, geostatistical). Geostatistical methods can incorporate secondary information such as elevation and distance to the regional maximum, but a relatively large number (generally more than 30) of measurement stations is required (Mair and Fares 2011). Alternatively, meteorological variables can be physically modelled across the terrain using empirical relationships that incorporate factors such as topography, elevation, and land cover (Granger 2000; Wilson and Gallant 2000).

Currently, interpolated rainfall and climate ‘surfaces’ are available for much of Australia (e.g. Jeffrey et al. 2001). These have two main shortcomings for quantitative hydrological analysis in mountainous terrain: 1) the spatial resolution is very coarse (e.g. 0.05 ° grid, about 5 km), and 2) there are no data for vapour pressure deficit. Temperature and vapour pressure deficit change strongly with topography in the high country of south-east Australia (as they do elsewhere) and it is important to investigate how this affects hydrological model inputs.

Other studies have mostly followed a ‘calculate-then-interpolate’ approach, where ET is first calculated and then interpolated across the terrain (Xu et al. 2006). However even studies that first interpolate input variables and then calculate ET, have focused on conventional interpolation methods (e.g. inverse distance weighting, various forms of kriging), rather than physically calculating these variables for each pixel (e.g. McVicar et al. 2007).

The aims of this study are twofold: 1) to test how the coupling of vegetation to atmospheric and soil water availability affects catchment water yield and 2) whether spatial aggregation of climate factors that largely influence ET improves model accuracy.

5.2 Methods

5.2.1 Site description

The Corin Catchment is located in the Namadgi National Park and is a part of the Cotter river catchment in the Australian Capital Territory (ACT), 50 km west of Canberra and lies
at the end of the Australian Alps (lat 35.6 °S, long 148.8 °E), encompassing an area of 148 km² (Figure 5.1).

Vegetation cover is native eucalypt forests and soils are derived from highly weathered Ordovician sediments. The soils are acidic and duplex in structure (Talsma 1983). The underlying bedrock of the area is granite, limestone and shale, and topography is mountainous.

The catchment is exposed to fogs, frosts and snowfall in winter, while summers are characterized as warm and often have hot and dry periods of between 6 and 8 weeks (Moore et al. 1993). Maximum and minimum temperatures are 4 °C and -1 °C in July (winter), and 24 °C and 10 °C in January (summer). Mean annual rainfall across the catchment is approximately 1150 mm. Snowfalls are common in winter (on the higher elevations only, hence not modelled here) but the soil never freezes (Woods and Raison 1983). Average annual evaporation and seepage losses from the catchment are estimated at 630 mm (White et al. 2006). Stream discharge typically peaks between August and September and reaches a minimum during late March to May.

5.2.2 Hydrologic model

A conceptual rainfall-runoff model, HBV (Seibert 1997), that operates on a daily time step, was used to test the hypotheses. The reason for using a low parameter model is that this will allow tracking of the different processes more directly. The HBV (Hydrologiska Byrånens Vattenbalansavdelning) model simulates discharge using rainfall, temperature and estimates of potential evapotranspiration. The model has previously been used to calculate the water balance in Norway (Beldring et al. 2002), to assess climate change impacts (Beldring et al. 2008), has been combined with an ecological model (L’Abee-Lund et al. 2004), and has been used for flash flood forecasting in Austria (Bloschl et al. 2007) and Slovenia (Grillakis et al. 2010).

The conceptual hydrological model consists of four main routines: 1) a snow routine that represents snowmelt using a degree-day method, 2) a soil moisture routine representing soil water storage and evaporation, 3) an impulse response function routine that describes water flow through three linear reservoir equations, and 4) channel routing using a triangular weighting function (Bergstrom 1995; Seibert 1997). Table 5.1 lists the most important parameters of the model. Section 5.2.3 describes the method for deriving inputs across the catchment.
Figure 5.1. Location of the Corin catchment, temperature and humidity measured within the catchment, and precipitation gauges. The circles mark the position of the rain gauges and the squares mark the plots where temperature and humidity is being measured between 2010 and 2012, on a 30 minute basis.

Within the model, soil moisture depends on the sum of rainfall and snowmelt previously calculated in the snow routine. This water input is divided a fraction that adds to the soil moisture \(S_s\) of the top layer, and \(Q_{rec}\) that contributes to runoff:

\[
Q_{rec} = \left( \frac{S_s}{FC} \right)^\beta \cdot (P + M) 
\]  

(5.1)

Where FC is the maximum soil water storage, \(\beta\) is a nonlinearity parameter, \(P\) is rainfall and \(M\) is snowmelt. Soil moisture \(S_s\) is only affected by actual evapotranspiration (ETa)
which is calculated from potential evapotranspiration ($ET_p$) as a linear function of the soil moisture:

$$
ET_s = \begin{cases} 
ET_p \cdot \frac{S_s}{FC \cdot L_p} & S_s \leq FC \cdot L_p \\
ET_p & \text{otherwise}
\end{cases}
$$

(5.2)

$L_p$ is a parameter that identifies the limiting soil storage for potential evapotranspiration. The amount of $Q_{rec}$ enters the upper zone of the first underlying catchment reservoir and leaves this reservoir through two main paths: (1) percolation to the lower zone ($Q_2$) and (2) outflow from the upper zone (as either $Q_0$ or $Q_1$). Parameters $S_{uz}$ and $S_{lz}$ define the storage in the upper and the lower zone respectively. The outflow from the upper zone either simply add to the outflow ($Q_1$) or if a threshold ($U_{zl}$) is exceeded it contributes through a very fast additional outlet ($Q_0$). Water flow from the storage reservoirs is computed as the sum of the outflows ($Q_{GW} = Q_0 + Q_1 + Q_2$). This flow is finally transformed by a triangular weighting function defined by parameter MAXBAS to give the simulated runoff:

$$
Q_{sim}(t) = \sum_{i=1}^{MAXBAS} c_i \cdot Q_{GW}(t - i + 1)
$$

(5.3)

Where

$$
c_i = \int_{i-1}^{i} \frac{2}{MAXBAS} - \left| u - \frac{MAXBAS}{2} \right| \frac{4}{MAXBAS^2} \, du
$$

(5.4)
Table 5.1. Parameters of the HBV model, their abbreviated names in the model, units, feasible range, and their description.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Feasible range</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>FC</td>
<td>mm</td>
<td>50 – 500</td>
<td>Maximum value of soil moisture storage</td>
</tr>
<tr>
<td>$L_p$</td>
<td>-</td>
<td>0.3 – 1.0</td>
<td>Fraction of FC above which $ET_a$ equals potential $ET_p$</td>
</tr>
<tr>
<td>B</td>
<td>-</td>
<td>1.0 – 6.0</td>
<td>Shape coefficient</td>
</tr>
<tr>
<td>$K_0$</td>
<td>day$^{-1}$</td>
<td>0.05 – 0.5</td>
<td>Recession coefficient (upper box)</td>
</tr>
<tr>
<td>$K_1$</td>
<td>day$^{-1}$</td>
<td>0.01 – 0.4</td>
<td>Recession coefficient (upper box)</td>
</tr>
<tr>
<td>$K_2$</td>
<td>day$^{-1}$</td>
<td>0.001 – 0.15</td>
<td>Recession coefficient (lower box)</td>
</tr>
<tr>
<td>$K_3$ (MAXBAS)</td>
<td>day</td>
<td>1.0 – 7.0</td>
<td>Length of triangular weighting function in routing routine</td>
</tr>
<tr>
<td>PERC</td>
<td>mm day$^{-1}$</td>
<td>0 – 3.0</td>
<td>Maximum rate of recharge between upper and lower groundwater boxes</td>
</tr>
<tr>
<td>$U_{z1}$</td>
<td>mm</td>
<td>10.0 – 100.0</td>
<td>Threshold for quick runoff</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>-</td>
<td>0 – 1</td>
<td>Reduction factor in response to VPD</td>
</tr>
</tbody>
</table>

5.2.2.1 Adjustment of the macroscopic evapotranspiration function

Empirical measurements of the actual rates of transpiration, vapour pressure deficit and soil moisture in the high country indicate strong control of maximum transpiration rates by atmospheric vapour pressure deficit when soil moisture is abundant (in the model this would mean $S_s > FC.L_p$, Table 5.2). This effect was included in the macroscopic evapotranspiration function within HBV (Equation 5.2), in order to improve estimations of $ET_a$ and thus $Q_{obs}$. The adjusted macroscopic evapotranspiration function is:

$$ET_a = ET_p \left(1 - \left|\sigma \cdot \ln(VPD)\right|\right) \cdot \min\left(\frac{S_s(t)}{FC.L_p}, 1\right)$$

(5.5)

Where VPD is the atmospheric vapour pressure deficit (kPa), given as an input at the daily scale and $\sigma$ is a reduction factor that theoretically depends on the sensitivity of $ET_a$ to VPD.
(Figure 5.2), and can be estimated from the shape parameters describing the relationship between transpiration and VPD (Figure 5.3, \( Y = a + b \log \text{VPD}, \sigma = b/a \)).

**Table 5.2.** Coefficient of determination \((r^2)\) of the relationship between average daily sap flow and VPD, separated for wet and dry periods. Wet periods include normalized soil moisture above 0.8 and dry periods include normalized soil moisture below 0.2. Rainy days were removed and VPD above 0.1 kPa was considered only. Data presented in this table are summarized from measurements in Chapter 2 and 4 (with the corresponding site numbers). Site no. 6 was excluded from this section as it was not within the Corin catchment.

<table>
<thead>
<tr>
<th>Site no.</th>
<th>Forest species</th>
<th>Dry</th>
<th>Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>E. delegatensis</em></td>
<td>0.30</td>
<td>0.91</td>
</tr>
<tr>
<td>2</td>
<td><em>E. radiata</em></td>
<td>0.36</td>
<td>0.58</td>
</tr>
<tr>
<td>3</td>
<td><em>E. pauciflora</em></td>
<td>0.45</td>
<td>0.90</td>
</tr>
<tr>
<td>4</td>
<td><em>E. delegatensis</em></td>
<td>0.79</td>
<td>0.81</td>
</tr>
<tr>
<td>5</td>
<td><em>E. radiata</em></td>
<td>0.85</td>
<td>0.78</td>
</tr>
<tr>
<td>7</td>
<td><em>E. dives</em></td>
<td>0.63</td>
<td>0.83</td>
</tr>
</tbody>
</table>

Data from **Ch.4** Gharun et al. (2013b) *E. radiata* 0.22 0.89

5.2.3 **Spatial aggregation of input data**

Lumped hydrological models require inputs data that can be collected from a single weather station, or from the average of several stations. Since climate variables are largely influenced by the terrain, it was hypothesized that spatially aggregated inputs are a better alternative. To test this hypothesis and the influence it might have on stream flow simulation, inputs were first derived as distributed over the catchment (at a 30 m resolution) and then lumped for the model application. In all cases the median of all grid cells was used to describe the lumped input. The median describes the “average” lumped value better than the arithmetic average owing to data spread. The model simulation period was 1 January 2009 to 31 December 2011, for which data was available. Daily precipitation and discharge observations were provided by the catchment management authority, ACTEWAGL, and daily minimum, maximum and average air temperature were extracted from the Bureau of Meteorology of Australia database (BOM).
Figure 5.2. Reduction of actual evapotranspiration (ET$_a$) depending on the soil moisture storage. Black solid line follows the original ET$_a$ response (Equation (5.2)) and dashed lines show this response adjusted per the formulation in Equation (5.5) for a) $\sigma = 0.2$ and b) $\sigma = 0.8$. Greater $\sigma$ values correspond to more sensitivity of ET$_a$ to VPD. Each line corresponds to a different VPD level for a VPD range between 0 and 3 kPa, typical of the study area.
Figure 5.3. Sap flow and VPD measurements collected from within the Corin catchment and in north-east Victoria (n= 2319 days), at an average daily scale (data summarized from Chapters 2-4). Least-squares regressions ($Y = a + b \cdot \log VPD$) are used to describe the relationship between sap flow and VPD. Parameter $\sigma$ is used to adjust the macroscopic ET function and theoretically is estimated from the shape of the relationship ($\sigma = b/a$).

5.2.3.1 Rainfall

Rainfall data from several stations inside and around the catchment (Figure 5.1) were used to derive time series of areal rainfall. To interpolate, inverse distance weighting (IDW) was applied, given the relatively sparse spatial coverage over the catchment and that IDW is known to outperform Thiesen polygon methods for hydrological modelling purposes at the catchment scale (Ly et al. 2011; Mair and Fares 2011).

5.2.3.2 Temperature

The model by Wilson and Gallant (2000, p.98) was modified to estimate minimum, maximum and average air temperature across the catchment, by including Normalized Difference Vegetation Index (NDVI) instead of Leaf Area Index (LAI):
where $z$ is the elevation of the grid point derived from a digital elevation model with 30 m resolution, $z_b$ is the elevation of the station where temperature is measured, $T_b$ is the temperature at the measurement station, $T_{\text{lapse}}$ is the temperature lapse rate (°C km$^{-1}$), $c$ is an empirical constant that links temperature and normalized difference vegetation index (NDVI). This is based on the theoretical notion that surface temperature is strongly affected by the surface albedo which in turn is controlled by land surface bio-physical characteristics reflected in NDVI (Pelgrum 2000). Parameter $s$ is the short wave radiation ratio at each location, which equals the ratio of the daily total or global short-wave irradiance on a sloping surface to that on an unobstructed horizontal surface. Potential solar radiation was estimated based on surface topography and the solar inclination using geographical information system software, SAGA (System for Automated Geoscientific Analyses). A complete description of how potential solar radiation is calculated is provided by Wilson and Gallant (2000).

NDVI was included instead of Leaf Area Index (LAI) in Equation (5.6) since; 1) NDVI represents the vegetation greenness and should be directly related to LAI, 2) remotely sensed NDVI is available at a higher spatial resolution (250 m instead of 1km) 3) both LAI and NDVI products are derived from MODIS surface reflectance data, but there is less uncertainty associated with the estimation of NDVI by satellite data, compared to LAI, for eucalypt forests of south Australia (see Appendix B). NDVI data from the Moderate Resolution Imaging Spectrometer (MODIS) were used and linearly interpolated to daily NDVI from the product which is available every 16 days (product MOD13Q1). While bare slopes can have maximum temperature differentials exceeding 10 °C, actively transpiring closed forest canopies may exhibit no slope-related differences (Running et al. 1987).

The temperature model (Equation (5.6)) was parameterized for local lapse rate and constants ($c$), separately for maximum and minimum, and average daily temperature, and using 50% of the actual measurements of air temperature at six locations within the catchment (more than 2000 days of data). The model was then validated against the remaining temperature measurements.
5.2.3.3 Vapour pressure deficit

Vapour pressure deficit can be estimated from air temperature following the model of (Granger 2000). This model was modified to include maximum air temperature rather than long-term mean air temperature, because at the daily scale, measurements in this study show that maximum air temperature is a strong predictor of average VPD with $r^2 = 0.53$ as opposed to $r^2 = 0.31$ for the relationship between VPD and average air temperature ($n = 2197$ days, pooled for six locations within the catchment). Measured VPD is a direct product of measurements of air temperature and relative humidity (Equation 2.5). With the new modifications VPD was calculated as:

$$VPD = 0.6459 + 0.02936 \times T + 0.03119 \times e \times T_{max} - 1.076 \times e$$  \hspace{1cm} (5.7)

Where $e$ is the daily saturation vapour pressure at temperature $T$:

$$e = 0.6108 \times e^{(17.27* T)/(T+237.3)}$$

The original and the modified model (Equation (5.7)) were both parameterized against half of the measured VPD and validated against the other half. Description of the locations where air temperature and VPD were measured within the catchment is given in Table 5.3.

5.2.3.4 Potential evapotranspiration

Potential evapotranspiration was based on the Priestley-Taylor equation (Priestley and Taylor 1972) due to limited data availability, which is common in Australia. Gardelin and Lindstrom (1997) analysed the effect of different potential evapotranspiration calculation methods on HBV performance, and found Priestley-Taylor to provide better results. Estimated air temperature and radiation are used to calculate $ET_p$:

$$ET_p = \frac{\alpha}{\lambda_w} \frac{\Delta_v}{\Delta_v + \gamma_{air}} (R_n - G)$$  \hspace{1cm} (5.8)

Where $\alpha$ is a constant equal to 1.26 (higher values recommended for more arid regions, Jensen et al. 1990), $\lambda_w$ is the latent heat of vaporization, $\Delta_v$ the slope of the saturation vapour pressure versus temperature curve, $\gamma_{air}$ is the psychrometric constant, $R_n$ is net radiation and $G$ is the soil heat flux. Potential evapotranspiration was calculated per pixel.
using the interpolated forcing variables (i.e. temperature, radiation). Median values of the spatially distributed model inputs were used for HBV.

Table 5.3. Specification of locations within the catchment where air temperature and relative humidity is measured. Site numbers correspond to numbers in Chapter 5 as well as Chapter 2.

<table>
<thead>
<tr>
<th>Site no.</th>
<th>Forest cover</th>
<th>Elevation (m a.s.l.)</th>
<th>Slope (%)</th>
<th>Aspect (degrees)</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>Eucalyptus radiata</td>
<td>1100</td>
<td>3</td>
<td>315</td>
<td>-35.65</td>
<td>148.83</td>
</tr>
<tr>
<td>3</td>
<td>Eucalyptus pauciflora</td>
<td>1650</td>
<td>57</td>
<td>81</td>
<td>-35.58</td>
<td>148.79</td>
</tr>
<tr>
<td>4</td>
<td>Eucalyptus delegatensis</td>
<td>1493</td>
<td>26</td>
<td>165</td>
<td>-35.60</td>
<td>148.78</td>
</tr>
<tr>
<td>5</td>
<td>Eucalyptus radiata</td>
<td>1130</td>
<td>47</td>
<td>227</td>
<td>-35.61</td>
<td>148.84</td>
</tr>
<tr>
<td>7</td>
<td>Eucalyptus dives</td>
<td>1234</td>
<td>18</td>
<td>310</td>
<td>-35.60</td>
<td>148.87</td>
</tr>
<tr>
<td>8</td>
<td>Eucalyptus dives</td>
<td>1138</td>
<td>21</td>
<td>48</td>
<td>-35.64</td>
<td>148.82</td>
</tr>
</tbody>
</table>

5.2.4 Model calibration

A Monte-Carlo approach was used to calibrate the model. An ensemble of 10,000 parameter sets was selected within the feasible parameter range for running the model. Table 5.1 contains a list of the parameters in the model, their units, description and a reasonable range for each parameter derived from a literature review (Gupta et al. 2009; Lawrence et al. 2009; Seibert 1997; Steele-Dunne et al. 2008).

The selection of specific efficiency criteria was a challenge in the calibration process (like any other hydrological modelling), since each criterion places different emphasis on different types of simulated and observed behaviours (Krause et al. 2005). The most common efficiency criteria in hydrological modelling are based on standard least square methods (e.g. Nash-Sutcliffe efficiency) where the differences between the observed and simulated values are calculated as squared values, and as a result larges values in a time series are strongly overestimated whereas lower values are neglected (Krause et al. 2005; Legates and McCabe 1999; Pechlivanidis et al. 2011).

In this study, a modified NSE that gives more weight to lower flows was used, because low flows dominate runoff in the catchment of study. A second criterion was the index of agreement (d) proposed by Willmot (1981) to overcome the insensitivity of NSE to
differences in the observed and simulated means and variances. Observed and simulated runoff were compared using the index of agreement \((d)\) and modified NSE:

\[
d = 1 - \frac{\sum_{i=1}^{n} (Q_{obs}^i - Q_{sim}^i)^2}{\sum_{i=1}^{n} \left| Q_{sim}^i - Q_{obs}^i \right| + \left| Q_{obs}^i - Q_{obs} \right|} \tag{5.9}
\]

\[
mNSE = 1 - \frac{\sum_{i=1}^{n} \left| Q_{obs}^i - Q_{sim}^i \right|^j}{\sum_{i=1}^{n} \left| Q_{obs}^i - Q_{obs} \right|^j} \quad \text{with } j \in N \tag{5.10}
\]

where \(Q_{obs}\) is observed discharge and \(Q_{sim}\) is simulated by the model. Selection of \(j = 1\) allows for producing lower values than the forms with squared values (Krause et al. 2005). Further increase in the values of \(j\) increases the sensitivity to high flows and can be used when high flows are of interest (e.g. for flood prediction).

The index of agreement (Willmot 1981, Equation (5.9)) has a range between 0 (no correlation) and 1 (perfect fit), and modified NSE (Nash and Sutcliffe 1970, Equation (5.10)) varies between \(-\infty\) and 1. A mNSE of 1 corresponds to a perfect fit, mNSE of 0 indicates that the model simulations are as accurate as the mean of the observed data, and mNSE less than zero (mNSE < 0) occurs when observed mean is a better predictor than the model.

Subjective selection criteria (mNSE > 0.5 and \(d > 0.8\)) were used to define “good” results. This approach is similar to the Generalized Likelihood Uncertainty Estimation (GLUE) originally proposed by (Beven and Binley 1992), where a range of possible values rather than a single value are selected, allowing calculation of a confidence interval for the calibration outcome. A general acceptable threshold is 0.5 for NSE at the monthly scale (Moriasi et al. 2007). The threshold in this study is set for daily data - a more rigorous approach.
5.3 Results

5.3.1 Spatial simulation of air temperature

Using Equation (5.6), temperature was simulated across the catchment. Simulated maximum, average and minimum air temperature agreed well with measured values with correlation coefficient ($r$) between 0.89 and 0.96 (Figure 5.4). The time scale was daily because climate data at weather stations were available at this scale.

Temperature lapse rates varied from -2.46 °C km$^{-1}$ for minimum temperature to -4.27 °C km$^{-1}$ for average temperature, and -8.7 °C km$^{-1}$ for maximum temperature. The magnitudes of temperature lapse rates are within the range of values observed in other studies (McVicar et al. 2007; Sheng et al. 2009; Wilson and Gallant 2000). Table 5.4 shows lapse rates and $c$ parameterized for average, maximum and minimum daily temperature. Temperature lapse rate is greatest for maximum temperature, reflecting large variations in maximum temperature with elevation. In contrast, vegetation greenness has the greatest influence on average daily temperature (largest $c$). This is logical, as minimum temperature represents night-time temperature with low radiation and little albedo effect, while maximum temperatures are dominated by radiation inputs and thus less affected by vegetation albedo than average temperature.

![Graph showing observed vs. simulated maximum air temperature](image-url)
Figure 5.4. Scatter plot depicting simulated and observed a) maximum daily air temperature (°C, $r = 0.96$), b) average daily air temperature (°C, $r = 0.95$), c) minimum daily air temperature (°C, $r = 0.89$) for 2600 days and fitted regression lines. The dashed lines show the 1:1 line.

Table 5.4. Temperature lapse rates and constant $c$ parameterized for average, maximum and minimum daily temperature.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Lapse rate (°C km$^{-1}$)</th>
<th>$c$ (-)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average temperature</td>
<td>4.27</td>
<td>1.38</td>
</tr>
<tr>
<td>Maximum temperature</td>
<td>8.70</td>
<td>1.19</td>
</tr>
<tr>
<td>Minimum temperature</td>
<td>2.46</td>
<td>0.89</td>
</tr>
</tbody>
</table>
5.3.2 Spatial interpolation of vapour pressure deficit and radiation inputs

VPD simulation with the modified model (Equation (5.7)) performed better than the original model as shown in Figure 5.5. This is mainly due to maximum temperature being included in the modified form of the model, on the basis of its relationship with VPD (see section 5.2.3.3 of this chapter).

The distribution of incoming radiation as a function of slope and aspect for the catchment is illustrated in Figure 5.6. At this latitude (35°S), radiation generally peaks at intermediate values of slope (15-25°) on the north facing aspects, and is at a minimum on steep south-facing terrain. An interesting feature of the radiation field is regions of similar radiation for different combinations of slopes and aspects. For example, a steeper south-facing surface and gentler east/west-facing surfaces can receive identical radiation and thus be expected to have similar evapotranspiration demands.

![Figure 5.5](image)

**Figure 5.5.** Scatter plot depicting simulated and observed vapour pressure deficit (VPD, kPa) and the regression lines for a) the parameterized Granger (2000) model \( r = 0.66 \) and b) the modified model (Equation (5.7), \( r = 0.76 \)). The dashed line shows the 1:1 line.

5.3.3 Estimated potential evapotranspiration

The range of plotted radiation values in Figure 5.6 corresponds to a range of 876 to 1223 mm of annual \( \text{ET}_p \) across the catchment (up to 30% variation in space).

The daily \( \text{ET}_p \) from the Corin catchment, estimated using the radiation and temperature data, ranged between 0.39 and 7 mm d\(^{-1}\) across the season. \( \text{ET}_p \) also shows a clear trend with season (Figure 5.7), with low values in winter and high values in summer due to available solar energy and latent heat flux. Rates of \( \text{ET}_p \) on the higher elevations and on
top of the mountain ridges is lower than within the lower elevations and valleys due to lower air temperature despite higher incoming solar radiation (Figure 5.8).

![Figure 5.6. Average daily potential incoming radiation ($Q_{pot}$, J min$^{-1}$ cm$^{-2}$) for 35 °S and 148 °E corresponding to the Corin catchment, as a function of slope and aspect. Exact south aspect is at 180°, and exact north aspect corresponds to 0° and 360°. The largest variation across the catchment was due to the radiation (Table 5.5). Variation in ET is much smaller than the variation in energy input (e.g. radiation) due to the non-linearity of the ET process compared to the meteorological inputs.](image)

**Table 5.5.** Coefficient of variation (%) for interpolated vapour pressure deficit (VPD), potential evapotranspiration ($ET_p$) and radiation ($Q_{pot}$) at the daily scale across the catchment, during a rain-free winter and rain-free summer day in 2010.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Variation in summer</th>
<th>Variation in winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>VPD (kPa)</td>
<td>17%</td>
<td>22%</td>
</tr>
<tr>
<td>$ET_p$ (mm)</td>
<td>4%</td>
<td>7%</td>
</tr>
<tr>
<td>$Q_{pot}$ (J min$^{-1}$ cm$^{-2}$)</td>
<td>15%</td>
<td>39%</td>
</tr>
</tbody>
</table>

The annual water budget of the catchment was 833 mm total measured rainfall, 1158 mm potential evapotranspiration and 112 mm measured river discharge for 2009, 1423 mm...
rainfall, 1113 mm potential evapotranspiration and 382 mm discharge for 2010, 1056 mm rainfall, 1097 potential evapotranspiration and 304 mm discharge for 2011. Based on a simple bucket model (net drainage = precipitation – evapotranspiration – discharge), it was concluded that there needs to be a contribution of some type of storage (possibly groundwater) to the river discharge, during the low rainfall and high evapotranspiration periods (e.g. year 2009, Figure 5.7) since the sum of potential evapotranspiration and discharge is 437 mm more than the measured incoming rainfall (assuming that the errors associated with estimating ET\textsubscript{p} and measuring rainfall and discharge are less than 437 mm on an annual basis.)

Figure 5.7. Observed daily discharge (\(Q_{\text{obs}}, \text{mm}\)) and rainfall (\(P, \text{mm}\)) and estimated potential evapotranspiration (ET\textsubscript{p}, mm) between 2009 and 2011.

5.3.4 Overall HBV model performance

The daily input surfaces (potential ET, temperature and rainfall) were calculated on a 30 m grid-cell basis from the outputs of the spatial interpolation and modelling. This suggests that changes in forcing variables such as topography (including elevation, slope, and aspect) and climate are implicitly accounted for. Inputs to the model were obtained by taking the spatial median of the resulting surfaces.
Time series of simulated and observed stream flow for the period of 2009-2011 are shown in Figure 5.9.

**Figure 5.8.** Relationship between potential evapotranspiration ($ET_p$) and elevation across the catchment.

**Figure 5.9.** Runoff estimated for those parameter sets that met the criteria of $m$NSE > 0.5 and $d$ > 0.8. Shaded area shows upper and lower boundary runoff simulated with selected parameter set, and dark line is the observed runoff between 2009 and 2011.
A comparison of the distribution of HBV output based on spatially aggregated and point-based inputs, and observed runoff are shown at a monthly scale in Figure 5.10. The boxplots in Figure 5.10 indicate the daily variations within each month. Model simulation generally improved after aggregating spatially variable inputs (Table 5.6), due to the data spread, especially for VPD, rainfall and minimum temperature, but not so much for radiation or maximum temperature (Figure 5.11). Estimating streamflow from point-based measurements leads to overestimation for the majority of the time period (Figure 5.10).
Figure 5.10. Runoff simulations for a) 2009, b) 2010 and c) 2011, with point-measured and with spatially-aggregated inputs, compared with measured runoff. Boxplots summarize data within each month.
Streamflow was simulated more accurately with the new evapotranspiration function (NSE = 0.70 vs. NSE = 0.61, and \( d = 0.91 \) vs. \( d = 0.89 \)). The model including the new ET function performed better especially during wet \( (P > ET_p) \) compared to dry periods \( (P < ET_p) \), with NSE = 0.79 during wet period compared to 0.66 in dry period. Parameter \( \sigma \) can physically be estimated from actual measurements of sap flow and VPD (Figure 5.3). Calibrated \( \sigma \) was in average 0.44 and when calculated for different species (Figure 2.4), \( \sigma \) was 0.23 \( E. \ radiata \) and 0.27 for \( E. \ pauciflora \) stands. An interpretation of \( \sigma \) and how it links vegetation physiological response to catchment water yield is given in section 5.4.2 of this chapter.

**Table 5.6.** Evaluation of HBV during 2009-2011. HBV was calibrated for this period with the original ET function, including the new ET function and with point-based measurements as inputs to the model. Root mean squared error (RMSE), Nash-Sutcliffe efficiency (NSE) and degree of agreement \( (d) \) are used for evaluating the model performance.

<table>
<thead>
<tr>
<th>Model type</th>
<th>( Q_{obs} ) (mm day(^{-1}))</th>
<th>( Q_{sim} ) (mm day(^{-1}))</th>
<th>RMSE  (mm day(^{-1}))</th>
<th>NSE (-)</th>
<th>( d ) (-)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Original ET function</strong></td>
<td>0.73</td>
<td>0.98</td>
<td>0.61</td>
<td>0.61</td>
<td>0.89</td>
</tr>
<tr>
<td><strong>New ET function</strong></td>
<td>0.73</td>
<td>0.98</td>
<td>0.52</td>
<td>0.70</td>
<td>0.91</td>
</tr>
<tr>
<td><strong>Original ET with point-measured inputs</strong></td>
<td>0.73</td>
<td>0.98</td>
<td>0.75</td>
<td>0.41</td>
<td>0.86</td>
</tr>
</tbody>
</table>
Figure 5.11. Distribution of climate variables across the catchment for one day (10 January 2011). Aggregated median of the surfaces (black dashed line) used in the mode is compared with median of available stations (blue dashed line).
5.4 Discussion

5.4.1 Spatial climate variables

Lumped hydrological models require inputs data that can be collected from a single weather station, or from the average of several stations. Since climate variables are largely influenced by the terrain, it was hypothesized that spatially aggregated inputs are a better alternative, and it was tested how this might influence model prediction. Sparse weather stations, even if numerously spread across the terrain, are unlikely to represent the actual distribution of the climate variable. Median of all grid cells described the “average” lumped value better than the median from a few stations and improved model performance.

One strength of the tested spatial temperature model was inclusion of NDVI as a proxy for vegetation cover, because vegetation influences dissipation of solar radiation in forested ecosystems (Tesař et al. 2008). In addition, using NDVI allows inclusion of the impact on surface temperature of changes to forest cover (e.g. as a result of bushfire). Bushfire is a common disturbance in Australia, and more frequent and more intense fires are predicted for south-east Australia (Lucas et al. 2007). Fires affect climate at local scales through the land cover effects on surface energy budgets (Liu et al. 2005). NDVI information from satellites is relatively easily available, either from the MODIS satellite or from LANDSAT (e.g. Appendix B; Wagendonk 2003).

In addition to season, there was a significant trend in $ET_p$ with topography (Figure 5.8), induced by the combination of radiation and temperature variations with altitude, slope and aspect (Liu et al. 2011). At the catchment scale, forest cover was relatively homogenous, in the sense that the native eucalypt forests did not differ widely in their canopy structures; hence the trend in $ET_p$ was only slightly affected by land cover and variations in surface vegetation greenness. $ET_p$ estimated in this study is thus a proxy for energy balance, as controlled by topography.

In general, spatial variations in environmental factors were larger in winter than in summer. This finding is consistent with other experimental observations in mountainous regions (Liu et al. 2011). The partitioning of radiation, VPD and $ET_p$ might be expected to be different and variability larger, in catchments with less homogenous covers (Liu et al. 2011).
5.4.2 Stream flow simulation

The HBV model required calibration of several parameters as summarized in Table 5.1. Calibration of parameters that are not physically measurable is an important feature of many conceptual models (Kavetski et al. 2006), but often very different sets of parameters can provide similar results (Seibert 1997), and sometimes those parameter sets which give good results during a calibration period may yield different results in other time (Harlin and Kung 1992).

Aggregated median values of spatially distributed inputs improved stream flow simulation. This adds to the observations of Boughton (1996) on how spatial variations in rainfall in the mountainous area due to uneven topography had large effects on the prediction of surface runoff in the Mount Lofty Ranges in South Australia. Considering that point-measured inputs lead to less accurate simulation of streamflow, it suggests that point based observations can be biased and not representative for actual climate variables at the catchment scale. The importance of this increases as catchments become more variable in topography. Spatially-aggregated inputs are thus important in montane catchments.

On the basis of the present study, it is not possible to assess the relative significances of spatial variation in ET on the one hand, and spatial variability of rainfall on the other. It might be expected that in a lumped model calibration, error in one estimate is partly balanced by the other. Future research might focus on the effects of spatial variation in ET and rainfall in terms of their contributions to predictive hydrology.

Sensitivity analysis of runoff response to the model parameters shows the model is most sensitive to the recession parameters of the upper and lower reservoirs that control the ability of soil to retain the water in these reservoirs (Kobold et al. 2003). Comparing calibrated parameter values in the present study to parameter values in catchments in other countries (e.g. Ireland, Steele-Dunne et al. 2008) indicates that the proportion of precipitation that directly contributes to runoff and the contribution of base flow to the river discharge is relatively low in the Corin catchment (relatively low beta and $k_2$). This would be expected for semi-arid catchments in Australia.

Among different atmospheric variables, vapour pressure deficit generally has the largest impact on transpiration, particularly in sparse canopies (see Chapter 2; Jarvis and McNaughton 1986). Especially when soil moisture is abundant, vegetation water use is strongly coupled to atmospheric demand (demand-limited). However, as soils dry,
vegetation water use is increasingly decoupled from vapour pressure deficit and becomes increasingly dependent on soil moisture (supply-limited, Table 5.2). The shift between supply-limited and demand-limited phase plays a crucial role in the movement of water through the soil-plant-atmosphere continuum (Barnard et al. 2010; Emanuel et al. 2010) and in general is not included in macroscopic evapotranspiration functions in hydrological models.

Although seasonal vegetation dynamics have large effects on evapotranspiration and fluctuations of the hydrologic system, at fine temporal scales (Donohue et al. 2007), seasonality of transpiration in response to soil moisture and VPD is not fully understood (Moore 2011). Vegetation is known to play a significant and dynamic role in determining catchment evapotranspiration. Nevertheless, it is expected for catchment processes to have relatively less sensitivity to the role of vegetation at bigger spatial and temporal scales (Budyko 1974; Farmer et al. 2003). In this study, it is highlighted how daily VPD modulates streamflow by controlling transpiration, which adds to previous understandings of signatures of vegetation transpiration response on streamflow, at the sub-daily basis (Barnard et al. 2010; Bond et al. 2002; Graham et al. 2012). Improving this understanding facilitates better space-time modelling of soil moisture which is fundamental in estimating catchment water balance. Model performance improved with the new function especially during wet periods (demand-limited), in agreement with the respective hypothesis.

Parameter $\sigma$ increases with sensitivity to VPD: drought sensitive species such as $E.\ pauciflora$ had greater $\sigma$ values compared to more drought tolerant ones ($e.g.$ $E.\ radiata$). Drought tolerance of the above-mentioned species is tested and widely discussed in Chapter 2. Physiologically, larger $\sigma$ is associated with earlier closure of stomata in response to high VPD (the asymptotic part of the relationship between transpiration and VPD, smaller $a$), and stronger response to VPD during the first part of the relationship (bigger slope of the linear part).

An average $\sigma$ of 0.44 for the entire catchment is not unexpected given mixed proportions covered by both drought sensitive and drought tolerant species. In a catchment covered solely by drought-sensitive species such as $E.\ pauciflora$ or $E.\ delegatensis$ ($e.g.$ catchments providing water to the city of Melbourne) a larger value for $\sigma$ is expected to better transfer coupling of vegetation to atmospheric and soil water availability affects on catchment water yield.
5.5 Conclusion

This study tested the adjusting of a supply limited evapotranspiration function with demand limitation, based on empirical data and theory (App.A Buckley et al. 2012; Ch.3 Gharun et al. 2013a, Ch.4 Gharun et al. 2013b), and how it affects catchment stream flow.

In summary, this study highlights the role of atmospheric drought on catchment water yield at the daily scale and demonstrates that 1) biophysical constraints of forest transpiration during non-limiting soil moisture periods determine variations in catchment water yield in south-east Australia and that 2) high resolution surfaces of ET in montane catchments can be spatially modelled, taking into account the influence of topography on the forcing variables, while improving stream flow simulations, compared to point-measured inputs.

Results from this study improve the understanding of how transpiration signals are transferred to the stream in forested catchments, which is of paramount importance in ecosystems where transpiration is a major part of the ET flux. In addition, the method tested in this study adds to the advantage of existing simplistic macroscopic ET functions that are normally hampered by methods that estimate ET from detailed weather information.
5.6 References


Farmer, D., Sivapalan, M., Jothityangkoon, C., 2003. Climate, soil, and vegetation controls upon the variability of water balance in temperate and semiarid landscapes:


6 Model of tree sap flux for high country forests of south-east Australia

Summary

Tree water use is a major component of the water balance in forested catchments of semi-arid areas, as more than 80% of the incoming rainfall may be used by overstory trees. Managers are unable to easily predict water use and thus water yield, for the majority of eucalypt-dominated catchments in south-east Australia, owing to the variety of dominant and co-dominant species and their relationships with landform, and the lack of species- and landform-specific knowledge. Moreover, the costs incurred to quantify input variables for available complex, process-based models, generally precludes their use, and alternative approaches are needed. One such alternative approach, suited to complex terrain such as the forests of south-east Australia, is application of data-learning techniques to empirical data.

In this study, the adequacy of using just two easily measured variables for estimating rates of tree water use, using a model derived from data-learning techniques, was tested. The inputs are 1) measured daily atmospheric demand for water and 2) potential incoming radiation derived from surface topography and solar declination. Artificial Neural Networks (ANNs) and Genetic Programming (GP) models were trained and validated using observations of vapour pressure deficit (VPD) and estimates of potential solar radiation ($Q_{pot}$), for a period of two years, at each of 10 forest stands across the high country of the states of New South Wales and Victoria. The models were tested using a random 50% of the collected data that was independent, i.e. not used in model development.

Atmospheric demand was selected because it strongly affected tree water use irrespective of site and species. Potential solar radiation was selected as a proxy for radiation, because it is relatively easy to estimate for any location for which elevation data are available in digital format, and since radiation strongly controls photosynthesis (through stomatal behaviour) and thermal balance.
Genetic programming resulted in models better able to predict rates of sap flux than ANNs. A selected GP model was able to describe the relationship between tree sap flux, VPD, and potential radiation with good accuracy, and was used to map tree water use, using available surfaces of input variables.

This study has significant economic and environmental implications for forested catchments, and their management across high country of south-east Australia.

6.1 Introduction

A significant portion of south-east Australia’s montane catchments are dominated by eucalypt forests (Office of Environment and Heritage, 2011). Water yield from these headwaters to the Murray Darling Basin is highly dependent on the influence of forest functional type on energy and water exchange across the catchment. Transpiration alone explains a significant proportion of the changes in the stream flow (Mitchell et al. 2012), while the sensitivity of catchment water balance to vegetation water use increases as the ratio of potential evapotranspiration to rainfall increases (Zhang 2004). Vegetation water use has only been well quantified for tall-open eucalypt forests (Buckley et al. 2012b; Dunn and Connor 1993; Jayasuriya et al. 1993; Pfautsch et al. 2010; Vertessy et al. 1995; Vertessy et al. 1996; Vertessy et al. 1997; Vertessy et al. 1998; Vertessy et al. 2001). There remains scant data and knowledge of key drivers of vegetation water use for the majority of the area of south-east Australian catchments.

Rates of tree water use are now routinely measured using sap flow sensors. Physically-based models that subsequently draw on such sap flow data are used internationally to predict vegetation water use (Chuang et al. 2006; Granier and Loustau 1994; Williams et al. 2001). Determinants of tree water use are complex. While physical processes are reasonably straightforward to represent mathematically, the biological processes are problematic. A general response within the literature is to greatly simplify these processes; albeit that the resulting models are then somewhat limited in their application. Consequently, there is a large number of experimental formulae for estimating tree water use. These include: 1) physically-based equations that describe the functions of the system and the physical laws that govern these processes (Chuang et al. 2006; Diaz-Espajo et al. 2012) - these equations require extensive input data which is seldom readily available at each location within a landscape; 2) empirically-based models that do not require
extensive inputs, but which need local parameterization and are not usable for species other than those studied (Buckley et al. 2012a; Dierick and Hölscher 2009; Langensiepen et al. 2006). Researchers have also built simpler forms of empirical models that are based on VPD and Photosynthetically Active Radiation ($Q$, specific to waveband ca. 400-700 nm of solar radiation). Even so, application of these simpler models across the landscape is still limited by the difficulty of parameter estimation (Dierick and Hölscher 2009; Dye and Olbrich 1993).

In general, limitations of available predictive models across a range of fields, has led to application of data-driven, machine learning techniques that solve optimization problems and find structure among potential relationships. Some of the most applied methods of such ‘soft computing’ in the field of hydrology and water resources, include Artificial Neural Networks (ANNs) and Genetic programming (GP). Their application has been encouraged by promising results for many prediction problems in hydrology (ASCE 2000).

For example, these methods have been successful in accurately estimating processes such as pan evaporation (Kişi et al. 2012; Terzi 2012), evapotranspiration (Aytek 2009; Cobaner 2011; Parasurman et al. 2007), reference evapotranspiration (Shiri et al. 2012), soil moisture estimation (Makkeasorn et al. 2006), precipitation (Kisi and Shiri 2011), ground water table depth fluctuations (Shiri and Kisi 2011), rainfall-runoff (Minns and Hall 1996; Savic et al. 1999; Whigham and Crapper 2001), suspended sediments in streams (Aytek and Kişi 2008), and risks in water supply (Babovic et al. 2001). Recently, GP was applied to modelling rainfall-runoff relationship in forested catchments affected by bushfires, and was found to be superior to other data-learning techniques, including Linear Regression, K-Nearest Neighbour, and Artificial Neural Networks (see Appendix C).

Meijun et al. (2007) and Li et al. (2009) used Neural Networks to predict transpiration from poplar trees and transpiration from fruit trees, however their models requires in-situ measurements of at least three inputs and lack a mathematical framework to describe underlying mechanisms.

In this study Artificial neural networks (ANNs) were tested since they provide a powerful tool which is more appropriate in studies where large amounts of data are available. Genetic programming was used to define the mathematical relationship between the
variables and the output, and then to optimize the variables and the constants of the relationship.

Evaporative demand and solar radiation have been tested as primary predictors of tree water use because amongst the various influencing climatic factors, humidity and radiation have the greatest effect on transpiration, vegetation function and dynamics (Chapter 2; Dye and Olbrich 1993). VPD and radiation can explain more than 90% of the variations in sap velocity in eucalypt forests of Australia (Zeppel et al. 2004), or deciduous forests of the northern hemisphere (Wullschleger et al. 2001). In some forests, atmospheric VPD does not have a strong influence on transpiration; for example in pine plantations with large leaf area indices (Teskey and Sheriff 1996). When tree canopies are sparse and well-coupled with the atmosphere (e.g. in eucalypt trees), atmospheric influence on tree water use becomes paramount (Jarvis and McNaughton 1986). VPD can be easily calculated from measurements of air temperature and relative humidity while solar radiation is highly dependent on topography (Hengl and Reuter 2009), and therefore, the apparent solar path can be easily and accurately calculated relative to any location and any surface (Wilson and Gallant 2000). Topography-driven variables can particularly be promising, since catchment topography is recognized as a critical control of the hydrological response and the resulting spatial organization of the vegetation patterns (e.g. Caylor et al. 2005; Coblentz and Riiters 2004).

The aim of this study was to test whether data-learning techniques trained with minimum input variables can estimate tree sap flux across a complex terrain with a range of eucalypts. To this date, no other study has tested ANNs or GP for estimating tree water use in the forested catchments of Australia.

### 6.2 Methods

#### 6.2.1 Data used

Sap flux and vapour pressure deficit (VPD, kPa) were measured at 10 sites between May 2010 and July 2012 from high country forests that cover the water catchments within Murray Darling Basin in south east Australia (MDB, between latitudes -35.58° to -36.46° and elevation between 700 and 1700 m above sea level). Collection of these data is described in details in Chapter 2 and 3. Briefly, the sites were chosen to capture the full
breadth of forests that vegetate the montane headwaters of the MDB: monospecific forest dominated by *E. delegatensis* or *E. pauciflora*, and mixed species forest dominated by *E. radiata*, *E. dives*, and *E. mannifera*.

Sap flux was measured at each site using the Heat Ratio Method (Burgess et al. 2001) and as described in section 2.2.2 of this thesis. Air temperature (*T*, °C) and relative humidity (*rH*, %) were directly measured 1 m above the forest ground every 30 minutes using electronic sensors. Average daily vapour pressure deficit (VPD, kPa) was calculated from measurements of temperature and relative humidity (World Meteorological Organization, 2008):

$$
VPD = \left( 0.6112 \times e^{\frac{17.62 \times T}{243.12 + T}} \right) \times \left( 1 - \frac{rH}{100} \right)
$$

VPD was selected because throughout this thesis, it strongly affected tree water use irrespective of site and species (see Chapter 2; Buckley et al. 2012b; Ch. 3, Gharun et al. 2013a, b). When direct measurements of temperature and relative humidity are not available, these data for the region can be collected from the Bureau of Meteorology of Australia for weather stations, or other climate databases such as SILO (enhanced climate databank hosted by Queensland Climate Change Centre of Excellence), that provide these data as spatially interpolated for any location within Australia (Jeffrey et al. 2001).

Figure 6.1 shows the location of selected sites within the Australian Capital Territory and Victoria in south-east Australia. The forests selected span a range of forest age, species and topography. Details of the measurement sites and species cover are given in Table 6.1.
Figure 6.1. Locations of selected sites in south-east Australian high country. Sites are in the high country of Australian Capital Territory and north eastern Victoria.

Table 6.1. Description of sites and species from which sap flux and VPD measurements were used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Elevation</th>
<th>Slope (%)</th>
<th>Aspect</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. dives a</td>
<td>826</td>
<td>27</td>
<td>302</td>
<td>-36.46</td>
<td>146.72</td>
<td>VIC</td>
</tr>
<tr>
<td>E. dives b</td>
<td>1234</td>
<td>18</td>
<td>310</td>
<td>-35.60</td>
<td>148.87</td>
<td>ACT</td>
</tr>
<tr>
<td>E. dives c</td>
<td>1138</td>
<td>21</td>
<td>48</td>
<td>-35.64</td>
<td>148.82</td>
<td>ACT</td>
</tr>
<tr>
<td>E. radiata a</td>
<td>1130</td>
<td>47</td>
<td>227</td>
<td>-35.61</td>
<td>148.84</td>
<td>ACT</td>
</tr>
<tr>
<td>E. radiata b</td>
<td>1100</td>
<td>5</td>
<td>315</td>
<td>-35.65</td>
<td>148.83</td>
<td>ACT</td>
</tr>
<tr>
<td>E. radiata c</td>
<td>742</td>
<td>24</td>
<td>272</td>
<td>-36.46</td>
<td>146.72</td>
<td>VIC</td>
</tr>
<tr>
<td>E. delegatensis</td>
<td>1493</td>
<td>26</td>
<td>165</td>
<td>-35.60</td>
<td>148.78</td>
<td>ACT</td>
</tr>
<tr>
<td>E. pauciflora a</td>
<td>1650</td>
<td>57</td>
<td>81</td>
<td>-35.58</td>
<td>148.79</td>
<td>ACT</td>
</tr>
<tr>
<td>E. pauciflora b</td>
<td>779</td>
<td>21</td>
<td>300</td>
<td>-36.46</td>
<td>146.72</td>
<td>VIC</td>
</tr>
<tr>
<td>E. pauciflora c</td>
<td>791</td>
<td>22</td>
<td>273</td>
<td>-36.44</td>
<td>146.72</td>
<td>VIC</td>
</tr>
</tbody>
</table>
Potential incoming radiation is the energy of solar radiation received by a particular surface point in one day, under clear sky conditions, and it depends on the components depicted in Figure 6.2. Average potential incoming solar radiation (0.4 – 1 µm, $Q_{pot}$, J min$^{-1}$ cm$^{-2}$) was estimated interactively, by combining a digital elevation model (approximately 30 m resolution, ASTER global DEM), and solar position within a geographic information system, SAGA (System for Automated Geoscientific Analyses, http://www.saga-gis.org). Incoming solar radiation is estimated within the software after calculating the shadowing effect of the surrounding land surface from the DEM, and integrating sun’s position on the sky. This approach combines sun’s position as the light source, and subsequent inclination angles and shadow effects; the angle at which radiation hits the earth’s surface, is corrected for slope and aspect for each point of the landscape (Hengl and Reuter 2009). Using this approach to describe changes in $Q_{pot}$ across time and space incorporates the interaction between radiation and topography, which is specifically important in forests covering complex terrain. Additional details concerning calculation of potential solar radiation are given in Böhner and Antonic (2009).

In total 3044 days of data were used in this study. Data were shuffled and split randomly in two halves to overcome autocorrelation issues. One half was used for deriving the models, and the other half for independently testing of the selected models. From the proportion of data used in the modelling, 70% was used for training and 30% for validation. For comparison purposes same approach was used for both ANNs and GP methods.

Figure 6.2. Factors influencing the potential direct solar radiation received by the earth surface (with modifications from Funk and Hoelze 1992).
6.2.2 Artificial Neural Networks (ANNs)

Artificial neural networks (ANNs) are semi-parametric regression techniques that are able to approximate any measurable function up to an arbitrary level of accuracy. This means ANNs are able to store the experimental knowledge gained through the process of learning and use it in the future (Haykin 1999).

The architecture of ANNs consists of layers of parallel processing elements, which are known as neurons. Figure 6.3 illustrates the architecture of a simple three-layer feed-forward neural network consisting of one input \((i)\), one hidden \((j)\) and an output layer \((k)\). Symbolically the architecture of the below ANNs is represented as ANNs \((i, j, k)\). Typically the input layer is connected to the hidden layer(s), and the hidden layer(s) is connected to the output layer with connection weights \((W)\). In a feed-forward network, the connection weights feed the activations only in one direction from an input layer to the output layer.

![Architecture of a simple feed-forward artificial neural network](image)

**Figure 6.3.** Architecture of a simple feed-forward artificial neural network

An ANN can have more than one hidden layer. The weights are initially selected and then systematically changed during the process of learning. Basically each ANN consists of three main steps: 1) setting the network architecture 2) training the network 3) testing the network. Here the input layer consists of nodes representing VPD and \(Q_{\text{pot}}\), and the output layer consists of a node representing sap flux. In this study, a multi-layer feed-forward ANNs was used and data was processed using a commercial software package (MATLAB 7.12, The MathWorks Inc., Natick, MA, 2011). The ANNs was trained under various
combinations of nodes in hidden layers, number of hidden layers, training functions and parameters of the training function to perform an input/output mapping to provide the set of rules on which the model was based.

6.2.3 Genetic Programming (GP)

Genetic programming was first proposed by Koza (1992), where a population of models are chosen using stochastic methods and are allowed to “evolve” according to a set of simple rules that mimic biological evolution. Output is a mathematical expression between a set of predicted and predictor values (Babovic and Keijzer 2000).

GP differs from other regression models, in that it does not require choosing a model structure a priori, it optimizes both variables and constants. Models are evolved and evaluated individually until a satisfactory solution is found based on a fitness measure. Each candidate model (potential solution) is coded in a parse tree (Figure 6.4) where the inner connection points are the functions (mathematical operators) and the terminal connection points are made up of variables and constants.

![Figure 6.4. The parse tree for a mathematical model](image)

The robustness of GP in modelling complex nonlinear processes has led to its application in a broad range of applications and for different purposes. GP has successfully been used in hydrological applications as mentioned in the introduction. However to our knowledge no other study has attempted to test this method for modelling the sap flux of eucalypt trees.
In the present work, the Eureqa program (Schmidt and Lipson 2009) was applied for the GP approach, since it provides a user friendly interface and each step is represented by one graphical interface sheet. Eureqa automatically shuffles the data before splitting them into training and validation datasets and verifies individual models on the automatically chosen validation data. The program provides the best solution with different levels of complexity. The level of complexity is related to the solution enlargement with progressive inclusion of additional permitted factors.

6.2.4 Performance evaluation

Performance of the model was evaluated based on a multi criteria approach including root mean squared error (RMSE) and correlation coefficient ($R$):

$$RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^{N} (y_i - \hat{y}_i)^2}$$  \hspace{1cm} (6.2)

$$R = \frac{\sum_{i=1}^{N} (y_i - \bar{y}) (\hat{y}_i - \bar{\hat{y}})}{\sqrt{\sum_{i=1}^{N} (y_i - \bar{y})^2} \sqrt{\sum_{i=1}^{N} (\hat{y}_i - \bar{\hat{y}})^2}}$$  \hspace{1cm} (6.3)

Where $y_i$ and $\hat{y}_i$ represent measured and modelled values respectively. Correlation coefficient evaluates the linear correlation between measured and modelled values, and root mean squared error describes the average difference between model results and observations, in units of average daily sap flux (cm hr$^{-1}$). Lower RMSE implies the better performance of the applied model.

6.2.5 Application across complex terrain

The selected model was applied to every pixel (30 m resolution) of a medium size catchment (Corin catchment, 148 km$^2$) to investigate variations of sap flux across the landscape. $Q_{pot}$ was derived from the available DEM for the catchment. The DEM is accessible from Earth Remote Sensing Data Analysis Centre (ERSDAC) of Japan and NASA’s Land Processes Distributed Active Archive Centre (LP DAAC). VPD was
extracted from VPD surfaces. For details of how VPD was interpolated across the landscape, see section 5.2.3.3 of this thesis.

6.3 Results and Discussion

Input variables were highly significant \((p < 0.001)\), with VPD alone explaining 41.5\% of the deviance in sap flow. Sap flow increased with an increase in VPD in a saturating fashion, with a greater increase during low VPD. As VPD increases transpiration commonly tends to saturate and stabilize at a maximum transpiration (Figure 6.5). Similar behaviour has been observed in forests of the northern hemisphere (Köcher et al. 2009; Pataki and Oren 2003).

The second variable is the potential incoming radiation that was calculated based on topography and location of sun in the sky \(Q_{pot}\). Radiation and VPD are often found to be the most important controls of tree water use (Chapter 2, Oren et al. 1999; Pallardy and Kozlowski 1979). VPD range was between 0.00014 and 2.9 kPa across the sites, and period of study, and \(Q_{pot}\) varied between 0.34 and 2.4 J min\(^{-1}\) cm\(^{-2}\).

![Figure 6.5. Relationship between sap flux \((V_s)\) and vapour pressure deficit (VPD) measured in Chapter 2 and 3.](image)

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6.3.1 Artificial Neural Networks performance

The final outcome of the ANNs training was a three-layer feed forward network (input, layer, hidden layer, output layer), with two nodes in the input layer (VPD and $Q_{pot}$), and 4 nodes in the hidden layer, constructed for predicting rates of sap flow.

The number of nodes in the hidden layer is related to several factors such as the number of input variables, the number of training cases, the complexity of the underlying processes and the amount of noise in the training data. The larger the number of nodes the lower the training error, but the higher will be the prediction error due to over fitting. Finding the optimal number of nodes in the hidden layer in ANNs remains an open challenge. The four nodes in the hidden layer was accepted as a reasonable performance, based on that it is suggested for the optimal number of nodes in the hidden layer to be equal or less than twice the number of input variables (Linoff and Berry 2011), or to be equal to log ($N$) where $N$ is the number of training samples (Wanas et al. 1998).

6.3.2 Genetic Programming performance

In order to find the optimal model for predicting sap flow, two main approaches were selected in applying the GP method: In the first approach (GP1), an initialization was based on preliminary function sets limited to a process-based model of Buckley et al. (2012a). This model was selected because: 1) it is driven by irradiance and evaporative demand with parameters that transparently represent stomatal physiology; 2) it has been successful in predicting whole tree sap flux in eucalypt forests (considering local parameterization is available).

In the second approach (GP2), initialization was based on Eureqa program’s default set of functions (i.e. $+, -, \times, \div, \sqrt[3]{\cdot}, \sqrt{\cdot}, \ln, e^x, x^2, \sin x, \cos x$, Arctgx), without assuming a specific mathematical form. Comparison of GP1 and GP2 showed that assigning the process-based model as initialization improved GP output, by increasing the correlation coefficient ($R$) and reducing root mean square error (RMSE).

The optimal equation evolved by GP for characterizing sap flux ($V_s$, cm hr$^{-1}$) is given by Equation (6.4) (GP1), and Equation (6.5) (GP2):
\[ V_s = \frac{(-0.36 - 22.12 \times Q_{pot} \times VPD)}{(-Q_{pot} - 1.29 \times VPD - 0.20 \times Q_{pot}^4 \times VPD)} \] (6.4)

\[ V_s = 7.97 \times \sqrt{VPD} + 2.82 \times VPD \times \sin \left( \frac{-14.05}{Q_{pot}} \right) \] (6.5)

According to GP1, sap flow increases with an increase in VPD, in a saturating fashion, where the upper limit of transpiration in high VPD conditions is influenced by radiation, especially at low and saturated light conditions (Figure 6.6). Physically, this is attributed to the offsetting effect of radiation and VPD on stomatal behaviour at the leaf level (Chapter 2; Buckley et al. 2012a; Meinzer et al. 1995; O’Biren et al. 2004).

**Figure 6.6.** A 3-dimensional representation of the model for sap flow based on solar radiation and vapour pressure deficit.

### 6.3.3 Model application at the tree scale

Table 6.2 represents the error statistics for training and testing with different methods. It can be concluded from this table that GP generally has superior performance in predicting
actual rates of sap flux. Both GP approaches performed better in predicting sap flux even though the ANNs trained the data better. Using a GP approach did not improve RMSE (2.3 and 2.18) but yielded greater $R$ (0.80) for predicting sap flux than did ANNs (0.75). In general the differences in the performance statistics between ANNs and GP models were modest.

Table 6.2. Comparison of ANNs and GP model performance against observed data.

<table>
<thead>
<tr>
<th>Model</th>
<th>Training</th>
<th></th>
<th>Testing</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R$</td>
<td>RMSE</td>
<td>$R$</td>
<td>RMSE</td>
</tr>
<tr>
<td>GP1</td>
<td>0.64</td>
<td>2.64</td>
<td>0.80</td>
<td>2.30</td>
</tr>
<tr>
<td>GP2</td>
<td>0.67</td>
<td>2.55</td>
<td>0.77</td>
<td>2.38</td>
</tr>
<tr>
<td>ANNs</td>
<td>0.75</td>
<td>2.17</td>
<td>0.75</td>
<td>2.18</td>
</tr>
</tbody>
</table>

The advantage of GP remains the explicit mathematical expression that it provides giving a platform for improving the knowledge about how radiation and evaporative demand influence tree water use, and the opportunity for finding new formulae. Therefore GP1 was selected as the most appropriate for predicting sap flux. The selected model (Equation (6.4)) captured sap flux behaviour well, almost in all sites, with best performance in $E.\ pauciflora$ and $E.\ radiata$ (Figure 6.7).

Figure 6.8 plots the measured and modelled sap flux as showing where model is over or underestimating actual rates. This plot suggests the model’s tendency to underestimate sap flux. Systematic deviations of the model from the data were tested by applying a multiple linear regression analysis on the residuals (measured data minus modelled), with VPD, $Q_{pot}$, and time used as independent variables. Table 6.3 summarizes the standardized regression slopes for any significant effects ($p < 0.05$). In most cases residuals were negatively correlated with VPD, and positively with $Q_{pot}$. This suggests that the model tends to underestimate in high radiation and low VPD, which within the landscape includes the flat areas on higher elevations and top of the ridges.
Figure 6.7. Rates of sap flux predicted for *E. pauciflora* and *E. radiata* over a five month period, using Equation (6.4). Top panel is modelled sap flux for the months December to April, and lower panel spans the period of July to December.

Some of the discrepancies in modelling the actual rates of sap flux can be attributed to the contribution of stored water in the tree stem, or changes in the soil to leaf hydraulic
conductivity (O’Grady et al. 1999). The contribution of stored water to tree water use varies among species and sizes, and has a significant effect on the relationship between water use measured at the base, and atmospheric VPD (Oren et al. 1999; Wullschleger et al. 1998).

![Figure 6.8](image)

**Figure 6.8.** Comparison between modeled and measured sap flux for all species.

A closer look into measured VPD revealed that variation of VPD used for training the model has a direct influence on the model performance. The more disperse the VPD data (measured here by coefficient of variation, CV), the better is the model built (Figure 6.9a). This is not unexpected, and it is logical that the validity of such models increases, when larger datasets from several locations and under a varying set of conditions is incorporated in the training process.
Another important source of uncertainty for the model is the location where the VPD is measured. Point-measured climate variables are not usually available exactly at the location where sap flux is to be modelled. Interestingly, within a complex terrain, differences in the elevation between where the VPD is measured and where sap flow needs to be modelled, has a larger influence on the model performance, than the distance between those two locations (Figure 6.9b).

6.3.4 Model application over the landscape

Application of the model to the catchment can assist us in visualizing and understanding some of the larger scale ecological processes that most affect vegetation water use and productivity distribution, and are normally hard to interpolate across the landscape, at a new spatial and temporal scale (Figure 6.10).
Figure 6.9. a) Improvement in model performance (during the testing process) with increase in VPD variation (during the training process), b) Changes in model performance with dH (dH shows the difference in elevation between where VPD is measured and the prediction location).

In this study for example, applying the model to every pixel of a catchment in south east Australia (Figure 6.11), reveals differences in tree sap flux, that are well-coupled with topography. Sap flux is significantly lower on higher elevations \((p < 0.001, r^2 = 0.98)\), which at the catchment scale is in equilibrium with soil water availability (Caylor and Dargoni 2009). In lowland areas and along stream rills, soil is wetter through re-infiltration of lateral overland flow (Niu et al. 2013). This subsidy of water provides plants with favourable transpiration supply (Hatton et al. 1997).

Modelled sap flux is greater on the southern slopes, and this can be explained by two main factors: radiation and precipitation. Tree water use and productivity are closely linked together, while topography plays an important role on vegetation water stress (Caylor et al. 2005; Emanuel et al. 2010; Jasper et al. 2006). In the north-facing aspects (between 0-90, and 270-360 degrees), excess radiation can limit productivity on steep slopes, induce soil moisture deficit, hence water stress (Jasper et al. 2006), and reduce vegetation water use. On southern slopes, greater rates of water use can be linked to precipitation distribution. Generally, topography influences precipitation patterns differently depending on the environment (Basist et al. 1994). In the area of study, among different topographic variables, slope explains the largest variation in spatial patterns of precipitation, more than elevation and aspect (Basist et al. 1994). In summary, forced ascent during cooler season and localized convection during the warm season leads to more precipitation on the higher slopes of the windward aspects. Practical implication of such information is in estimating
weighted potential impact of for example forest management practices on catchment water balance at different locations within the landscape.

The great advantage of the model proposed here is that it incorporates all wavelengths within the incoming radiation instead of those deemed photosynthetically active radiation (a required parameter for most empirically-based models of tree water use), enabling it to be easily predictable from topography from a digital elevation model. The role of VPD in constraining transpiration is especially observed in instantaneous and short time scales (Motzer et al. 2005). Observations in this study however prove strong control of VPD at a daily time scale, and the model proposed is established on daily VPD for which data collection is easier. The second input (insolation) can be a proxy for terrain-modulated water balance conditions and productivity patterns across the landscape (Flores Cervantes et al. 2012).

Figure 6.10. Tree sap flux modelled for the Corin catchment, at an average monthly scale, during 2010.
The advantage of the methodology used in this study is its simplicity; models can be produced and tested in the absence of data that are required to describe complex processes underlying tree water use. The shortcoming however is that data-learning models are limited in performance by the variance in the training data. The possible approach to develop the methodology proposed in this study would be to incorporate larger datasets from several locations to increase the range of variation in the input data set. More local training of the model might as well improve the prediction power, but at the same time limits model applicability in other locations.

**Figure 6.11.** Coordination of modelled sap flux with slope and aspect across the Corin catchment. Data is average of sap flow during 2010.

### 6.4 Conclusion

Tree sap flux indicates rates of transpiration for a single tree, as well as for whole stand and catchment, using suitable upscaling methods. Process-based models for tree water use are limited in their applicability for catchment managers, as parameterisation requires substantial input variables that often require specialist equipment and are difficult to obtain. Data-learning techniques (ANNs and GP) were applied to predict rates of sap flux in eucalypt trees of mixed species forests in south east Australia, using evaporative demand and potential radiation as the input variables.

The solution finding power of GP is advantageous in this particular application, as unlike ANNs “black box” approach to model input-output relationships, GP has delivered an
equation that could readily be used by catchment managers to estimate sap flux in the montane eucalypt forests of south-east Australia. Application of the selected model for mapping tree sap flux provided a powerful tool for exploring spatial variability in tree water use, within the landscape.
6.5 References


7 General Discussion

7.1 Introduction

Much research in hydrology has been unconnected to the ecological characteristics that make the interplay between climate, soil and vegetation specific to a region. To improve hydrologic tools and methods, it is fundamental that we develop a better understanding of the climate and physiological characteristics of the particular biome type (Rodriguez-Iturbe 2000).

In south-east Australia, forested catchments supply water to millions of people while water yield is largely governed by the loss to the atmosphere via plants (evapotranspiration in some parts accounts for 100% of the annual rainfall). In the State of Victoria, almost 79% of the total forested area is dominated by mixed-species eucalypt forest (Attiwill 1994). Even so, most eco-hydrological studies have been confined to ash-type eucalypt forests, and we have little knowledge of the linkage between hydrology and ecology for millions of hectares of mixed-species eucalypt forests.

The aims of this study, as explained in detail in the preceding chapters, were to 1) collect base-level estimates of tree water use across mixed-species eucalypt forests and determine the most important environmental and physiological underpinnings of water use for the range of forest types, 2) investigate the impact of bushfire on canopy transpiration, 3) validate existing models for simulating canopy transpiration, 4) investigate hydrological links between vegetation response to the atmospheric and soil moisture, and catchment water yield, and to 5) identify and test suitable methods for modelling tree sap flux across the landscape.

This conclusion chapter summarizes the findings and discusses their implications in the context of natural resources management and outlines research perspectives for the future, including the filling of gaps in data and knowledge.
7.2 Environmental underpinnings of water use in mixed-species eucalypt forests

Atmospheric conditions and soil moisture control tree water use albeit with substantial differences among species and sites (Buckley et al. 2012; Dierick and Hölscher 2009; Medhurst et al. 2002; Oren and Paraki 2001; Oren et al. 1999a; Oren et al. 1998; Wullschleger et al. 2001). In eucalypt forests, climatic variables such as radiation ($Q$) and vapour pressure deficit (VPD) explain a considerable proportion of variation in tree water use, with accompanying diurnal and seasonal variations (O’Grady et al. 1999; Pfautsch et al. 2010; Zeppel et al. 2004).

In the high country, tree water use was on average 6700 L ha$^{-1}$ day$^{-1}$ and sap flow was largely governed by the atmospheric environment, mainly VPD and radiation, compared to upper soil moisture and wind speed. On a daily timescale, VPD (averaged) and $Q$ (integrated) were the most important variables. This however varied depending on the time scale; on a sub-daily basis, VPD had more effect on tree water use than $Q$. These findings inform a growing understanding of the central role of atmospheric drought in the physiological ecology of high country forests.

That wind speed had little influence on tree water use seems very likely to be a reflection of the well-ventilated canopies of eucalypts. Leaf area index in the high country eucalypt forests is generally low (1.1 m$^2$ m$^{-2}$ in average in this study). Numerically, canopy coupling with the atmosphere is often described by an empirical decoupling coefficient ($\Omega$, Jarvis and McNaughton 1986), and relatively low values of $\Omega$ have been reported for eucalypt forests (Hutley et al. 2000; Mielke et al. 1999; Morris et al. 1998; Zeppel and Eamus 2008). Strong coupling with the atmosphere is reflected in close coupling of transpiration rates to atmospheric VPD, and changes in stomatal conductance and VPD exert a larger impact on transpiration than aerodynamic conductance, since VPD at the leaf surface is increasingly coupled with that in the air (Jarvis and McNaughton 1986). These findings are important for informing mechanistic models of tree water use where the role of aerodynamic and stomatal conductance is explicitly included.

It is generally accepted that trees close their stomata at night when there is no opportunity for carbon gain (Dawson et al. 2007; Fisher et al. 2007; Kramer and Boyer 1995; Meidner and Mansfield 1965; Ritchie 1974; Sharkey and Ogawa 1987), in order to minimize transpiration water loss. In the studies described in this thesis, tree water use did not cease
at night. Sap flow measurements instead indicated consistent rates of night-time transpiration of up to 11% of diel transpiration, which is within the range observed in other eucalypt forests (Benyon 1999; Buckley et al. 2011; Phillips et al. 2010; Zeppel et al. 2010). The observations recorded here also show that night-time water use is not limited to summer periods.

Night-time sap flow is either a result of actual transpiration of the canopy (Benyon 1999) or is used for recharging the internal water storage that was depleted during daytime transpiration (Caspari et al. 1993; Daley and Phillips 2006), or both. Previous studies show that relative reliance on stored water increases with tree size in some species (Phillips et al. 2003), and that trees use larger amount of stored water in more dry conditions (Ford et al. 2004; Phillips et al. 2003). Rates of night-time sap flux however were not related to tree size for these eucalypt species \( (p > 0.05) \).

To distinguish actual transpiration from stem recharge, a separate set of measurements (Goldstein et al. 1998) or analysis such as the mathematical technique proposed by Buckley et al. (2011) are required. Although potential capacitance effects were not addressed in this study, the presence of significant night-time sap flow changes current understanding of how these eucalypt forests interact with their environment. This has important implications for water yield modelling that frequently assumes zero water loss by trees in the absence of radiation.

7.3 Physiological underpinnings of water use in mixed-species eucalypt forests

In addition to environmental variables, tree water use (expressed either as sap velocity or volume flux) depends on a range of biological factors, such as tree hydraulic properties associated with tree size and age, and stomatal regulation of transpiration.

The results of the studies in this thesis did not support a relationship between tree size and sap velocity, in marked contrast to tropical forests (Horna et al. 2011; Meinzer et al. 2001), but consistent with observations from other eucalypt species in western and south-east Australia (Macfarlane et al. 2010; Roberts et al. 2001; Vertessy et al. 2001). Determination of stand water use often requires measurements on individual trees to be scaled spatially, usually at least to the stand and often the landscape. An important implication is that size-
class approaches for scaling individual tree water use to whole stands, where trees are divided into size classes and transpiration is weighted according to the number of trees in each class (Köstner et al. 2002), is unlikely to be reliable for eucalypt forests.

Sap velocity and tree water use almost universally increased with increasing vapour pressure deficit (VPD) - a response similar to that documented for a range of functional types of forests including temperate and tropical hardwood forests of the northern hemisphere (Bovard et al. 2005; Meinzer et al. 1997; Pataki et al. 1998; Zeppel et al. 2004). Radiation and VPD are alone able to explain more than 90% of variations in sap velocity (Lu et al. 2003; Wullschleger et al. 2001; Zeppel et al. 2004). In this thesis, once the roles of radiation and VPD were confirmed (Chapter 2), a model was proposed for estimating sap flux for mixed-species eucalypt forests (Chapter 6).

At the tree scale, and during high radiation periods, transpiration increases linearly with increase in VPD until, under conditions of high VPD, transpiration becomes relatively insensitive to either Q or VPD. This is explained by short-term responses of stomatal conductance to changes in VPD and Q (Motzer et al. 2005; Zeppel et al. 2004); after sunrise, assimilation and transpiration increase primarily due to radiation-induced stomatal opening. In the afternoon, stomatal conductance becomes light-saturated and when VPD peaks (usually later in the day), stomata close in response to increased evaporation from the epidermis (Sheriff 1979), and prevent further increases in transpiration.

Thus, while transpiration is directly affected by VPD, it is also affected indirectly by the effects of VPD on stomatal conductance (Passioura 1988; Whitehead et al. 1983; Zelitch and Waggoner 1962). A decreasing response of stomata to VPD is a complex mechanism (Buckley 2005; Streck 2003) that can be hypothetically explained as either a ‘feed-forward’ response triggered by the Abscisic acid (ABA) of the leaves (Bunce 1996; Tardieu and Simonneau 1998), or a ‘feedback’ response due to decreased leaf water potential (Monteith 1995; Stewart and Dwyer 1983). In isohydric species, stomatal closure at high VPD is mostly regarded as a feed-back response that prevents excessive dehydration and physiological damage by maintaining leaf water potential above a minimum limit (Saliendra et al. 1995).

Stomatal conductance generally decreases as VPD increases, with species-specific relationships existing for leaf hydraulic conductance (Bond and Kavanagh 1999), sensitivity to drought (Kolb and Stone 2000; Oren et al. 1999b), competition for light
In this thesis, species-specific responses of stomatal conductance to VPD are discussed in the light of drought tolerance, and the significance of differences is discussed in relation to eucalypt distribution patterns.

7.3.1 Species sensitivity to drought

Species-specific response to atmospheric drought was tested in three dominant species, occupying different environments within the catchment; *Eucalyptus pauciflora* grows at the highest elevations and experiences the greatest variation in temperature, *E. delegatensis* grows on southern aspects and protected slopes, and *E. radiata* is a generalist found at the lowest elevation on all aspects.

Drought tolerance has a direct role in determining species distribution with respect to local and regional water availability (Engelbrecht et al. 2007). Water availability, as controlled by slope, aspect, and annual rainfall, is an important factor controlling distribution of eucalypt species (Martin and Specht 1962; Pook et al. 1966). In Australia, Pook (1966) and (Morgan 2004) suggest occasional periods of severe summer-autumn drought as a contributory factor in distribution of dry sclerophyll species (e.g. *E. radiata*) within the study area. The less isohydric behaviour allows the *E. radiata* species to grow on drier sites with shallow rocky soil and tolerate drought better (McDowell 2011). In addition to physiologic responses, plants adjust their leaf morphology in order to maximise carbon gain whilst limiting water loss. In summary, both water relations and stomatal anatomy varied with species and corresponded well with their distinct distributions within the catchment. For example more conservative, lower-risk strategies (*g*$_s$ sensitive to VPD, well-developed cuticular ledge) supports the distribution of *E. delegatensis* that suggests a pattern of avoidance of soil drought, and being strongly restricted to less water limited slopes and protected southern aspects (Adams 1995).

From an ecosystem perspective, under a scenario of severe drought, changes in atmospheric drought (e.g. due to increase in temperature) would have a different effect on the drought-sensitive species compared to more generalist trees. The more isohydric behaviour of the drought-sensitive species might enable them to maintain a more stable condition, with an advantage in terms of growth and carbon assimilation (Kumagai and Porporato 2012). Under optimal to moderate water availability, however, the less isohydric behaviour of the generalist species could be in favour of higher productivity (Kumagai and
Porporato 2012; McDowell 2011; Sade et al. 2012) that supports their wider distribution. These results have important implications for catchment-scale models of carbon and water fluxes that need to reflect such variation in structure and function, to fully capture species effects on water balance and yield.

7.4 Impact of bushfires on forest water use

Previous research on seed-regenerating eucalypt species (e.g. ash-type eucalypts) posits that water use by regenerating forests increases quickly after fire and may exceed that of mature forests (by more than 100%, App.A Buckley et al. 2012) for periods of many decades. This hypothesis has not been tested in forests dominated by re-sprouting eucalypts. In this thesis the effect of fire on tree and stand-level water use was examined in a re-sprouting mixed species eucalypt forests close to Stanley in north-east Victoria, Australia.

In general, rates of water use in regenerating mixed-species eucalypt forests three years after fire were similar to those for adjacent unburnt mature forests. These results strongly contrast post-fire patterns in water use for the seeder (ash-type) eucalypt forests. This clear difference between resprouters and seeders corresponds to: slower sap velocity in resprouting trees; a comparatively limited increase in sapwood area index (22% compared to 70% in Alpine Ash forests); and a 20% decrease in total leaf area index after the fire.

At the leaf level, greater stomatal conductance in the resprouting stands can be partially related to morphological differences of the leaves that lead to adult foliage being hydrologically more conservative compared to the young foliage. This requires further research.

Resprouting mixed species forests exhibit a slower recovery of canopy leaf area (and a gradual reduction in ground and understorey leaf area) after fire, when compared to ash forests. In general it seems highly unlikely that foliage cover in regrowth stands would exceed pre-fire cover, within the first decade after fire. These results are consistent with catchment-scale observations that showed no significant change in water yield within the first few years after bushfires in catchments forested with mixed-species eucalypts (White et al. 2006).

The other types of fire that are of significance to management are the prescribed or fuel-reduction fires used to reduce fuel loads. These fires are managed to be of lower intensity
and not affect the overstorey canopy. In general, however, they do remove the understorey and ground layer vegetation. Regrowth of these layers after such fires is highly variable and the subject of much contention as to their species composition. The hydrological benefits (in terms of water yield) of that regrowth are likely to persist irrespective of species composition.

The study in Chapter 3 shows that fire impact on the hydrology of mixed species eucalypt forests is much less than on that of even-aged ash forests. In part, it must be recognized that the increase in water use by ash-type species after fire is at least partly due to there being more water available to use (Hatton et al. 1997). The much poorer soil and climatic conditions that prevail over the mixed-species forest estate, and consequently greatly reduced water availability, are in no small part the drivers of the lack of fire effects for this large proportion of the Australian forest estate.

Observations in this thesis might extend to other tree genera that respond vegetatively to fire and are able to resprout after fire, such as forest trees in Chile (Armesto and Pickett 1985), in South Africa (Kruger et al. 1997), or in California (Hanson and North 2006).

7.5 Modelling tree water use with a soil-plant-atmosphere model

The ability to predict forest transpiration, both with reasonable accuracy and in response to changes in the environment, is essential for catchment management. In that note, a soil-plant-atmosphere model (SPA, Williams et al. 1996) was validated for 222 days in a mature, mixed species forest of north-east Victoria, using measurements of overstorey transpiration (*Eucalyptus radiata* and *E. goniocalyx*) and site-specific climate and vegetation parameters. Validations against direct measurements showed that the biological representation of transpiration in SPA is adequately representative of the real world conditions. Such models (e.g. SPA) should be able to represent plant responses to VPD under water-stressed conditions.

In terms of predicting forest water use, models that combined Penman-Monteith relationships (Monteith 1965) with one of the many empirical or process-based models of stomatal conductance, have been widely and successfully used (Granier and Loustau 1994; Leuning et al. 1991; Lhomme et al. 1998). While the underlying assumption of stomatal control of water loss holds, there is still considerable debate over the mechanisms behind the control processes (Buckley 2005; Bunce 1996; Jarvis and McNaughton 1986;
Pieruschka et al. 2010). While that debate should continue, hydrological predictions of forest water use in south-east Australian foothill forests will benefit greatly from models that express stomatal conductance as a function of soil and atmospheric variables (Damour et al. 2010).

This thesis shows that SPA provides estimates of stand water use with reasonable accuracy, despite limited soil information. A sensitivity analysis suggests that among the various required inputs, leaf area index (LAI) is the most important, and accurate estimates of LAI could significantly improve estimation of stand transpiration.

In eucalypt forests, water use converges with leaf area (Zeppel 2013). In the context of upscaling ecohydrological processes, this allows for LAI to be a robust tool to scale water fluxes to regional or continental scales.

Leaf area index can be measured with a range of techniques, including remote sensing. For example, high temporal resolution data from the Moderate Resolution Imaging Spectroradiometer (MODIS) have been used in landscape-scale estimates of evapotranspiration (e.g. Vetter et al. 2012; Kim et al. 2012) and global circulation models (e.g. Randerson et al. 2009; Kvalevag et al. 2010). However, accuracy of satellite-based LAI needs to be tested for each biome type (Hill et al. 2006; Myneni et al. 2002) before application. In that note, a recent study (see Appendix B), raises questions about the validity of MODIS LAI for high country Australia, and suggest this product to be used with caution in modelling of carbon and water flux.

7.6 Linkage between ecological responses and catchment hydrology

In Australia, evapotranspiration (ET) sometimes approaches 100% of incoming rainfall (Bren and Hopmans 2007; Eamus et al. 2006). Evapotranspiration is spatially influenced by topography (Bertoldi et al. 2012; Mitchell et al. 2012) as well as vegetation structural (e.g. leaf area, canopy structure) and functional (e.g. stomatal conductance) properties (Detto et al. 2006; Zhang et al. 2001). Temporal controls include the shifting role of atmospheric demand and soil moisture supply on evapotranspiration. The interacting spatial and temporal controls on the catchment ecohydrology affect the movement of water in the soil-plant-atmosphere continuum (Emanuel et al. 2010). Among different processes included in evapotranspiration (e.g. transpiration, soil and leaf evaporation, canopy
transpiration is the most important component, especially in forested catchments of south-east Australia (Mitchell et al. 2012).

The overall observations from more than two years of concurrent measurements of canopy transpiration, VPD and soil moisture in several forest sites confirmed that during periods when soil moisture is abundant, transpiration is limited by the plant demand for water, and regulation of water loss at the leaf level is strongly coupled to atmospheric demand. Once atmospheric demand reaches a certain level, stomata begin to close and this limits transpiration to a constant level (Chapter 2; Ch.3, Gharun et al. 2013a, b). In contrast, down-regulation of plant water use with increasing atmospheric demand when soils are dry can be negated in response to soil water deficit (Oishi et al. 2010). Transpiration, when stomatal conductance is independent from soil moisture (Emanuel et al. 2007), is a function of biochemical demand for carbon assimilation, and is coupled with the atmosphere (demand-limited). When soil moisture becomes limiting, stomatal conductance responds to plant hydrodynamics and soil moisture, hence transpiration becomes increasingly decoupled from the atmosphere (supply-limited). The shift on the controls of ET (from atmosphere to soil) during the transition from demand-limited to supply-limited, is associated with vegetation water stress (Emanuel et al. 2010), and plays a crucial role in the movement of water through the soil-plant-atmosphere continuum.

In conceptual hydrologic modelling, ET is commonly represented simplistically in response to relative soil moisture only (Zhao et al. 2013). According to this general form, ET is not limited when soil moisture is not limiting. However, empirical data collected in this thesis showed transpiration is constrained by stomatal response to high VPD, even when soil moisture is not limiting. Including biophysical constraints of transpiration within a conceptual frame work in Chapter 5, improved stream flow simulation and the understanding of how transpiration signals are transferred to stream flow in forested catchments.

Physiologically, the additional parameter ($\sigma$, varying between 0 and 1) was linked to species-specific sensitivities to atmospheric drought previously tested in Chapter 2. An average $\sigma$ of 0.44 was not unexpected, given mixed proportions of drought sensitive and drought tolerant species that cover the catchment of study. In a catchment covered solely by drought-sensitive species, such as *E. pauciflora* or *E. delegatensis* (e.g. catchments providing water to the city of Melbourne), a greater value for $\sigma$ is expected to more accurately transfer affects of vegetation coupling with atmospheric and soil water
availability, to stream flow, because of greater slope of transpiration response to atmospheric drought (greater numerator) and lower earlier stomata closure hence smaller maximum transpiration (smaller denominator) for drought sensitive species.

These results inform hydrological modelling with improved understanding of how ET affects catchment water yield, which is of paramount importance in water-limited ecosystems where transpiration is a major component of the ET flux.

The HBV model used for testing the hypothesis in this study is a conceptual model with relatively low number of parameters, that does not represent the explicit role of topography and channel network on the water and energy balance. The underlying processes and processes interactions that may occur at the catchment in the presence of natural heterogeneities and the natural self-organization of landscape characteristics (e.g. catchment area and shape, drainage network, geology, soil, vegetation) therefore, are not accounted for. Furthermore, catchment hydrological processes can be very complex with nonlinearities, thresholds and paradoxes that challenge existing process theories that do not embed within them the effects of natural heterogeneities. For example while most models are predicted on porous media flow theory based on Darcy’s law, non-Darcian flow that underlies the ‘old water paradox’ has been observed in many field studies (Tromp-van Meerveld and McDonnell 2006), where stream flow is highly responsive to recent rainfall, but passive tracers that move with the water are largely different to the recent rainfall (Kirchner 2003). This happens due to the rapid release of stored water and contribution of pre-event soil water (old water) to the event flow, and has been explained through a variety of concepts including the water movement through macropore (McDonnell 1990; Torres et al. 1998; Williams et al. 2002).

In the catchment of study, contribution of spatially stored water to the event flow can be particularly important as deep roots of eucalypts enhance the macropore channel through their biological activities (Aubertin 1971; Beven and Germann 1982), and influence the exchange of matrix and macropore flow (McDonnell 1990).

### 7.7 Mapping tree sap flux

Process-based models of tree water use are limited in their applicability for catchment managers, as parameterisation requires substantial input variables which often require
specialist equipment and are thus difficult to obtain. One such example is the SPA model validated in this thesis. As an alternative, application of data-driven, machine learning techniques that solve optimization problems and find structure among potential relationships were tested in this thesis.

Artificial Neural Networks (ANNs) and Genetic Programming (GP) were applied to a large amount of real-time tree water use measurements. Genetic programming has robustness in modelling complex non-linear processes, and no other study had attempted to test this method for modelling the water use from eucalypt trees. Recently GP was used in comparison with other data-learning techniques to model rainfall-runoff relationship in eucalypt forested catchments affected by bushfire (see Appendix C), and outperformed Linear Regression, K-Nearest Neighbour, and Artificial Neural Networks.

Vapour pressure deficit and potential incoming radiation (as a proxy for radiation) were selected as primary predictors, because amongst various influencing climatic factors, humidity and radiation have the greatest effect on transpiration, vegetation function and dynamics (Chapter 2, Dye and Olbrich 1993). The incoming radiation is a proxy for terrain-modulated water balance conditions and productivity patterns across the landscape (Flores Cervantes et al. 2012).

GP had superior performance in predicting sap flow across the high country. The advantage of GP remains the explicit mathematical expression that it provides, giving a platform for improving the knowledge about how radiation and evaporative demand interact to influence tree water use, and the opportunity for finding new formulae.

According to the GP model (Equation 6.4), sap flow increases with an increase in VPD in a saturating fashion, however the upper limit of transpiration in high VPD conditions is influenced by solar radiation especially at very low and saturated light conditions. Physically, this can be attributed to the effect of radiation and VPD on stomatal behaviour at the leaf level (Chapter 2; Meinzer et al. 1995; O’Brien et al. 2004). Radiation and VPD typically co-vary and are known to have offsetting effects on stomatal conductance (i.e. simultaneous stomatal opening and closing). While stomatal conductance ($g_s$) generally increases with increasing solar radiation, $g_s$ saturates at a threshold level that is photosynthesis-related (Buckley et al. 2003; Farquhar and Sharkey 1982). This threshold varies across the catchment with plant water status and hydraulic properties (Meinzer et al.
1995; Will and Teskey 1999) and was lower for species exposed to much higher levels of radiation (e.g. *E. pauciflora* in this study).

The great advantage of the model proposed in this thesis is that it incorporates all wavelengths within the incoming radiation, instead of just those deemed photosynthetically active radiation (a required parameter for most empirically-based models of sap flux), enabling it to be easily predictable for every location, from a digital elevation model. In addition to the observed role of VPD in constraining transpiration on instantaneous and short time scales (Motzer et al. 2005), results in this thesis confirm strong control of VPD on a daily time scale. Subsequently the model was constructed from daily variables for which data collection is relatively easier as well.

Application of the model to every location within the catchment allowed visualization of tree water use on a larger spatial scale. In the landscape studied here, differences in tree water use are well-coupled with topography; modelled sap flux is greater on southern slopes, explained by two main factors: radiation and precipitation. Tree water use and productivity are closely linked. In the north-facing aspects (between 0-90, and 270-360 degrees), excess radiation can limit productivity on steep slopes and reduce vegetation water use. On southern slopes greater rates of water use can be linked to precipitation distribution; generally topography influences precipitation distribution differently depending on the environment (Basist et al. 1994). In the area of study, slope explains the largest variations in spatial patterns of precipitation (more than elevation and aspect, Basist et al. 1994). Briefly, forced ascent during cooler season and localized convection during the warm season leads to more precipitation on the higher slopes of the windward aspects.

Based on the modeled sap flux, and because of increased vegetation activity (e.g. photosynthesis, growth, transpiration, root water uptake), trees play a more active role on moisture re-distribution in terms of depending and controlling soil water availability, on lower elevations and southern aspects where rates of sap flux are greater, (Rodriguez-Iturbe and Porporato 2004). Greater wetness due to thicker soil reservoirs and larger run-on contributions on lower elevations also facilitates more rapid cycling of organic matter and nutrient availability that could enhance vegetation productivity and water use (Knoepp et al. 2008). At higher elevations where soils are shallow and modelled sapflow is low, vegetation absorb lesser fractions of the incoming rainfall, and soil water status will be more directly related to atmospheric conditions. Practical implications of a spatial tree water use model include being able to explore the weighted contribution of different stands
to catchment water balance, impact of disturbance or management options, relative to the position within the landscape.

7.8 Conclusions

The investigations completed as part of this thesis realised the following:

- The primary environmental controls of water use at the leaf- and tree scale for high country eucalypt forests are light and vapour pressure deficit. Water relations and stomata anatomy vary with species that in turn have distinct distributions within the landscape.

- Mixed-species forests exhibit a more resistant response to fire compared to even-aged ash forests, that are better described as resilient. A few years after crown-removing fires, water use by resprouting mixed-species eucalypt forests was not different to nearby mature forests. These results strongly contrast post-fire patterns in water use for the seed-regenerating eucalypt forests (mono-specific), and are consistent with catchment-scale observations of fire impact on water yield.

- In terms of predicting the hydrology of mixed-species eucalypt forests, the soil-plant-atmosphere mode of SPA successfully predicted stand transpiration over several seasons. Accurate estimates of leaf area index, above all other inputs, could significantly improve model estimation of stand water balance.

- During periods when soil moisture is abundant, transpiration is limited by plant demand for water, and regulation of water loss at the leaf level is strongly coupled to atmospheric moisture. In contrast, down-regulation of plant water use with increasing atmospheric demand when soils are dry can be negated in response to soil water deficit (supply-limited transpiration).
• In water-limited ecosystems, where transpiration is the major component of the ET flux, biophysical constraints of transpiration influence catchment stream flow through controlling ET during demand-limiting periods.

• A framework was proposed for mapping tree sap flux over the high country. The framework takes into account surfaces of physically interpolated VPD and potential incoming radiation, and a mathematical expression derived from application of genetic programming to measurements of tree sap flux. Accordingly, tree sap flux is lowest on higher elevations, and is greatest on protected steep southern aspects. Patterns emerging from the modelled tree sap flux might be a restatement of the Eagleson’s hypothesis, a theoretical bridge between ecology and hydrology; that vegetation productivity (hence water use) is in equilibrium with the availability of water.

7.9 Future research

Many additional questions were raised during this study, while trying to answer others. There is thus clear opportunity to investigate several of the most pressing. Those that might be tackled in the near future are outlined here:

A range of parameters were considered when assessing species tolerance to atmospheric drought, however these did not include xylem vulnerability to cavitation which is a promising criterion of drought tolerance among species (as discussed in section 2.4.3). This criterion is suitable because it is predominantly associated with genotypes, rather than environment conditions, and is an important determinant of the limits to species distribution (Bond et al. 2008). Xylem cavitation can be measured using a range of methods (Sperry and Saliendra 1994), including ultra-sonic methods (Jackson and Grace 1996) that detect acoustic emissions by the plants under water stress, as a result of cavitation in the water-conducting pathways.

When stomatal sensitivity to VPD was investigated, measurements did not include the interacting role of season and soil drying on stomatal response to the atmosphere. It would be interesting to know whether species-specific sensitivities observed here depend on the state of soil moisture, as for example observed in the tropical forests of Australia (Thomas
et al. 2000). Measuring gas exchange during longer periods, than undertaken in this study allows for differentiating stomatal response between wet and dry seasons. Once the potential role of climatic shifts on the distribution of species is established, an optimal management strategy can be defined using landscape evolution modeling and simulation of various scenarios, to ensure for an intended distribution (e.g. for biodiversity or other forest ecosystem services).

Evapotranspiration and rainfall were spatially prepared for model application in Chapter 5, however on the basis of the present study; it is not possible to assess the relative significances of spatial variation in ET on the one hand, and spatial variability of rainfall on the other. It might be expected that in a lumped model calibration, error in one estimate is partly balanced by the other. Future research could focus on the effects of spatial variation in ET and rainfall in terms of their contributions to predictive hydrology in high country catchments of south-east Australia.

Measurements of soil moisture in this study are not sufficient for identification and quantification of water sources to the plants. Stable isotopes in combination with sap flow data are likely to be a powerful tool for this purpose. Isotopic techniques are an increasingly common means to trace water sources and a comparison of the isotopic composition of groundwater, soil water, river water and xylem water can be used to determine sources of water used by the trees (Dawson 1996).
7.10 References


A. Differences in water use between mature and post-fire regrowth stands of subalpine *Eucalyptus delegatensis* R. Baker

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Abstract

We estimated plot level water use from sap flux measurements over a 9-month period, in post-fire regrowth and mature plots of *Eucalyptus delegatensis* R. Baker (Alpine Ash) in high elevation catchments near Falls Creek, Victoria, Australia, seven years after a major stand-replacing bushfire. Water use was more than double (460 ± 100 mm yr⁻¹ more) in regrowth as compared to mature plots, whereas sap flux was similar between age classes. This difference in water use reflected 72% greater sapwood area index and 35% greater leaf area index in regrowth than in mature plots. A small part of the difference in water use can be attributed to nocturnal transpiration, which was greater in regrowth than in mature plots (10.3 ± 0.8% vs 7.3 ± 0.8% of diel totals). As evaporative demand was 41% greater in mature than in regrowth plots, these data suggest mean transpiration rate and stomatal conductance per unit leaf area were approximately 1.6 and 2.3 times greater, respectively, in the regrowth. However, mid-day leaf water potential and photosynthetic capacity were similar in both age classes. Evaporative demand was the primary environmental driver of water use in all cases, whereas soil moisture was not a strong driver of either water use or
canopy conductance (estimated as sap flux/evaporative demand). Together, our results suggest (a) stand water use rapidly recovers after fire in these high elevation forests and quickly surpasses rates in mature stands, confirming projections by Kuczera (1987) for lower-elevation Mountain Ash (*E. regnans*) forests and highlighting the potential impact of tree water use on water yield in the first decade of forest regeneration after fires, and (b) stomatal conductance and sapwood area/leaf area ratio are all less in tall, older Alpine Ash trees, whereas leaf water status and photosynthetic capacity appear to be sustained – consistent with predictions from optimisation theory but not Pipe-Model Theory.

### A.1 Introduction

Water use by forest vegetation often declines with age (e.g. Vertessy et al. 2001; Delzon and Loustau 2005; Ryan et al. 2006). The reasons differ among sites and species, and may involve reductions in stomatal conductance or leaf area index (Ryan et al. 2006). A consequence of the age-related decline in water use is that, following major disturbance such as a stand-replacing fire, the new, rapidly growing young trees may use more water than the older trees that they have replaced (Langford 1976; Kuczera 1987; Cornish 1993; Hornbeck et al. 1993). This has potentially serious implications in regions that depend on runoff from forested catchments for urban or agricultural water supply.

Forested catchments in the mountains of southeastern Australia supply water to millions of people in the region and to an agricultural industry that is vital to the region's economy. These forests are subject to periodic stand-replacing fires, notably in 1939 and more recently in 2003 and 2006. Previous studies estimated the impact of such fires on catchment water balance using runoff data from high-rainfall (1700-1800 mm year\(^{-1}\)) and moderate-elevation (~900 m) sites 50 km east of Melbourne, dominated by Mountain Ash (*Eucalyptus regnans* F. Muell.). Langford (1976) reported a decline in streamflow from catchments in this area after the 1939 fires, beginning 3-5 years after the fires. Kuczera (1987) later analysed 41 years of post-fire runoff data for these catchments, and fitted those data with an empirical model (the "Kuczera curve") that predicted a rapid but saturating decline in yield – reaching 50 and 100% of maximum yield reductions at an average of 7.6 and 33 years after the fires, respectively. Long-term yield reductions (after 15 years) in these Mountain Ash forests were shown to result from reduced stand sapwood area and to a lesser extent from reduced leaf area, by measurements of sap flow and stand
characteristics by Dunn and Connor (1993) and Vertessy et al. (1995; 1997; 2001). Other eucalypt forests have shown varying trends, however. For example, yield reductions were found 2-3 years after logging in old-growth eucalypt forests of central New South Wales (Cornish 1993), whereas Cornish and Vertessy (2001) reported an initial increase in water yield after logging in mixed eucalypt forested catchments near Sydney, and a clear reduction in yield only after 12 years. A paired catchment study in mixed eucalypt forest also found an initial increase in yield followed by a clear reduction after 4 years for patch-cut sites, but an initial yield increase with no subsequent reduction in thinned sites (Lane and Mackay 2001).

It is clear that the dynamics and extent of changes in water yield from eucalypt forests after disturbance vary widely. Although differences in transpiration of regrowing trees probably contribute to this variation, the role of tree water use in the early phase of post-fire regeneration remains poorly understood, because few studies have directly measured tree water use in the first decade after fires. Most direct measurements have been carried out for fairly short periods and/or in older stands (Dunn and Connor 1993; Vertessy et al. 1995; Vertessy et al. 1997; Roberts et al. 2001; Vertessy et al. 2001; Eichelmann et al. 2005). Moreover, little is known about the response of stand water use to fire in *Eucalyptus delegatensis* R. Baker (Alpine Ash) – a higher elevation species that dominates a large part of the Victorian Alps, which supply most of the region's agricultural water – and a recent modeling study of water yields from catchments including *E. delegatensis* highlighted the need for better information about stand water use in the early post-fire years (Lane et al. 2010). *E. delegatensis* is also of particular interest because it is one of a minority of tree species (McDowell et al. 2002; Mokany et al. 2003; Macfarlane et al. 2001) that apparently contradict the "pipe model theory" of Shinozaki (1964a, b), which predicts tall trees produce more sapwood area per unit leaf area in order to counteract the burdens of height growth on water transport. Measurements of the structural, physiological and environmental controls on water use in relation to stand age in Alpine Ash may inform ongoing debate about the physiological ecology of transpiration in tall trees (Ryan and Yoder 1997; Koch et al. 2004; Ryan et al. 2006).

The objective of this study was to measure plot water use in subalpine (~1300m) stands of Alpine Ash that germinated after the 2003 fires, and to compare these results with data from adjacent mature stands that survived the fires. We measured sap flux with the heat ratio method (Burgess et al. 2001) in relation to environmental variables in 11 mature trees.
of AA (71 years old and 40-50 m tall) and 10 young trees (7 years old and 4-6 m tall) growing in monospecific stands in the Alpine National Park near Falls Creek, Victoria, Australia, and analysed results for 213 days from December 2009 to August 2010 (late spring to late winter), during which data were continuously available for all trees. To inform future attempts to predict effects of fire on stand water on a process basis, we also measured physiological variables (stomatal conductance, photosynthetic capacity and leaf water potential).

A.2 Methods

A.2.1 Study sites

Our study sites are located near the town of Falls Creek (36° 51’ S, 147° 16’ E) in the Victorian Alps of Australia, approximately 230 km NE of Melbourne. The sites are in mountainous terrain in the upper Kiewa Valley, roughly 5 km N/NW of Falls Creek. The mature sites (M1 and M2) are stands that germinated following a major stand replacement fire in 1939. M1 is on a shallow, slightly south-facing slope (i.e., facing away from the sun), and M2 is on a steeper, north-facing toe slope. Neither site has significant understory. The regrowth sites (R1 and R2) are in pure stands of Alpine Ash that germinated following major fires in December 2003. Plot size varied according to stem density and to our need to sample the range of stem diameters found in each stand. We thus used 50 x 50 m (2500 m$^2$) plots in the mature stands and 10 x 10m (100 m$^2$) plots in regrowth stands. The fires that killed the previous mature trees at R1 and R2 were slowed and reduced in intensity at a track that formed a fire break between those sites and M1 and M2. R1 and R2 were located adjacent to M1 and M2, respectively, for logistical purposes, but they have different slopes and aspects than the mature sites. R1 is on a moderate east-facing slope and R2 is on a steeper north-facing slope. During a pilot study in 2006-2008, R1 and R2 comprised roughly equal populations of *E. delegatensis* and *Daviesia mimosoides*, but by the time of this study, *E. delegatensis* dominated and *Daviesia* represented a negligible portion of total leaf area. A third pair of sites, M3 and R3 (mature and regrowth, respectively), located between M1/R1 and M2/R2 on the same track, were chosen for measurements of crown water potential to permit crown access with a boom lift. Descriptive data for these sites are given in Table A.1.
A.2.2 Atmospheric and soil measurements

Air temperature, relative humidity and soil relative water content were measured within each site using sensors supplied by ICT International (Armidale, NSW, Australia). Relative water content was measured using standing wave soil moisture sensors (MP406, ICT Int'l) installed at 20 and 50 cm depths at one location near the center of each plot. Temperature/relative humidity sensors (HT1, ICT Int'l) were placed in radiation shields 1 m above the ground. Air water vapour saturation deficit (evaporative demand) was calculated from air temperature and relative humidity. Onset of darkness (for estimation of nocturnal transpiration fraction; see below) was identified from photosynthetically active radiation, which was measured using a HOBO weather station (Onset Corp, Pocasset, MA, USA) at Howman's Gap, approximately 600 m from M1 and R1 and 1400 m from M2 and R2, at similar altitude.

A.2.3 Sap flux

We used the heat-ratio method (HRM), as developed and presented theoretically by Burgess et al. (2001) and validated by Bleby et al. (2004). For this study, we inserted one probe set at breast height (1.30 m) under the bark of each sample tree. To minimise bias due to azimuthal variation, probes were installed at the same azimuth in all trees. We characterised azimuthal variation by installing an additional five probe sets at 60 degree azimuth steps in one tree at each of the mature sites (M1 and M2), and accounted for this variation in our estimates of confidence intervals for plot-level sap flow. (We did not gauge azimuthal variation in trees at the regrowth sites because of the likelihood of bias arising from disproportionate anatomical damage if we were to install numerous probes in these small-diameter stems.) Each probe set consisted of three probes, 0.13 cm in diameter and 3.5 cm in length, spaced 0.5 cm apart axially in the bole. A drill guide (ICT Int'l) was used to minimise errors in spacing and probe alignment. The centre probe contained a heater wire, and the upper and lower probes contained two thermocouples each, located 1.25 and 2.75 cm from the probe hub, which was situated at the outside of the stem after removing a small area of bark. In each tree, the thermocouple pair at 1.25 cm depth comprised the "outer sensor," and that at 2.75 cm depth comprised the "inner sensor." Heat pulses (40 or 50 J) were triggered by a 16-bit microprocessor unit attached to the tree adjacent to the probes, approximately 10 cm to the side of the probe insertion point, and temperature ratios were recorded 80 s after each pulse. Measurements were recorded every
30 min. The probe interfaces were connected to ICT SmartLogger dataloggers, powered by one or two 12-volt truck batteries that were continuously recharged by solar panels.

Table A.1. Descriptive data for the sites used in this study. Environmental data are means for 02 Dec 2009 – 01 June 2010 (minus a gap from 21 Jan – 22 Feb 2010), the period used for analysis of environmental controls on sap flux. DBH, diameter at breast height (1.30 m); VPD, air vapour pressure deficit; RWC, relative water content.

<table>
<thead>
<tr>
<th>site name</th>
<th>mature</th>
<th>regrowth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M1</td>
<td>M2</td>
</tr>
<tr>
<td>elevation /m</td>
<td>1300</td>
<td>1280</td>
</tr>
<tr>
<td>slope /%</td>
<td>5-10</td>
<td>10-25</td>
</tr>
<tr>
<td>aspect /°</td>
<td>196</td>
<td>0</td>
</tr>
<tr>
<td>approx. mean height /m</td>
<td>40</td>
<td>45</td>
</tr>
<tr>
<td>range of diameter at breast height /cm</td>
<td>29.1–82.5</td>
<td>25.2–86.0</td>
</tr>
<tr>
<td>mid 50% of diameter at breast height /cm</td>
<td>42.2–57.1</td>
<td>41.8–56.5</td>
</tr>
<tr>
<td>air temperature °C</td>
<td>12.1</td>
<td>11.7</td>
</tr>
<tr>
<td>relative humidity /%</td>
<td>9.7</td>
<td>9.3</td>
</tr>
<tr>
<td>evaporative demand /kPa</td>
<td>0.44</td>
<td>0.45</td>
</tr>
<tr>
<td>soil relative water content (20 cm) /%</td>
<td>22.3</td>
<td>24</td>
</tr>
<tr>
<td>soil relative water content (50 cm) /%</td>
<td>21.0</td>
<td>21.2</td>
</tr>
</tbody>
</table>

Raw heat pulse velocities were calculated using values of thermal diffusivity \((k = 2.18 \text{ to } 2.32 \times 10^{-3} \text{ cm}^2 \text{ s}^{-1})\) measured in one tree core at each of the four sites, and corrected for wounding using a homogeneous third-order polynomial (Burgess et al. 2001), assuming a wound diameter of 1.8 mm. The flux of xylem water through sapwood (this is “sap velocity on a total sapwood area basis” in the terminology of Edwards et al. 1997) was calculated by multiplying corrected heat pulse velocities by the bulk density and heat.
capacity of fresh wood, and dividing by the bulk density and heat capacity of sap (water) (Marshall 1958; Burgess et al. 2001; Buckley et al. 2011). Fresh wood density and heat capacity were measured on cores from one tree at each site; the resulting conversion factors ranged from 0.701 to 0.759 (dimensionless) for mature trees, and from 0.742 to 0.816 for regrowth trees.

We could not fell trees or cut through stems to ensure zero-flow for probe calibration in mature trees because our sites are located within a national park. Instead, we estimated baselines *in situ* by analysing periods in which relative humidity remained above 99.5% for at least 24 hours. The mean heat pulse velocity during the final 25% of the longest such period available for each sensor was taken as the baseline for that sensor. This assumes that refilling of depleted bole water stores is complete within 18 hours – an assumption strongly supported by the time-course of sap flux on nights with low evaporative demand, as described previously (see Buckley et al. 2011). For consistency, we applied this same zeroing method to regrowth stands as well.

Single-point data gaps were filled by linear interpolation between the adjacent points; larger gaps were not filled. For sap flux data, high frequency noise was reduced by local weighted linear least squares smoothing (loess) with a 5-point window and a tri-cube weight function.

Additional details concerning the analysis of sap flux (partitioning sapwood area into inner and outer bands, separating transpiration from refilling of bole water stores, scaling sap flux measurements to the plot level, and generating 95% confidence intervals for scaled estimates of plot water use) are provided in Appendix A.6.

### A.2.4 Sapwood area and leaf area

Sapwood area was estimated from two cores taken from each sample tree, and partitioned into "outer" and "inner" bands by defining the boundary between these bands as the midpoint between outer and inner sensors (2.0 cm sapwood depth). Leaf area was estimated from point measurements made in each plot with hemispherical photography, following the method of Macfarlane et al. (2007). Within each stand, images were taken using a Nikon Coolpix 5700 digital camera located at 1.3 m height. Images were processed with the WINPHOT image processing tool (ter Steege 1996). LAI was averaged for 10-11 images in each plot.
A.2.5 Physiological measurements

In November 2006 and January, February and November 2007, we measured aspects of leaf physiology in mature crowns and at two heights in regrowth crowns ("upper", within 50 cm of the crown top; and "lower", between 1.5 and 2 m below the crown top). These measurements include stomatal conductance (which was measured at two times of day: morning [8-11 am] and afternoon [1-3 pm], with a porometer [Decagon SC-1, Decagon, Pullman, WA, USA]), and photosynthetic capacity (carboxylation capacity, $V_{m25}$, and maximum potential electron transport rate, $J_{m25}$, both measured with an infrared gas analyser [Li-Cor 6400, Li-Cor, Lincoln, NE, USA]). Mature crowns were accessed by a tree climber who excised branches with a pole saw. Measurements were completed within 15 minutes of excision, and showed no consistent trends during that time (not shown). Conductance was measured for three leaves, chosen haphazardly. In regrowth plots, all three leaves were from different individuals, but for mature plots, the difficulty of crown access made this impossible, so all three leaves were from the same individual in each case. Photosynthetic capacity was measured for one leaf from one individual in each plot. Additional details for measurement of photosynthetic capacity are given in Appendix A.7.

In December 2009 and February and May 2010, we measured leaf water potential on three leaves of each of three individual trees, at predawn (5-6 am) and mid-day (12-1 pm) with a Scholander-type pressure chamber (PMS model 1000, PMS Instrument Co, Corvallis, OR, USA) at sites M3 and R3. Leaves were excised with clean razor blades and sealed in the pressure chamber for measurement within 20 seconds of excision.

A.2.6 Statistical analysis

We assessed differences in the measurements described above among age classes, months in the study and time of day where applicable, by analysis of variance and regression analysis. Further details are provided in Appendix A.8.

A.3 Results

A.3.1 Sap flux

We collected sap flux and environmental data for 534 days between March 2009 and November 2010. Because periods of available data differed among sites and sensors,
statistical comparisons of sites using all available data may be biased. Comparative analyses therefore focused on 213 days (03 Dec 09 to 13 Aug 10, excluding a gap from 21 Jan 10 – 22 Feb 10) during which data were available for all sap flux sensors simultaneously. Analyses of environmental data and their effect on sap flux focused on 148 days (03 Dec 09 – 01 Jun 10, excluding the gap from 21 Jan 10 – 22 Feb 10), because data were unavailable for several environmental sensors after that period.

Mean sap flux \( (f, \text{cm}^3 \text{cm}^{-2} \text{hr}^{-1}, \text{Table A.2}) \) from Dec 09 – Aug 10 differed significantly among months, but not between age classes or between sites for each age class. By contrast, estimated sapwood area index did differ between age classes, and was 72% greater in regrowth than mature plots (Figure A.1). However, leaf area index (Figure A.1) was only 35% greater in the regrowth than in the mature sites. As a consequence, the mean plot-level ratio of sapwood area to leaf area was greater, albeit not significantly, in the regrowth (6.8 ± 1.7 vs 5.5 ± 1.4 cm\(^2\) m\(^{-2}\); means ± 95% CIs, Figure A.1). It should be noted that leaf area index differed greatly between the two mature sites (M1: 1.98 m\(^2\) m\(^{-2}\); M2: 1.24 m\(^2\) m\(^{-2}\)), and much less between the two regrowth sites (R1: 2.22 m\(^2\) m\(^{-2}\); R2: 2.13 m\(^2\) m\(^{-2}\)).

The nocturnal fraction of diel transpiration, estimated from sap flux by the method of Buckley et al. (2011), was significantly greater in regrowth plots (10.3 ± 0.8%) than in mature plots (7.3 ± 0.8%) (means ± SE), and also differed significantly between sites for each age class. The time constant for refilling of bole water stores was similar among age classes and sites (2.57 ± 0.16 hr; mean ± SE).
Table A.2. Diameter at breast height (1.3 m, cm), areas of outer and inner sapwood bands (cm²), and mean sap flux (cm³ cm⁻² hr⁻¹) during the study period (03 Dec 2009 – 13 Aug 2010) for outer and inner sensors. Where inner values are not given, this means inner sensors were not in sapwood. M1 and M2 are mature sites; R1 and R2 are regrowth sites.

<table>
<thead>
<tr>
<th>site</th>
<th>tree</th>
<th>diameter at 1.3 m</th>
<th>sapwood area outer</th>
<th>sapwood area inner</th>
<th>sap flux outer</th>
<th>sap flux inner</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>1</td>
<td>44.0</td>
<td>238.4</td>
<td>42.5</td>
<td>4.40</td>
<td>6.64</td>
</tr>
<tr>
<td>M1</td>
<td>2</td>
<td>45.0</td>
<td>220.9</td>
<td>-</td>
<td>5.46</td>
<td>-</td>
</tr>
<tr>
<td>M1</td>
<td>3</td>
<td>66.3</td>
<td>371.3</td>
<td>143.2</td>
<td>3.58</td>
<td>3.47</td>
</tr>
<tr>
<td>M1</td>
<td>4</td>
<td>52.5</td>
<td>285.9</td>
<td>17.7</td>
<td>6.28</td>
<td>2.90</td>
</tr>
<tr>
<td>M1</td>
<td>5</td>
<td>35.8</td>
<td>174.0</td>
<td>-</td>
<td>3.63</td>
<td>-</td>
</tr>
<tr>
<td>M1</td>
<td>6</td>
<td>58.5</td>
<td>324.8</td>
<td>46.6</td>
<td>3.96</td>
<td>3.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean ± SE</td>
<td>4.55 ± 0.45</td>
<td>4.23 ± 0.83</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M2</td>
<td>1</td>
<td>76.4</td>
<td>428.5</td>
<td>150.1</td>
<td>2.81</td>
<td>6.76</td>
</tr>
<tr>
<td>M2</td>
<td>2</td>
<td>48.2</td>
<td>176.1</td>
<td>-</td>
<td>8.07</td>
<td>-</td>
</tr>
<tr>
<td>M2</td>
<td>3</td>
<td>53.0</td>
<td>289.0</td>
<td>31.6</td>
<td>8.13</td>
<td>2.73</td>
</tr>
<tr>
<td>M2</td>
<td>4</td>
<td>44.1</td>
<td>204.0</td>
<td>-</td>
<td>7.48</td>
<td>-</td>
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<tr>
<td>M2</td>
<td>5</td>
<td>61.3</td>
<td>332.6</td>
<td>115.1</td>
<td>5.43</td>
<td>4.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean ± SE</td>
<td>6.39 ± 1.02</td>
<td>4.79 ± 1.16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R1</td>
<td>1</td>
<td>8.5</td>
<td>53.0</td>
<td>-</td>
<td>5.92</td>
<td>-</td>
</tr>
<tr>
<td>R1</td>
<td>2</td>
<td>7.8</td>
<td>44.9</td>
<td>-</td>
<td>8.64</td>
<td>-</td>
</tr>
<tr>
<td>R1</td>
<td>3</td>
<td>8.5</td>
<td>39.3</td>
<td>-</td>
<td>8.27</td>
<td>-</td>
</tr>
<tr>
<td>R1</td>
<td>4</td>
<td>8.6</td>
<td>62.9</td>
<td>-</td>
<td>7.27</td>
<td>-</td>
</tr>
<tr>
<td>R1</td>
<td>5</td>
<td>8.1</td>
<td>45.9</td>
<td>-</td>
<td>7.85</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean ± SE</td>
<td>7.59 ± 0.48</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R2</td>
<td>1</td>
<td>8.2</td>
<td>31.2</td>
<td>-</td>
<td>4.22</td>
<td>-</td>
</tr>
<tr>
<td>R2</td>
<td>2</td>
<td>8.7</td>
<td>50.1</td>
<td>-</td>
<td>6.70</td>
<td>-</td>
</tr>
<tr>
<td>R2</td>
<td>3</td>
<td>9.0</td>
<td>44.7</td>
<td>-</td>
<td>7.33</td>
<td>-</td>
</tr>
<tr>
<td>R2</td>
<td>4</td>
<td>9.0</td>
<td>37.4</td>
<td>-</td>
<td>5.16</td>
<td>-</td>
</tr>
<tr>
<td>R2</td>
<td>5</td>
<td>8.6</td>
<td>48.5</td>
<td>-</td>
<td>6.69</td>
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<td></td>
<td></td>
<td>mean ± SE</td>
<td>6.02 ± 0.57</td>
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<td></td>
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</tr>
</tbody>
</table>
Figure A.1. Leaf area index (right axis, open bars), sapwood area index (grey bars, left axis), and the plot level ratio of sapwood area to leaf area (black bars, left axis) in mature and regrowth plots. Bars are means of two plots. Error bars are 95% confidence intervals.

A.3.2 Evaporative demand and soil moisture

We measured environmental variables for 148 days from December 2009 – June 2010. During this period evaporative demand differed among months (Figure A.2) and was greater in mature than regrowth plots, although the latter difference was significant only during April and May 2010. Soil relative water content at 50 cm differed among months (Figure A.2), and was significantly lower in mature than regrowth plots in all months except May. However, soil relative water content at 20 cm depth did not differ significantly among months or between age classes.
Figure A.2. Daily means of soil relative water content at 20 cm (a) and 50 cm (b), and of evaporative demand (c), averaged for the two regrowth plots (dashed lines) and the two mature plots (solid lines).

A.3.3 Effect of environmental variables on sap flux

Multiple linear regression found that evaporative demand was a strong predictor of mean sap flux in outer sensors in all cases ($p < 0.0001$ in all cases; $r^2_{adj}$ ranged from 0.639 to 0.782; $df_{error} = 145$), but that soil relative water content was not a significant predictor of sap flux in any site ($p > 0.05$). Moderate variance inflation factors (up to 2.0) suggested
slight multicollinearity between these two environmental variables, reflecting the tendency for evaporative demand to increase and soil moisture to decline over time after rain events (e.g., Figure A.2). Simple regressions using only soil relative water content as a predictor variable and the ratio of sap flux to evaporative demand (a proxy for crown conductance, intended to isolate the effect of soil moisture on water use) found significant regression slopes for in most cases (Table A.3). However, coefficients of determination were very low (average and maximum $r^2_{adj} = 0.075$ and 0.250, respectively) and regression slopes were negative in 4 of 12 cases. These results suggest that soil moisture does not strongly or consistently control water use in our sites.

A.3.4 Plot water use

Estimated sap flow at the plot level (Figure A.3) was similar between the two regrowth plots (R1, $2.24 \pm 0.28$ mm d$^{-1}$; R2, $2.45 \pm 0.25$) and between the two mature plots (M1, $0.97 \pm 0.19$ mm d$^{-1}$; M2, $1.17 \pm 0.46$), but was greater in the regrowth than in the mature plots (R, $2.35 \pm 0.19$ mm d$^{-1}$; M, $1.07 \pm 0.20$ mm d$^{-1}$; means $\pm$ 95% CI). These estimates of water use in the mature plots used observed relationships between inner and total sapwood area (see Appendix A.6.1) to weight sap flux estimates from inner and outer probes (no inner probes were in sapwood in the regrowth plots). We estimated upper and lower bounds on mean plot water use in the mature sites by assuming outer probes or inner probes, respectively, were indicative of flow through all sapwood (mean flux was greater in outer than inner probes in all cases); this led to estimates of 0.92 and 1.08 mm d$^{-1}$ for mean water use in the mature plots. Using the upper estimate for water use in the mature plots to be conservative, we conclude that plot water use was at least $1.27 \pm 0.28$ mm d$^{-1}$ greater in the regrowth plots. Equivalently, water use was approximately 120% greater in the regrowth plots.
Table A.3. Standardised regression slopes (\( \beta \)) and coefficients of determination (\( r^2_{adj} \)) for regressions with the ratio of mean sap flux in outer sensors to evaporative demand as the dependent variable and soil relative water content (measured at 20 or 50 cm depths) as the predictor variable. \( \text{df}_{\text{error}} = 146. \) *** \( , p < 0.0001; \) ** \( , p < 0.005; \) * \( , p < 0.05; \) ns, not significant (\( p \geq 0.05 \)).

<table>
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<td>0.042</td>
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</table>

These calculations of water use were based on data from a 9-month period (Dec 09 – Aug 10), so extrapolation to annual averages may be biased. However, we also have sap flux data from three of the four plots (M1, R1 and R2) spanning an entire year from Sep 09 – Aug 10 (data from Sep-Nov 09 were excluded from our statistical analysis due to missing data from environmental sensors and sap flux sensors at site M2). Plot means of sap flux within that year-long dataset (not shown) were each within 2-6% of the respective means in our 9-month analysis period, suggesting the 9-month period was fully representative of whole-year averages.

Uncertainty in estimated water use was attributable to different factors at each plot. Differences in sap flux among sampled trees contributed 23.1 and 48.8% of the total variance at M1 and M2, respectively, and 17.2 and 29.2% at R1 and R2, respectively. In the mature plots, the remaining variance in water use estimates came predominantly from azimuthal variation (which contributed 75.0 and 49.0% at M1 and M2, respectively). Uncertainty in the inference of sapwood area from stem diameter contributed 2.9 and 2.2% of variance at M1 and M2, respectively, and 82.8 and 70.8% at R1 and R2, respectively.
A.3.5  Leaf physiology (2006-2007 and 2009-2010 campaigns)

Stomatal conductance measured in 2006-2007 was consistently greater in upper-regrowth crowns than in either lower-regrowth crowns or mature crowns (Figure A.4). Stomatal conductance was also greater in the afternoon than in the morning in mature crowns. Photosynthetic capacity did not differ significantly among positions/ages, and neither conductance nor photosynthetic capacity differed between sites for each age class, nor among campaigns. Pre-dawn leaf water potential measured in 2009-2010 at sites M3 and R3 was higher in regrowth than mature trees, but mid-day leaf water potential was similar between age classes (Figure A.6), and did not differ among campaigns.

Figure A.3. Plot level water use in mature and regrowth sites (mean of two plots each). Error bars are 95% confidence intervals.
Figure A.4. Stomatal conductance measured in campaigns during 2006 and 2007, in mature crowns and lower and upper regions of regrowth crowns, prior to installation of sap flux sensors in the regrowth trees. LS means ± SEs from ANOVAs, as described in the text. Different letters above bars represent significantly different means \((p < 0.05,\) Tukey's LSD post-hoc tests).  

Figure A.5. Carboxylation capacity and maximum potential electron transport rate, measured in mature (M), lower regrowth (RL) and upper regrowth (RU) crowns in campaigns during 2006 and 2007, prior to installation of sap flux sensors in the regrowth trees. LS means ± SEs from ANOVAs, as described in the text. Different letters above bars represent significantly different means \((p < 0.05,\) Tukey's LSD post-hoc tests).
Figure A.6. Leaf water potential in mature and regrowth crowns at sites M3 and R3, respectively, measured at predawn and mid-day in three campaigns in 2009-2010. LS means ± SEs from ANOVAs, as described in the text. Different letters represent significantly different means ($p < 0.05$, Tukey's LSD post-hoc tests).

A.4 Discussion

We measured water use by young Alpine Ash trees that grew from seed after a stand-replacing fire in 2003, and by mature trees in adjacent plots that survived the fire. Our data suggest plot-level transpiration is about 120% greater, or $1.3 \pm 0.3$ mm d$^{-1}$ (460 ± 100 mm year$^{-1}$) greater in the regrowth than in the mature plots, seven years after the 2003 bushfire. Our results are consistent with the rapid initial decline in catchment water yield predicted by the "Kuczera curve" (Kuczera 1987; Watson et al. 1999). Those predictions were based on measurements of water yield from catchments near Melbourne dominated by Mountain Ash (E. regnans F. Muell.), a close relative of Alpine Ash that grows at lower elevation sites (e.g., 300-700m), often with greater rainfall (up to 1800 mm) and on deeper soils. Lane et al. (2010) recorded that mixed-species catchments that included some E. delegatensis yielded less water after fire. While we did not measure water yield, our results verify that the biological component of catchment water balance in these high elevation Alpine Ash forests responds quickly following stand-replacing fires. Several sap-flux studies in the Mountain Ash catchments studied by Kuczera (Dunn and Connor 1993; Vertessy et al. 1995; Vertessy et al. 1997; Vertessy et al. 2001) supported the Kuczera
curve projections for stand ages of 15 – 240 years in age. The present study complements the insights provided by those earlier works by documenting the rapid increase in stand water use, measured seven years after fire.

Our results suggest that the greatest potential to mitigate the effect of fire on water yield through stand thinning may lie in the first decade after fire. This requires reconsideration of the costs and benefits of pre-commercial thinning, to include not only the economic value of the water yield that can be preserved by thinning (Attiwill and Adams 2008), but also the potential enhancement of wood production in later years if thinning is performed in the first decade of regeneration (Rawlins 1991; Fagg 2006). The need for, and potential economic benefits of refined and scientifically-informed management of ash forests could well increase if fire frequencies increase in the coming century with climate change (Lucas et al. 2007), and as warmer conditions continue to increase water use from these forests (Pfautsch et al. 2010).

Our data suggest a 55% reduction in either leaf area index or in sapwood area would be needed to offset greater water use in the regrowth, and potentially maintain water yield. Based on the observed relationship between sapwood area and stem diameter at breast height in the regrowth plots, and on the observed distribution of stem diameters in those plots, this would require removing all stems with a diameter less than approximately 6.8 - 7.1 cm and a concomitant reduction in stand density by 64%, from around 5900 stems ha$^{-1}$ to 2100 stems ha$^{-1}$. While such thinning is technically feasible, there are many commercial, social and other ecological issues that need further study (e.g., Attiwill and Adams 2008).

A.4.1 Why is water use greater in the regrowth?

A clear understanding of the reasons for greater water use in the regrowth, based on measurements of stand properties and both environmental and physiological variables, is useful for the development and testing of process-based models of forest water use. The earlier studies cited above reported similar mean sap flux (flow per unit sapwood area) among stands of differing age (Dunn and Connor 1993; Vertessy et al. 1997), and our data corroborate those findings. Structurally, the difference in water use with stand age in this study can be attributed to 72% greater sapwood area index in the regrowth plots. Previous work in ash forests yielded similar results: Vertessy et al. (2001), Watson et al. (1999) and Dunn and Connor (1993) found a steep decline in sapwood area with age in *E. regnans*, as did Roberts et al. (2001) in another ash species, *E. sieberi*. However, those declines in
sapwood area were not matched by commensurate declines in leaf area index. Data given by Watson et al. (1999) suggest overstory leaf area index is approximately 35% greater in 7-year old than 70-year old *E. regnans*. In the present study, *E. delegatensis* overstory leaf area index was also 35% greater in the regrowth than in the mature plots. This increased leaf area is not sufficient to explain the greater water use in regrowth as compared to mature stands. Watson et al. (1999) likewise found that the observed changes in leaf area index with stand age in *E. regnans* were not great enough, when incorporated in a catchment model, to predict observed changes in water yield, and they concluded that water use per unit leaf area must also be greater in younger ash trees.

Our data for *E. delegatensis* imply that transpiration per unit leaf area, $E$, was ~61% times greater in the 7-year-old regrowth than in the approximately 71-year-old mature plots. Since evaporative demand (VPD) was also 41% greater in the mature plots, leaf conductance must have been greater still – approximately 128% greater – in the regrowth to account for the extra water use, and boundary layer effects are probably not responsible because the regrowth canopy is much nearer to the ground. Therefore, stomatal conductance was likely much greater in the regrowth than in the mature plots. Limited canopy access prevented extensive direct measurements of conductance to confirm this inference during the study period for which we report sap flux data. However, campaigns in 2006-2007 (when regrowth stems were too small for installation of sap flux sensors) indeed found 175% and 52% greater stomatal conductance in upper and lower regrowth crowns, respectively, than in mature crowns (Figure A.4). Other studies on eucalypts have also found greater stomatal conductance in young trees (Connor et al. 1977; Velikova et al. 2008).

We might question then, why stomatal conductance should be so much greater in the regrowth. Environmental variables may explain part of the difference: soil relative water content at 50 cm was greater in the regrowth, which generally favours enhanced stomatal conductance. However, soil relative water content at 20 cm did not differ between age classes, and we found only very weak relationships between soil moisture and the ratio of sap flux to evaporative demand (a proxy for conductance) across the study period (Table A.3). Declining photosynthetic function also cannot explain the inferred difference in conductance, because photosynthetic capacity was similar in the two age classes (Figure A.5; measured in 2006-2007). Many previous studies have attributed reduced stomatal conductance in taller trees to the need to sustain leaf water status under burdens of water
transport in tall trees (Yoder et al. 1994; Bond and Kavanagh 1999; Hubbard et al. 1999; Delzon et al. 2004). We found similar mid-day leaf water potential in mature and regrowth trees despite greater pre-dawn leaf water potential in the regrowth (Figure A.6 measured in 2009-2010 at sites M3 and R3, near our sap flux study sites), suggesting that changes in stomatal conductance with age in this species do indeed achieve a degree of hydraulic homeostasis. Anatomical changes may contribute to reduced leaf conductance with age and height in ash, as suggested by a recent study on *E. regnans* (England and Attiwill 2006) that found thickened cuticles and waxy deposits blocking stomata in leaves of older, taller trees.

It is intriguing that the community-level ratio of sapwood area to leaf area was slightly greater in the regrowth sites than in the mature sites (Figure A.1). This is consistent with earlier studies on Alpine Ash (Mokany et al. 2003) and Mountain Ash (Watson et al. 1999), which found that sapwood:leaf area ratio declines with increasing age and height in these ash species. However, most species show the opposite trend (McDowell et al. 2002), as predicted by "pipe-model theory" (Shinozaki et al. 1964a, b). That theory suggests that, in order to sustain water transport, sapwood:leaf area ratio should increase as trees grow in height to counteract the effects of increased pathlength and gravitational head on xylem pressure gradients. By contrast, a tree growth model based on optimising carbon profits from carbon allocation, DESPOT (Buckley and Roberts 2006a, b), predicts a shift in carbon allocation away from sapwood production due to the increasing carbon cost of water transport in taller trees. That strategy requires substitution of nitrogen for water as a photosynthetic resource – i.e., increased photosynthetic capacity to compensate for reduced stomatal conductance – which, in turn, requires substantial plasticity in the coordination of photosynthetic resource use (Buckley and Roberts 2006b). The hydraulic effect of reduced sapwood:leaf area ratio may also be offset by an increase in sapwood permeability with height and age, which has in fact been observed in both *E. delegatensis* (Mokany et al. 2003) and *E. regnans* (England and Attiwill 2007). The occurrence of two such distinct patterns in the coordination of tree growth and leaf gas exchange may reflect a fundamental divergence in the underlying ecological strategies of different species, perhaps due to differences in physiological plasticity at the leaf level, and is worthy of more intensive study. For the present, our data support the view that young eucalypt leaves are adapted to exploit abundant resources in order to maximise carbon gain, whereas adult
leaves are more resilient. In general, eucalypts are physiologically plastic in the face of changing resource availability (James and Bell 2000, 2001).

A.5 Conclusion

Measurements of sap flux over 9 months in 2009-2010 showed that 7-year-old post-fire regrowth stands of *E. delegatensis* consume 2.2 times more water (an increase of 460 ± 100 mm year\(^{-1}\)) than adjacent 71-year old mature stands that survived the 2003 bushfires. This confirms the rapid increase in water use after fire in ash forests suggested by the "Kuczera curve" (1987), and extends the results of earlier studies on post-fire water use by Mountain Ash (*E. regnans*). Changes in leaf area index were insufficient to explain the greater water use and evaporative demand was 41% greater in the mature sites, implying that transpiration and stomatal conductance on a leaf area basis were 1.6 and 2.3 times greater, respectively, in the regrowth. A small part (~3%) of the increased transpiration rate reflected greater nocturnal water use in the regrowth. Similar photosynthetic capacity and mid-day leaf water potential between regrowth and mature trees but lower conductance in the mature trees suggested that the negative impacts of height growth on water transport – increased hydraulic pathlength and gravitational head – are compensated in this species by changes in photosynthetic resource allocation at the leaf level. This is consistent with predictions from optimisation theory (Buckley and Roberts 2006a, b) and a previous study in this species (Mokany *et al.*, 2003), but it contrasts the prediction that sapwood area per unit leaf area must increase to sustain stomatal conductance, as predicted by "pipe-model theory" (Shinozaki et al. 1964a, b) and supported by data from many northern hemisphere species (McDowell et al. 2002). This knowledge can be used improve predictions of Australian forest water use in a changing climate.

A.6 Detailed methods for analysis of sap flux

A.6.1 *Inner vs outer sap flux*

Inner probes were not in sapwood in any regrowth trees, but they were in sapwood in 7 of 11 mature trees (Table A.2). To address uncertainty in the attribution of different sap flux values to different bands of sapwood in those mature trees, we computed values of water use and its confidence intervals (see below), using three different assumptions: (i) Sap flux
measured by outer sensors applies to all sapwood area in each tree. (ii) Sap flux measured by inner sensors applies to all sapwood area in each tree. (iii) sap flux measured by inner probes applies to a band of sapwood whose area we estimated from total sapwood area based on an observed linear relationship (area of inner band = 0.472 \times \text{[total area]} - 111.85 \text{[for total area > 237]}, r^2 = 0.92, df_{error} = 7), and sap flux measured by outer probes applies to all other sapwood.

A.6.2 Separation of transpiration and refilling

We estimated the nocturnal fraction of diel transpiration by separating the transpiration and bole refilling components of sap flux using a simple flow model; full details and a derivation are given in Buckley et al. (2011). Briefly, the model assumes fluxes across basal sensors and into/out of bole water stores are driven by water potential gradients, which are linked to xylem water content by a constant capacitance. In the model, the ratio of storage resistance and xylem resistance modulates the flows; we assumed a ratio of unity to ensure our estimates of nocturnal transpiration were conservative, as suggested by Buckley et al. (2011). The model also requires estimates for the time constant for refilling bole water stores in the absence of transpiration, which we obtained from sap flow data following Buckley et al. (2011).

A.6.3 Scaling to the plot level

We estimated average plot-level sap flow in mm d^{-1} from measurements of sap flux in cm^{3} cm^{-2} hour^{-1} made by individual sensors as follows, for each plot. First, we calculated the mean sap flux for each sensor during the study period, separately for inner and outer sensors. Second, for every stem in the plot, we estimated sapwood area from measured diameter at breast height, using linear regressions for observations in sampled trees. For R1, this equation was [sapwood area in cm^{2}] = 5.7356 \times \text{[diameter in cm]} - 5.9332, r^2 = 0.7816, df_{error} = 6, p = 0.0036; for R2, the equation was [sapwood area] = 4.9662 \times \text{[diameter]} - 7.2177, r^2 = 0.9115, df_{error}=10, p < 0.0001. Regression parameters did not differ significantly between M1 and M2, so we pooled those data into a single relationship: [sapwood area] = 11.239 \times \text{[diameter]} - 271.21, r^2 = 0.9067, df_{error} = 9, p < 0.0001. Third, for each stem we multiplied sapwood area by estimates of sap flux from inner or outer sensors, or a weighted sum of both, as described above. Finally, we summed the flows over all stems in each plot and divided by plot area.
We used sap flux data rather than scaled sap flow estimates to compare responses of mature and post-fire regrowth trees to environmental conditions to avoid confounding the latter analysis with uncertainties arising from the scaling process.

A.6.4 Confidence intervals for plot-level sap flow

We computed 95% confidence intervals (CIs) for estimated values of plot water use as \( \pm 1.96 \times \text{standard error for water use} \), where 1.96 is the normal quantile for \( \alpha = 0.95 \). We calculated the standard error for water use from the sum of variances in estimated flow for all stems in the plot. Variance for each stem flow estimate was computed as the sum of relative variances for flux and sapwood area estimates. For flux, this included variances both among azimuths and among sampled trees, and for sapwood area, the variance was calculated from the standard deviation of prediction from regressions of sapwood area vs diameter at breast height.

A.7 Measurement of photosynthetic capacity

To calculate photosynthetic capacity (carboxylation capacity and maximum potential electron transport rate), we measured relationships between leaf net CO\(_2\) assimilation rate and intercellular CO\(_2\) mole fraction under saturating photosynthetic photon flux density (2000 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)) and leaf temperature 22.2 ± 2.3°C (mean ± s.d.; temperature varied less than 0.5°C during each response curve) with a LI-COR 6400 infrared gas analyser (Li-Cor, Lincoln, NE, USA) equipped with an LED light source (Li-Cor) and the standard 2 x 3 cm leaf chamber. Carboxylation capacity was estimated by fitting the RuBP-carboxylation-limited phase of the model of Farquhar et al. (1980) by least-squares regression to 4-5 points at low intercellular CO\(_2\) below a visible transition to RuBP-regeneration limitation. Maximum potential electron transport rate was estimated by applying the values of assimilation rate and intercellular CO\(_2\) measured at saturating CO\(_2\) (ambient CO\(_2\) ≈ 600 \(\mu\)L L\(^{-1}\)) to the RuBP-regeneration-limited phase of the Farquhar model. All estimates were corrected to a common temperature of 25°C using temperature responses given by Bernacchi et al. (2001) for carboxylation capacity and by de Pury and Farquhar (1997) for electron transport. This procedure was performed for one leaf from one individual per plot in Nov 06 and Jan 07, and from one leaf from each of three individuals per plot in Nov 07. Branches bearing measured leaves had been cut under
water with sharp secateurs, with the cut end subsequently kept in water during measurements.

A.8 Detailed methods for statistical analyses

We performed analyses of variance (ANOVAs) on ten independent variables, with effect structures as given in Table A.4. We assessed effects of evaporative demand and soil relative water content on sap flux measured by outer sensors using two sets of linear regressions. First, we performed multiple linear regressions on daily means, separately for soil relative water content measured at 20 or 50 cm depth. These regressions invariably showed evaporative demand to be the dominant driver of sap flux ($p < 0.0001$ in all cases), with relative water content being an insignificant predictor in all cases. To isolate the effect of relative water content on sap flux, we performed simple regressions using the ratio of sap flux to evaporative demand (a proxy for canopy conductance) as the dependent variable. Significant fixed effects from ANOVAs reported in the Results had $p$ values less than 0.05. The identity and sense of significant treatments were assessed by Tukey's LSD post-hoc tests. All statistical comparisons were performed in SAS Enterprise Guide 4.3, running SAS System version 9.2. Quantitative variables were log-transformed to increase normality.
Table A.4. Effect structure of analyses of variance (ANOVAs) used in this study. Each successive effect listed in each row was nested in the nearest effect to the left, except for campaign, which was not nested. For example, age class was nested in month for ANOVAs on sap flux. Treatment levels for "position/age class" were mature, regrowth-upper crown, and regrowth-lower crown. Levels for "time of day" were morning or afternoon for stomatal conductance, and pre-dawn or midday for leaf water potential.

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A.9 References


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B. NDVI and LAI mismatch complicates remote sensing data use in hydrological and carbon models

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Abstract

Accurate estimates of evapotranspiration are essential for water resource assessment and can be based on estimated leaf area index (LAI). We compared a decade of Collection 5 MOD15A2 LAI (LAIMOD) to NDVI derived from MODIS (NDVIMOD) and Landsat ETM+ (NDVIETM) for eucalypt forests in south-eastern Australia and deciduous broadleaf forest in north-eastern USA. For eucalypt forests, NDVIMOD was underestimated by, and only weakly correlated ($r = 0.27$) to, NDVIETM. Generalized additive models fitted to seasonal and long-term trends for NDVIMOD and LAIMOD differed between Australian and US forests. A mismatch between seasonal NDVIMOD and LAIMOD could be caused by understorey reflectance. LAIMOD should be used with considerable caution in global circulation modeling, and preferably cross-checked against ground-based data for leaf area.

B.1 Introduction

Accurate estimates of evapotranspiration (ET) are essential for water resource assessment and environmental management at various scales (Bastiaanssen et al. 2005) and depend on quantifying leaf area. Spatiotemporal resolution of remotely-based ET has arguably improved to the point where it may be applied in models (Anderson et al. 2012). For example, high temporal resolution data from the Moderate Resolution Imaging Spectroradiometer (MODIS) has been used in landscape-scale estimates of ET (e.g. Vetter et al. 2012; Kim et al. 2012) and global circulation models (e.g. Randerson et al. 2009; Kvalevag et al. 2010). The MODIS leaf area index (LAI) product, MOD15A2 LAI (LAIMOD), is a key input for the recently developed algorithm to predict terrestrial ET (Mu et al. 2011). LAI is strongly correlated to maximum evaporation demand (Teuling and
Troch 2005) and basal area (O’Grady et al. 2000). LAIMOD has been used to estimate ET at regional scales (Zhang et al. 2008; Leuning et al. 2008) and run-off prediction in un-gauged catchments (Li et al. 2009) in Australia. In these uses, LAIMOD was optimized to observed data. In more general use, however, the accuracy of LAIMOD estimates for temperate eucalyptus forests in south-eastern Australia is unknown. The previously available Collection 4 (c4) is known to have over-estimated LAI in mature, tall Eucalyptus forest (Hill et al. 2006), which range from 2.65 to 4.1 m²m⁻² in the field (Pook 1984; Vertessy et al. 1995; Roberts et al. 2001; Buckley et al. 2012). The currently available Collection 5 (c5) data set includes re-calculated vegetation classes (Shabanov et al. 2007), and it seems likely that the resultant LAI estimates may be improved (De Kauwe et al. 2011), as suggested by recent work in tropical savannas in Australia (Sea et al. 2011). Simple comparisons of c4 and c5 data are no longer possible because c4 is unavailable (NASA Land Processes Distributed Active Archive Center, pers. comm. 2012).

Vegetation indices have long been associated with LAI (e.g. Jordan 1969). They are globally well correlated with LAI across various canopy structures and species (Huete et al. 2002). Normalized Difference Vegetation Index (NDVI) has been used to upscale LAI from plot to LAIMOD scale (e.g. Aragao et al. 2005; Yang et al. 2006; Sea et al. 2011). In Australia, NDVI derived from Landsat 5 Thematic Mapper explained 87% of the variation of ground-based LAI over south-western Australia, with a root mean square of 0.28 m²m⁻² (Boer et al. 2008); in south-eastern Australia, regression of Landsat Multi-Spectral Scanner derived NDVI and ground-based data yielded a strong correlation ($r =0.84$, Coops et al. 1998).

An important development is recognition that mean differences between red and near infra-red (NIR) from MODIS and Landsat 7 Enhanced Thematic Mapper (ETM) are < 0.013 (red) and < 0.015 (NIR) for broad-leaf forest over north-American sites (Fang and Liang 2005). There is thus a reasonable a priori assumption that NDVI derived from MODIS and ETM should be directly comparable to MODIS-based estimates of LAI.

In light of earlier studies, and given the availability of MODIS and ETM products, we sought first to test whether NDVI derived from MODIS (NDVIMOD) and Landsat ETM+ (NDVIETM) are interchangeable. Secondly, we tested the validity of the LAIMOD product through correlation of c5 LAIMOD to c5 NDVIMOD over temperate, evergreen eucalypt forest in Australia (Corin catchment, CC; near Canberra, ACT) and deciduous
broad-leaf forest in north-eastern America (Hubbard Brook, HB; near Plymouth, New Hampshire).

B.2 Methods

B.2.1 Data

MOD15A2 has a 1 km\(^2\) resolution and is a composited output over eight days (Tian et al. 2002; Myneni et al. 2003; De Kauwe et al. 2011; Sea et al. 2011). We downloaded scene h30v12 for 2001–2012 from the NASA Land Processes Distributed Active Archive Center Data Pool. Using the MODIS Reprojection Tool (Version 4.0), the LAIMOD scenes were cut to the study areas (Table B.1) and the quality flags were extracted. Quality scores were unpacked with MODIS Land Data Operational Product Evaluation Tools (Roy et al. 2002). All LAIMOD with a quality score of zero, representing best possible results, were selected and temporally smoothed, as suggested by Gu et al. (2006). For each time step, we excluded LAIMOD for a given pixel if it was \(\geq 1.5\) times the moving, 32 day inter-quartile LAIMOD range for that pixel (Hwang et al. 2011).

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude (m)</th>
<th>Longitude (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC</td>
<td>13448404.337</td>
<td>–3964509.716</td>
</tr>
<tr>
<td>HB</td>
<td>–6212162.799</td>
<td>5229897.834</td>
</tr>
</tbody>
</table>

We calculated NDVI directly from surface reflectance. MOD09A1 provides a measure of surface reflectance and has a 500 m\(^2\) resolution. We chose MOD09A1, which is temporally compositied over eight days, rather than other daily surface reflectance at larger spatial scales, e.g., MOD09GA, or NDVI at larger temporal scales, e.g., MOD13Q1. For each eight-day composite period, surface reflectance is calculated on the basis of high observation coverage, low angle of view, absence of clouds or cloud shadow, and low loading of aerosols (Vermote et al. 2011). Using scene h30v12 for 2001–2012 from the NASA Land Processes Distributed Active Archive Center (LPDAAC) Data Pool, surface
reflectance bands one (red, 620–670 nm) and two (NIR, 841–876 nm) were extracted and cut to the study areas (Table B.1). NDVIMOD was calculated using:

\[
\text{NDVI} = \frac{\varrho_{\text{NIR}} - \varrho_{\text{RED}}}{\varrho_{\text{NIR}} + \varrho_{\text{RED}}}
\]

(7.1)

where \( \varrho_{\text{NIR}} \) is the NIR and \( \varrho_{\text{RED}} \) the red portion of the electromagnetic spectrum. To aggregate NDVIMOD to a 1 km\(^2\) resolution, mean NDVIMOD was calculated from all NDVIMOD pixels within a LAIMOD pixel.

Similarly, NDVIETM was calculated from reflectance data at a 30 m\(^2\) resolution, every 16 days. Scene P090R085 was downloaded for 2001-2012 from the United States Geological Survey Earth Resources Observation and Science Center (EROS). Scenes highly contaminated with cloud, as indicated by EROS, were excluded. Digital Numbers in each scene were converted to top-of-atmosphere radiance and then reflectance using metadata (National Atmospheric and Space Agency 1998). Bands two to six were used to derive a cloud mask via the Fmask method (Zhu and Woodcock 2012). Values in bands three (red, 630–690 nm) and four (NIR, 770–900 nm) deemed cloud, cloud shadow or snow were excluded from the data and the rest were used to calculate NDVI (Equation (B.1)). These were re-projected using bilinear interpolation to a sinusoidal, 1984, coordinate system to match LAIMOD and NDVIMOD. Normality and the mean of all high-resolution NDVIETM pixels within the boundaries of a single LAIMOD pixel were calculated. Only the mean NDVIETM from normally distributed NDVIETM populations within a single LAIMOD pixel were used as upscaled NDVIETM.

**B.2.2 Observations**

NDVIMOD and NDVIETM were compared for the CC only. We matched dates for NDVIMOD with the nearest earlier date from NDVIETM (Bhandari et al. 2012). The maximum number of days between each dataset was 11 and we assumed this had no bearing on leaf phenology. Derived estimates of NDVI from all dates and locations were lumped and linearly regressed.
Subsequently, a generalised additive model (GAM) was fitted to the LAIMOD, NDVIMOD and NDVIETM series for each study area to identify seasonal and long-term trends:

\[
LAIMOD = \beta_0 + \beta_1 f_1(\text{Season}) + \beta_2 f_2(\text{Trend}) + \varepsilon
\]  

(B.1)

Here, using LAIMOD as an example, \(f_1\) and \(f_2\) are smooth spline functions of the different trends and optimized to the data (Wood 2006; van Ogtrop et al. 2011).

**B.3 Results and Discussion**

**B.3.1 NDVIMOD and NDVIETM interchangeability**

Surprisingly, and across time and space, NDVIETM was over-estimated, and only weakly correlated \((r = 0.27, \text{results not shown})\) to NDVIMOD. The linear regression was significant, but again weak \((r^2 = 0.07, p < 0.05, \text{results not shown})\). In contrast, much higher correlations are reported for global datasets \((r = 0.9 \text{ at a } 0.5^\circ \text{ resolution with MOD13Q1-derived NDVI}; \text{Beck et al. 2011})\) and boreal \((r = 0.83 \text{ at a } 250 \text{ m}^2 \text{ resolution with MOD13Q1-derived NDVI}; \text{Steinberg et al. 2006})\) and savanna \((r^2 \geq 0.95 \text{ at a } 500 \text{ m}^2 \text{ resolution with MOD09-derived NDVI}; \text{Fensholt and Sandholt 2005})\) landscapes. Systematic over-estimation may be related to differences between MODIS and ETM in red and NIR bandwidths and in attenuation by various atmospheric constituents (Steinberg et al. 2006). This may be linked to several reflectance-complicating factors: bare ground, greenness, leaf orientation and solar elevation, and viewing angle (Sellers, 1985), all of which, inter alia, combined are the reflected radiation received at the satellite sensor (Kumar 2007). If the reflectance detection difference with bandwidth is irrelevant, then viewing angle could be a source of difference between NDVIMOD and NDVIETM. We considered it unlikely that over-estimation was related to up-scaling NDVIETM. Particularly since NDVIETM and NDVIMOD data were collected, at most, within 11 days of each other and NDVIMOD was only compared to NDVIETM derived from normal distributions.
Some of the correlations improved if we focused on data points in time for single pixels ($r^2 = 0$ to $0.66$; Figure B.1) or across space (all pixels in the catchment) at each date ($r^2 = 0$ to $0.45$; Figure B.2). For either type of NDVI disaggregation, variation in correlations did not coincide with removal of data due to cloud cover or failure of the scan line corrector within the upscaled NDVIETM pixels.

**B.3.2 LAIMOD validation**

The dynamics of the evergreen CC and deciduous HB are captured by LAIMOD (Figure B.3). Furthermore, LAIMOD HB is similar to reported field-based LAI of other New Hampshire forests, ranging from $1.73$ to $3.61 \text{ m}^2 \text{ m}^{-2}$ (Smith et al. 2002). In contrast, LAIMOD CC is greater than measured overstorey LAI, $0.5$–$1.3 \text{ m}^2 \text{ m}^{-2}$ (Gharun et al. 2013a, b). NDVIMOD CC is similar in pattern and range to Advanced Very High Resolution Radiometer over open, eucalypt forest (see Figure 5b in Lu et al. 2003).

Similarly, mean NDVIMOD CC ($\mu = 0.63$, $\Omega = 0.13$) is comparable to forest in south-eastern Australia (e.g. NDVI range from $0.37$ to $0.64$ over Tarra Bulga and Wombat forests, Coops et al. 1998). The NDVIMOD we calculated (inter-quartile range maximum < $0.92$) for HB exceeds other NDVI estimates in the region (e.g. < $0.5$, Jenkins et al. 2002).

Interestingly, the GAM-based seasonal and long-term trends for NDVIMOD and LAIMOD are not consistent for the study areas and time scales (Figure B.4). The trend term, which represents long-term cycles (i.e. those longer than one year) is generally in phase for both CC and HB. However, the periods 2000–2003 and 2010–2012 are out of phase for CC and HB, respectively. Generally, the long-term NDVIMOD and LAIMOD trends confirm earlier work by Coops et al. (1998). The seasonal terms for LAIMOD HB and NDVIMOD HB are in phase. Hence, the assumption of maximum greenness and maximum LAI holds for deciduous forests in north-eastern America. This is logical because of the colour change that occurs prior to, and during, leaf-fall. In contrast, seasonal NDVIMOD CC (and NDVIETM CC) and LAIMOD CC are out of phase. We suggest that this is related to changes in red light adsorption due to leaf drop of the overstorey in autumn and exposing the normally shaded understorey to the satellite recorder.
**Figure B.1.** NDVIMOD and NDVIETM regression across a subset of randomly selected times for each pixel (CC, 2001–2010). Numbers represent pixel identifiers within the catchment.
Figure B.2. NDVIMOD and NDVIETM regression across a subset of randomly selected times (CC, 2001–2010). Numbers represent pass dates in years and Julian day.
Figure B.3. Full range (black fill) and inter-quartile range (red fill) of NDVIMOD (top panels) and LAIMOD (bottom panels) over the CC (left panels) and HB (right panels), 2000–2012. The decrease in NDVIMOD at the beginning of 2003 over the CC corresponds to a wildfire that burnt much of the catchment. The non-response in LAIMOD is likely due to smoothing.
Figure B.4. Seasonal (right panel) and long-term (left panel) mean NDVIMOD (blue dashed line), NDVIETM (blue full line) and LAIMOD (red line) and associated standard errors (thinner lines) for the CC (top panels) and HB (bottom panels) from 2000 to 2012 derived by fitting GAMs. NB: seasonal data is from all years, but is arbitrarily displayed over one year, 2000.

The implication of these findings is that the use of LAIMOD for hydrological simulations might not be straightforward, due to local variations in vegetation distributions and landscape. Evidently, the LAIMOD does reflect both the seasonal and long-term overstorey LAI trend. However, given limited field observations and published data, caution is needed in the use of LAIMOD for water resource planning in evergreen forests.
across the globe. The mismatch has wider implications for global circulation modeling. While the southern hemisphere contributes less to overall CO$_2$ capture (Siegenthaler and Sarmiento 1993), mismatches in actual and assumed LAI can skew overall ET estimations and results.

**B.4 Conclusion**

Our aim was to validate c5 LAIMOD over temperate, evergreen eucalypt forest in Australia for water resource modeling. The two MODIS products indicated a seasonal mismatch over the CC, but not in the deciduous HB, while long-term trends were similar. At a seasonal scale, LAI was inverse to NDVI over the CC. Furthermore, comparing NDVIMOD to NDVIETM seasonal and long-term trends were similar, but the correlation between NDVIETM and NDVIMOD was weak. NDVI, as a surrogate for reflectance, is inappropriate to validate LAIMOD over the CC and caution is needed for use of LAIMOD in hydrological and other modeling.
B.5 References


C. Modelling rainfall-runoff relationship of a mixed-species forested catchment in Australia, following the 2003 bushfires

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Abstract

Rainfall-runoff relationships of forested catchments vary and depend in part on human activities such as logging and roading, long-term land use and changes therein (e.g. switches between plantations and natural forests), and major disturbances such as bushfires. In countries where forested catchments provide most of the water for human consumption and industries including agriculture, this relationship can be critical to actual and predicted water yield. Previous studies have shown that, in effect, bushfires create new relationships between water yield of forested catchments and rainfall, and that these vary with vegetation cover and age of regenerating forests. The aim of the present study is to model such new relationships, using as test the Corin catchment in south-east Australia that is dominated by mixed-species eucalypt forests and which is part of the system of catchments and dams that meet the water needs of Canberra, Australia’s capital. This catchment was severely affected by a large ($>10^6$ Ha) bushfire in 2003.

We compared and contrasted a range of practical, data-driven modelling approaches, including Linear Regression, K-Nearest Neighbour, Artificial Neural Networks (ANNs) and Genetic Programming. Inputs to our models include precipitation, time since fire, and remotely sensed Normalized Difference Vegetation Index (NDVI), as an index of vegetation cover. A runoff model derived from Genetic Programming was superior across all goodness-of-fit criteria. The NSE = 0.64 and Corr = 0.79 for the training-test stage, as well as NSE= 0.60 and Corr= 0.80 for the validation stage, are indicative of the predictive power of the preferred model.
C.1 Introduction

In Australia, high country catchments are often largely forested and provide most of the water to cities, agriculture, industry and the environment. For example, almost all of the City of Melbourne’s water is supplied from forested catchments (Vertessy et al. 2001), with similar scenarios for the cities of Sydney, Perth, Canberra and Brisbane. Forested catchments also supply the water for much of the irrigated agriculture within the Murray Darling Basin, and have been exposed to numerous bushfires in the past decade. Climate change is predicted to increase the intensity and frequency of such bushfires (Lucas et al. 2007).

Bushfires affect catchment hydrology through changing the structure and density of forests, leading to changes in evapotranspiration and streamflow over the regeneration period, usually for at least several decades. Past studies of relationships between tree- and stand-level hydrology and stream flow suggest that regenerating forests use more water than the mature forest (Buckley et al. 2012; Dunn and Connor 1993; Haydon et al. 1997; Jayasuriya et al. 1993; Pfautsch et al. 2010; Vertessy et al. 1996; Vertessy et al. 2001). Most of the abovementioned studies have focused on even-aged ash-type eucalypt forests that are mono-specific. The hydrology of mixed-species eucalypt forests is much less well known. The imbalance in hydrological knowledge is all the more stark if it is considered that eucalypt forests which cover water catchments within the high country of south-east Australia are largely mixed-species. Mono-specific ash-type forests dominate much smaller areas. The ash forests also differ from the mixed-species forests in that the former regenerate after fire almost solely via seeds, while the latter are almost completely dominated by species that resprout after fire via epicormic buds. Regenerating via epicormic sprouts is, in fact, the norm for eucalypts - less than 10% of the more than 700 eucalypt taxa are obligate seeders (Nicolle 2006). Research on water yield from mixed-species forests has mostly focused on logging effects, despite fires being the major disturbance of these forests, much more so than logging (Attiwill and Adams 2008). A few studies have recorded the hydrologic effects of logging after fire, or of seeding (Lane and Mackay 2001).

Currently, estimation of streamflow responses to forest disturbance rely on applying traditional computational/statistical tools (i.e. empirical models) or on the physical representation of governing processes within process models (Kuczera 1987; McMichael and Hope 2007; Shiklomanov and Krestovsky 1988; Watson et al. 1999). These have some
disadvantages: 1) large numbers of required parameters which introduce uncertainties (e.g. Macaque model of Watson et al. (1999) has more than 70 parameters); 2) empirical models of streamflow being based on even-aged ash forests can provide inaccurate predictions of yield from mixed-species forests (Lane and Mackay 2001; Macfarlane et al. 2010; White et al. 2006).

Limitations of such approaches have led to development and application of data-driven techniques. Amongst the more commonly applied methods of soft computing in the field of water science include Linear Regression (LR), K-Nearest Neighbour (K-NN), Artificial Neural Networks (ANNs) and Genetic programming (GP). These have yielded satisfactory results for numerous hydrological issues. For example, these methods have been successfully applied to the problems of estimating: pan evaporation (Kisi et al. 2012; Terzi 2012), evapotranspiration (Aytek 2009; Cobaner 2011; Parasuman et al. 2007), reference evapotranspiration (Shiri et al. 2012), soil moisture (Makkeasorn et al. 2006), precipitation (Kisi and Shiri 2011), ground water table depth fluctuations (Shiri and Kisi 2011), rainfall-runoff and streamflow (Minns and Hall 1996; Savic et al. 1999; Whigham and Crapper 2001), suspended sediments in streams (Aytek and Kisi 2008), and risks in water supply (Babovic et al. 2001).

In the current study, we analysed and compared capabilities of data-driven methods in modelling rainfall-runoff relationships. We used the Corin catchment as a model, as it incorporates the effects of wildfires and has a prevalence of resprouting eucalypts.

C.2 Case study and data sources

The Corin catchment is located in the Namadgi National Park and is a part of the Cotter river catchment in the Australian Capital Territory (ACT). The catchment lies some 50 km west of Canberra, at the northern end of the Australian Alps (lat 35.6 °S, long 148.8 °E), and encompasses an area of 148 km². The catchment is almost completely covered by native eucalypt forests. These include mono-specific forests of snow gum (*Eucalyptus pauciflora*) and tall-open forests of Alpine Ash (*E. delegatensis*). The bulk of the catchment is, however, dominated by mixtures of broad-leaved peppermints (*E. dives*), narrow-leaved peppermints (*E. radiata*), manna gums (*E. viminalis*), mountain gums (*E. dalrympleana*) and brown barrel (*E. fastigata*). All soils of the area are derived from highly weathered Ordovician sediments and are acidic and duplex in structure (Talsma 1983). The
underlying rock types of the catchment are granite, limestone and shale, and the
topography is mountainous (steep with rocky outcrops). The catchment is exposed to fogs,
frosts and snowfall in winter. Summers are characterized as warm and often hot, with dry
periods of between 6 and 8 weeks (Moore et al. 1993). In winter (July), mean daily
maximum and minimum temperatures in sheltered locations (mid-slope) are, respectively,
14 and -1, while in summer (January) the respective temperatures are 24 and 10. Mean
annual rainfall is approximately 1150 mm. Snowfalls are common in winter but soils never
freeze (Woods and Raison 1983). Annual evaporation and seepage losses from the
catchment are estimated to be 630 mm (White et al. 2006). Stream discharge typically
peaks between August and September and reaches a minimum between March and May.
Identification and documentation of fires within the Australian Capital Territory (ACT)
date back to 1730. In the past 100 years, there has been major bushfires in the catchment
and surrounding areas in the summers of 1920, 1926, 1939, 1983 and 2003. With the
exception of the 1920 fire, all have followed severe droughts where rainfall in the months
preceding the fire was well below average (Sparks et al. 2008). Most recently, bushfire in
2003 affected very nearly 100% of the catchment. With the exception of parts of east and
south facing slopes, all understorey species were completely burnt and re-seeding
eucalypts (ash-type) were killed.
Previously, precipitation, vegetation cover, and the age of the forest after fire ($T_{bush}$) have
been used as key variables in predicting post-fire runoff from forested catchments
(Kuczera, 1987; Green et al. 1997; Vertessy et al. 1998; Watson et al. 1999; Turner et al.
1999; Vertessy et al. 2001; Xavier and Vettorazzi 2004). Here, in addition to precipitation
and $T_{bush}$, we used Normalized Difference Vegetation Index (NDVI) as an index of
vegetation cover. Our time series data encompass the period between the latest bushfire in
the study catchment (January 2003) and July 2011.
Data from the hydrometry station of Corin Dam rainfall gauges within the catchment were
made available by ACTEWAGL (the utility that supplies water to Canberra) and are the
basis of daily time series of streamflow and precipitation (Figure C.1). Time series of
MODIS NDVI version 5, derived from red (0.62-0.67 µm) and near-infrared (0.841-0.876
µm) reflectance data, were extracted and used directly. MODIS NDVI was selected as it
provides an estimate of vegetation condition and changes in cover (Huete et al. 1999). Data
obtained from the MODIS-TERRA sensor (MOD13Q1 product version 5) has a 250 m
spatial resolution and is a composited output over 16 days. Version-5 MODIS/Terra NDVI
is validated over a widely distributed set of locations and time periods (Solano et al. 2010). We downloaded scene h30v12 of the product, from the NASA Land Processes Distribution Active Archive Centre Data Pool. Using the MODIS reprojection tool (version 4.1), the NDVI scenes were cut to the study area (Figure C.1) and median values were calculated for the catchment.

Since NDVI is available every 16 days, other dependent and independent variables were reformed to 16-day intervals by accumulation of daily data. The $T_{bush}$ variable for $n^{th}$ 16-day interval after the bushfire can be calculated as $n \frac{16}{365}$.

![Figure C.1. Case study area and location of hydrometry stations and precipitation gauge.](image)

### C.3 Standardization and goodness of fit criteria

Given the natural range of all dependant and independent variables was equal to or greater than 0, the most simple and efficient method for standardizing variables was:

$$y_{\text{standardized}} = \frac{y}{\text{Max}(y)}$$  \hspace{1cm} (C.1)

Where, $y_{\text{standardized}}$ is the amount of variable $y$ after standardization and Max ($y$) is the maximum of variable $y$ within the time series. Following goodness of fit criteria were used in comparing the results of different data driven methods:
C.3.1 Root Mean Square Error (RMSE)

\[
RMSE = \sqrt{\frac{\sum (obs_i - for_i)^2}{n}}
\]  
(C.2)

C.3.2 Volume Error (VE)

\[
VE = \frac{\sum |obs_i - for_i|}{n}
\]  
(C.3)

Where, \(obs_i\) and \(for_i\) are observed and predicted value of the dependent variable at time step \(i\) respectively, and \(n\) is the total number of time steps.

C.3.3 Correlation (Corr)

\[
Corr\% = \frac{Cov(obs, for)}{\sigma_{obs} \times \sigma_{for}}
\]  
(C.4)

Where, \(Cov(\text{obs}, \text{for})\) is the covariance between observed and predicted values, \(\sigma_{obs}\) and \(\sigma_{for}\) are standard deviation of observed and predicted values respectively.

C.3.4 Nash-Sutcliffe Efficiency (NSE)

NSE is used to evaluate the predictive power of hydrological models (Nash and Sutcliffe 1970; Moriasi et al. 2007). It is presented as:
\[
NSE = 1 - \frac{\sum_{i=1}^{n} (Q'_{\text{obs}} - Q'_{\text{sim}})^2}{\sum_{i=1}^{n} (Q'_{\text{obs}} - \bar{Q}_{\text{obs}})^2}
\]  
(C.5)

Where \(Q_{\text{obs}}\) is observed discharge, \(Q_{\text{sim}}\) is modelled discharge, \(Q_{\text{obs}}^{1}\) is observed discharge at time step \(t\) and \(\bar{Q}_{\text{obs}}\) is the average of observed discharge from \(t = 1:T\). NSE can range from \(-\infty\) to 1. NSE = 1 corresponds to a perfect match of modelled discharge to the observed data. NSE = 0 indicates that the model predictions are as accurate as the mean of the observed data, whereas NSE < 0 occurs when the observed mean is a better predictor than the model or, in other words, when the residual variance is larger than the data variance.

### C.4 Prediction models

In the current study, Linear Regression (LR), K-Nearest Neighbour (K-NN), Artificial Neural Networks (ANNs), and Genetic programming (GP) were tested for their ability to predict streamflow. Each of these models is briefly outlined in the following sections.

#### C.4.1 Linear Regression (LR)

LR can estimate unknown coefficients of predictors by fulfilling a least squares fit. Here, LR is applied in the following form:

\[
y = \left( \sum_{i=1}^{n} c_i x_i \right) + c_{n+1}
\]  
(C.6)

Where, \(x_1\) to \(x_n\): \(n\) predictor variables, \(c_i\): coefficients of predictors and \(c_{n+1}\): constant of the model.
C.4.2 The K-Nearest Neighbour (K-NN)

K-NN method is one of the most widely used nonparametric models in rainfall-runoff forecasting (Karlsson and Yakowitz 1987), in re-sampling hydrological time series (Lall and Sharma 1996), in real-time flood forecasting (Toth et al. 2000) and in data fusion (Azmi et al. 2010). The K-NN method develops a distribution function of predicted values using a nonparametric kernel distribution function. The concept is based on observing predictor variable values at a given time (usually the present) and searching for similar conditions in the past, within the time series. These similar conditions can be considered as possible solutions depending on the degree of similarity between predictor variables at current and past time points.

We used the equation \( K = \sqrt{n} \) to estimate the best number of neighbours, where, \( n \) is the length of the time series and \( K \) is the number of neighbours according to the K-NN method (Tarboton et al. 1993). Further, weights of all predictor variables are considered equal (\( w_i = 1; i = 1 \): number of predictor variables).

C.4.3 Artificial Neural Networks (ANNs)

ANNs are semi-parametric regression techniques that are able to approximate any measurable function up to an arbitrary level of accuracy. This means ANNs are able to store acquired experimental knowledge through a learning process and use it in future (Haykin 1999). The architecture of ANNs consists of layers of parallel processing elements, which are known as neurons. Figure C.2 illustrates the architecture of a simple three-layer feed-forward neural network consisting of one input (\( i \)), one hidden (\( j \)) and an output layer (\( k \)). In a feed-forward network, the connection weights feed the activations only in one direction from an input layer to the output layer. Basically each ANN consists of three main steps: 1) setting the network architecture 2) training the network 3) testing the network. In forecasting issues using ANNs, input layers are predictor variables, and the output layer is the predicted variable.
C.4.4 Genetic Programming (GP)

GP was first proposed by Koza (1992), where a population of models are chosen using stochastic methods and are allowed to “evolve” according to a set of simple rules that mimic biological evolution. Output is a mathematical expression between a set of predicted and predictor values (Babovic and Keijzer 2000). GP differs from other regression models in that it does not require choosing a model structure a priori, it optimizes both variables and constants, models are evolved and individual models are evaluated until a satisfactory solution is found based on a fitness measure. Each candidate model (potential solution) is coded in a parse tree (Figure C.3) where the inner connection points are the functions (mathematical operators) and the terminal connection points are made up of variables and constants.

![Figure C.2. Architecture of a simple feed-forward artificial neural network.](image)

![Figure C.3. The parse tree for a mathematical model $f(x, y, z) = (x + y + 5) \times z$.](image)
C.5 Results

We divided the time series into three blocks. We used a first block as part of a calibration (training) stage. This block included 70% of the time series. The second and third blocks were used for verification (test) and validation, with each block including 15% of the complete time series. Data were randomly clustered into the three blocks. We attempted to ensure that each block included high and low flow events, in addition to more normal flows.

Weights of the linear regression equation were derived using the linear programming within the Lingo optimization modelling software (Lindo Systems Inc., Chigaco, IL). The rainfall-runoff relationship derived from the LR method can be presented as following:

\[
Q = (-0.44 \times NDVI) + (0.44 \times Precipitation) + (0.12 \times T_{bush}) + 0.33
\]  

MATLAB (The MathWorks Inc., Natick, MA) was used in programming the K-NN, ANNs and GP methods. As for K-NN, based on section 4.2, all weights are considered equal to 1 and the best number of neighbour is calculated 14. As for ANNs, a three-layer feed-forward neural network with 5 neurons in the hidden layer was used. The best number of neurons in the hidden layer was found with trial and error. The “trainlm” and RMSE were chosen as the training function and performance function respectively. As for GP, five main mathematical operators of +, -, /, × and ^ were used. A variety of mathematical functions such as exponential, trigonometric and logarithmic functions were also used. The derived rainfall-runoff relationship from GP can be presented as follows:

\[
Q = \frac{(T_{bush} \times NDVI) - Sin(T_{bush}) + (0.231 \times Precipitation) + 0.11}{Sin(53.3 \times T_{bush}) + 1.26}
\]  

Final results of goodness of fit criteria for four mentioned estimating models at three stages of training-test, validation and the entire data are presented in Table C.1. Accordingly, GP produced the best correlation (at the validation stage, 0.84) and K-NN the worst (for the entire dataset, 0.63). Using the RMSE criterion, the best performance was shown by GP at the validation stage (0.08) and worst by K-NN at the validation stage (0.21). Similarly for VE, GP again performed best (validation stage, 0.58) and K-NN the worst (validation...
stage, 3.57). Finally, using the NSE criterion, GP showed the best performance (validation stage, 0.68) and K-NN the worst performance (validation stage, -0.54).

In a pair-wise comparison between K-NN and LR (Table C.1), LR was superior 12 times out of a possible 12 times. Pair-wise comparison between LR and ANNs shows the superiority of ANNs for 11/12 times, while the pair-wise comparison between ANNs and GP again suggested the superiority of GP for 12/12 times. Clearly, GP was the superior approach.

**Table C.1.** Final results of estimations using data-driven methods

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<th>Training-Test (85% of data)</th>
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<td>RMSE</td>
<td>VE%</td>
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<td>1.63</td>
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<td>0.11</td>
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</tr>
<tr>
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<td>0.79</td>
<td>0.10</td>
<td>0.62</td>
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</tbody>
</table>

The data shown in Figure C.4 to Figure C.7, covering both training-test and validation stages, suggest all models underestimated extreme high observations and overestimated extreme low observations. For instance in Figure C.4, K-NN overestimated observed data points < 0.25 during the training-test stage and subsequently underestimated the remaining data. All four models used in this study estimated more normal data better than they did data extremes. GP was again clearly superior to other models in this respect.

**C.6 Discussion and Conclusion**

Stream flow in forested catchments after fire is often profoundly different to that before fire, and depends on patterns of regeneration, both temporally (e.g. recovery of leaf area) and spatially (e.g. distribution of re-sprouting eucalypts vs. that of eucalypts regenerating from seed). Most studies apply a recovery of leaf area index and changes in evapotranspiration that is based on mono-specific forests (Watson et al. 1999); even though fire in mixed–species forests has different effects on stand hydrology to that in
mono-specific forests (White et al. 2006; Gharun et al. 2013). We assessed the capabilities of data-driven methods in modelling

**Figure C.4.** Final results of estimations using K-NN method. Data are standardized modelled and observed stream flow.

**Figure C.5.** Final results of estimations using LR method. Data are standardized modelled and observed stream flow.
Figure C.6. Final results of estimations using ANNs method. Data are standardized modelled and observed stream flow.

Figure C.7. Final results of estimations using GP method

the rainfall-runoff relationship of a mixed-species forested catchment in south-east Australia following the 2003 bushfires, using precipitation, remotely sensed Normalized Difference Vegetation Index (NDVI) and time after the fire, as input variables.

An encouraging aspect of the LR and GP models tested in this study is that they can be presented in straightforward fashion as mathematical equations describing rainfall-runoff relationships. Such derived equations can be easily applied by non-specialists, as well as by specialists. Of these two models, GP outperformed LR in predicting stream flow over the study period. The ‘non-black box’ nature of the GP model is unlike that of ANNs, where inputs and outputs are known but formulation is implicit.

Attempts have been made to overcome the problems associated in dealing with flow extremes. An example is the use of new performance function networks with ANN models.
(Coulibaly et al. 2001). In addition, the accuracy of estimation of extremes of streamflow using GP can be strongly improved by dividing data sets into extreme and normal groups and then modelling each one separately (Charhat et al. 2009).

We suggest that the GP approach offers significant advantages over the others tested here for modelling rainfall-runoff relationship of the Corin mixed-species forested catchment following the 2003 bushfires and presents a simple and user-friendly mathematical function. We suggest further that, in other mixed-species forested catchments with similarities to the current case study area; we may be able to use the GP equation derived here with some confidence, with only moderate calibration and without the need for remodelling. Further improvements in the models presented here could be gained from longer periods of continuous data.

Concluding, the models developed here have advantages for catchment managers and water utilities: 1) they are built from observations in a catchment dominated by mixed-species forests, and 2) they require only readily available inputs. NDVI, for example, is accessible free of charge in Australia and has a 250 m spatial resolution. Precipitation data are freely available from a range of sources (Jeffrey et al. 2001). Genetic programming is a reasonable approach for the estimation of streamflow after fire in the absence of extensive climate, soil and vegetation data. Further testing a wider range of data-driven or physically-based/conceptual alternative models for the mixed-species forested catchments in Australia are encouraged for the choice of the most appropriate approach.
C.7 References


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