COMPARATIVE ECOPHYSIOLOGY OF *EUCALYPTUS* WOODLANDS ALONG A DEPTH-TO-GROUNDWATER GRADIENT

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CERTIFICATE OF ORIGINAL AUTHORSHIP

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

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List of abbreviations, acronyms and symbols

AGB	Above-ground biomass (Mg C ha^{-1})
ANOVA	Analysis of variance
ANPP	Above-ground net primary productivity (Mg C ha^{-1})
BA	Basal area (m^2 ha^{-1})
BNPP	Below-ground net primary productivity (Mg C ha^{-1})
CCA	Canonical correlation analysis
C_{FT}*	Absolute capacitance (g m^{-2} MPa^{-1})
C_{FT}	Capacitance at full turgor (MPa^{-1})
CSIRO	The Commonwealth Scientific and Industrial Research Organisation
C_{TLP}	Capacitance at turgor loss point (MPa^{-1})
DBH	Diameter at breast height (cm)
DGW	Depth-to-groundwater (m)
EWR	Environmental water requirement
ET	Evapotranspiration (mm day^{-1})
ET_0	Reference evapotranspiration (mm day^{-1})
ET_{act}	Actual evapotranspiration (mm day^{-1})
ET_{eq}	Equilibrium evapotranspiration (mm day^{-1})
ET_P	Potential evapotranspiration (mm day^{-1})
GDEs	Groundwater dependent ecosystems
GPP	Gross primary productivity (Mg C ha^{-1})
H_V	Huber value (mm^2 mm^{-2})
K_L	Leaf specific conductivity (Kg m s^{-1} MPa^{-1} m^{-2})
K_S	Branch sapwood specific conductivity (Kg m s^{-1} MPa^{-1} m^{-2})

LAI	Leaf area index (m^2 m^{-2})
MANOVA	Multivariate analysis of variance
Non-GDEs	Non groundwater dependent ecosystems
NPP	Net primary productivity (Mg C ha^{-1})
NSW	New South Wales
P	Precipitation (mm)
PLC$_{50}$	Water potential associated with 50% loss in hydraulic conductance (MPa)
PLC$_{88}$	Water potential associated with 88% loss in hydraulic conductance (MPa)
P-V curve	Pressure- volume curve
RO	Run-off
RWC$_{TLP}$	Relative water content at turgor loss point
SCA	Sydney catchment authority
SLA	Specific leaf area (cm^{-2} g^{-1})
SWC	Saturated water content (g cm^{-3})
T	Transpiration
VIC	Victoria
VOC	Volatile organic compounds
VPD	Vapour pressure deficient (kPa)
WA	Western Australia
Ψ_{min}	Minimum leaf water potential (MPa)
Ψ_{pd}	Pre-dawn leaf water potential (MPa)
Ψ_{TLP}	Leaf water potential at turgor loss point (MPa)
ε	Bulk modulus of elasticity (MPa)
π_{100}	Osmotic potential at full turgor (MPa)

Abstract

A major challenge for groundwater research is to consider the complex relationships amongst groundwater resources, vegetation (function and structure) and climate. Transpiration from vegetation (especially trees when present) is the principal pathway for discharge of water from vegetated landscapes. Whilst it is known that the ability to access groundwater can help plants survive drought conditions and in particular the importance of groundwater in arid and semi-arid areas is well documented, there have been few studies that compare ecophysiological (e.g. leaf water relations), structural (e.g. basal area, leaf area index) and functional (e.g. rates of tree water-use, above-ground net primary productivity; water-use-efficiency) attributes of trees along a naturally occurring gradient in depth-to-groundwater, especially in mesic environments.

The aim of this research was to establish whether differences in groundwater depth along a transect influences ecophysiological, functional and structural attributes of remnant woodlands in southeast of Australia growing in a region with relatively high annual rainfall. The study area was located in the Kangaloon bore-field area, NSW, where depth-to-groundwater varies from 2.4 m to 37.5 m. To address this aim; seasonal measurements were made at seven sites at three scales (leaf-, tree- and stand-scales).

Structural attributes of woodlands, above-ground productivity were significantly different across sites. The three shallowest sites with 2.4m, 4.3 m and 5.5 m depth-to-groundwater had significantly larger above-ground biomass and productivity than the four deepest sites (sites where depth-to-groundwater was more than 9.8 m). A significant shift occurred in all measured variables when depth-to-groundwater increased from 5.5 m to 9.8 m. This result was found consistently for each structural trait examined (LAI, tree height, BA, ANPP, AGB, stem density). There were no differences in three structural traits (BA, height and LAI) nor ANPP across the four

deepest sites. All these traits were significantly smaller at these deepest sites compared to the three shallowest sites.

Rates of stand transpiration rate tended to be smaller at all sites compared to many other studies conducted in a similar environment. This result was attributed to larger-than-average rainfall received across all sites across the entire study period, with concomitant reductions in solar radiation, temperature and VPD compared to long term means. Despite this, there were significant differences across sites and these differences were not consistent with my initial hypothesis: namely that as depth-to-groundwater decreases stand transpiration rates will increase. Rates of stand transpiration at the shallowest groundwater site (2.4 m) were the same as those at the deepest groundwater site (37.5 m) despite significantly larger tree density, BA, LAI at the shallowest site compared to the deepest site. Rates of stand transpiration were consistently the largest at the 4.3 m site compared to all other sites.

Tree hydraulic architecture was the least affected by depth-to-groundwater. Hydraulic architecture of trees was examined by measurement of the following traits: Huber value, branch hydraulic conductivity (leaf and sapwood specific), xylem sensitivity to embolism and sapwood density. Huber value (H_V) increased significantly as depth-to-groundwater increased, in agreement with my initial hypothesis: namely that H_V is larger at drier sites (deeper groundwater sites) than sites with shallow groundwater. Neither sapwood density nor branch hydraulic conductivity (sapwood and leaf area specific) varied significantly across sites, in contrast to expectations. Xylem vulnerability to embolism was assessed in summer and winter by determining the water potential associated with both a 50% and 88% loss of conductance (PLC_{50} and PLC_{88} respectively). PLC_{50} in both seasons was significantly and negatively correlated with depth-to-groundwater.

Leaf-scale measurements showed that trees occupying sites with the shallowest water table were more sensitive to drought stress than those growing at sites with the deepest water-tables. There were significant changes across some leaf traits, including: leaf turgor loss point, osmotic potential at full turgor and the relative water content at turgor loss point (RWC_{TLP}). All of these traits declined as depth-to-groundwater increased. In contrast, leaf volumetric elasticity was independent of depth-to-groundwater. The form of the relationship between depth-to-groundwater and leaf-scale and stand-scale structural traits differed between the two sets of data. In the former a negative and linear response to increasing depth-to-groundwater was observed but in the latter an exponential decay response was observed.

When all leaf-scale, tree-scale and stand-scale traits were normalized (zero to one) to produce a single, average response across all traits, as a function of depth-to-groundwater, a significant step-function response to increase in depth-to-groundwater was observed. For the three shallowest sites, there were minimal changes as a function of depth-to-groundwater but as depth-to-groundwater increased from 5.5 m to 9.8 m there was a significant reduction in mean normalised trait value. When depth-to-groundwater was larger than approximately 9-10 m a consistent reduction in normalised trait value occurred, with no significant difference across the four deepest sites.

This thesis has demonstrated that even in a mesic environment, groundwater can have an important impact on ecophysiological, structural and functional traits of trees. Understanding how trees respond to changes in groundwater availability is a crucial knowledge gap in our current understanding about groundwater and vegetation interactions. Determining this response function has management and conservation applications which indicate potential changes in ecosystem function, structure, growth and ultimately survival. It can also potentially determine the safe limit threshold for groundwater drawdown.

Whilst it is acknowledged that variation in traits along environmental gradients in the field are, by definition, correlative (that is correlated with variation in the environmental variable identified along the gradient), the use of multiple sites across a very small spatial gradient strongly supported the conclusion that trait variation was associated with variation in groundwater depth and not with variation in climate. Furthermore, consistency in trends across the gradient in groundwater depth also support the conclusion that trait variation identified in this thesis can be attributed to variation in groundwater depth, rather than randomly occurring in space.

Chapter 1 General Introduction

Groundwater in Australia

Groundwater[1] is often the only reliably available source of water in semi-arid[2] and arid[3] regions. Groundwater plays an important role in alleviating problems arising from water scarcity because of its physical and storage characteristics (Pereira et al. 2009). As human population has increased, groundwater-use has also increased, especially during the past century in Australia and globally (Llamas and Martínez-Santos 2005). Australia is the driest permanently inhabited continent on the Earth, with the majority of its land area classified as semi-arid and arid (Eamus 2003; O'Grady et al. 2010) and annual evaporation exceeds annual rainfall across most of the continent (O'Grady et al. 2011). As a result a significant fraction of the ecology, industry and population of Australia are highly dependent on groundwater resources.

In Australia utilization of groundwater for human consumption has increased exponentially in the past 150 years (Nevill et al. 2010). A large proportion of agricultural industries, many rural towns and large cities such as Perth are dependent on groundwater resources. Groundwater usage has almost doubled (1983-1996) across the country to support irrigation, mining and drinking water; in some States (WA and NSW), the rate of increase has been even larger (Eamus et al. 2006b). As a result in many catchments groundwater is being over-extracted (Eamus et al. 2006b; Polglase and Benyon 2009). This happens when the rate of extraction is larger than

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1 - Groundwater has been described as the saturated zone of the regolith and its associated capillary fringe (Eamus et al 2006b).

2 - Semi-arid regions receive more rainfall than arid regions but it is still too low and unreliable for crops to be grown with certainty (Eamus et al 2006b).

3 - Arid regions are defined as those areas in Australia receiving less than 250 mm in the south or 350 mm of rainfall per year in the north (Eamus et al 2006b).

the rate of recharge and this represents a challenge for land and water resource managers (Polglase and Benyon 2009).

The key role that groundwater resources have in the Australian water cycle is well understood but the role that groundwater plays in controlling Australian ecosystem structure and function is not well understood (Hatton and Evans 1998; O'Grady et al. 2006a). In addition to humans who depend on groundwater resources, a number of ecosystems and species depend on having access to groundwater. These ecosystems are called groundwater dependent ecosystems (GDEs).

Groundwater dependent ecosystems

Groundwater dependent ecosystems (GDEs) are important elements in the landscape that rely on an input of groundwater to maintain their current composition, structure and function (Eamus et al. 2006b; Laio et al. 2009). Ecosystem services such as water filtration, erosion control, soil formation, recreation, nutrient cycling, habitat provision, maintaining biodiversity and genetic resources are provided by groundwater dependent ecosystems and may be impossible or extremely costly to replace (Eamus et al. 2005; Kløve et al. 2011; O'Grady et al. 2002; O'Grady et al. 2006a; O'Grady et al. 2006c). GDEs include a variety of both terrestrial and aquatic communities (Kløve et al. 2011). These communities can be divided to three groups: those which rely on the surface expression of groundwater resources (e.g. some riparian forests, base-flow rivers, wetlands); those that rely on a sub-surface expression of groundwater (e.g. terrestrial vegetation, including some woodlands and forests); and stygofauna located in aquifers or groundwater-fed caves (Eamus et al. 2006a). Groundwater dependent vegetation uses groundwater when it is within reach, via roots accessing groundwater at depth or through groundwater discharge to the surface, for example, through flooding and consequent soil water recharge (Eamus and Froend 2006). Terrestrial ecosystems that depend on groundwater are generally characterized as having greater structural complexity, higher floristic diversity, or higher leaf area compared with neighbouring non-groundwater dependent ecosystems (O'Grady et al. 2007).

Management of GDEs

Groundwater dependent ecosystems are becoming increasingly influenced by human activities (Edmunds and Shane 2008). Because of excessive and unsympathetic groundwater abstraction and land use changes, decline and mortality of groundwater dependent vegetation, such as wetlands and woodlands, have been observed throughout Australia (Eamus and Froend 2006; Nevill et al. 2010). Although it has long been understood that groundwater exploitation must be managed to prevent irreversible degradation or loss of water supplies, the need to ensure the protection of ecosystems associated with groundwater has only been recognised as a key aspect of water management after the 1970s (MacKay 2006). Many land use practices, including exploitation of groundwater resources for irrigation and consumptive use, significantly alter groundwater levels and dynamics (Hatton and Evans 1998). Any activities that have the potential to alter groundwater levels and dynamics can have an adverse effect on GDEs.

The dependence of ecological processes on groundwater availability is based on one or more of the basic groundwater attributes, namely: depth of the saturated zone, the quality of the groundwater, the location of discharge and the normal patterns in the rate of change in groundwater depth (Eamus et al. 2006a; Sinclair Knight Merz 2001). GDEs have adapted to natural variation in these groundwater attributes (level, pressure, flux and quality) over thousands or millions of years (Nevill et al. 2010). Man-made variation in groundwater attributes are expected to impact GDEs through an influence several processes, including rooting depth, water-use-efficiency, fluxes of water and carbon, leaf water potential and productivity.

Managers of water resources face a complex decision when managing environmental water requirements and consumptive use in Australian landscapes: how to ensure that future development of water resources is managed sustainably? (O'Grady et al. 2006c). This is the ultimate challenge for water resources managers: how to include environmental water requirement (EWR) within water allocation planning programs. There is due to increasing concern about potential impacts of changes in groundwater regimes on GDEs. Hatton and Evans (1998) highlighted the importance of groundwater dependent ecosystems in Australia as well as our limited understanding of the types and nature of groundwater dependency (e.g. obligate *versus* facultative dependence; see below).

Since the 1994 Council of Australian Government's frameworks for water reform, the allocation of groundwater resources for the maintenance of ecosystem processes has been identified as a pressing issue. Arguably, one of the main concerns is how much water should be allocated to the environment (Murray et al. 2003). For groundwater resource managers a key question they must address is: "what are the safe limits to changes in groundwater availability?" (Eamus et al. 2006a). A second, perhaps equally important question for groundwater managers is: what measure can be applied to monitor the response of GDEs to changes in groundwater availability? To minimise the future impact of groundwater extraction on GDEs, the effective management of groundwater resources requires information about the following:

1- Identification of the location of these ecosystems

The first step in managing GDEs is to find the location of these ecosystems. There are many different ways to determine whether an ecosystem is dependent to groundwater (Eamus et al. 2006a). For terrestrial vegetation if groundwater is within the rooting depth of vegetation there is a very high chance that they use groundwater either intermittently, continually or seasonally (Naumburg et al. 2005). Alternative methods that can be employed include a comparison of stable isotopes of groundwater and xylem water (Cook and O'Grady 2006), comparison of leaf area indices across a catchment and comparisons of leaf water relations and phenology of potential GDEs and adjacent ecosystems (Eamus et al. 2006a).

The Atlas of GDEs of Australia was developed in 2012 by the National Water Commission, CSIRO, the Bureau of Meteorology and consultancy services provided by Sinclair Knight Merz. The Atlas was developed using existing information on GDEs from every State and Territory in Australia. The Atlas incorporates previous field-based work, published and unpublished literature and previously mapped GDEs to provide information about the location and characteristics of known and potential GDEs around the country. This will help recognition of GDEs in natural resource management including water and environmental planning (http://www.bom.gov.au/water/groundwater/GDE).

2- Timing and degree of dependency

Vegetation dependency on groundwater differs among ecosystems, from being entirely dependent ecosystems (obligate GDEs) to limited and opportunistic use of groundwater (facultative GDEs). Furthermore, the entire ecosystem might be reliant on groundwater (for example, baseflow dependent rivers and some wetlands) or only one or a sub-set of the species present may be dependent on groundwater. Understanding to what degree an ecosystem is dependent on groundwater is important to the management of these ecosystems. Obligate GDEs always require the supply of groundwater for the maintenance of their structure and function, but facultative dependent ecosystems can survive without groundwater input (Murray et al. 2003). Obligate GDEs may rely on groundwater all year or throughout all stages of their life cycle. Such GDEs may not be using groundwater all the time but access to groundwater during specific times during their life span is critical to survival. Absence of groundwater can result in loss of an entire population in these ecosystems or permanent changes in structure and function of the ecosystem. The probability of their being obligate phreatophytes (plants using groundwater) is higher in sites with shallow groundwater than sites with deeper groundwater resources. Facultative GDEs use groundwater in some stages in their life or some times in a year. They use groundwater when it is available and accessible. Although access to groundwater is an advantage for these ecosystems, the absence of groundwater can be accommodated for months or years. While groundwater may constitute a small proportion of water-use in facultative species, it may still be important for their long-term survival. However, in practice it is very difficult to determine if and to what extent an ecosystem is dependent on groundwater. Plant species may be strongly groundwater dependent even if they only use a small proportion of groundwater, or only use groundwater infrequently for a short period each year (Murray et al. 2003). Thus, O'Grady et al. (2006c) found that many tree species in riparians zone use groundwater during the dry season but not during the wet season when soil water is used preferentially.

Knowing the extent and timing of ecosystem dependency on groundwater is important for water resource managers because this information can inform planning in relation to optimising the timing of groundwater extraction to minimise the impact of extraction on GDEs. Until such information about groundwater dependency has been established the impact of different managements scenarios cannot be identified (Lamontagne et al. 2005). Currently our understanding of the nature (timing, extent, degree of dependency and quantity) of groundwater dependence in terrestrial vegetation is severely limited (Eamus et al. 2006b). Groundwater-use is likely to be a function of several factors including depth to water table, maximum rooting depth, root distribution, rainfall, potential evaporation rate and soil water reserves (O'Grady et al. 2006a).

3- Study the interaction between groundwater and GDEs and ecosystem responses to changes in groundwater availability

The answer to the question of "How does ecosystem health[1] respond to changes in groundwater availability?" is perhaps the biggest unknown area related to

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1- Assessment of ecosystem health is one of the hotspots in ecosystem management. Ecosystem health is a broad concept for which there is not agreement on the precise and exact definition of the concept (Peng et al 2007), so it may be better to use the term ecosystem function inste groundwater dependent ecosystems. Assessment of ecosystem responses to changes in groundwater availability is a key issue for water and landscape managers. To-date, a lack of quantitative data precludes an answer to this question. Ecosystem responses to changes in groundwater availability has been hypothesised to be a linear, curve-linear or, step function response with minimum damage until a threshold is reached (Eamus et al. 2006b) (Fig. 1-1). Horton et al. (2001) studied the relationship of depth-to-groundwater and tree physiology of three species of riparian vegetation in Arizona, USA and found a step function response. However, there are few studies that have determined response functions to changes in groundwater availability, particularly in Australia.

Vegetation responses to changes in groundwater depth tend to be the focus of many studies because it is vegetation that shows the proximal and immediate utilization of groundwater (Eamus et al. 2006b). Information on how vegetation adapts to differences in water supply is also critical for predicting vegetation survival, growth and water-use, which, in turn, have important impacts on site hydrology (Carter and White 2009; McDowell et al. 2008). The development of species' response curves to reduced water availability would significantly enhance our understanding of water requirements and perhaps lead to the identification of response thresholds. Such thresholds could be used to identify the limits of reduction in water-source availability, a useful parameter for characterising water requirements for resource and conservation management (Froend and Drake 2006). However, it is likely that ecosystem responses to changes in groundwater availability differ with ecosystem age, the rate of change of groundwater availability, the time-of-year and the type of the ecosystem.

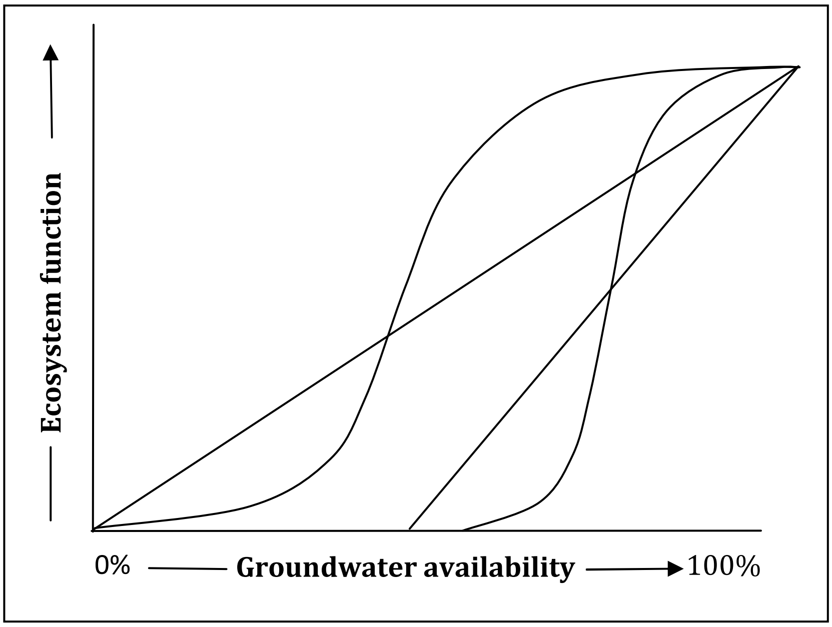


Figure 1-1: Theorical ecosystem response function to changes in groundwater availability (Eamus et al. 2006b).

4- Quantify water requirements of GDEs

Exploitation of groundwater resources will almost inevitably impact groundwater dependent ecosystems. To minimize the negative impact of groundwater extraction the water requirements of GDEs needs to be better understood and quantified (Lamontagne et al. 2005). The water requirement of a GDE is the water regime needed to sustain its key ecological values, including species composition, productivity and persistence through time. The water requirement of GDEs must be understood if the management of groundwater resources is to be consistent with the principles of ecologically sustainable development (Eamus et al. 2006a). The water requirement of phreatophytes can be a complex function of several attributes of groundwater systems (both quality and quantity) (Lamontagne et al. 2005). The pattern of groundwater-use by vegetation can also have significant effect on hydrological balance of landscapes (Kray et al. 2012; Newman et al. 2006a).

The scope of this thesis

Groundwater dependent ecosystems are essential components of many landscapes and have a key role in the hydrological cycle of their catchment. There is a clear need to better understand their function, how they impact their environment and how they are affected by their environment. This information will provide a valuable tool to assist in predicting the nature and scale of ecosystem responses to variation in groundwater availability. Such research should be focused on developing a better understanding of the interaction between groundwater and vegetation, specifically trees, which because of their deeper roots, tend to access groundwater more consistently than understory species. Studying trait diversity and convergence of traits across sites differing in depth-to-groundwater among species or within species will provide a better understanding of the separation of niches of different species or how individuals within one species adapt to variation in resource availability (Mitchell 2009). Interactions among vegetation and groundwater availability are a focus of renewed research interest globally, particularly in semi- arid and arid areas.

This thesis focuses on trees and their potential interaction with groundwater. The reason trees have been chosen is because trees tend to be more deeply rooted than herbs and grasses and may interact more consistently with groundwater, especially when groundwater depth exceeds 2 m. This thesis has focused on a comparative analysis of the ecophysiological traits of *Eucalyptus* trees across a gradient of depth-to-groundwater from shallow (2.4 m) to deep (37.5 m) to answer the following questions.

1- Are these any differences in functional attributes across a gradient of depth-to-groundwater?

There is an extensive literature pertaining to the comparative analyses of tree functional traits (for example: rates of photosynthesis, wood density, specific leaf area; Huber value, hydraulic conductivity of sapwood) along aridity gradients arising from differences in annual rainfall along a transect (e.g. Lane et al. (2000), White and Hood (2004)Hood (2004), Ellis and Hatton (2008), Taylor and Eamus (2008), Turner et al. (2008), and Buis et al. (2009)). In contrast, there have been few studies that have looked at differences in vegetation functional traits across a depth-to-groundwater gradient. Figure 1-2 shows that the distribution of the few studies on the ecophysiology of GDEs in Australia (O'Grady et al. 2010). Most research in this area in Australia has focused either on riparian forests[1] (Drake and Franks 2003; O'Grady et al. 2006c), wetlands[2] (Rodriguez-Iturbe et al. 2007) or ecosystems in arid and semi-arid environments (Froend and Drake 2006; Miller et al. 2010). In contrast to these studies, the work described in this thesis examines the impact of groundwater depth on functional attributes of trees in a mesic environment (South-East Australia). Measurements have been made at leaf, tree and stand-scales (Fig. 1-3) at sites with contrasting depth-to-groundwater. Each variable was measured in different seasons to provide a clear description of the ecophysiology of these trees.

1- Riparian forests are forests located on the banks of a river or other water body (Eamus et al., 2006b).

2- wetlands are areas those are regularly flooded and have a water table that stands at or above the land surface for at least part of the year (Eamus et al., 2006b).

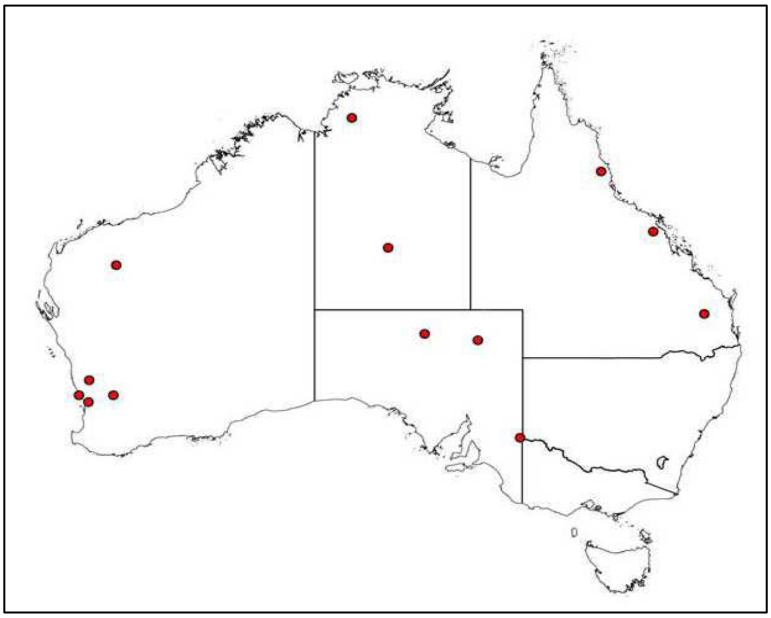


Figure 1-2: Distribution of ecophysiological studies that have identified groundwater as a contributor to evapotranspiration (O'Grady et al. 2010). Red points show where these studies were conducted.

2- What should be measured to monitor tree responses to changes in groundwater availability?

Adaptations to water stress occur at several temporal and spatial scales. In the short term, water loss and leaf water status are controlled by changes to stomatal conductance (Tyree and Sperry 1988). In the medium term, osmotic or elastic adjustment of leaf tissue may occur in response to declining water availability to maintain gradients of water potential between soil and leaf and to maintain flow of water leaves and hence maintenance of leaf turgor (Ladiges 1975; White et al. 2000). Over longer time frames, plants may change their growth rates, decrease their leaf area (Grier and Running 1977), increase allocation to roots (Cannell 1985) or alter xylem structure to limit the risks inherent in loss of sapwood conductance arising from xylem embolism (Nardini and Salleo 2005; Tyree and Zimmermann 2002). These adjustments not only impact vegetation growth, but also vegetation water-use, which may have large impacts on site water balance (Carter and White 2009; Gazal et al. 2006; O'Grady et al. 2009). However, these responses are usually studied by either (a) examining the response of vegetation at a site to localised drought/water stress or (b) comparing the ecophysiology of vegetation along aridity gradients (Buis et al. 2009; Santiago et al. 2004a; Taylor 2008). In contrast, in this study, the ecophysiological traits of trees were compared along a natural gradient in depth-to-groundwater within a single climate envelope within a single type of ecosystem (Eucalypt woodland).

Figure 1-3 identifies the physiological and structural measurements that have been conducted in the current study at different scales. Both functional and structural traits were measured at three scales (leaf, tree and stand), to assess the responses of a wide-range of traits to changes in groundwater availability and thereby attempt to answer the question: which attributes provide a measure of tree responses to differences in groundwater depth? Answering this question will help groundwater resource managers in future assessments of groundwater abstraction regimes.

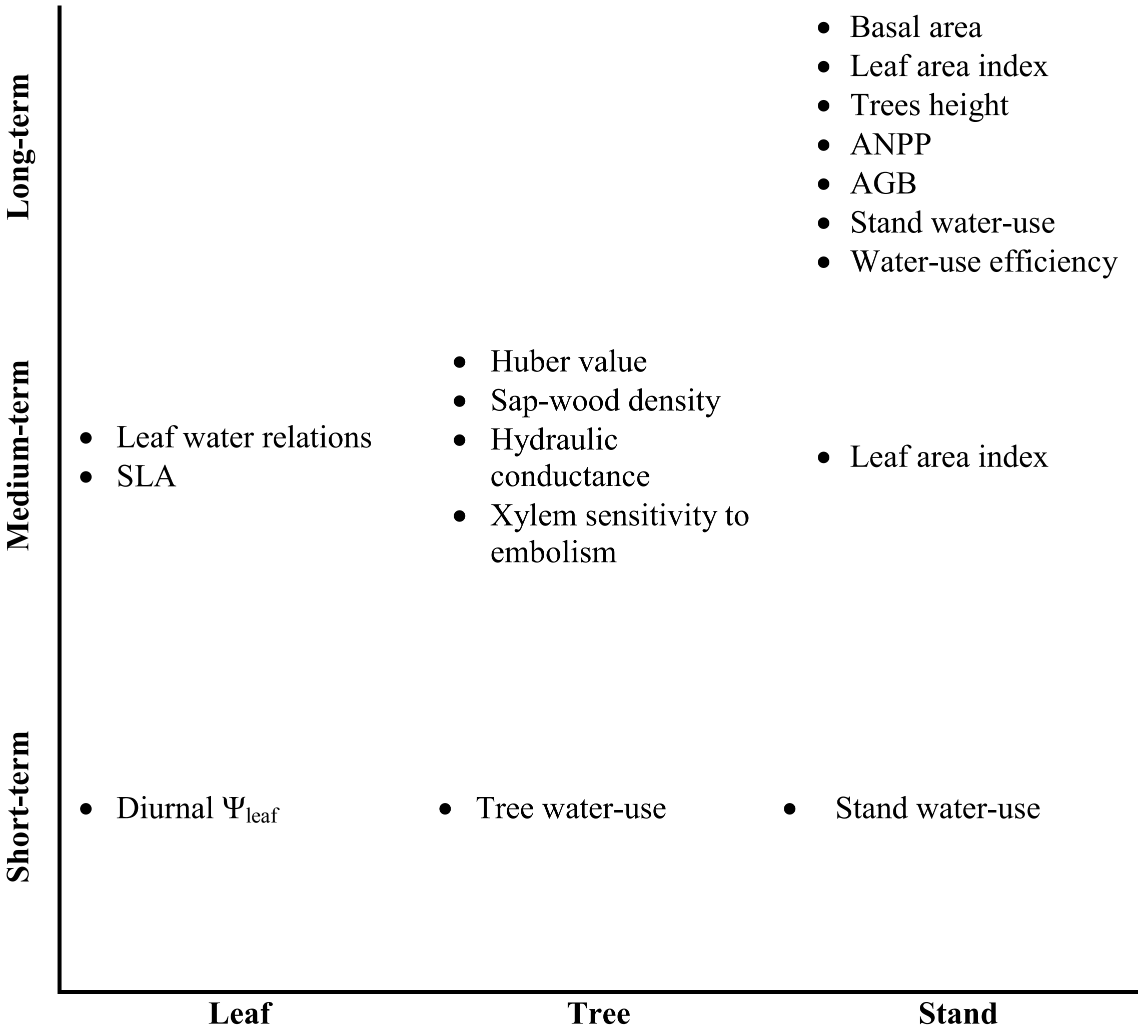


Figure 1-3: Traits that were measured in this research at different spatial and temporal scales.

3- Can response functions to differences in depth-to-groundwater be identified across a range of traits?

Determining the response function of a species, species assemblage or ecosystem to variation in groundwater depth is difficult because measurements before, during and after periods of change in groundwater depth are rarely available.

There are number of researchers (mostly in USA) who compared riparian vegetation adjustment both physiologically and morphologically to water stress arising from increased groundwater depth (Cooper et al. 2003; Naumburg et al. 2005; Scott et al. 1999; Stromberg et al. 1996). Species composition and species resistance to drought change along topographical gradients of depth-to-groundwater (Stromberg et al. 1996). Similarly, plant height, leaf area, leaf size and xylem potential have been shown to vary as a function of depth-to-groundwater (Cooper et al. 2003; Stromberg et al. 1996). However, Froend and Sommer (2010) suggested that not all vegetation communities show similar responses to those of riparian vegetation. The rate, magnitude and duration of drawdown of groundwater can determine how vegetation responds to this issue (Froend and Sommer 2010; Scott et al. 2000a; Scott et al. 1999).

In the work described in this thesis, comparisons of ecophysiological traits of trees growing at sites along a depth-to-groundwater gradient were used to determine whether traits showed persistent trends that were consistent with differences in water availability across sites.

It is expected that outcomes of this thesis will help to fill some research gaps by expanding our knowledge of:

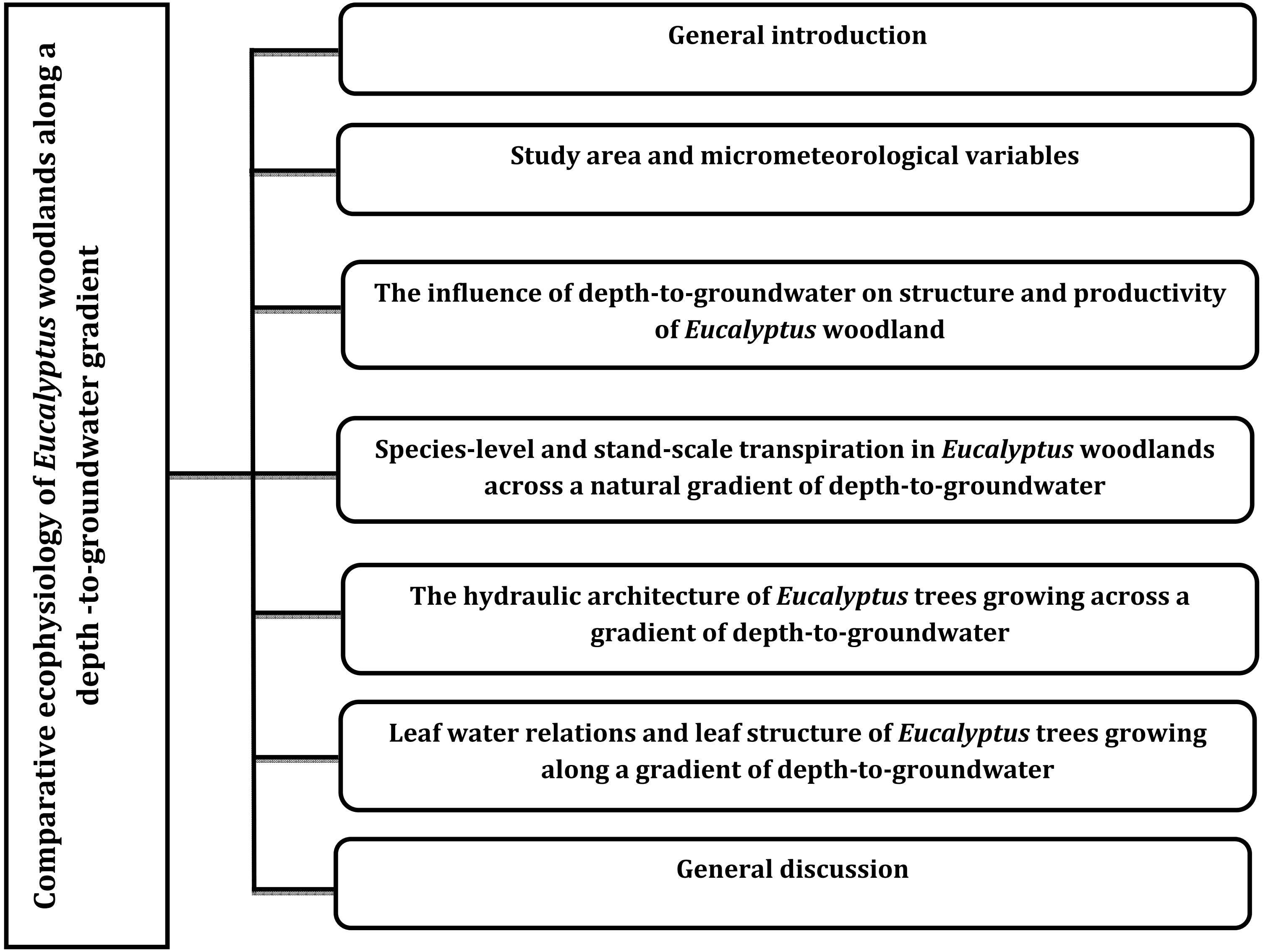
1- Comparative ecophysiology (functional attributes) of different species across a gradient of depth-to-groundwater, examined at different scales (leaf, tree and stand-scale);

2- Comparative rates and patterns of water-use across a depth-to-groundwater gradient at tree and stand-scales;

3- The most important traits in vegetation that can be used to compare vegetation responses to differences in depth-to-groundwater and

4- Response curves defining trends in terrestrial vegetation attributes as a function of groundwater availability.

The Figure below shows how each of these aims are addressed in different chapters.


Comparative ecophysiology of *Eucalyptus* woodlands along a depth -to-groundwater gradient
General introduction
Study area and micrometeorological variables
The influence of depth-to-groundwater on structure and productivity of *Eucalyptus* woodland
Species-level and stand-scale transpiration in *Eucalyptus* woodlands across a natural gradient of depth-to-groundwater
The hydraulic architecture of *Eucalyptus* trees growing across a gradient of depth-to-groundwater
Leaf water relations and leaf structure of *Eucalyptus* trees growing along a gradient of depth-to-groundwater
General discussion

Chapter 2 Study area and micrometeorological variables

Site description

The study site was located in relatively pristine Eucalyptus woodlands in the Upper Nepean catchment, on the Great Dividing Range (also known as the Eastern Highlands), on the Woronora Plateau to the east of Bowral, to the north of the township of Robertson and east of Wingecarribee Reservoir. The Upper Nepean River is located 110 km south west of Sydney in New South Wales, Australia (Fig. 2-1).

The Kangaloon Bore-field area (Fig 2-1), within which this study was undertaken is characterised by relatively undisturbed dry sclerophyll Eucalyptus woodlands, forests and upland swamps (Beadle 1954, 1966; NPWS 2003). The geology is described as Hawkesbury Sandstone covered by Remnant Wianamatta Shales and Tertiary Basalt occurs at higher elevations, often capping hills in the area (Kodela 1990). The main aquifers of the Kangaloon area are within Robertson Basalt and Hawkesbury Sandstone, with groundwater in the basalt mainly limited to higher regions of the catchment. Groundwater in the aquifers is recharged by rainfall along ridgelines and discharges in mid slope areas providing base-flow to several small streams and springs.

The area is owned and managed by the Sydney Catchment Authority (SCA). Several bores that are located in areas with different depth-to-groundwater have been monitored frequently by the SCA since 2006. Based on the information from these bores, seven sites were chosen to span a wide range of average depth-to-groundwater: 2.4 m, 4.3 m, 5.5 m, 9.8 m, 13 m, 16.3 m and 37.5 m along an 11 km transact. These sites were identified by the SCA as 3J, 3F, 3C, 3A, 5M, 4M and 10A, respectively (Fig. 2-2).

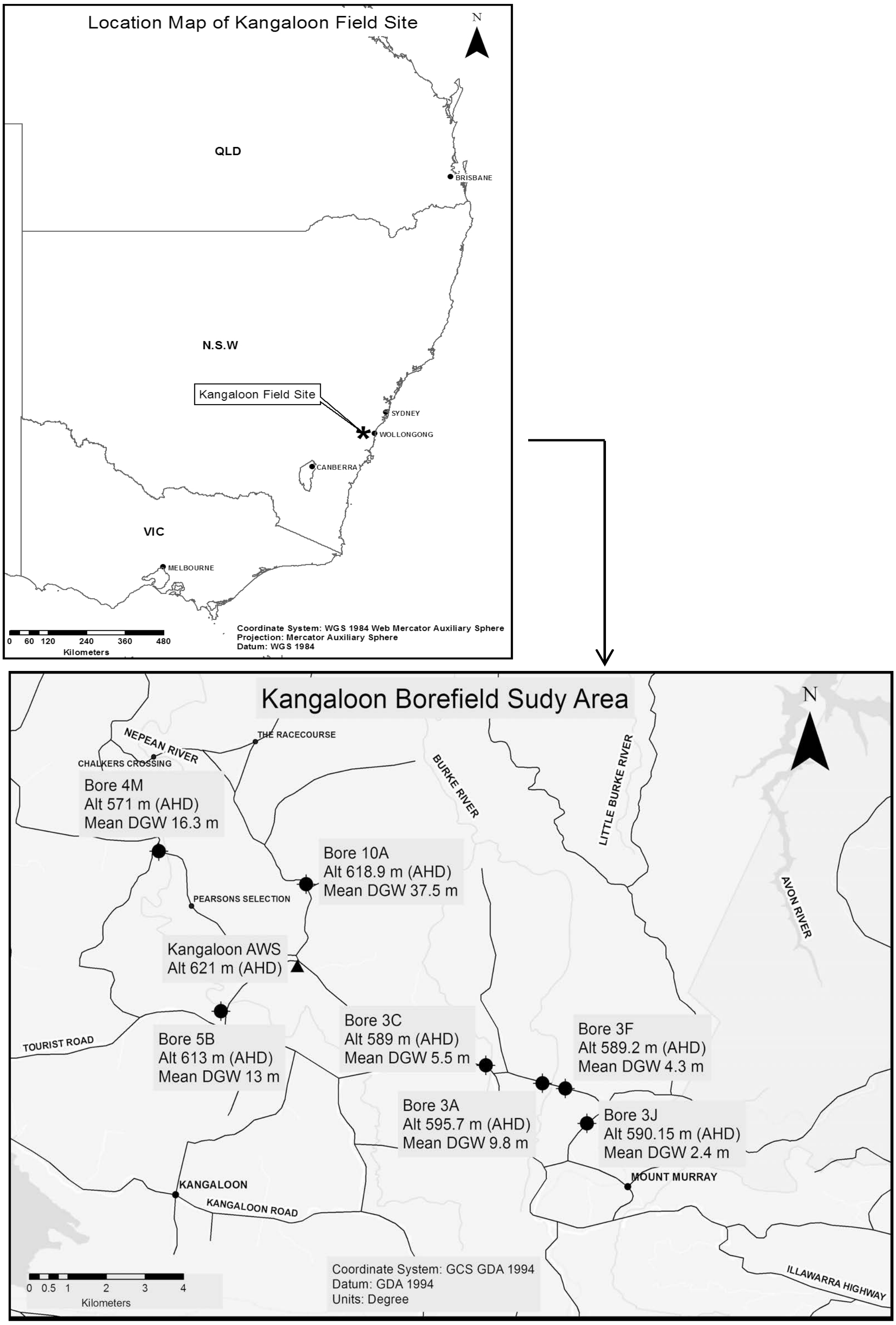


Figure 2-1: Study area; location of site within Australia (Top panel) and location of bores (lower panel).

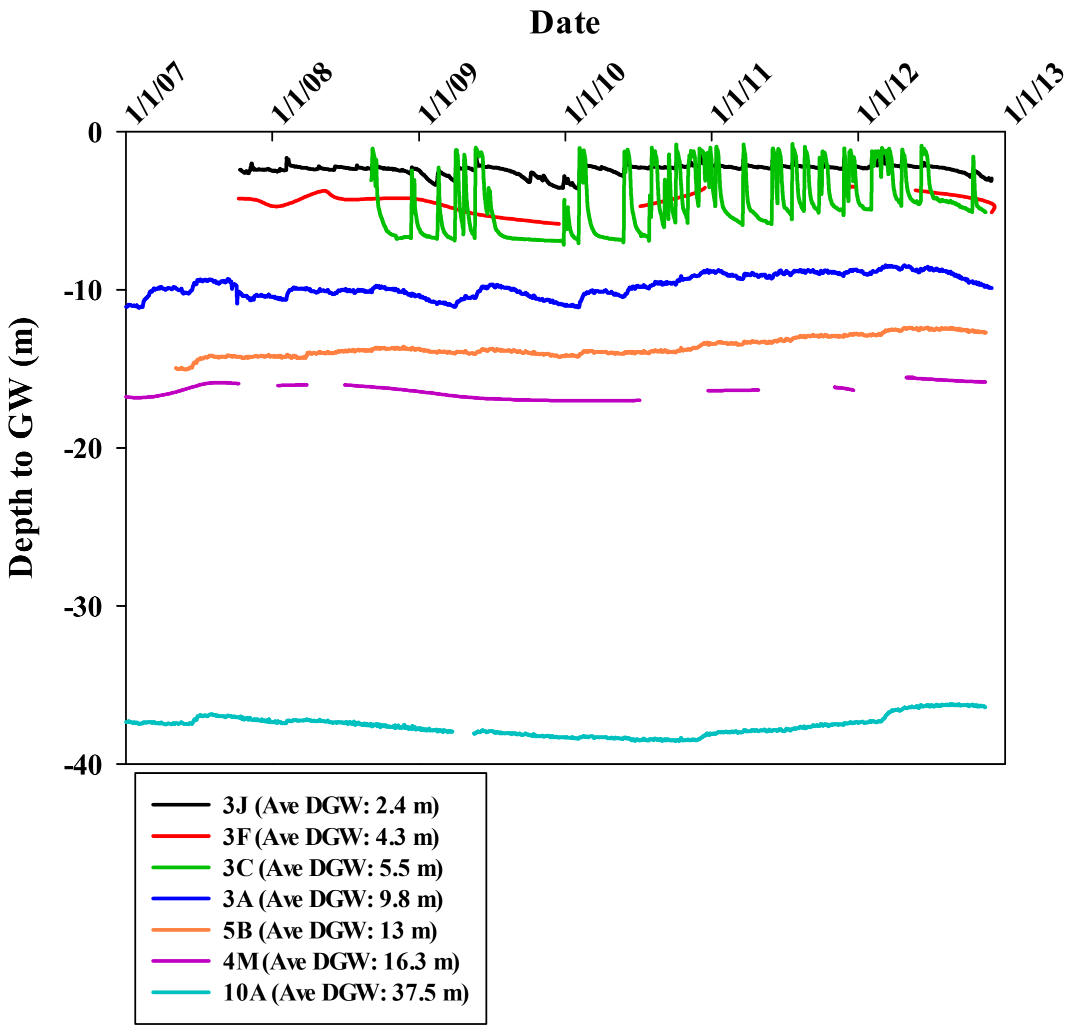


Figure 2-2: Fluctuations of water table depth at the seven study sites between January 2007 and December 2012.

Micro-meteorology, weather and soil water content

The study area has an average annual rainfall of approximately 1067 mm (2000-2010, BOM station no. 68243). The highest monthly rainfall occurs in February (average of 186 mm) and the lowest in August (average of 51 mm). Average minimum temperature occurs in July (2.7 ^{o}C) and average highest temperature in January (24.3 ^{o}C) (2000-2012 From SCA meteorological station in East Kangaloon) (Fig. 2-3).

Micro-meteorological information, including relative humidity, air temperature, wind speed, wind direction, net solar radiation and rainfall were recorded at a meteorological station installed less than 7 km of all study sites. A temperature and relative humidity probe, (model; HMP45C; Vaisala, Logan, Utah) was installed in a cleared field (> 3 ha in area) (Fig. 2-1) in a screened meteorological station. Solar radiation was measured using NR-Lite Net radiometer sensor; manufactured by Kipp & Zonen, Netherlands. Vapour pressure deficit was calculated from the difference between saturation vapour pressure (SVP, kPa) and vapour pressure (kPa), at the observed air temperature (T) and observed relative humidity. Saturation vapour pressure was calculated using FAO (Food and agriculture organization of United Nations) method:

$$SVP = 0.6108 \times Exp((17.27 \times T))/(T + 237.3) \qquad \text{(Equation 1)}$$

Figure 2-4 shows daily rainfall and daily average temperature, VPD and daily sum of Rs measured across the two year study period (January 2011 to December 2012). Vapour pressure deficit (VPD) was relatively low and for most of days remained below 1 kPa (Fig. 2-4), reflecting the relatively wet two-year period of the study. Total annual amount of rainfall in 2011 was 1561 mm and 1188 mm in 2012, which was or 46 % and 11 % larger than the long term average of 1067 mm (Fig. 2-5).

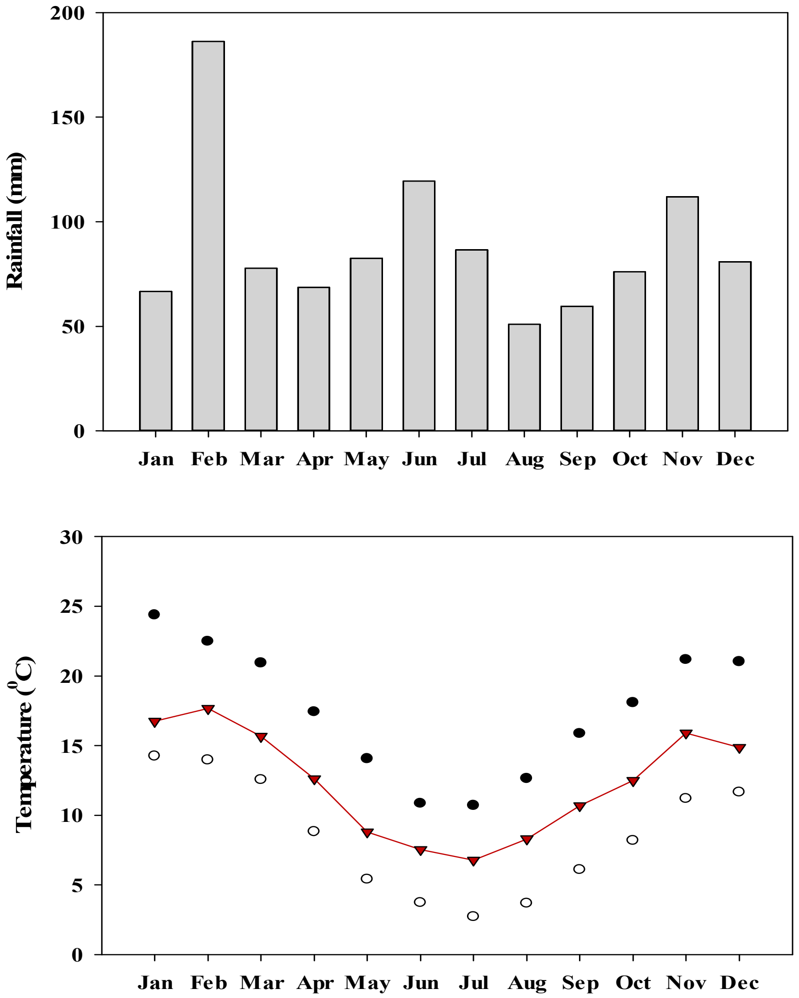


Figure 2-3: Top panel: Average monthly rainfall at the study area; 12 years (2000-2012) from BOM station no. 68243; lower panel shows minimum (open circles) and maximum (closed circles) average monthly temperature in the study area for 12 years. Red triangles show average monthly temperature. Data from: SCA meteorological station; East Kangaloon.

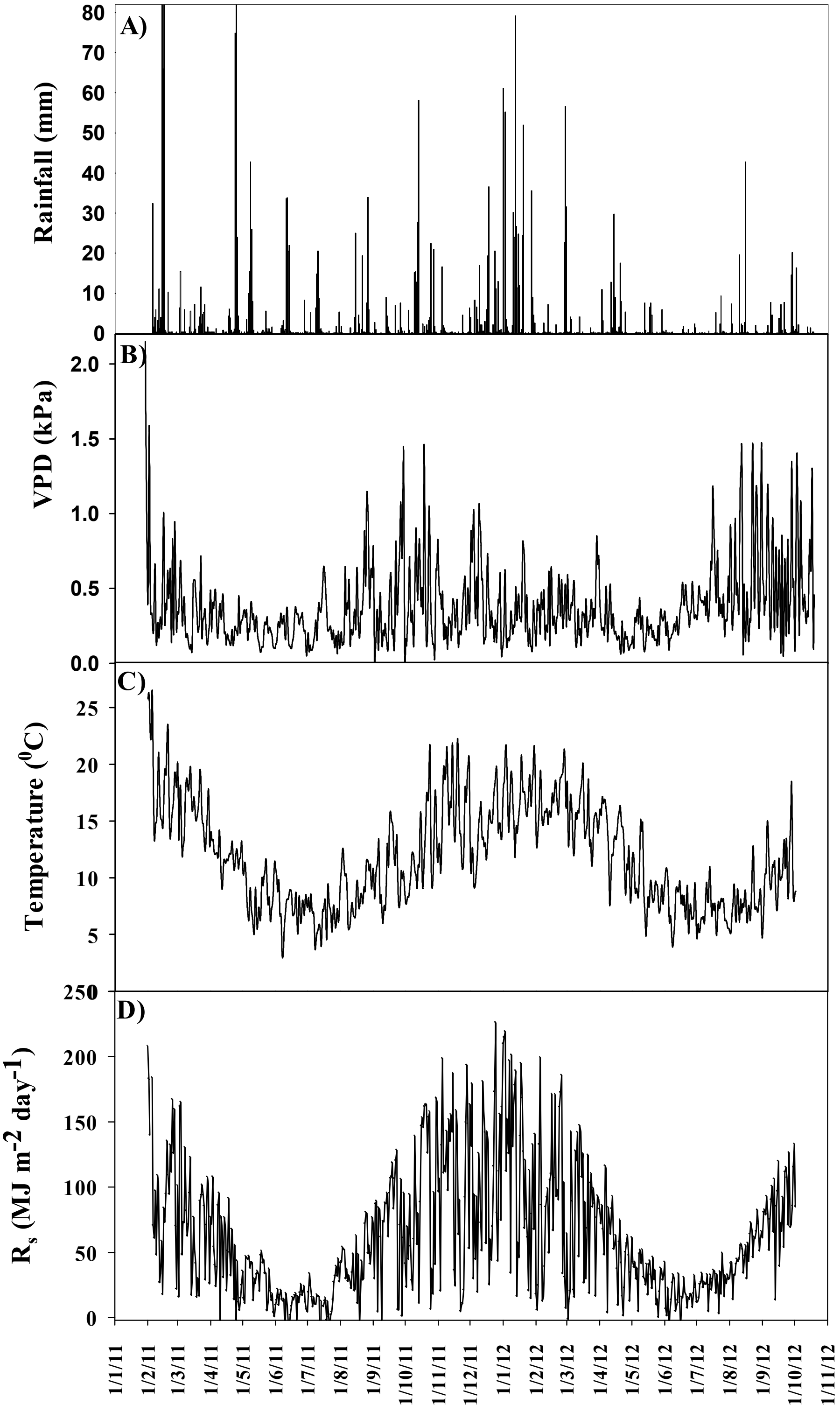


Figure 2-4: Meteorological measurements over the years 2011–2012: A) rainfall (mm day^{-1}), B) average vapour pressure deficit (kPa), C) average daily temperature (^{0}C) and D) mean daily solar radiation (MJ m^{-2} day^{-1}).

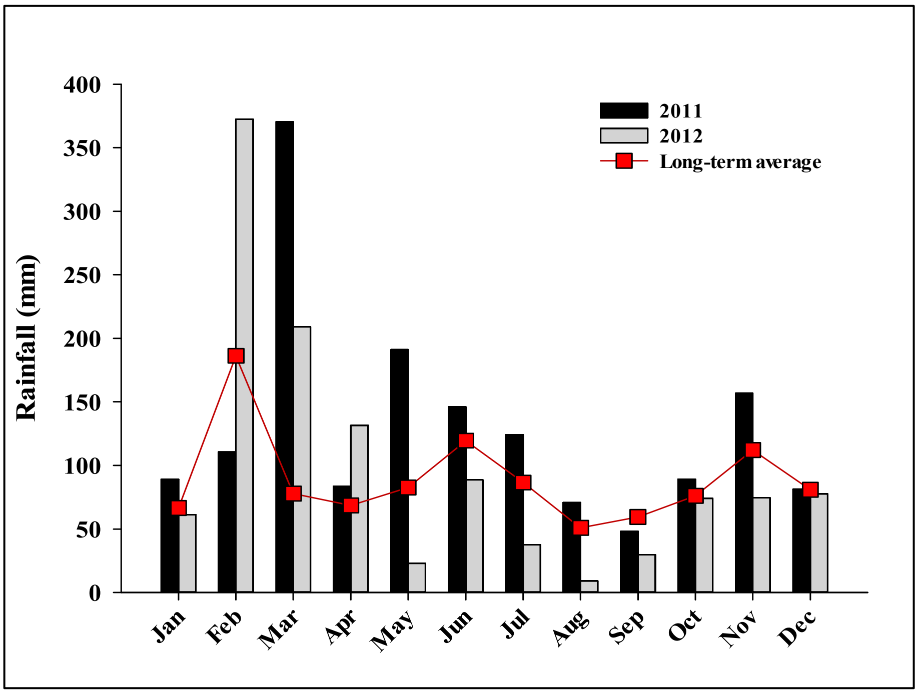


Figure 2-5: Total rainfall in two years (2011 and 2012) measured with the an automated weather station installed within the study area compared with the long-term average rainfall acquired from East Kangaloon BOM station.

Volumetric soil moisture content was measured with Theta probes which were installed in all four sites that were instrumented with sapflow sensors (see below). These probes were buried horizontally at depths of 10 cm, 30 cm and 50 cm in sites having 2.4 m and 4.3 m DGW and at 10 cm and 30 cm in sites having 9.8 m and 37.5 m DGW. Limited numbers of sensors were available and hence there we no sensors at 50 cm in the two deeper groundwater sites (9.8 m and 37.5 m DGW).

Soil water content measurements during 2011 and 2012 showed that the site with deepest water-table (37.5 m DGW) had the lowest soil water content in 2011 which reached to a maximum of 0.29 (g cm^{-3}); while soil water content at the site 9.8 m DGW reached 0.54 (g cm^{-3}) (Fig. 2-6). Also during 2012 measurement, the site with 4.3 m DGW constantly had larger soil water content (maximum of 0.61 g cm^{-3}) while the site 37.5 m DGW soil water content was smallest except a short period in early march (Fig. 2-7).

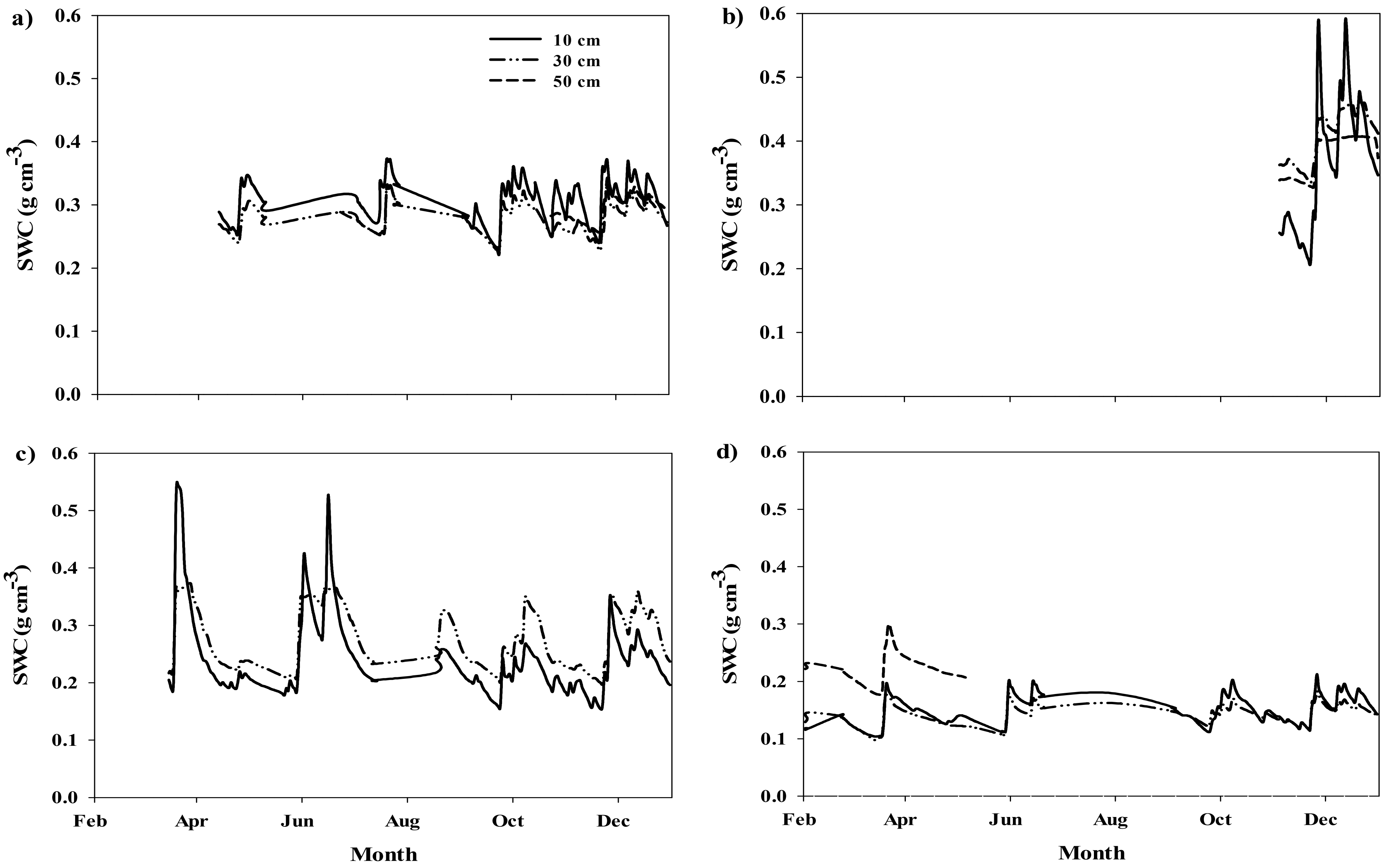


Figure 2-6: Soil water content (g cm^{-3}) at 4 sites in 2011; site 2.4 m DGW (panel a), 4.3 m (panel b), 9.8 m (panel c) and 37.5 m (panel d). Data collectetion started in November 2011 at site 4.3 m DGW.

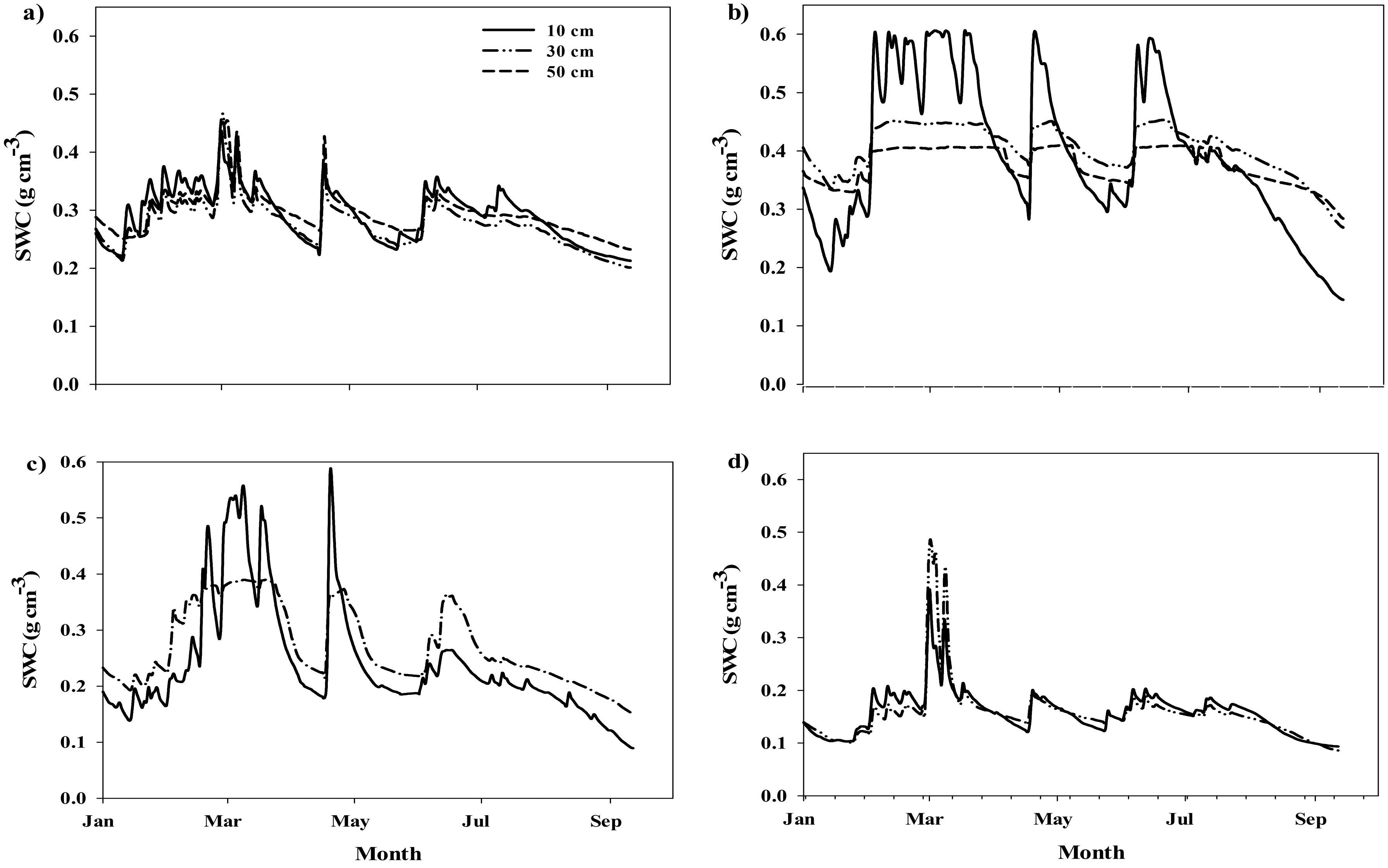


Figure 2-7: Soil water content (g cm^{-3}) at four sites in 2012, site 2.4 m (panel a), 4.3 m (panel b), 9.8 m (panel c) and 37.5 m (panel d).

The study area is characterised by extensive areas of relatively undisturbed native woodland. Based on field surveys, the dominant tree species were identified at each site. A list of the names of the dominant tree species within each site is presented in Table 2-1. The suite of measurements that were collected at each site depended on the time and labour required for each measurement (Table 2-2). Each set of measurements is described in detail in subsequent chapters.

Table 2-1: Dominant species at each site. The asterisk shows the presence of the species on the corresponding site. Information were taken from Brooker and Kleining (1999).

Species	**Common name**	**Ssubgenus**	**Family**	**Average depth to GW (m)**						
				2.4	4.3	5.5	9.8	13	16.3	37.5
Eucalyptus radiata	Narrow-leaved Peppermint	*Eucalyptus*		*	-	-	-	-	-	-
Eucalyptus globoidea	White Stringybark	*Eucalyptus*	Capilulus	*	*	*	*	-	-	*
Eucalyptus piperita	Sydney Peppermint	*Eucalyptus*	Cineraceae	*	*	*	*	-	-	*
Eucalyptus sieberi	Silver-top Ash	*Eucalyptus*	Cineraceae	-	*	-	*	-	-	*
Eucalyptus sclerophylla	Scribbly Gum	*Eucalyptus*	Cineraceae	-	*	-	*	*	*	*

Table 2-2: Measurements collected at each site

DGW (m)	Stand basal area	Tree height	Tree stem density	Overstorey leaf area index	Litterfall	Specific leaf area	Pressure-volume analysis	Diurnal leaf water potential	Branch hydraulic conductivity	Xylem embolism vulnerability curve	Sapwood density	Huber value	Rates of tree water-use
2.4 m	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
4.3m	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
5.5 m	✓	✓	✓	✓	✓	-	-	-	-	-	✓	-	-
9.8 m	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
13 m	✓	✓	✓	✓	✓	✓	✓	✓	-	-	✓	✓	-
16.3 m	✓	✓	✓	✓	✓	✓	✓	-	-	-	✓	✓	-
37.5 m	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

Chapter 3 The influence of depth-to-groundwater on structure and productivity of *Eucalyptus* woodland

Introduction

Forest productivity has been long considered to be one of the most important characteristics of forest health (Rapport et al. 1998). For example, a recent study used changes in daily net primary productivity (NPP) across a two year study as a measure of forest health (Eamus et al. 2013a). Multiple factors have an impact on ecosystem productivity and these include soil nutrients (Chapin et al. 1987; Harpole et al. 2011), water resources (Ford et al. 2008; Pita and Pardos 2001; Teskey and Hinckley 1986), climate (Tian et al. 1998) and anthropogenic disturbance. Changes in any of these factors can have an adverse effect on total net productivity of terrestrial ecosystems (Poorter and Nagel 2000). Understanding the regulation of forest productivity and structure as a function of water availability is critical for sustainable management of water and ecosystems.

Variation in biomass allocation is a fundamental process leading to variations in the structure, and consequently productivity, of forest ecosystems (Seidl et al. 2010). In terrestrial ecosystems, differences in biomass allocation are a result of adaptive responses to environmental drivers such as climate and water resource availability (Binkley et al. 2004; Poorter 2001). Several studies have suggested that allocation in plants tends to maximize growth rates by partitioning carbon into organs that optimize harvesting of the resources that limit growth (Aragago et al. 2009; Litton et al. 2007; Newman et al. 2006b; Roa-Fuentes et al. 2012; Zerihun et al. 2006). General ecological theory also predicts that carbon is allocated to those structural tissues that improve acquisition of the most limiting resources (Newman et al. 2006b); for example preferential allocation to below-ground biomass in drier habitats

(Litton et al. 2007). Forest productivity and allocation of biomass is consequently influenced by soil moisture availability, nutrient availability and forest structure, which is, in turn, influenced by species composition, canopy height, stem density, basal area and leaf area index (LAI; the ratio of projected leaf area to ground area). Large investment in foliage production and the resulting large LAI increases interception of light and consequently carbon uptake (Bonan 1993; Malhi et al. 2004). Thus LAI is an indicator of ecosystem productivity that impacts growth, structure and function, including transpiration (Cermák et al. 2008). To understand the function of forest ecosystems and their responses to environmental drivers, it is essential to understand their structure and dynamics.

Net primary productivity (NPP) is the difference between gross primary productivity (GPP; total carbon gain per unit land area per unit time) and autotrophic respiration (Kirschbaum et al. 2001). Net primary productivity is influenced by stand age (Chen et al. 2002; Gower et al. 1996), species composition (Hector et al. 1999) and site conditions such as temperature (Newman et al. 2006b), soil moisture availability and nutrient availability (Chen et al. 2003; Schuur and Matson 2001). Temperature and precipitation are considered to be the most important environmental drivers of daily and seasonal variations in productivity (Newman et al. 2006b). Several studies demonstrate the importance of variation in water availability on productivity and biomass allocation in terrestrial ecosystems (Binkley et al. 2004; Ellis and Hatton 2008; Zerihun et al. 2006). Above-ground biomass increases with long-term average soil moisture content and the proportion of below-ground biomass tends to decline with increasing availability of soil moisture (Malhi et al. 2004; Zerihun et al. 2006). This dependency of standing above-ground biomass on rainfall is most clearly apparent in arid and semi-arid ecosystems where water supply is the principle limit to plant growth (Heisler-White et al. 2008; Shiping et al. 2009; Wu et al. 2011). For regions with large annual rainfall, the response of biomass accumulation and productivity tend to an asymptote as other factors, such as temperature, become more limiting (Campos et al. 2013).

Despite the extensive literature on the environmental controls of NPP, our understanding of the response of NPP to differences in depth-to-groundwater is relatively poorly known, especially in mesic environments. Although several studies of the impact of groundwater depth on structure and productivity have been conducted in riparian forests and groundwater dependent ecosystems of arid and semi-arid regions (Naumburg et al. 2005; O'Grady et al. 2010; Stromberg et al. 1996), there are far fewer such studies published for mesic regions.

Forest productivity is determined across a given interval of time as the combined masses of new organic material that is retained by live plants and organic matter that was produced during the same interval and lost from plants by the end of the interval (Binkley et al. 2004; Clark et al. 2001a). Estimation of NPP in terrestrial ecosystems can be divided into above-ground and below-ground net primary productivity (ANPP and BNPP respectively). Measurement of below-ground productivity is time and labour consuming, thus BNPP is not typically measured and is assumed to be proportional to ANPP (Binkley et al. 2004; Zerihun et al. 2006).

Total above-ground productivity ($\mathrm{ANPP}_{\mathrm{total}}$) in forests can be estimated as the sum of above-ground stem biomass increment ($\mathrm{NPP}_{\mathrm{stem}}$), canopy productivity ($\mathrm{NPP}_{\mathrm{canopy}}$), above-ground losses to consumers, and emission of biogenic volatile organic compounds (VOC) (Clark et al. 2001b; Malhi et al. 2004). Canopy productivity ($\mathrm{NPP}_{\mathrm{canopy}}$) can be estimated from litterfall measurements, although this can be underestimated due to decomposition or consumption by herbivores before collection (Binkley et al. 2004; Keeling and Phillips 2007; Malhi et al. 2004). The amount of VOC that is lost is typically assumed to be negligible and is not considered in most studies. A strong relationship exists between $\mathrm{NPP}_{\mathrm{canopy}}$ and $\mathrm{NPP}_{\mathrm{total}}$, thus $\mathrm{NPP}_{\mathrm{canopy}}$ is generally accepted as being the most appropriate single predictor of $\mathrm{NPP}_{\mathrm{total}}$ (Clark et al. 2001b). This suggests that biomass allocation to leaves is often prioritised and this enhances canopy rates of photosynthesis and thus total productivity (Chave et al. 2010).

Biomass allocation in plants and its effect on growth involves a trade-off amongst available resources and their limitation on productivity (McConnaughay and Coleman 1999; Weiner 2004). Biomass accumulation is influenced by rates of nutrient turnover, vegetation structure and function and carbon storage; thus biomass is perhaps the most fundamental characteristic of natural ecosystems. Biomass is defined on an area basis as the amount of organic matter per unit area of ground and is usually expressed as dry organic matter (e.g. Mg C ha^{-1}) (Keeling and Phillips 2007). Similar to NPP, biomass accumulation by forests can be partitioned into above-ground and below-ground biomass (AGB and BGB respectively). Together these constitute a significant component of total ecosystem carbon stock (Zerihun et al. 2006). The production of above-ground biomass is an important share of total net primary production forests, especially in ecosystems where water resources are not scarce.

The aim of this study was to investigate how differences in groundwater depth across a landscape influence patterns of growth and forest structure in mesic, pristine forests of southern New South Wales, Australia. I hypothesised that depth-to-groundwater is negatively correlated with ANPP and AGB. This hypothesis was tested using estimations of above-ground biomass, above-ground net primary productivity and measurements of basal area, litterfall and leaf area index at seven sites along a gradient of groundwater depths (2.4–37.5 m).

Methods

Basal area

At each site, two plots, each covering an area of 2500 m^2 were established. Within each plot the diameter at breast height (DBH) of all plants (including trees and shrubs) that were larger than one centimetre diameter was measured. The height of all plants with a DBH larger than one centimetre was measured using a clinometer

(Haglöf Electric Clinometer, HEC; Sweden). A scaling relationship between DBH and basal area (BA) was derived for each plot from plot measurements:

$$BA\ (m^2) = 7.854 \times 10^{-5}\ [DBH(cm)]^2 \qquad \text{(Equation 1)}$$

Above-ground biomass (AGB)

Two methods are most commonly used to estimate above-ground biomass in a forest: harvesting and allometric regression. Empirical allometric models are developed from regressions between AGB and tree structural attributes (e.g. diameter at breast height, height and wood density) in destructively harvested samples. These relationships are used to calculate stand biomass based on inventory measurements of all trees in a plot. Many different equations have been developed, including species specific (Chave et al. 2005), site specific (Eamus et al. 2000a) and general equations (Chave et al. 2005; Williams et al. 2005).

Inventory measurements of forest structural characteristics were used to estimate above-ground biomass (AGB) using the general allometric equations developed by Williams et al. (2005). Williams et al. (2005) developed two allometric equations from inventory data (one using tree height and the other using tree height and DBH) to estimate above-ground biomass in Australian *Eucalyptus* woodlands. Two, best-fit general equations included height (H, m) and DBH (cm) to calculate ABG (kg) were proposed by Williams et al (2005):

$$\ln(AGB) = -2.0596 + 2.1561 \ln(DBH) + 0.1362 \ln(H)^2 \qquad \text{(Equation 2)}$$

$$\ln(AGB) = -2.2111 + 2.4831 \ln(DBH) \qquad \text{(Equation 3)}$$

The reason equation 3 (using DBH as the only predictor of AGB) was used was due to the concerns regarding the practical difficulty of accurately measuring the height of standing trees in the field.

Litter baskets

Litterfall was collected for two years (December 2010–May 2013) at each of seven sites. Thirty-five litter baskets were made from nylon mesh and set in a PVC frame (60 cm diameter) and mounted 100 cm above the ground surface (Fig. 3-1). Litter baskets were emptied monthly, except when the sites were inaccessible due to bad weather. Litter was sorted into leaves, woody parts (stem and branches), bark, fruit, flowers and others (animal and bird remaining or unidentified materials) following Bray and Gorham (1964) and Binkley et al. (2004). Litter fall mass (kg ha^{-1}) was estimated from litter that was oven dried to a constant weight.

Figure 3-1: A litter basket

Above-ground Net Primary Production (ANPP)

Forest ANPP represents the difference between the amount of new organic material that is produced during a given interval of time and biomass that is lost by plants during the same interval. In forests, ANPP is estimated from the sum of above-ground biomass increment, fine litter fall, above-ground losses to consumers, and emission of biogenic volatile organic compounds (Clark et al. 2001b). Above-ground loss to consumers and emission of biogenic volatile organic compounds are commonly small and neglected in most studies of ANPP (Keeling and Phillips 2007). In cases where one measurement is unavailable, an estimate of ANPP is still possible using only litterfall and AGB. In the present study, ANPP was calculated at the seven sites using four combinations of two methods:

1- In a global model, Bray and Gorham (1964) showed that NPP is strongly correlated with total litterfall. Total NPP was calculated as 3.1 times total litterfall (Murphy 1975).

2- Clark et al. (2001b) developed two logarithmnic relationships between AGB increment and litterfall ($r^2 = 0.69$) or above-ground biomass ($r^2 = 0.53$):

3- AGB increment ($\text{Mg ha}^{-1}\ \text{y}^{-1}$) = 1.13 ln (fine litterfall) + 0.57 (Equation 4)

4- AGB increment ($\text{Mg ha}^{-1}\ \text{y}^{-1}$) = 1.05 ln (AGB)-2.91 (Equation 5)

Altogether, four combinations of these methods were used to determine ANPP: 1) from litterfall alone (i.e. 3.1 × litterfall, Murphy 1975) or from AGB increment that was determined from 2) fine litterfall (Eqn. 4) or AGB that was estimated from 3) BA as a function of DBH and tree height (Eqns. 2 and 5) or 4) BA as a function of DBH alone (Eqns. 3 and 5). In each case, it was assumed that 50% of the total dry mass was equal to the carbon content of the materials (Basuki et al. 2009; Chambers et al. 2001; Clark et al. 2001b).

Leaf area index

Canopy leaf area index (LAI) was measured indirectly using digital photography (Macfarlane et al. 2007). This method applies gap fraction analysis to upward looking digital images to estimate canopy LAI. Image analysis was conducted using an automated procedure in MATLAB (Fuentes et al. 2008).

Photographs were taken at seven sites during each of four seasons across two years. Photographs were taken along a 100 m transect that was centred on a random location in each site. Transects were sampled every five meters (i.e. 30 images per site), and the camera was mounted at a height of 1.5 m above the ground. Upward-facing images were levelled to ensure a match to the zenith angle.

Data analysis

The relationship between each measured trait with depth-to-groundwater was tested using regression analysis. Two-way analysis of variance was used to test the null hypothesis H_0: that LAI, BA, tree height and stem density did not differ between sites. Pearson correlation was used to find the correlation between BA, stem density, tree height and LAI. Analyses were performed using IBM SPSS STATISTICS version 19, Armonk, NY, USA.

Results

As DBH increased tree height increased asymptotically for all sites (Fig. 3-2 &3-3). Additional stand structural characteristics obtained from the inventory are presented in Table 3-1. Significantly taller ($p< 0.001$, $F=107.32$) trees (26 m ± 0.66) occupied the sites with the three shallowest groundwater depths (2.4 to 5.5 m DGW; Table 3-1 and Fig. 3-2) compared to sites with deeper groundwater (15.84 ± 0.20 m) (Table 3-1 and Fig. 3-3). Stand basal area and stem density were similarly significantly ($P < 0.001$) larger at the three “shallow” sites than at the four sites with deeper groundwater (DGW below 9.8 m depth). Maximal basal area (82 ± 19.2 m^2 ha^{-1}) was observed at the shallowest water table site (2.4 m DGW) while the minimum (18 ± 0.4 m^2 ha^{-1}) occurred at the site where DGW was 13 m. There were significant positive correlations between structural traits (BA, maximum tree height, stem density and LAI) (Table 3-2) and sites with taller tress were associated with a larger stem density, larger basal area and larger LAI (Fig. 3-4).

Values of AGB that were calculated with and without use of tree height data(Equations 2 and 3) were similar to each other at all sites except for the shallowest site, where ABG was much larger using the height × DBH equation (> 500 Mg C ha^{-1}) than when using the single-factor DBH model (*ca.* 300 Mg C ha^{-1}; Table 3-1). All these traits (BA, tree height, stem density and AGB) showed a significant decrease where depth-to-groundwater reached 9.8 m and more. Maximum AGB (363 ± 33 Mg C ha^{-1}; using Equation 3) was estimated at the 5.5 m DGW site following by 302 ± 85 Mg C ha^{-1} at site 2.4 m DGW and smallest AGB (65 ± 11 Mg C ha^{-1}) was estimated at the 13 m DGW site.

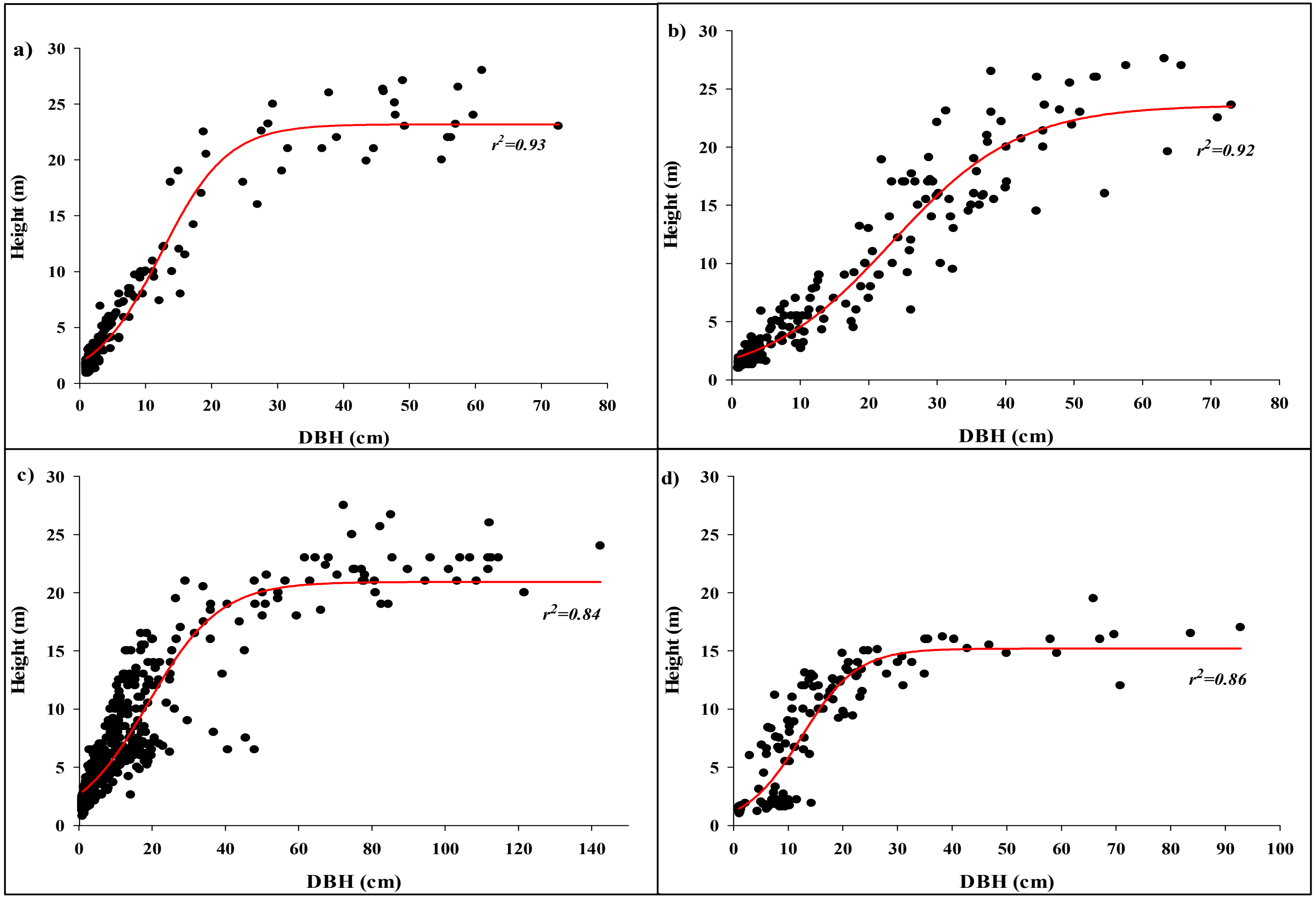


Figure 3-2: The relationship between diameter at breast height (DBH, cm) and height (m) across sites with the four shallowest depths-to-groundwater: a) 2.4 m, b) 4.3, c) 5.5 and d) 9.8 m DGW.

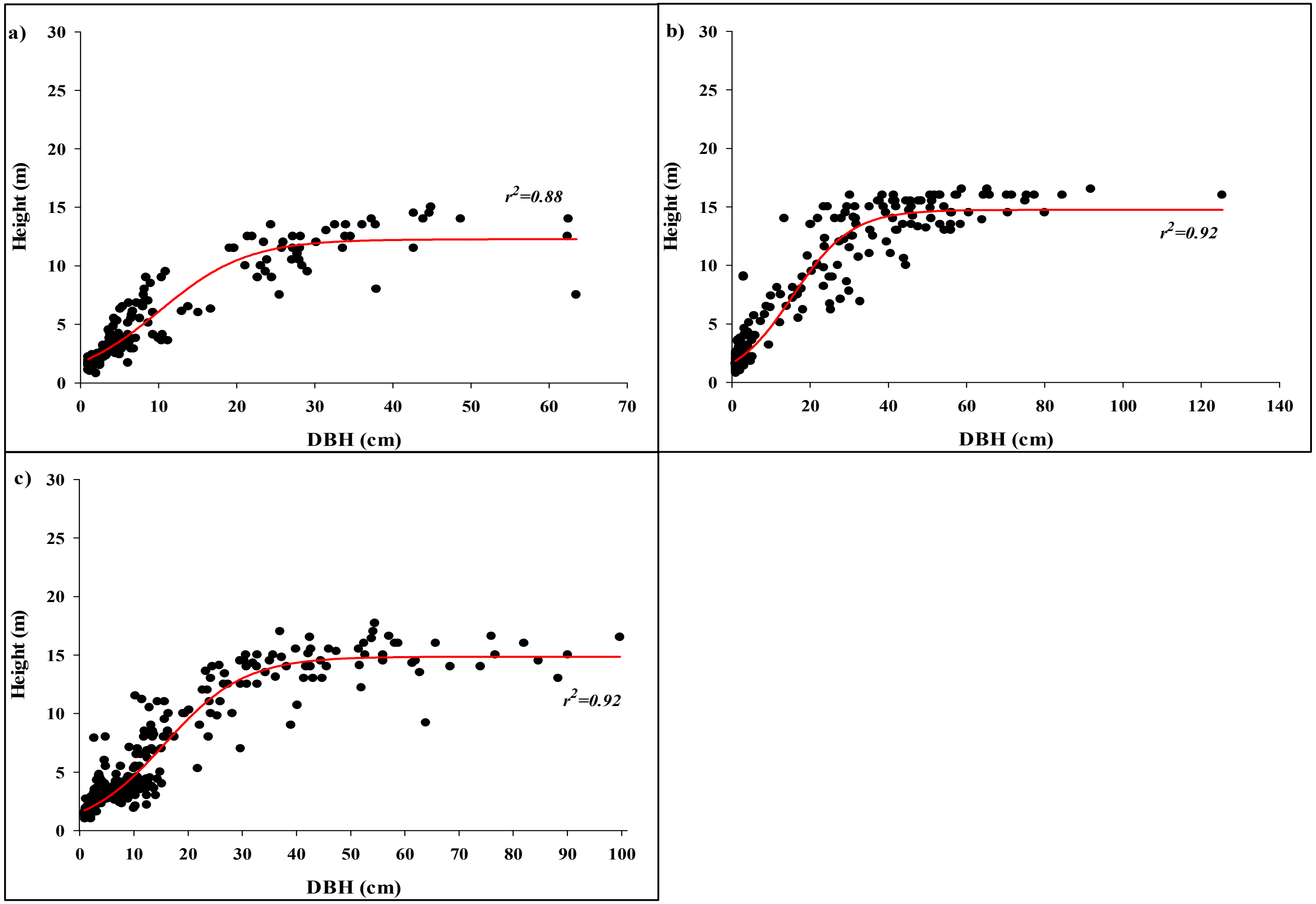


Figure 3-3: The relationship between diameter at breast height (DBH, cm) and height (m) at the three sites with the deepest depths-to-groundwater: a) 13 m, b) 16.3 and c) 37.5 m DGW.

Table 3-1: Stand characteristics of the seven sites across the gradient in depth-to-groundwater (stand mean ± SE). Letters within rows indicate which means are significantly different from each other ($p < 0.05$).

Stand parameter	**2.4 m**	**4.3 m**	**5.5 m**	**9.8 m**	**13 m**	**16.3 m**	**37.5 m**
Stand Basal area (m^2 ha^{-1})	82.0 ± 10.2 **a**	52.4 ± 2.4 **a**	64.2 ± 0.7 **a**	23.3 ± 1.5 **b**	18.4 ± 0.4 **b**	37.9 ± 8.2 **ab**	32.6 ± 2.1 **b**
Max tree height (m) (n = 10)	26.5 ± 1.0 **a**	26.1 ± 0.5 **a**	25.2 ± 0.1 **a**	16.1 ± 0.3 **b**	14.05 ± 0.1**c**	16.1 ± 0.07 **bc**	16.3 ± 0.1 **b**
Stem density (stems ha^{-1}, > 1cm)	2466 ± 101 **a**	1440 ± 103 **b**	1455 ± 42 **b**	648 ± 32 **c**	673 ± 56 **c**	692 ± 192 **c**	809 ± 126 **c**
AGB (Mg C ha^{-1})*	535 ± 182 **a**	245 ± 29 **b**	348 ± 38 **c**	96 ± 9 **d**	56 ± 1 **e**	152 ± 44 **d**	117 ± 2 **d**
AGB (Mg C ha^{-1}) **	302 ± 85 **ab**	208 ± 13 **b**	363 ± 33 **a**	95 ± 8 **c**	65 ± 11**c**	185.3 ± 52 **cb**	151 ± 15 **c**

* $\ln(AGB) = -2.0596 + 2.1561 \ln(DBH) + 0.1362 \ln(H)^2$

** $\ln(AGB) = -2.2111 + 2.4831 \ln(DBH)$

Carbon content was assumed to be 50% of dry mass as suggested by (Baldocchi and Ryu 2011; Zeppel et al. 2006)

Table 3-2: Pearson's correlation (r) matrix of structural traits (BA, max tree height, stem density and LAI)

Structural trait		BA	Max tree Height	Stem density	LAI
BA (m^2 ha^{-1})	*r*	1			
	P-value				
Max tree height (m)	*r*	0.90^{**}	1		
	P-value	0.005			
Stem density (stems ha^{-1})	*r*	0.94^{**}	0.86^{*}	1	
	P-value	0.001	0.01		
LAI (m^2 m^{-2})	*r*	0.91^{**}	0.98^{**}	0.86^{*}	1
	P-value	0.004	0.000	0.01	

**** correlation is significant at the 0.01 level**

*** correlation is significant at the 0.01 level**

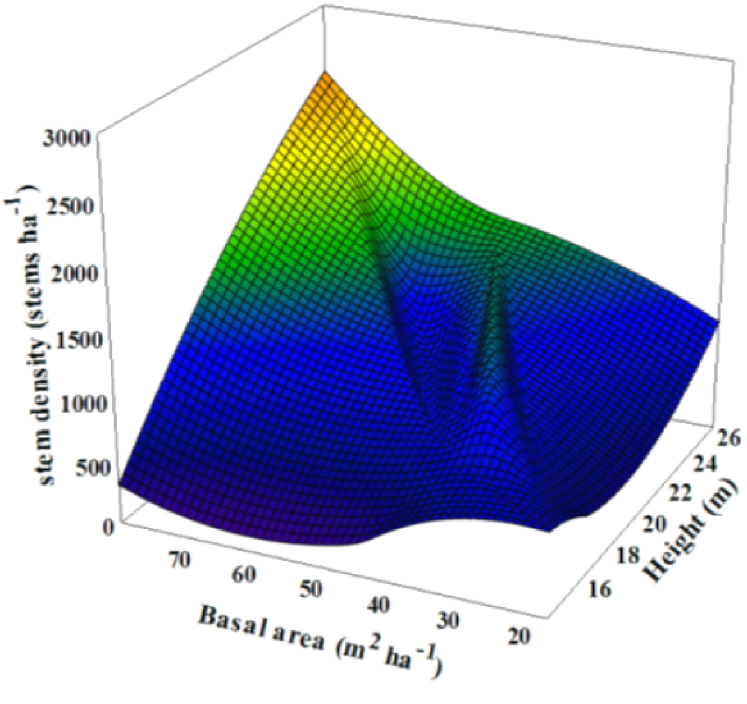


Figure 3-4: 3 dimensional plot showing the relationships among BA, max tree height and stem density.

The amount of material collected in litter baskets at the site with the shallowest groundwater (9.10 Mg ha^{-1} y^{-1}) during the first year of collection (Dec 2010–Nov 2011) was nearly twice as large as that at the site with the deepest groundwater (4.86 Mg ha^{-1} y^{-1}). The smallest litterfall collection was obtained at the site with 13 m DGW (2.59 Mg ha^{-1} y^{-1}). The relationship between DGW and total litterfall was very similar across both years: total litterfall declined exponentially with increased depth-to-groundwater in both the first ($r^2 = 0.74$, $p = 0.04$, df = 1) and second year of study ($r^2 = 0.96$, $p = 0.005$, df = 1; Fig. 3-5).

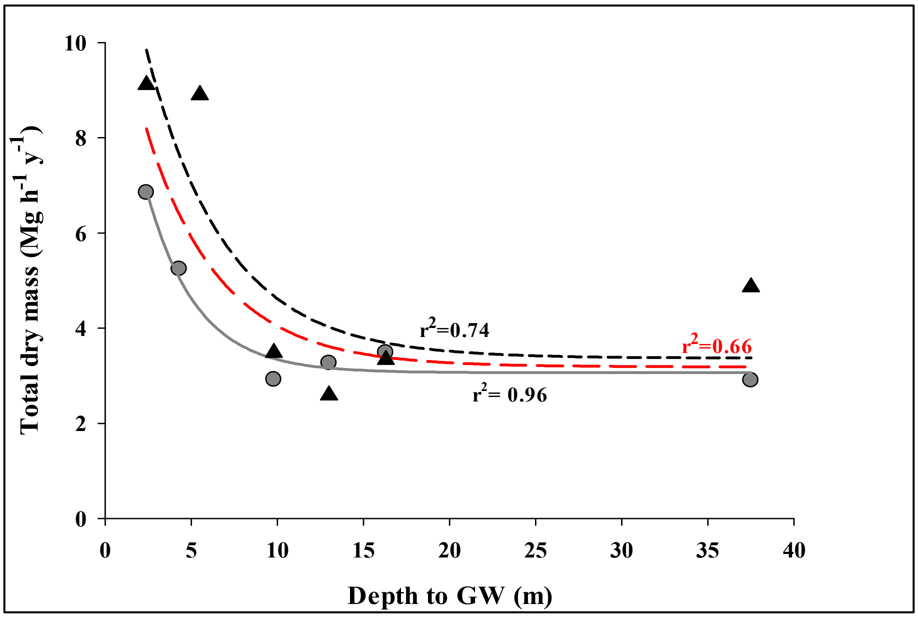


Figure 3-5: Total litterfall (Mg ha^{-1} y^{-1}) as a function of depth-to-groundwater depth (m) in the first (2011, triangles) and second (2012, circles) years. The combined curve (combining both years' data) is shown in the red dashed line.

Figures 3-6 and 3-7 show the composition of the monthly litter collections across all sites during the first and second years, respectively. Both years followed similar patterns in seasonal patterns in the rate of litterfall. More litter was collected during summer than during winter in both years (F = 21.08, $p < 0.001$, df = 23). The largest amount of litter was collected during the summer of the first year (Dec- Feb). In the second year the largest litterfall was collected during the latter half of summer and early autumn (Jan-March). The smallest amount of litter was collected during June 2012 across all sites. Despite the similar pattern in seasonal litterfall, the amount of material that was collected in two consecutive years was not the same (Table 3-3). In spring of the second year (Aug-Nov 2012), the amount of material collected from all sites was larger than the same period of the first year (up to 2 times larger). Leaves contributed 57–59% of total material and this did not vary between sites. A significantly larger total amount of litterfall was collected at the three shallowest sites (F = 32.47, $p < 0.001$, df =6) than at sites where the water table was deeper (9.8–37.5 m DGW). The maximum difference between sites was observed during summer and early autumn of both years.

LAI at the three shallowest sites was significantly larger than at the four deeper sites (i.e., at sites where the water table was deeper than 9 m; Fig. 3-8). Seasonal changes in LAI were minimal at the four deeper sites, while at the three shallowest groundwater sites LAI was smallest during autumn and winter. Similarly, the other structural characteristics (BA, stem density, AGB and tree height) were largest at the three shallowest groundwater sites than at the four deeper sites (Tables 3-1 & 3-2).

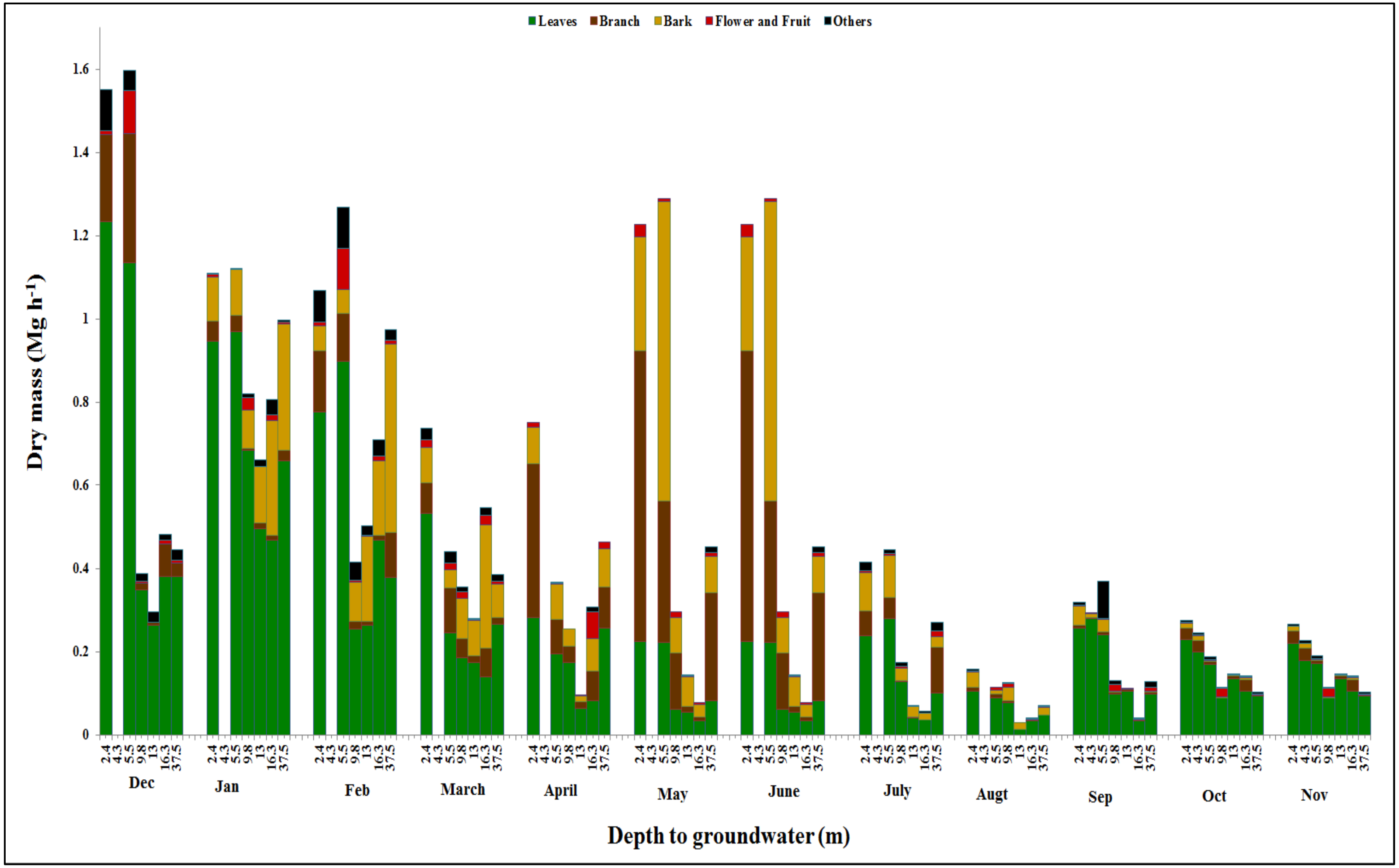


Figure 3-6: Monthly total litterfall collected (Mg ha^{-1}) during year one (Dec. 2010–Nov. 2011) as leaves, branches, bark, flower, fruits and un-identified materials (others) Litter baskets were placed at the 4.3 m DGW site in September 2011.

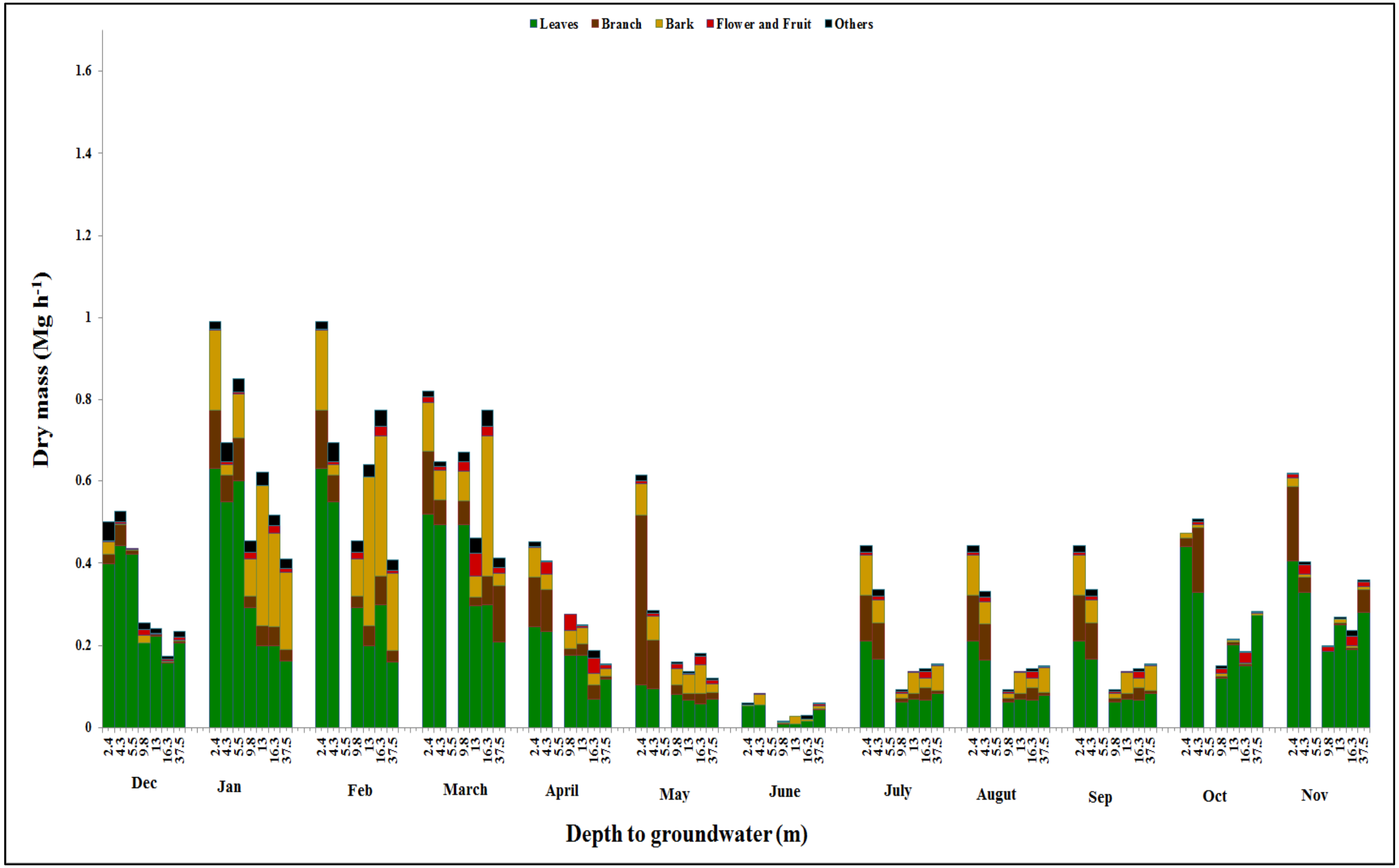


Figure 3-7: Monthly total litterfall collected (Mg ha^{-1}) during year two (Dec. 2011–Nov. 2012) were as leaves, branches, bark, flower, fruits and un-identified materials (others). Litterfall collection ceased at the 5.5 m DGW site in February 2012.

Table 3-3: Average of seasonal litterfall (Mg ha^{-1}) across the two years study period (Dec 2011-Nov 2012) at seven sites having different depth-to-groundwater. NA indicates data were not collected at the site.

DGW (m)	**2011**				**2011**	**2012**				**2012**
	Summer	**Autumn**	**Winter**	**Spring**	**Total**	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
2.4	1.24 ± 0.12 **a**	0.90 ± 0.15**a**	0.60 ± 0.30**a**	0.28 ± 0.01**a**	**9.10**	0.82 ± 0.07**a**	0.63 ± 0.10**a**	0.31 ± 0.05**a**	0.51 ± 0.05**a**	**6.84**
4.3	NA	NA	NA	0.25 ± 0.01 **a**	**NA**	0.64 ± 0.02 **a**	0.50 ± 0.08 **a**	0.24 ± 0.04 **b**	0.41 ± 0.05 **a**	**5.24**
5.5	1.40 ± 0.13 **a**	0.70 ± 0.07 **b**	0.61 ± 0.31 **a**	0.25 ± 0.04 **a**	**8.90**	0.64 ± 0.01 **a**	NA	NA	NA	**NA**
9.8	0.54 ± 0.14 **c**	0.30 ± 0.03 **c**	0.19 ± 0.05 **a**	0.12 ± 0.005 **b**	**3.48**	0.39 ± 0.06 **b**	0.36 ± 0.06 **bc**	0.06 ± 0.03 **c**	0.14 ± 0.03 **b**	**2.91**
13	0.47 ± 0.11 **c**	0.17 ± 0.05 **c**	0.08 ± 0.03 **a**	0.13 ± 0.01 **b**	**2.59**	0.50 ± 0.13 **ab**	0.28 ± 0.08 **b**	0.09 ± 0.02 **cd**	0.20 ± 0.03 **b**	**3.24**
16.3	0.63 ± 0.07 **bc**	0.31 ± 0.13 **c**	0.05 ± 0.01 **a**	0.10 ±0.03 **b**	**3.35**	0.48 ±0.10 **b**	0.38 ±0.09 **bc**	0.10 ±0.07 **cd**	0.18 ±0.02 **b**	**3.48**
37.5	0.81 ±0.10 **bc**	0.43 ±0.02 **bc**	0.26 ±0.11 **a**	0.11 ± 0.008 **b**	**4.86**	0.35 ± 0.05 **b**	0.22 ± 0.09 **b**	0.12 ± 0.05 **d**	0.22 ± 0.05 **b**	**2.90**

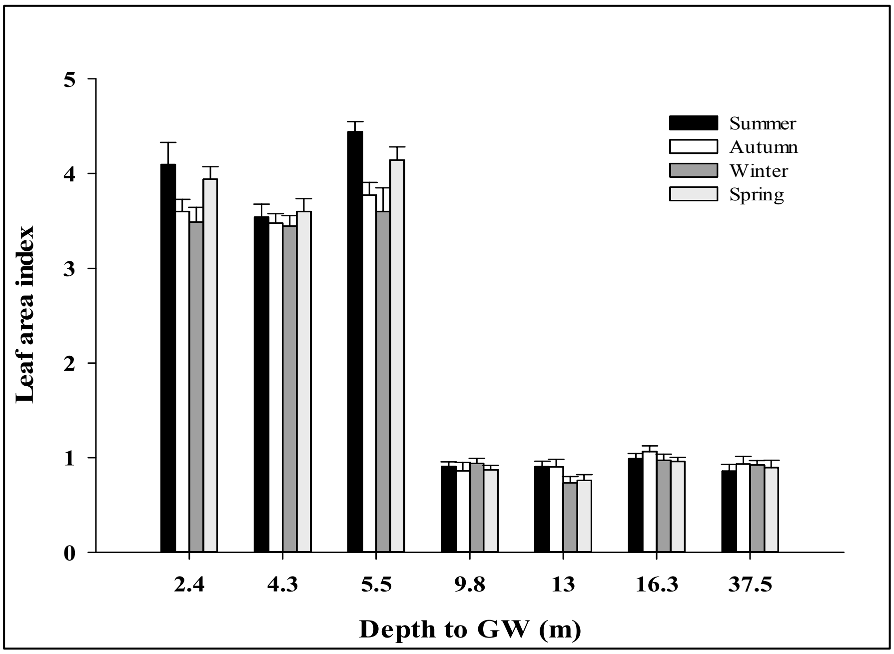


Figure 3-8: Leaf area index (LAI) as a function of depth-to-groundwater (m). LAI was measured at a height of 1.5 m.

Use of different methods for calculating ANPP resulted in small and inconsistent differences in ANPP across sites (except that the Global model (Bray and Gorham 1964) which generated almost always the smallest value) (Fig. 3-9). Regardless of the method of calculation, ANPP decreased exponentially as depth-to-groundwater increased (r^2=0.92, p=0.005, F=24.98) (The analysis was conducted on average ANPP of different methods of calculation and for a 5 month period when data from all sites were available; Sep 2010-Jan 2012). Results from the site with 4.3 m DGW (first year) and the 5.5 m DGW site (second year) were not included because a full year of data were not available because of damage to the litter baskets. Above-ground net primary productivity was larger in the first year than the second year at all sites except for sites with 13 m and 16.3 m DGW. The largest reduction in ANPP in the second year was at the site with 37.5 m DGW (> 30% decrease) while the site 2.4 m DGW had a 20% reduction in ANPP in the second year compared to the first (Fig. 3-9).

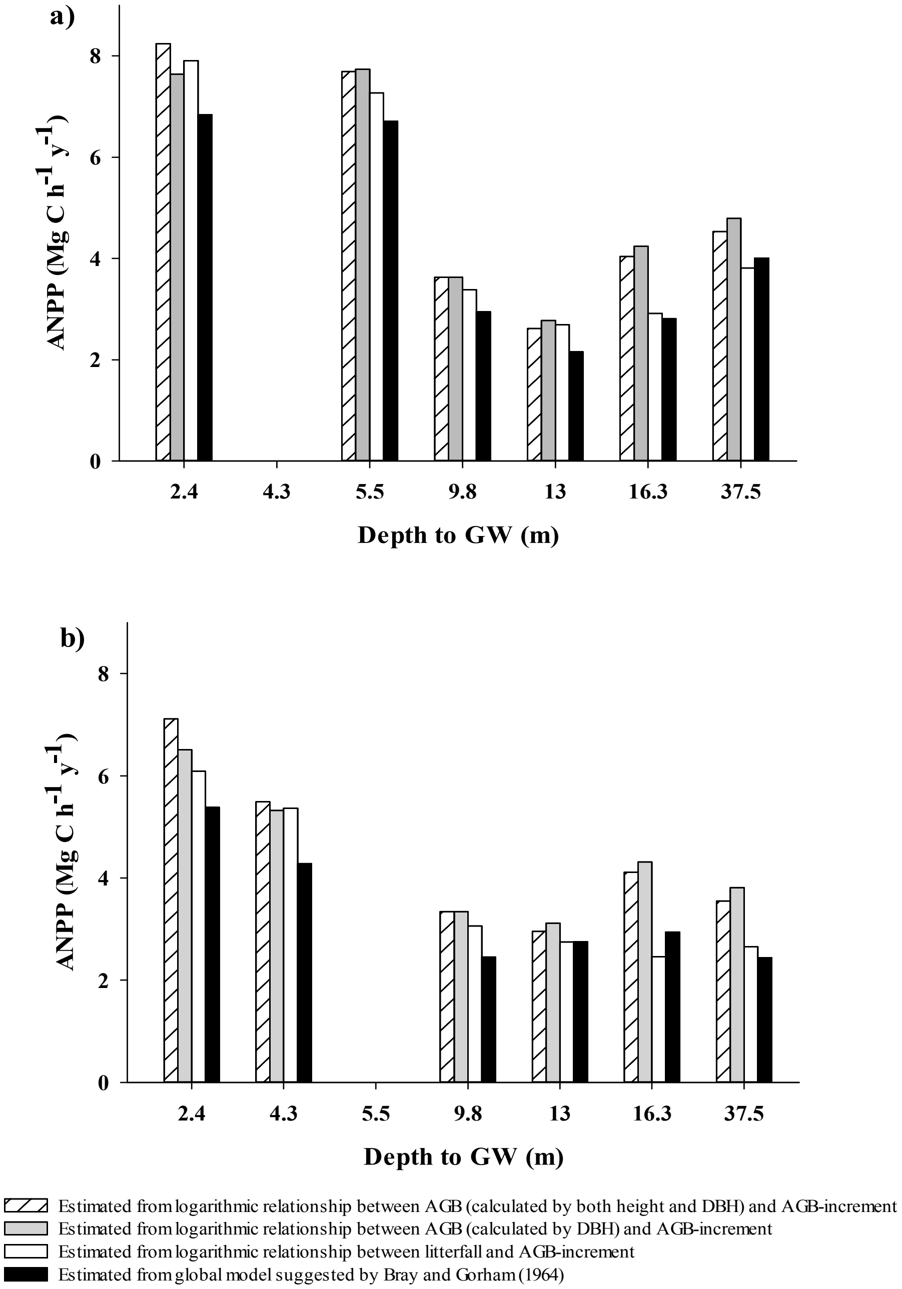


Figure 3-9: Average above-ground net primary productivity (Mg C ha^{-1} y^{-1}) estimated using different methods across a gradient of depth-to-groundwater (m) for two years; A) December 2010–November 2011 and B) December 2011–November 2012.

Discussion

I hypothesised that above-ground productivity increases with reductions in depth-to-groundwater in the temperate mesic forests used in the present study. This hypothesis was based upon the additional hypotheses that at mesic sites with a large average annual rainfall of 1067 mm, increased access to groundwater will still exert a positive influence on canopy structure (for example increased basal area and LAI) and hence increased site productivity. To test these hypotheses, canopy structure and above-ground productivity were studied at seven sites across a 2.4–37.5 m gradient in depth-to-groundwater.

Structural characteristics of forests were significantly different between the three shallow sites and the remaining four sites with deeper water tables. The shallowest groundwater site (2.4 m DGW) contained taller trees, more stems per hectare, larger total tree basal area, larger LAI, larger above-ground biomass, larger annual rates of litterfall production and consequently a larger ANPP than the four sites with a deeper water table. Furthermore, these characteristics did not change significantly amongst the three shallowest sites (2.4 m, 4.3 m and 5.5 m). However as depth-to-groundwater increased from 5.5 m to 9.8 m there was a significant decline in all of the above attributes. Beyond 9.8 m, structural characteristics of the forest varied little with DGW (i.e. reached a minimum plateau). These findings support the main hypothesis of this chapter, namely that depth-to-groundwater plays a key role in forest structure and productivity.

The relationship between each of these individual traits and depth-to-groundwater was not the same for all traits and was not a simple negative linear one. Rather, for all structural traits (LAI, BA, stand density, tree height and litterfall) as depth-to-groundwater increased beyond approximately 9.8 m depth, there was very little change in the value of any structural trait. For groundwater depths less than approximately 9.8 m, there was either a step-function response, most clearly evident in the LAI response (Fig. 3-8) but also apparent in the response of tree height (Table

3-1) to depth-to-groundwater. Alternatively there was a steeply declining almost exponential response in litterfall, tree density and basal area as depth-to-groundwater increased across the three shallowest groundwater sites. In a comparable study in an arid ecosystem in California, USA total plant cover increased as depth-to-groundwater increased; however, surprisingly the shallowest site did not have the largest plant cover (McLendon et al. 2008). In contrast to the result of current study and McLendon et al. (2008), a linear relationship between plant cover and depth-to-groundwater was found in eastern California, USA (Elmore et al. 2006).

A threshold of between 5.5 – 9.8 m was apparent in the response of structural traits to differences in depth-to-groundwater. This shift in traits across sites may be explained by the depth-to-groundwater and root depth of *Eucalyptus* trees in a mesic habitat. It may be concluded that somewhere between 5.5 to 9.8 m depth-to-groundwater trees loose access to groundwater at these sites. As water table declines below the rooting depth and is not accessible for trees, they become insensitive to further increase in water table depth (Elmore et al. 2006) and this explains the minimum plateau in the response of trees above a depth of between 5.5 and 9.8 m.

It is well documented that increasing annual precipitation results in larger leaf area index (Ellis and Hatton 2008; Harrington et al. 1995; Jose and Gillespie 1997; Meier and Leuschner 2008; Newman et al. 2006b; Pfeifer et al. 2012). Groundwater can provide an alternative water resource for terrestrial ecosystems, thereby resulting in increased leaf area index and productivity. Recent studies in Australian arid and semi-arid and riparian ecosystems confirm that groundwater dependent ecosystems can support significantly larger LAI (Carter and White 2009; O'Grady et al. 2011). Consistent with predictions, the present study showed that LAI at the three shallowest DGW sites was about four times larger than at sites with deeper groundwater. The range of LAI of this study (0.8-4.0) is comparable to other Australian woodlands (Ellis and Hatton 2008; Whitehead and Beadle 2004). The response of LAI to declining depth-to-groundwater occurred over a narrow range of depths, in contrast to LAI responses that are often linear as a function of gradients in precipitation (Ellis and Hatton 2008; Lane et al. 2000; Pfeifer et al. 2012).

Comparisons of the LAI of adjacent stands of trees within the same climate envelope can be used as an indication of access to groundwater resources (Eamus and Froend 2006). The sudden decline of the LAI after 5.5 m DGW and minimum change from 9.8 m and beyond is strongly supportive of the hypothesis that groundwater access occurs for shallow sites but not at deep sites and maybe indicative of the maximum rooting depth of trees in these sites.

There were significant positive correlations amongst BA, height, stem density and LAI. The tallest trees occupied sites with the largest BA, stem density and LAI. Plant growth is a function of resource supply and the efficiency in resource use (Binkley et al. 2010; Forrester et al. 2013). Leaf area index determines light interception within the canopy and a larger leaf area index results in a larger proportion of incoming solar radiation being intercepted by the stand. Although increased LAI is associated with increased self-shading (Ackerly and Bazzaz 1995; Anten et al. 1995; Posada et al. 2012) an almost linear positive relationship has been found between leaf area index and light absorption (Campoe et al. 2013; Forrester et al. 2013) in woodlands and forests. With increased LAI and light interception comes increased carbon gain and hence increased ecosystem productivity (Niinemets 2010). Several studies showed a strong positive relationship between light interception and ecosystem productivity and this is reflected in larger BA, stem growth and tree height. Nunes et al. (2013) found a linear relationship between BA and LAI in a *Pine* and *Oak* forest in Portugal. Similarly Forrester et al. (2013) found positive linear relationship in *Eucalyptus* plantation in South-Eastern of Australia. Overall, larger trees (taller trees and larger diameter trees) grow as a result of more light interception. Also trees that intercepted more light are more efficient in light use (Binkley et al. 2013; Binkley et al. 2010; Campoe et al. 2013). Consistent with these findings larger LAI at shallower water table sites is resulted in larger AGB and ANPP which will now be discussed.

Above-ground biomass (AGB) was calculated from inventory data based on two different general equations developed by Williams et al. (2005). Including height as a predictor resulted in larger estimates of AGB at the sites with a shallow water table (i.e. < 9.8 m DGW) and smaller estimates of AGB at sites with deep water table (i.e.

> 5.5 m DGW) relative to AGB determined from DBH alone. This was due to significant differences in tree height between sites in which taller trees grew at the sites with shallow groundwater. It has been suggested that DBH is the best predictor for AGB (Basuki et al. 2009; Chave et al. 2005) because of the smaller errors associated with DBH measurements (compared to that associated with tree height (Montagu et al. 2005)). However, regardless of the calculation method, AGB decreased sharply between 5.5 and 9.8 m DGW (Table 3-1) and was significantly larger at site where depth-to-groundwater was less than 5.5 m than those at the deeper water table sites.

For calculation of ANPP; the global model was assumed to provide better results in the current study because it was developed and tested across different ecosystems globally, in contrast to most models, which were developed for tropical forests and tend to overestimate productivity. ANPP estimated in the present study ranged from 2.7-7.9 Mg C ha^{-1} y^{-1}, which is similar to ANPP in other Australian ecosystems (Chen et al. 2003; Coops et al. 1998) and overlaps, at the shallowest sites, the most productive sites within tropical rainforests (Chambers et al. 2001).

The patterns of litterfall production and ANPP followed the same step-change responses to increase in depth-to-groundwater as LAI and AGB. Litterfall production is positively correlated to rainfall (Chave et al. 2010; Newman et al. 2006b), which is similar to the relationship between groundwater and litterfall in the present study (Figs. 3-6 and 3-7). The non-linear response function observed in the current study shows the negative impact of increase in depth-to-groundwater on forest structure and productivity which was apparent in all measured traits. Within a pine savanna of south-eastern America (Georgia USA), LAI, AGB, stem density and ANPP increased linearly with decreasing depth-to-groundwater (Ford et al. 2008). Similar decreases in vegetation cover as a result of groundwater drawdown has been documented for different ecosystems such as for *Banksia* woodlands in WA, Australia (Sommer and Froend 2011), floodplain forest South-eastern Australia (Horner et al. 2009), multiple sites at California, USA (McLendon et al. 2008) and riparian forest, Spain (González et al. 2012). Positive correlations between water resources availability and ANPP are common and can exhibit a step function (McLendon et al. 2008; Zerihun et al. 2006) or linear response (González et al. 2012; Knapp and Smith 2001; Lane et al. 2000) unless excessive amount of soil water content results in decrease in productivity.

Litterfall collected across sites for two years showed that litter production significantly decreased during winter at all sites. Seasonal variation in productivity was related to solar radiation and temperature, which were both lower in the winter (cf. chapter 2). The rate of litterfall in June 2011 was significantly larger than in June 2012 at all sites, which was due to heavy storms before litterfall collection that mechanically delivered pre-senescent material to the litterfall baskets. The apparent decrease in litterfall production during the second year (cf. Figs. 3-5, 3-6 and 3-8) are more difficult to explain using contemporary meteorological measurements. The above average rainfall received by the study area during 2010 and 2011 (30% above long term average) may explain the larger litterfall during 2011 and consequently larger ANPP. Changes in ANPP have been shown to lag behind environmental change (e.g. reduction in precipitation) by one year (Brienen and Zuidema 2005; Vasconcelos et al. 2012).

The plateau observed for all traits which showed minimal changes beyond 9.8 m DGW clearly indicates a threshold of access to groundwater by trees. Sensitivity of vegetation to changes in groundwater depth occurs to a critical depth, beyond which groundwater becomes inaccessible and consequently beyond that depth ecosystem structure and productivity is controlled by other factors (Elmore et al. 2006; McLendon et al. 2008). This critical point is largely a factor of the maximum rooting depth of the species and the height of capillary rise (Mata-González et al. 2012; McLendon et al. 2008) and for the current study is likely to be somewhere between 5.5 - 9.8 m DGW.

The current study has illustrated the importance of groundwater depth in influencing forest structural attributes and hence ANPP, even in mesic regions, as opposed to arid and semi-arid regions. In the present study this depth occurred between 5.5 and 9.8 m. Where aquifers are de-watered below this threshold, a significant shift in ecosystem structure and function (e.g. productivity) is likely to be observed. Identification of groundwater thresholds from species-specific response curves can be used to identify the limits of drawdown, thereby providing guidance for resource and conservation management.

Chapter 4 Species-level and stand-scale transpiration in *Eucalyptus* woodlands across a natural gradient of depth-to-groundwater

Introduction

Worldwide demand for fresh water supplies will continue to grow in response to increasing population size and economic (agricultural and industrial) development (MacKay 2006). With a finite amount of freshwater, changes in global climate creates uncertainty in water supply. Thus, concerns about the availability and quality of freshwater resources are at the top of the world's environmental agendas (Gleick et al. 2006). The imbalance between supply and demand affects the allocation of water resources across competing human and biotic demands. There is conflict at the moment for water allocation among commercial (industry, irrigation), domestic and environmental sectors.

To manage limited fresh water resources sustainably, the demand of all sectors must be quantified and considered. However, the water requirements of the environment have traditionally received little attention and are often neglected or underestimated (Eamus et al. 2005). Allocation of water to the environment has frequently been limited to an allocation of water to ensure river flows (Murray et al. 2003). However, it is now understood that environmental water allocations goes far beyond this and environmental needs now include allocations to wetlands, woodlands, mound springs and a myriad of ecosystems that require groundwater to maintain their current structure and function (Eamus et al. 2006b).

Sustainable management of water, vegetation and land resources requires a clear understanding of the water balance of a landscape. Major challenges in understanding the water balance are the complex relationships among water resources, climate and vegetation function (Boulain et al. 2009). The two largest components of a site water balance are evapotranspiration (ET), which is comprised of evaporation from wet surfaces and transpiration through stomata, and rainfall (P) (Lawrence et al. 2007; Whitley et al. 2012; Zeppel et al. 2008b).

Compared to measurements of rainfall, measurement of actual evapotranspiration (ET_{act}) is relatively difficult (McMahon et al. 2012) and as a result ET is usually estimated using different models developed over many years using mainly meteorological data as a key factor. Reference ET (ET_0) is generally calculated using the Penman-Monteith equation for a grass reference crop height which is assumed to be regulated by energy, atmospheric demand and surface conductance (both plants and soil). Equilibrium evapotranspiration (ET_{eq}) represents the ET rate based solely on energy supply and doesn't account for atmospheric demand. Potential evapotranspiration (ET_p) is calculated by multiplying ET_{eq} by the Priestley–Taylor coefficient and reflects the dual control of ET by energy supply and atmospheric demand on evapotranspiration (Baldocchi and Ryu 2011; McMahon et al. 2012). Budyko (1974) introduced a curve to show the relationship between ET_{act} and an aridity index (ET_p/P; where ET_p is potential evapotranspiration and P is precipitation) as a function of annual rainfall (Baldocchi and Ryu 2011; Gerrits et al. 2009). A Budyko curve describes the theoretical energy and water limits on the catchment water balance and clarifies which one of these factors is the dominant determinant of a catchment water balance (McKenney et al. 2007; O'Grady et al. 2011).

Transpiration by trees can be a major determinant of the hydrological balance of catchments because trees use the largest volume of available water compared to grasses or shrubs (Dragoni et al. 2009; Eamus et al. 2006b; Eamus et al. 2005; Hernández-Santana et al. 2009; Zeppel and Eamus 2008). To predict the impact of hydrological changes on vegetation function and *vice versa*, knowledge of vegetation water-use strategies is important. Thus, understanding the water balance of forested catchments helps for sustainable management of water resources (Eamus et al. 2005; Zeppel 2006). The aim of the work described in this chapter is to measure rainfall and transpiration of the dominant tree species present across a natural gradient of depth-to-groundwater.

The measurement of sapflow provides a widely applicable method of estimating water-use of single trees (Eamus et al. 2006b; Zeppel et al. 2008b) or plots of trees (Lagergren and Lindroth 2004; Nadezhdina et al. 2002). Measuring rates of sapflow with sapflow gauges has advantages over other measures of tree water-use in that they can be operated at a range of spatial and temporal scales and are portable and easily automated (Eamus et al. 2006b; Zeppel 2006). If sapflow is measured in a sufficiently large number and size range of individuals, these data can be up-scaled for partitioning of stand water-use (Meinzer et al. 1997). Information about stand water-use is generally more important than water-use of individual trees for evaluating the water balance of a site (Eamus et al. 2006b; Lubczynski 2009). Stand transpiration depends on the total number of trees in the stand, species composition, soil properties and climatic conditions (Lubczynski 2009).

Rates of tree water-use vary widely in space, time and between species. This variation can be explained by species-specific physiological and structural properties such as variation in rooting depth, hydraulic architecture, active xylem area and properties, leaf area and tree size (Dragoni et al. 2009; Maseda and Fernández 2006; O'Grady et al. 2007; O'Grady et al. 2006c; O’Grady et al. 2009; Vertessy et al. 1995; White et al. 2002). Water-use within plant communities is also a function of a number of variables including plant health, age, density and cover (Baird et al. 2005; Maseda and Fernández 2006). Finally, environmental factors such as solar radiation, vapour pressure deficit, soil moisture content (Maseda and Fernández 2006; O'Grady et al. 2006c; Whitley et al. 2012; Zeppel and Eamus 2008), seasonality, topographic location (Whitley et al. 2012; Zeppel and Eamus 2008) and access to water resources influence sap velocity of trees (Dragoni et al. 2009; Maseda and Fernández 2006; Rossatto et al. 2012; Whitley et al. 2012; Zeppel et al. 2008a).

In some ecosystems at some sites, trees have the potential to access more than one source of water. Three sources of water are traditionally identified for trees: a) recent rainfall in the upper soil profile; b) water deeper in the profile from past rainfall events; and c) groundwater and its associated capillary fringe (Eamus et al. 2006b). Plants that can acquire groundwater from a shallow aquifer are commonly referred to as phreatophytes (Naumburg et al. 2005). Apart from depth-to-groundwater, factors that affect vegetation access to groundwater include root attributes (depth and distribution profile) and soil characteristics (Groom 2004; O'Grady et al. 2006a; Zencich et al. 2002). Access to groundwater affects plant growth, survival, rate of water-use and consequently impact on site water balance (Carter and White 2009; Miller et al. 2010; Zencich et al. 2002). There are a few studies that compare both structural (basal area, leaf area index) and functional (rates of tree water-use) attributes along a *naturally occurring* gradient in depth-to-groundwater (Carter and White 2009; Gazal et al. 2006; Lamontagne et al. 2005). There is extensive evidence of groundwater-use by trees growing over shallow water tables. For example, access to groundwater is often identified by rates of actual evapotranspiration that exceed annual rainfall (Cleverly et al. 2006; Feikema et al. 2010). In addition, groundwater-use can be inferred when transpiration is insensitive to large fluctuations in the moisture content of the upper soil profile (Mereu et al. 2009; O'Grady et al. 2006a) or significantly larger transpiration than in adjacent ecosystems that have no access to groundwater (O'Grady et al. 2007). Similarly, Carter and White (2009) found that rates of stand water-use in a mallee *(Eucalyptus* sp.) plantation (Western Australia) were four times larger in shallow groundwater sites than that of trees over deep groundwater sites. Thus, differences in rates of stand water-use can in some circumstances be explained by differences in groundwater availability and this is generally inferred from groundwater depth (Baird et al. 2005; O'Grady et al. 2007).

The pattern of groundwater-use by vegetation has a significant effect on the hydrological balance of landscapes (Kray et al. 2012; Newman et al. 2006a). Trees may transpire a significant amount of groundwater and this should not be neglected in estimating groundwater balances, modelling and management. Estimating annual rates of groundwater-use in terrestrial vegetation is difficult without an understanding of the temporal and spatial nature of tree water-use and the contribution of groundwater to transpiration (O'Grady et al. 2006a). Changes in depth-to-groundwater, which arise from natural or anthropogenic modifications, almost inevitably impact vegetation that is reliant on groundwater (Cooper et al. 2003; Rood et al. 2000; Scott et al. 1999). These effects result in changes in plant physiology and plant structure (e.g. wood density) as well as community dynamics, particularly in arid regions where groundwater can be the primary water source for many plants. To minimize negative impacts of changes in groundwater depth, the environmental water requirements of these ecosystems need to be better understood and quantified (Lamontagne et al. 2005; Naumburg et al. 2005). However, quantifying the water requirement of phreatophytes can be complicated and requires understanding of the complex interacting processes controlling water uptake (Lamontagne et al. 2005). Understanding an ecosystem's water requirement helps to ensure that decision makers have the opportunity to include the water requirements of GDEs as a vital component of catchment water budget (Baird et al. 2005).

Despite the importance of understanding water requirement of GDEs, quantification of water-use by GDEs has not been a major focus of research (Loheide et al. 2005; Lubczynski 2009; Murray et al. 2003; Yang et al. 2011). Of those studies that have examined rates of water-use of phreatophytes, most have focused on riparian forest (Cleverly et al. 2002; Drake and Franks 2003; O'Grady et al. 2006b; Snyder and Williams 2000) and generally in water limited (arid and semi-arid) ecosystems (Lubczynski 2011; Miller et al. 2010). Comparisons of rates of tree water-use across a depth-to groundwater gradient are even less common (Zencich et al. 2002). Knowledge of groundwater-use at different depths to the water table will contribute to our understanding of the effect of groundwater drawdown on trees water-use. It has been assumed that with increase in depth-to-groundwater, transpiration decreases (Butler et al. 2007; Landmeyer 2012). However, Baird et al. (2005) hypothesised that transpiration rates for a given functional type (except obligate wetland species) would be largest at intermediate depths-to-groundwater and decline with increasing and decreasing depths-to-groundwater. They explained this counter-intuitive result on the suggestion that anoxia of the root zone caused a reduction in water uptake at the shallowest groundwater levels.

The impact of groundwater depth on stand transpiration in a mesic temperate habitat climate has not been, to my knowledge, examined in detail. This chapter tests the following hypotheses in a mesic temperate Eucalypt woodland along a naturally occurring gradient of depth-to-groundwater:

1) The rate of stand water-use will decrease as depth-to-groundwater increases;

2) Intra-specific variation in water-use across sites will follow the same decline with groundwater depth as stand water-use; and

3) Seasonal differences (i.e. between summer and winter) in transpiration rates will be larger for trees over deep groundwater sites that at shallow sites.

4) During relatively dry periods, rates of transpiration will decline more at the deepest depth-to-groundwater sites than at the shallower sites.

Methods

The research reported in this chapter is a detailed assessment of daily and seasonal transpiration over 16 months in south-eastern Australian woodland dominated by *Eucalyptus* species. The interactions between groundwater depth and tree transpiration were studied across a depth-to-groundwater at four sites that differ in depth-to-groundwater: 2.4, 4.3, 9.8 and 37.5 m (the study area is fully described in chapter 2). The dominant species were identified during field surveys of basal area. Each site contained 2–3 dominant tree species. In a total of 10 healthy trees across the 2 or 3 dominant species, rates of tree water-use were measured using the heat dissipation sapflow method (described below). Sensors were made in the TERG group laboratory (UTS). Trees were selected across a range of DBH to allow scaling from individual tree to stand-scale. Sapflow measurements commenced in January 2010 (summer) at the 37.5 m DGW site and continued until December 2012 (summer). Establishment of measurements followed at the remaining sites until measurements began at the fourth site in September 2011 (spring), after which concurrent measurements of sapflow were available at all four sites for a 16 month period (Sep 2011–Dec 2012 inclusively).

Sapflow measurement

Xylem sapflow measuring systems are commonly used to quantify whole plant water-use. There are several different methods to measure xylem sapflow (heat dissipation, heat ratio and heat pulse methods). The heat dissipation method (Granier 1985) was used in the present study. This method is popular because of its simplicity, accuracy, and relatively low cost (Do and Rocheteau 2002; Lu et al. 2004). A basic Granier system consists of two sensor probes. The two probes were inserted radially into the stem sapwood 10 cm apart at breast height. The upper probe contains an electric heater that is continuously heated at constant power (0.2 W) and a thermocouple while the lower probe contains only a thermocouple to measure the ambient temperature of the wood. The two temperature sensors measure the heat dissipation from the heating element (via the sapwood and xylem water), which increases with sapflow and results in cooling of the heated probe. This approach enables the measurement of xylem sapflow velocity from the relationship between ΔT and sap velocity. When sapflow velocity is zero, the temperature difference (ΔT) between the two sensors is maximal. Granier defined a flow index (K), calculated from the measured temperature difference between the upper heated sensor and the lower reference sensor (ΔT) and the maximum measured temperature difference, occurring at zero flow velocity (ΔT_{max}):

$$K = \frac{(\Delta T_{\max} - \Delta T)}{T_{\max}} \qquad \text{(Equation 1)}$$

The value of ΔT is found from the differential voltage measured between the upper and lower thermocouple. Granier then found an empirical relation between the value of K and the actual sapflow velocity (Equation 2) (Lu et al. 2004):

$$V = 0.0119 \times K^{1.231} \text{ cm/s} \qquad \text{(Equation 2)}$$

In the current study, no fewer than one 3-probe sensor was used in each tree along with one 2-probe sensor. Three probes systems are useful because they record the natural temperature gradient between the upper and lower probes. The natural temperature gradient was subtracted from the measured ΔT. The third probe is located at the same height of the heated probe with the same longitudinal distance (10 cm) from lower reference probe (Fig. 4-1).

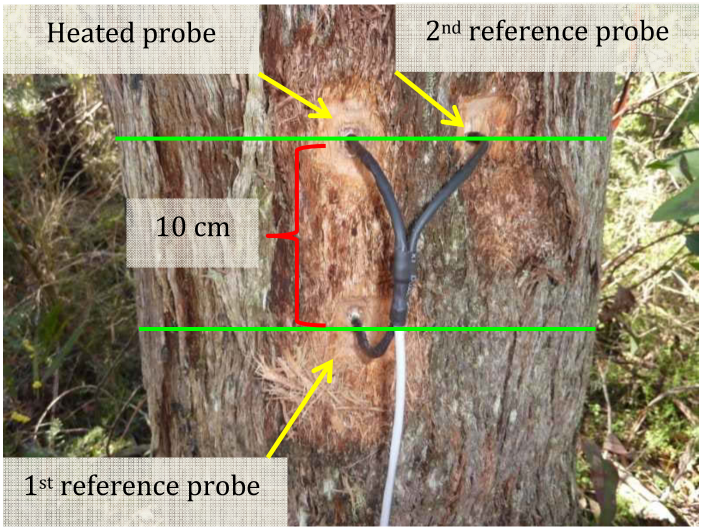


Figure 4-1: Position of installed three probe sensor

1- Zero flow

To calculate K, the maximum temperature difference (ΔT_{max}) which occurs when water flux is zero needs to be determined. There are different factors that may prevent the occurrence of zero flow including nocturnal transpiration and capacitive recharge of the tree's internal water storage (Bucci et al. 2004a; Hultine et al. 2003; Regalado and Ritter 2007). The contribution of nocturnal transpiration to the 24 hour sum of sapflow is variable often ranging from 0-28% (Mitchell et al. 2008; Regalado and Ritter 2007; Zeppel et al. 2010). Sapflow at night can cause an under-estimation of the true ΔT_{max}, so if ΔT_{max} is determined for each night, possible nocturnal flow of that night will be masked. Considering this and as was suggested by Lu et al. (2004), in the current study, ΔT_{max} was determined for every 7 days` throughout the study period, based on a double regression method.

Having ΔT_{max} calculated for every seven days, K was calculated for each tree using Equation 1. Sap velocity was calculated using Equation 2 for each sensor (m s^{-1}).

2- Sensor installation

Prior to installation of sapflow sensors, bark was removed carefully to prevent damage to the underlying phloem and xylem. For each sensor, two or three holes were drilled to a depth of 1 cm with a separation of 10 cm using a drill guide. Because sapflow rates vary around the circumference of trees (Cienciala et al. 2000), two sets of sensors were inserted at breast height into each tree trunk to minimise the impact of such variation. One set of each pair per tree was a three sensor system, which is used to measure radial thermal gradients for estimation of the natural background correction. Following insertion, probes were sealed against moisture with silicone. To avoid the effect of external thermal gradients on velocity measurements, the outer surface of the trunk was insulated with bubble wrap and a thermal blanket that circumscribed the tree for a distance of 15 cm above and below each sensor (Do and Rocheteau 2002; Lu et al. 2004). Temperature differences between sensors were measured once per minute and recorded as 10 minute averages in a CR 3000 Campbell Scientific data logger.

Representative days in both summers and winter were chosen from days with relatively similar VPD and temperature. 3 days were identified in each period that characterized by the VPD, T for that period.

Sapwood area

Estimation of sapwood area is critical for scaling flow rates to whole tree and stand scales. Sapwood cross sectional area was determined at each site using a 6 mm diameter increment corer on a range of tree sizes in each species. Two cores were taken from each tree. Sapwood was distinguished from heartwood by visual inspection of a distinct colour change. When the boundary between sapwood and heartwood was not clear, sapwood was stained with Methyl orange to determine depth. The sapwood depth was used to calculate sapwood area by assuming a circular cross-section.

Spatial scaling

Scaling sapflow measurements from measurements of individual trees to stand-scales requires information about the sapwood area of each tree species per unit ground area. Within each site, DBH of all trees within three replicate plots (20 m × 20 m) were measured, from which the total sapwood area per hectare of land was estimated for each species ($SWA_{species}$). The relationship between DBH and sapwood area was evaluated using a power function regression equation (Meinzer et al. 2005). Analysis of covariance (ANCOVA, IBM SPSS STATISTICS version 19, Armonk, NY, USA) was used to test the null hypotheses that 1) the regression coefficients were equal to zero amongst all species and 2) the slope of the DBH-sapwood area relationship did not differ amongst species. The average sap velocity of each species for each hour ($SV_{species}$) was multiplied by $SWA_{species}$ to calculate sapflux (J_s) (Zeppel et al. 2008b):

$$J_S = \sum SWA_{species} \times SV_{species} \qquad \text{(Equation3)}$$

In each 24 hour period, 10-minute J_s was summed to give the daily sapflow that was expressed as a volume (cm^3 day^{-1}) (Zeppel et al. 2006) and as sapflow per unit ground area per day (mm day^{-1}). For those species that were not used in measurements of sapflow (which accounted for less than 20 % of the basal area of each site), J_s was estimated using the average velocity of all trees measured at each site (SV_{site}) and $SWA_{species}$. At each site, daily rates of stand transpiration of all tree species were calculated by summing J_s for each species.

Daily transpiration for each species, expressed as volume of water transpired per unit ground area per day (mm day^{-1}), was calculated within sites. Stand transpiration that was calculated by summing the daily transpiration of each species measured at a site.

Micro-meteorology

Micro-meteorological information, including relative humidity, air temperature, wind speed, wind direction, net solar radiation and rainfall were recorded at a meteorological station installed in a cleared field (the map of the study area which includes the location of the met-station and sites with sapflow systems is shown in chapter 2). Reference evapotranspiration (ET_0) was computed using the FAO (Food and agriculture organization of united nations) Penman-Monteith method (Allen et al. 1998) using the following equation:

$$ET_0 = \frac{\Delta(R_n - G) + \rho_a C_p D r_a^{-1}}{\lambda\left[\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)\right]} \qquad \text{(Equation 4)}$$

where λ is the latent heat of vapourization (2.45×10^6 J kg^{-1} at 20 °C), Δ is the slope of the saturation vapour pressure curves with temperature (Pa K^{-1}), R_n is net radiation, G is ground heat flux, ρ_a is the density of moist air, C_p is the heat capacity of moist air, D is the vapour pressure deficit, and γ is the psychrometric coefficient (approximately 67 Pa K^{-1}). Following (Allen et al. 1998), daily totals were used to parameterise FAO56 (e.g. R_n in MJ m^{-2} day^{-1}), in which case G can be assumed to be negligible and was not included. Measurements of wind speed were made in a forest meadow with similar canopy structure to the grass reference, thus aerodynamic resistance (r_a) was computed as 208 / u_2, in which u_2 is the wind speed measured two metres above the ground (Allen et al. 1998). The bulk surface resistance (r_s) was estimated using the leaf stomatal resistance for a well-illuminated leaf in a reference grass crop (r_l = 100 s m^{-1}) and the leaf area index (LAI) of each forest: $r_s = r_l / 0.5$

LAI. In the calculation of ET_0, the average LAI of each site was used instead of that of the reference crop (2.8 LAI) (Allen et al. 1998).

Potential evapotranspiration (ET_p) was calculated using the Penman equation (Li et al. 2013; Shuttleworth 1993):

$$ET_P = \frac{\Delta}{\Delta + \gamma}(R_n - G) + \frac{\gamma}{\Delta + \gamma}\left(\frac{6430(1 + 0.54)(D)}{\lambda}\right) \qquad \text{(Equation 5)}$$

The information for the calculation of ET_P and ET_0 were obtained from the micro-meteorological station installed in the study area.

Budyko-Curve

As there was no estimation of ET_{act} for the current study, Budyko curve was established using the relationship between ET_0/P (as an evaporation index on y-axis) *versus* ET_p/P (as an aridity index on x-axis).

Results

Climate

Total rainfall in 2011 was 1561 mm and 1188 mm in 2012 which was substantially larger in the first year than the long term average (10 years) of rainfall (1067 mm yr^{-1}). Vapour pressure deficit (VPD) was relatively small and generally remained below 1 kPa (Fig. 4-2). During the 694 days that measurements of sapflow were collected, rainfall was received on 415 days. A detailed analysis of measured climate variables can be found in chapter 2.

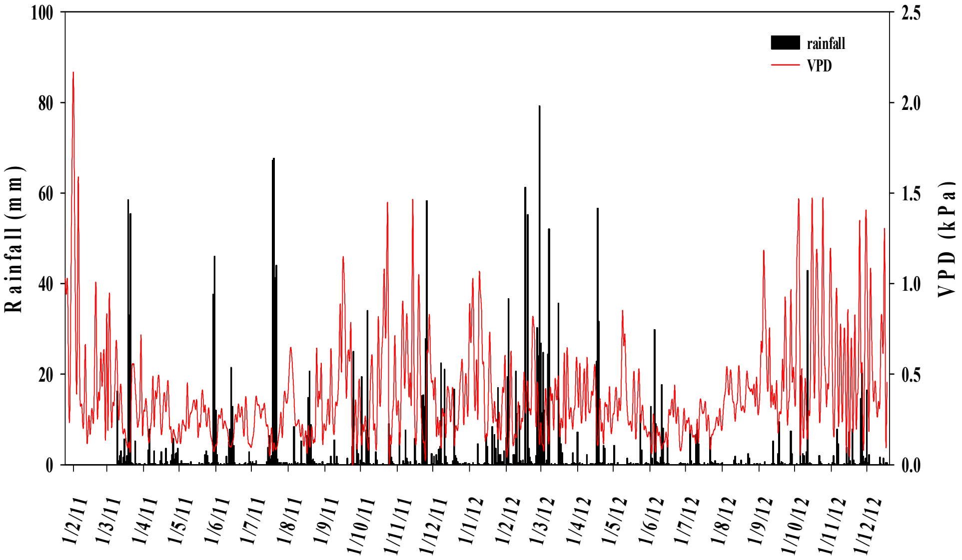


Figure 4-2: Daily rainfall (mm-bars) and vapour pressure deficient (kPa-red line) over the 2 year study period.

Relationships amongst DBH and sapwood area

The relationship between tree diameter at breast height (DBH) and sapwood area (cm^2) was investigated for all species used in the study of sapflow and across all sites. Species sampled at each site covered the range of tree sizes upon which sapflow measurements were conducted. As DBH increased, sapwood area increased for all species and across all sites (Fig. 4-3). The relationship between sapwood area and DBH varied significantly between species except at site 9.8 m DGW (species × site, F = 1.106; p = 0.35; df = 2,19). Likewise, the coefficient of regression was different between species within each site except at the deepest site (37.5 m). Additionally, regression coefficients were significantly different across sites in all species. Stem diameter explained 87–97% of variation in sapwood area.

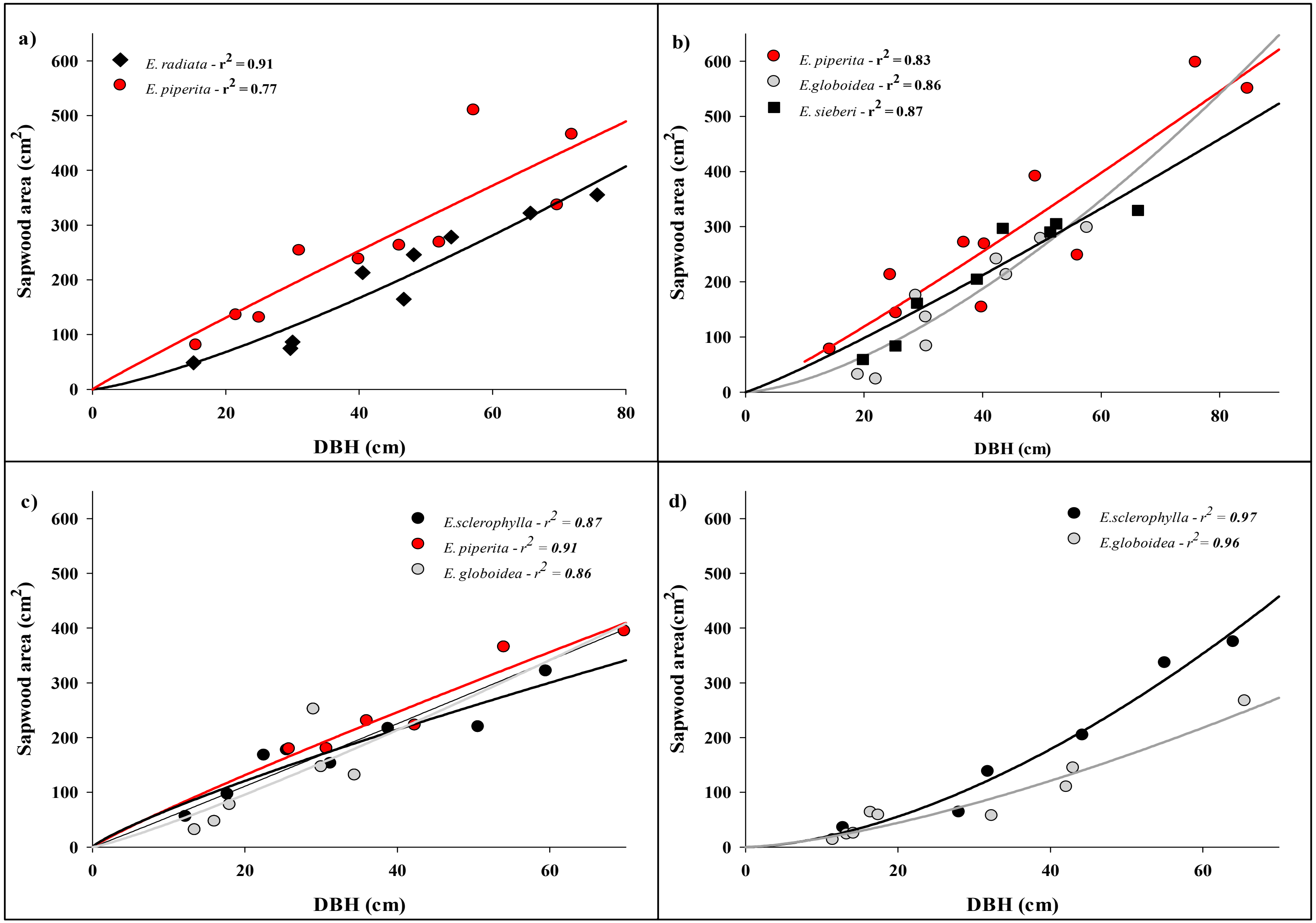


Figure 4-3: The relationship between DBH (cm) and sapwood area (cm^2) for individual species growing at the four study sites: a) 2.4 m, b) 4.3 m , c) 9.8 m and d) 37.5 m depth-to-groundwater. Each point represents one tree.

Sapflow density

Figures 4-4 to 4-6 show the diurnal pattern of sapflow density (cm^3 cm^{-2} h^{-1}) for three representative days in summer 2012 (Fig. 4-4), winter 2012 (Fig. 4.5) and summer 2013 (Fig. 4-6). As expected, transpiration followed a pattern of increasing rates in the morning and declining rates in the late afternoon. Climate conditions of the study area during those three days are shown in Table 4-1.

Table 4-1: Climatic conditions of the study area during 3 representative days in summer 2012, winter 2012 and summer 2013. T_{max} (°C) (maximum temperature), T_{min} (°C) (minimum temperature), VPD (vapour pressure deficit, kPa), rainfall (mm), average daily net radiation (MJ m^{-2} d^{-1}), and ET_0 (reference evapotranspiration).

Year	**T_{max} (^{0}C)**	**T_{min} (^{0}C)**	**VPD (kPa)**	**Rain (mm)**	**Radiation (MJ m^{-2} day^{-1})**	**ET_0 (mm day^{-1})**
Summer 2012	28.01±1.11	7.12±2.64	0.80±0.07	0.07±0.08	18.52±0.28	1.30±0.15
Winter 2012	14.21 ±1.37	1.64±0.98	0.31±0.01	0.13±0.16	2.91±0.23	0.70±0.29
Summer 2013	27.79±1.97	11.91±0.51	0.91±0.23	0.47±0.57	No data	No data

During summer 2012 sapflow density was larger in the two deepest sites (9.8 m and 37.5 m DGW) than the two shallowest sites. Sapflow density of *E. globoidea* in summertime reached a maximum of 13.75 cm^3 cm^{-2} h^{-1} at site 37.5 m DGW in comparison to a minimum of 8.90 cm^3 cm^{-2} h^{-1} at site 4.3 m DGW (Fig. 4-4). Overall sapflow density was lower during winter than in the summer (Fig. 4-5), because of reduced solar radiation inputs and lower temperatures, which combined with shorter days, resulted lower rates of daily water loss from these evergreen trees during winter.

Within sites, sapflow density was not significantly different between species during summer 2012. In contrast, inter-specific differences in water-use were observed at site 9.8 DGW in the winter of 2012, site 37.5 DGW during summer 2013 and site 4.3 DGW in both winter of 2012 and summer 2013. Sapflow density in *E. piperita* was significantly lower than for other species at site 4.3 DGW (F=10.76, p<0.001; df=2,213) in winter. In contrast at site 9.8 m DGW, sapflow density of *E. piperita* was significantly larger than in co-occurrence species (F=5.58, p=0.004; df=2,213). During the summer of 2013 *E. sieberi* at site 4.3 m DGW (F=8.81, p<0.001; df =2,213) and *E. globoidea* at site 37.5 m DGW (F=12.58, p=0.001; df=1,139) had significantly larger sapflow density compared with the other species at those sites (Fig. 4-6). For average seasonal sapflow density of all species and all sites see appendix A.

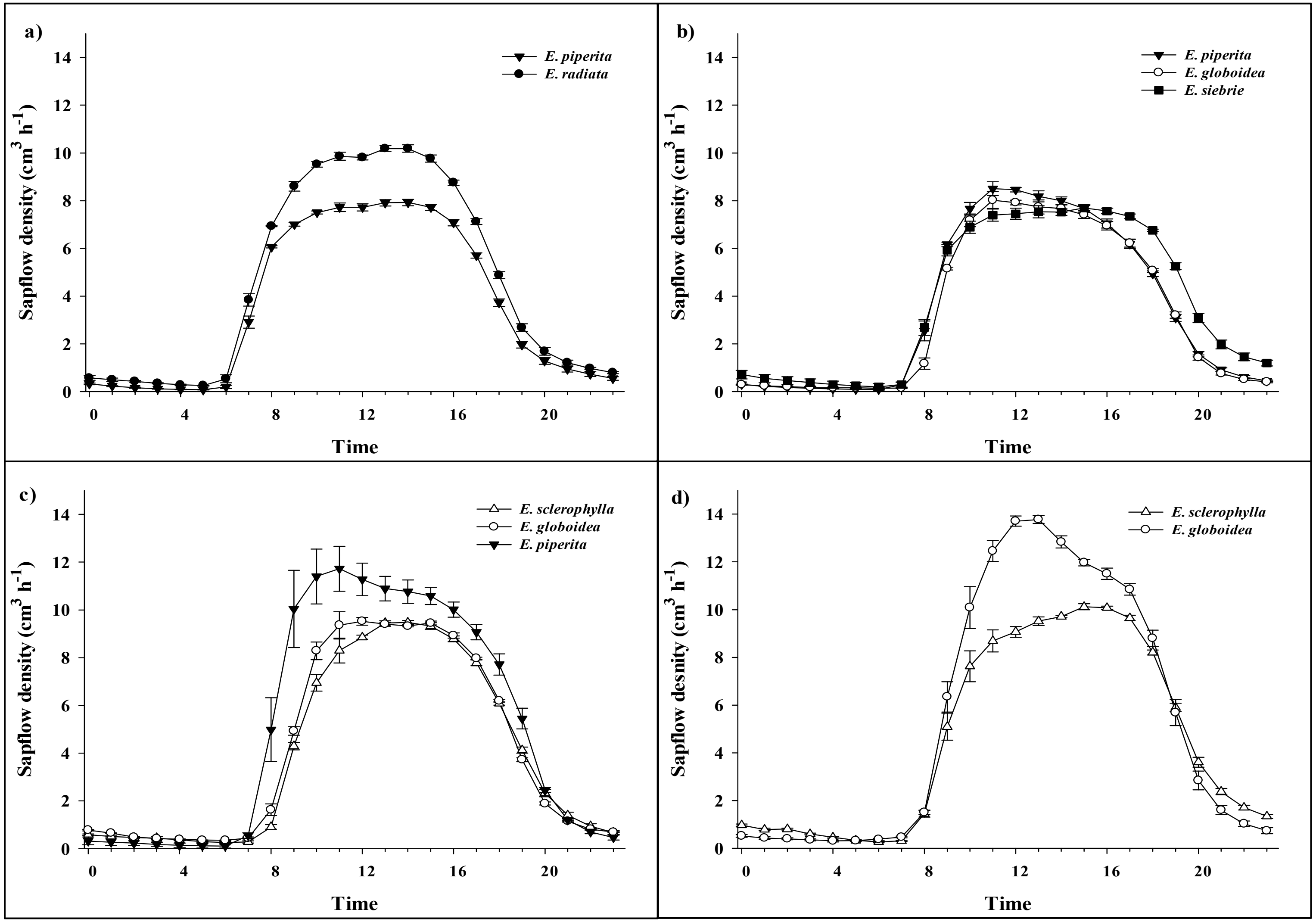


Figure 4-4: Diurnal patterns of water- use of each tree species for the 4 sites a) 2.4 m, b) 4.3 m, c) 9.8 m and d) 37.5 m depth-to-groundwater); 3 representative days in summer 2012. See Appendix supplemantry Fig. A1.

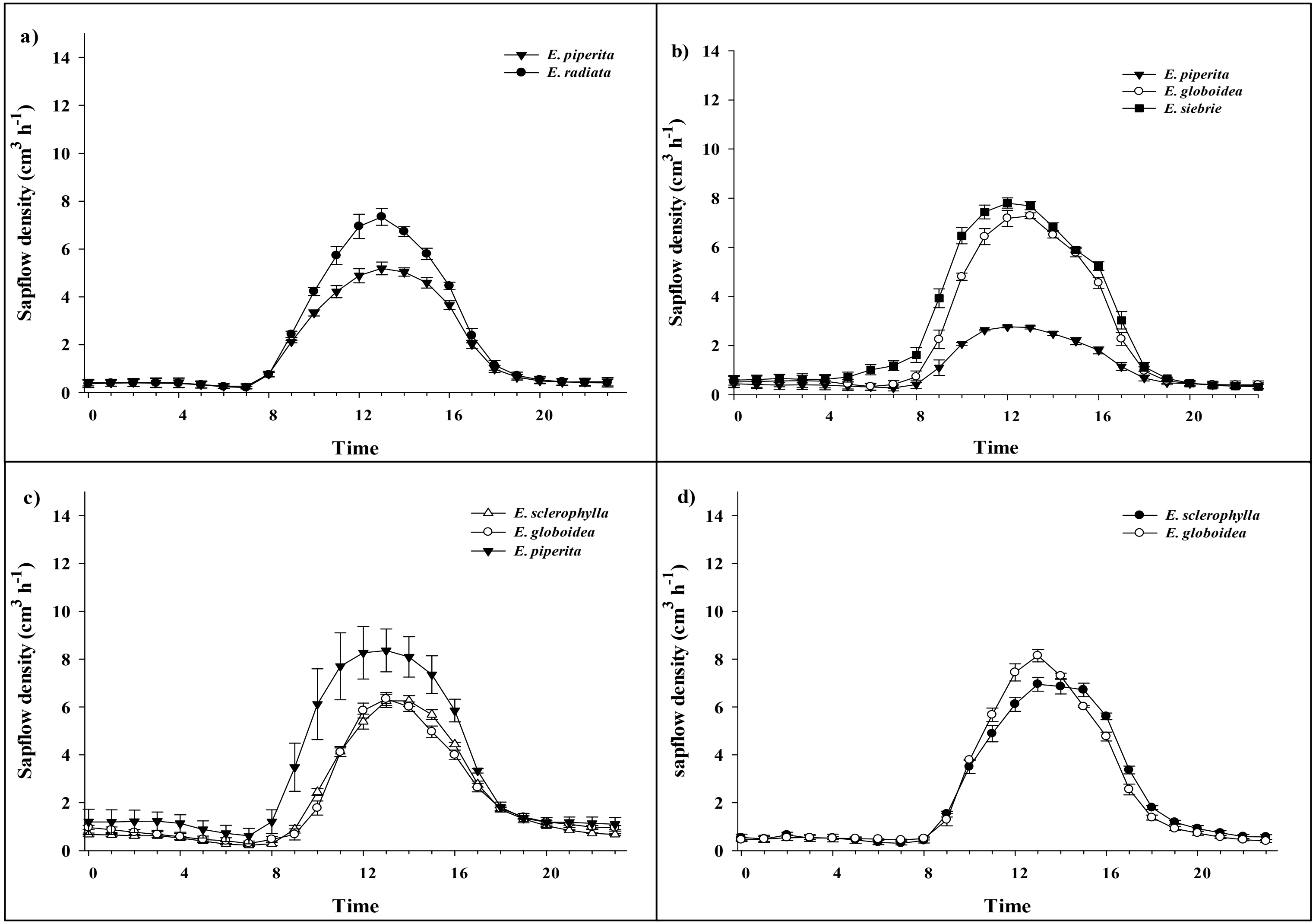


Figure 4-5: Diurnal patterns of water- use of each tree species for the 4 sites: a) 2.4 m, b) 4.3 m, c) 9.8 m and d) 37.5 m depth-to-groundwater); 3 representative days in winter 2012. See Appendix supplumentary Fig. A2.

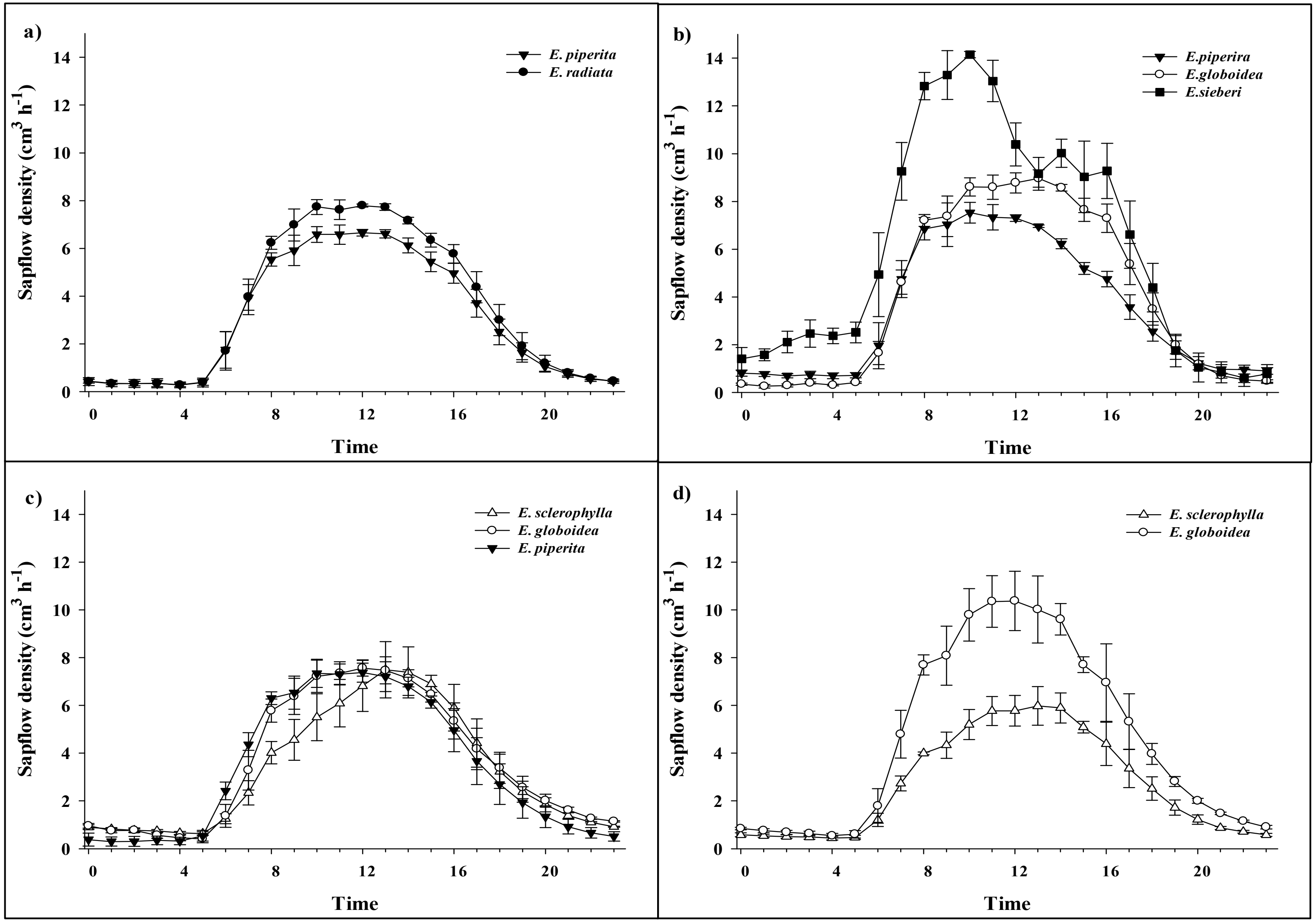


Figure 4-6: Diurnal patterns of water- use of each tree species for the 4 sites: a) 2.4 m, b) 4.3 m, c) 9.8 m and d) 37.5 m depth-to-groundwater) for three representative days in summer 2013. See Appendix supplemantry Fig. A1.

Before up-scaling transpiration from individual trees to stand level, the relationship between sap velocity and tree size (DBH) was tested using regression analysis across sites for all tree species. The slopes of all regression lines were not significantly different from one (F=0.47, p=0.57; df=1,358), which indicates that there was not a significant size effect on sap velocity in all species and across all sites. Thus up-scaling was relatively simple and the results were reliable.

Stand transpiration at the 2.4 m DGW reached a maximum of 0.35 mm day^{-1} (*E. radiata*). Transpiration rate for *E. radiata* was substantially larger than the co-occurring *E. piperita* (Fig. 4-7a) across the study period. Both species exhibited a larger daily rate of transpiration in summer than winter because of the longer sunlit period and the warmer weather, with a larger daily average VPD in summer than winter (up to two times larger in summer).

The daily rate of transpiration of *E. globoidea* growing at the 4.3 m DGW site was larger than that of the other two species (maximum 0.62 mm day^{-1}) across the entire study period (Fig. 4-7b) but the difference was larger in summer than winter. The lowest rate of daily transpiration for the three species at the 4.3 m DGW was recorded for *E. sieberi* except during a short period of time in September 2012, when transpiration of *E. sieberi* was larger than that of *E. piperita* (Fig. 4-7b).

Daily transpiration rates at the two deeper sites are presented in Figure 4-8 *E. sclerophylla* was present in both sites and showed the largest transpiration rate compared to the other species at these sites. At site 9.8 DGW *E. sclerophylla* transpired a maximum of 0.46 mm day^{-1}. *E. globoidea* maintained the lowest transpiration rate compared to the other two species in that site (Fig. 4-8a). At the site 37.5 m DGW throughout the entire measurement period, *E. sclerophylla* maintained a larger transpiration rate than *E. globoidea* (Fig. 4-8b). The rate of transpiration of *E. sclerophylla* at 9.8 m DGW was approximately twice that observed at site 37.5 m DGW (Fig. 4-8 a, b).

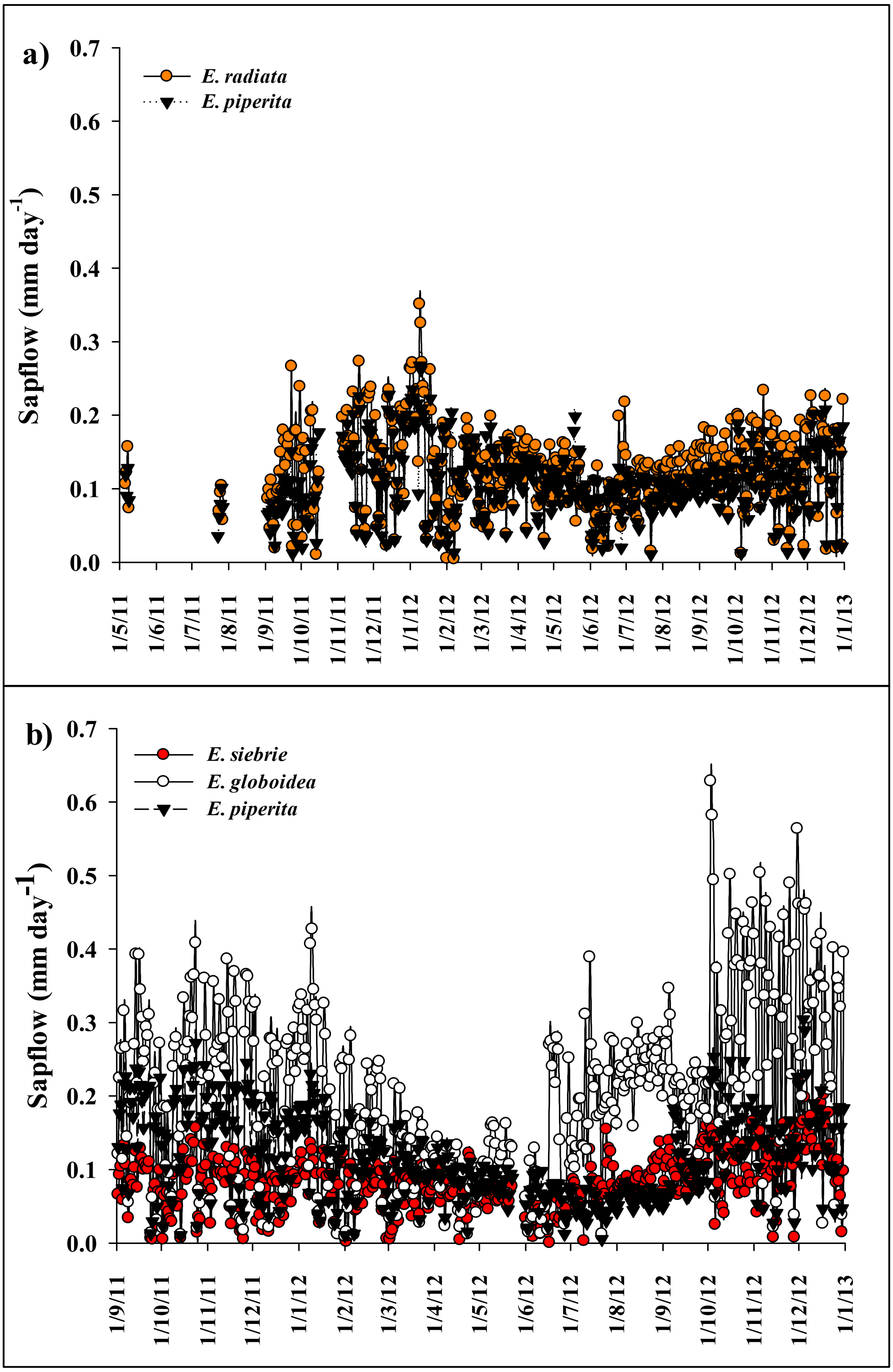


Figure 4-7: Daily sums of the rate of water- use for each species scaled individually within a stand for the study period for sites a) 2.4 m and b) 4.3 m depth-to-groundwater. (Missing data indicate periods of power supply or instrument failure).

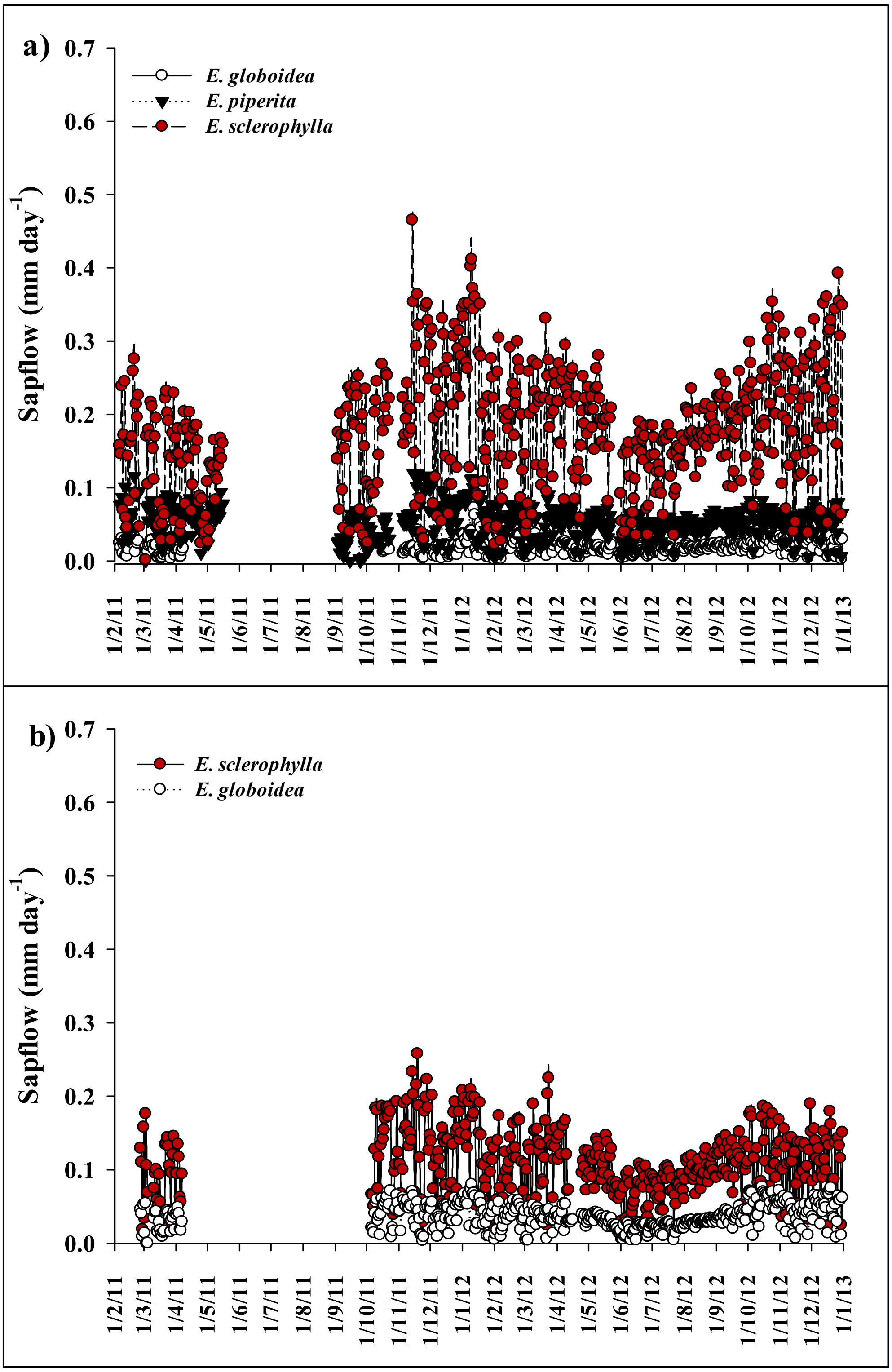


Figure 4-8: Daily sums of the up-scaled rate of water- use for each species scaled individually within a stand for the study period for sites a) 9.8 m and b) 37.5 m depth-to-groundwater. (Missing data indicate periods of power supply or instrument failure).

The average daily transpiration of each species that occurred at more than one site showed significant differences across sites. Average daily sapflow of *E. piperita* ranged from 0.04 mm day^{-1} at site 9.8 m in winter 2012 to 0.15 mm day^{-1} at site 4.3 m DGW in summer 2013. During the full study period, transpiration of *E. piperta* was 50% smaller at the site 9.8 m DGW than at the two shallower sites (2.4 m and 4.3 m DGW). Transpiration rates of *E. piperita* were significantly larger during summer than winter at the two shallower water table sites (Table 4-2). Average daily sapflow of *E. globoidea* was significantly larger (≈ 80%) at site 4.3 m DGW than at sites 9.8 m and 37.5 m DGW (Table 4-2). Average daily transpiration of *E. globoidea* reached a maximum of 0.29 mm day^{-1} at site 4.3 m DGW during summer 2013 and was as little as 0.02 and 0.04 mm day^{-1} at site 9.8 m and 37.5 m respectively. Last among the species that were present at multiple sites, the average daily transpiration in *E. sclerophylla* was significantly larger (up to 44% ; F=157.1, p<0.001; df=1,426) at site 9.8 m DGW than at the deepest water table site (37.5 m DGW) (Table 4-2). Transpiration in *E. sclerophylla* was significantly larger in summer of both years at both sites 9.8 m DGW; (F=23.47, p<0.001; df=2,211) and 37.5 m DGW, (F=17.66, p<0.001; df=2,211).

Table 4-2: Details of the measurement of transpiration across sites; total reference evapotranspiration (ET_0, mm) per year and during the study period, species studied, number of days of continuous measurements at each site, total sum of transpiration during the study period and average daily transpiration (mm day^{-1}).

DGW	**ET_0 (mm $year^{-1}$) 2012**	**ET_0 (mm)study**	**Species**	**No. of days of data collection**	**Total T (mm)**	**Average daily T (mm day^{-1})**
2.4 m	612	1173	*E. radiata*	473	59.67	0.12±0.002
			E. piperita	476	52.15	0.11±0.002
4.3 m	606	1163	*E. piperita*	479	54.58	0.11±0.002
			E. globoidea	479	96.72	0.20±0.005
			E. sieberi	468	39.13	0.08±0.001
9.8 m	455	876	*E. piperita*	553	29.37	0.05±0.001
			E. globoidea	475	9.44	0.02±0.0004
			E. sclerophylla	559	99.95	0.18±0.003
37.5 m	455	876	*E. globoidea*	479	17.47	0.03±0.0007
			E. sclerophylla	476	50.92	0.10±0.002

Table 4-3: Average daily sapflow per unit of ground area ± SE of each site at three periods; summer 2012, winter 2012 and summer 2013 at different sites for each species. Letter in the last column shows difference between sites within each season. Symbols under the column depth-to groundwater show the difference within each site as a function of season. *E. sieberi* and *E. radiate* were present only at one site.

Species	**Season**	**DGW**	**Average sapflow (mm day^{-1})**	
E. piperita	**Summer 2012**	**2.4 m** *	0.13 ± 0.006	**a**
		4.3 m ○	0.12 ± 0.005	**a**
		9.8 m ●	0.06 ± 0.002	**b**
	Winter 2012	**2.4 m** **	0.08 ± 0.003	**a**
		4.3 m ○○	0.05 ± 0.001	**b**
		9.8 m ●/ ●●	0.04 ± 0.001	**b**
	Summer 2013	**2.4 m** *	0.13 ± 0.009	**a**
		4.3 m ○○○	0.15 ± 0.01	**a**
		9.8 m ●●	0.05 ± 0.003	**b**
E. globoidea	**Summer 2012**	**4.3 m** ○	0.18 ± 0.01	**a**
		9.8 m ●	0.02 ± 0.001	**b**
		37.5 m ◊	0.04 ± 0.001	**b**
	Winter 2012	**4.3 m** ○	0.18 ± 0.008	**a**
		9.8 m ●	0.01 ± 0.0004	**b**
		37.5 m ◊	0.02 ± 0.0007	**b**
	Summer 2013	**4.3 m** ○○	0.29 ± 0.02	**a**
		9.8 m ●	0.02 ± 0.001	**b**
		37.5 m ◊	0.04 ± 0.003	**b**
E. sclerophylla	**Summer 2012**	**9.8 m** ●	0.20 ± 0.01	**a**
		37.5 m ◊	0.11 ± 0.005	**b**
	Winter 2012	**9.8 m** ●●	0.14 ± 0.005	**a**
		37.5 m ◊◊	0.08 ± 0.003	**b**
	Summer 2013	**9.8 m** ●	0.23 ± 0.01	**a**
		37.5 m ◊◊	0.10 ± 0.007	**b**
E. sieberi	**Summer 2012**	**4.3 m** ○	0.07 ± 0.003	
	Winter 2012	**4.3 m** ○	0.06 ± 0.004	
	Summer 2013	**4.3 m** ○○	0.13 ± 0.008	
E. radiata	**Summer 2012**	**2.4 m** *	0.14 ± 0.007	
	Winter 2012	**2.4 m** **	0.10 ± 0.004	
	Summer 2013	**2.4 m** *	0.14 ± 0.01	

Figure 4-9 shows stand transpiration that was calculated by summing the daily transpiration of each species measured at a site. At all sites, the rate of stand transpiration was larger in summer (Dec-Feb) than winter (Jun-Aug). Throughout most of the period from September 2011 to December 2012, the rate of stand transpiration was largest at the 4.3 m DGW site where peak summer and winter rates of stand transpiration were approximately 1.35 mm day^{-1} and 0.80 mm day^{-1} respectively (Fig. 4-9). In contrast, the deepest site (37.5 m) exhibited the lowest rate of stand transpiration across the 16 month study period with peak summer and winter rates of 0.57 mm day^{-1} and 0.30 mm day^{-1} respectively (Fig. 4-9). The rates of stand transpiration at the shallowest (2.4 m DGW) and intermediate depth (9.8 m DGW) sites were intermediate and overlapped considerably across the 16 month study: peak summer rates were 0.76 mm day^{-1} (2.4 m DGW) and 0.71 mm day^{-1} (9.8 m DGW) while winter stand transpiration was 0.42 mm day^{-1} and 0.37 mm day^{-1} respectively.

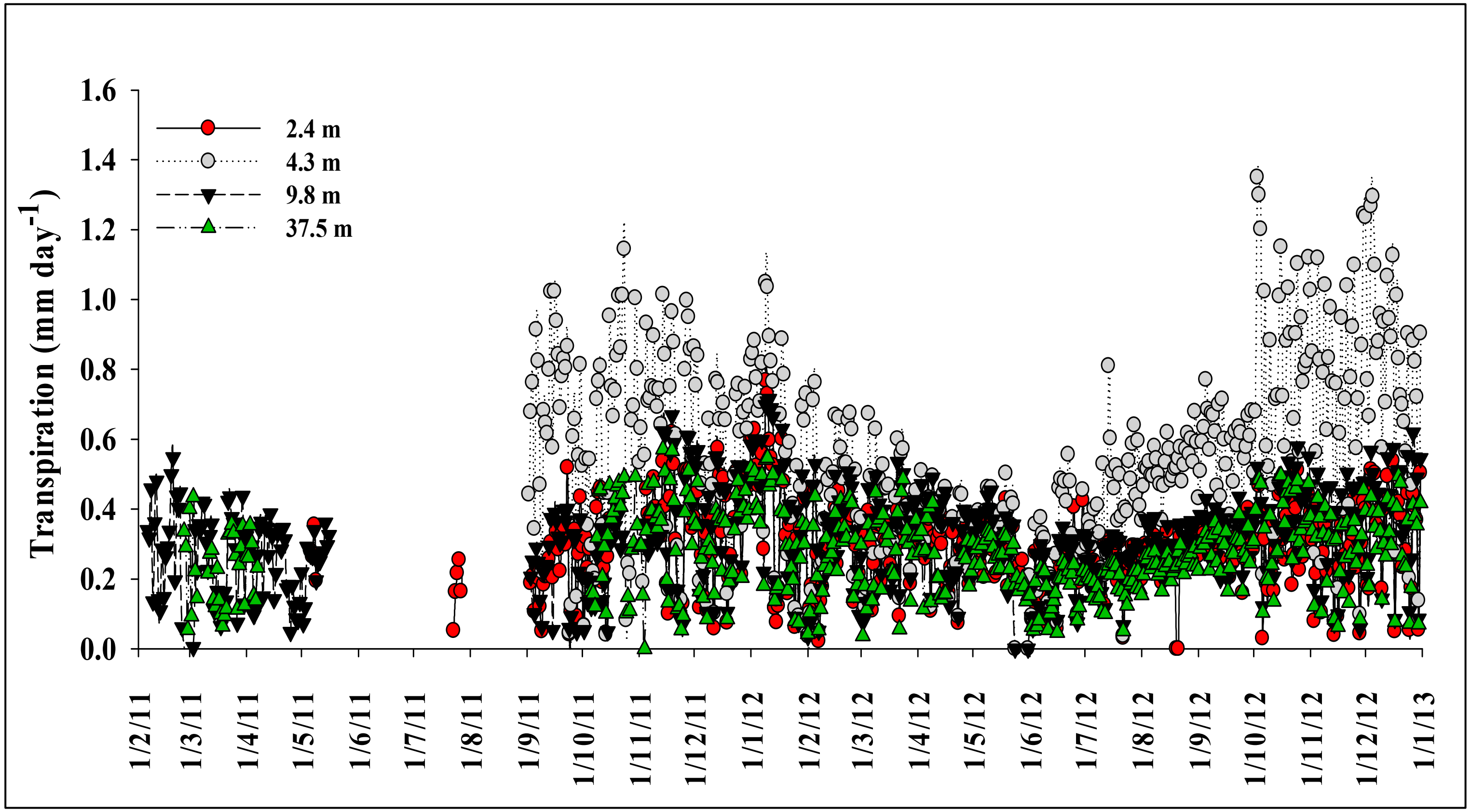


Figure 4-9: Daily stand transpiration of the four study sites based only upon the species sampled for sapflow, (missing data indicate periods of power supply or instrument failure).

Figure 4-10 shows the relationship between daily total stand transpiration *versus* reference evapotranspiration (ET_0) at each site. Maximal ET_0 was 6.38 mm day^{-1} in summer 2011-12 and 5.36 mm day^{-1} during the following summer (2012–3). Transpiration was much smaller than ET_0 at all sites but especially at the deepest site. Reference evapotranspiration ranged from 32-41% of site rainfall in 2011 to 36-47% in 2012.

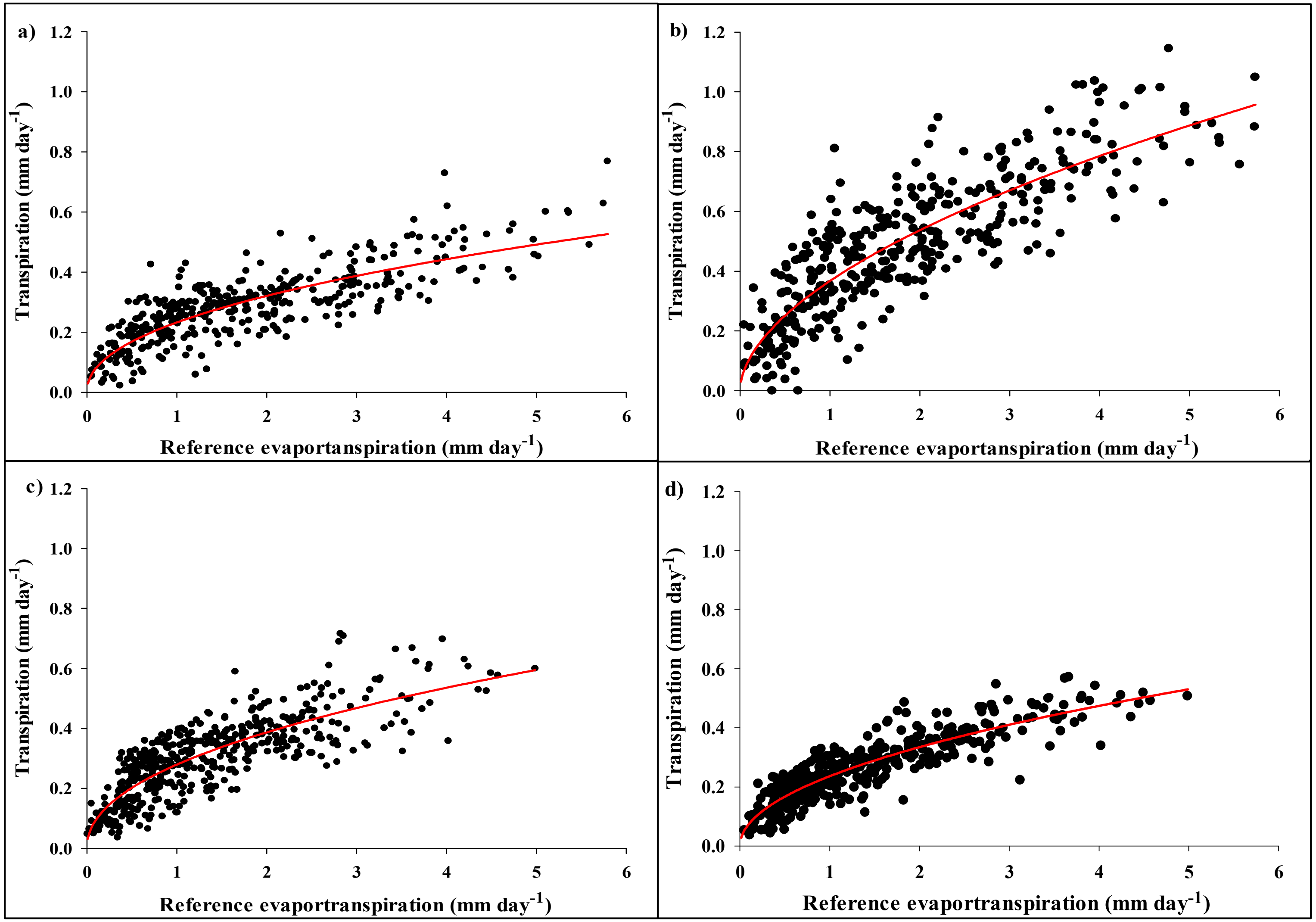


Figure 4-10: Daily stand transpiration (mm per day) as a function of reference daily evapotranspiration (mm per day) for the 4 sites: a) 2.4 m, b) 4 m, c) 9.8 m and 37.5 m depth-to-groundwater.

The Budyko curve has been used to show the relationship between forest evapotranspiration (actual ET or ET_0) and potential evapotranspiration (ET_P) after accounting for differences in precipitation (P). All sites had a water surplus ($ET/P < 1$) in both years and are limited by energy, not water (Fig. 4-11). Differences between sites were more pronounced in 2011, especially at the two sites with a shallower water table, both of which have a smaller ET deficit (i.e., ET_0/P near unity; Fig. 4-11) and consequently contribute less run-off.

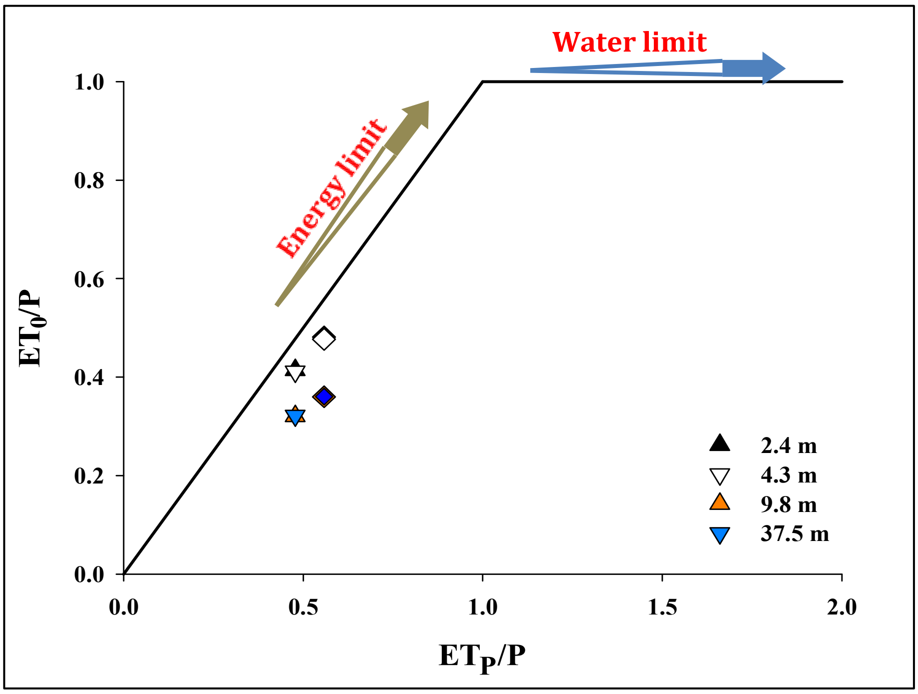


Figure 4-11: Budyko curve for two years across sites. Triangle symbols represents year 2011 and 2012 are in diamond symbols. The horizontal line represents water and vegetation limitations *versus* the 1:1 line, which represents energy and atmospheric demand limitations on evaporation.

Monthly total stand transpiration for each site was calculated using either only the species that had been measured (Fig. 4-12a) or for all species present at each site (Fig. 4-12b). Monthly totals for stand transpiration showed the expected seasonal variation, with larger rates in summer (5 -18 mm month^{-1} for sampled species, or 9 – 25 mm month^{-1} for all species present) than winter (2.5 - 12 mm month^{-1} for sampled species, or 5 – 17 mm month^{-1} for all species present) across sites (Fig. 4-12a, b). The largest rate of monthly transpiration (18.51 mm month^{-1}, October 2012) was consistently observed at site 4.3 m DGW although the difference was largest in summer and smallest in winter. The smallest monthly rate of total stand transpiration (2.55 mm month^{-1}, June 2012) was observed at the deepest (37.5 m) DGW site with the remaining two sites showing intermediate rates of monthly stand transpiration (Fig. 4-12).

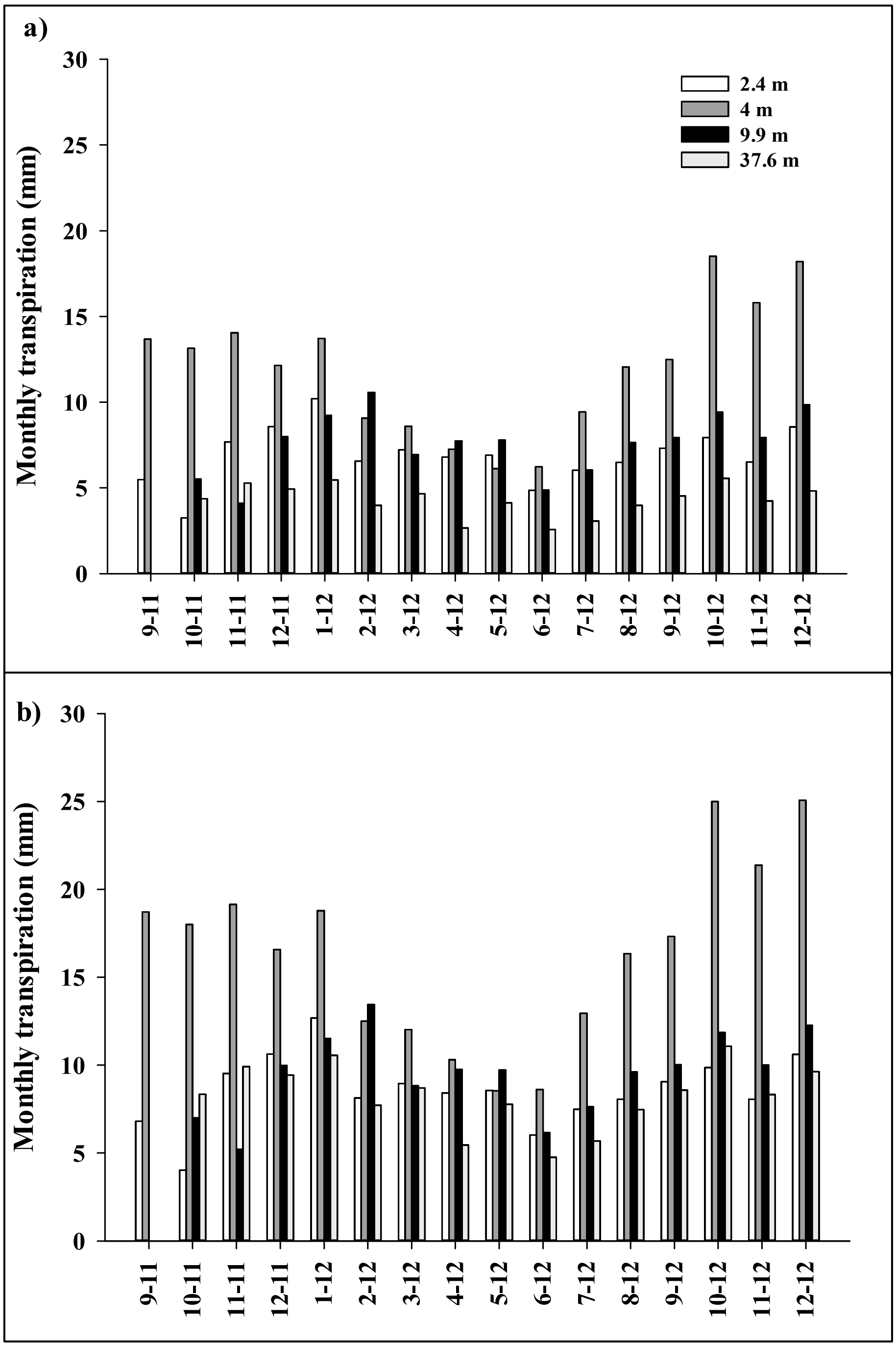


Figure 4-12: Stand-scale monthly water- use (mm per month) for (a) all tree species measured and (b) all tree species present each site.

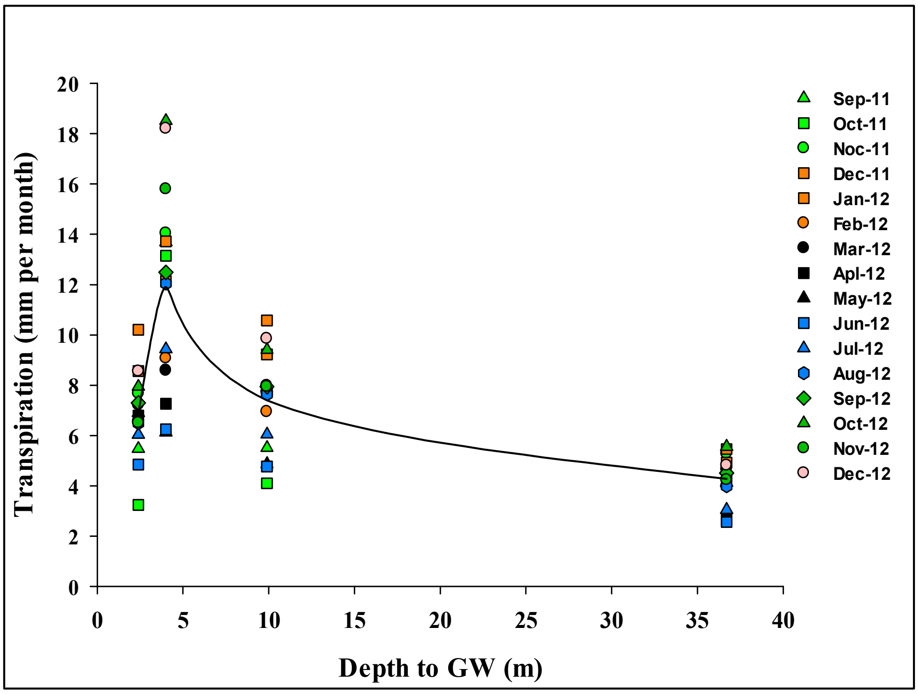


Figure 4-13: Monthly transpiration as a function of depth-to-groundwater (m)

Monthly total stand transpiration (for all tree species present) showed a pronounced peak at 4.3 m DGW, with rates of water-use declining rapidly to either side of 4.3 m groundwater depth (Fig. 4-13). Inter-monthly variability in monthly stand transpiration was largest at the 4.3 m site and least at the deepest groundwater site (37.5 m DGW).

Cumulative stand transpiration (all tree species present) and rainfall are presented for the year 2012 in Figure 4-14. Cumulative rain fall during 2012 at study area was 1188 mm. Total stand transpiration was maximal at site 4.3 m DGW (261 mm) and was minimal at the site 37.5 m DGW (95 mm). The slope of the increase in amount of transpiration was largest in summer and smallest in winter at all sites, which indicates that the amount of transpiration was most similar between sites during winter, except the site 4.3 m DGW where transpiration was always larger (Fig. 4-14).

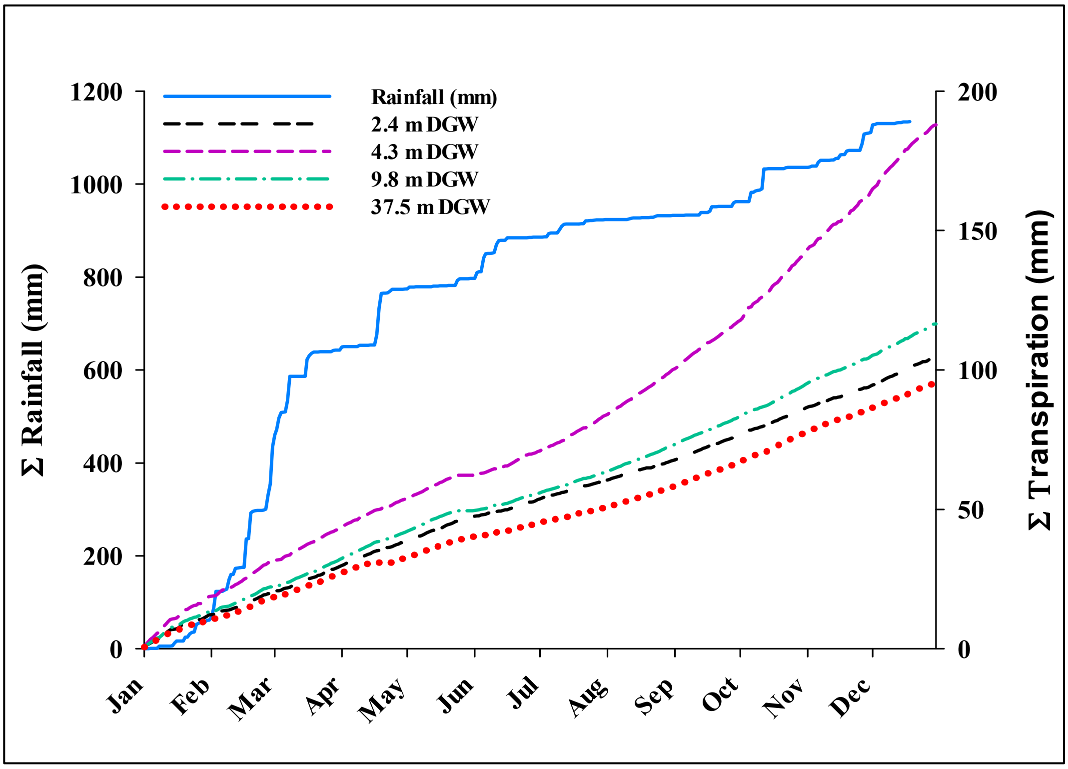


Figure 4-14: Cumulative stand transpiration at each site (all tree species present included) and rainfall in 2012.

Discussion

Climate and weather

Mean summer and winter temperatures were 16 and 7°C respectively (see Chapter 2), and mean summer and winter VPD were 0.45 and 0.25 kPa respectively. Thus the climate of these sites is best described as temperate mesic with warm summers and cool winters. Rainfall measured at the site in 2011 and 2012 was 32 and 11 % larger than the long-term average. Similarly, average daily net radiation was 62.73 and 61.70 MJ m^{-2} day^{-1} in 2011 and 2012 respectively (chapter 2), whilst the long-term average is 193 MJ m^{-2} day^{-1} (2000-2012; BoM, station no 68243). It is apparent that 2011 and 2012 were wetter, cooler and more humid than the long-term average values, which had the net effect of inhibiting transpiration.

Relationship between sapwood area and DBH

The relationship between tree size (DBH) and sapwood area was used to scale the sapflow measurements from individual trees to the stand-scale. A close relationship was found between sapwood area and DBH at all sites and for all species, which is consistent with the results of studies across a range of different species and ecosystems (Cienciala et al. 2000; Eamus et al. 2000b; Kelley et al. 2007). Sapwood area increased following a power function of increasing tree size (DBH; Fig. 4-3) as has been found in earlier studies (Gebauer et al. 2008; Meinzer et al. 2001). In the current study, the relationship between DBH and sapwood area was close (r^2= 0.77–0.97), thus making stem diameter a reliable predictor of sapwood area contributing to confidence in stand scale estimates of transpiration.

Sap velocity

The relationship between evaporative demand (which is a function of VPD, solar radiation and temperature) and sap velocity has been examined extensively for different species and environments (Rosado et al. 2012; Schipka et al. 2005; Zeppel et al. 2004). The low sap velocities observed in the present study in winter can be partially explained by low VPD, low temperature and short day length, which results in low solar radiation input and very low evaporative demand of the atmosphere. Sap velocity for all sites was higher during summer than winter, which is a function of increased evaporative demand, which arose because of the larger temperature, increased solar radiation input (up to a factor of 10 larger in summer than winter; see chapter 2) from a higher solar angle in summer than winter (Eamus et al. 2013b) and larger average VPD.

Transpiration

Both species (*E. piperirta* and *E. radiata*) growing at the shallowest groundwater site (2.4 m DGW) exhibited very similar diurnal patterns and rates of water-use. This agrees with studies by O'Grady et al (1999) and Kelley et al. (2007) who found convergence in transpiration rates between species within one site. In contrast, the various dominant species at all other sites exhibited a different rate of transpiration from the other species present even though there were no significant differences in sapflow density between species (Figs. 4-4 & 4-5 & 4-6). The differences in transpiration rate between species in mixed stands can be due to the species-specific differences in water-use (Bowden and Bauerle 2008; Bugmann 2001; Dierick and Hölscher 2009) or driven by total amount of sapwood area per ground unit area of that species (Jonard et al. 2011; Kumagai et al. 2007; Vertessy et al. 1997; Wullschleger et al. 2001). Considering the total sapwood area of each species within each site, the results of the current study shows the contribution of each species to stand level transpiration is largely driven by total sapwood area per unit of ground area rather than species-specific differences in sap velocity, in agreement with the study of Jonard et al. (2011).

Perhaps most importantly, the rate of transpiration (per unit ground area) was always larger for trees growing at a shallower groundwater site than for trees of the same species growing at the deeper groundwater site. Just as with inter-specific differences in transpiration, intra-specific differences across sites were the result of larger sapwood area per tree at shallower sites than at deeper sites, whilst sap velocities were not different between sites. Total stand transpiration at all sites and estimated for all species at a site, was low compared with some previous studies (Table 4-4). The maximum rate of canopy transpiration observed in the current study was 1.34 mm day^{-1} at site 4.3 m DGW, which is considerably lower than the maximum canopy transpiration in other woodlands in Australia (Carter and White 2009; Forrester et al. 2010; Zeppel 2006) (compare Table 4-4 and Table 4-3). However, the rates observed in the present study are comparable to rates observed at some other Australian studies (Mitchell et al. 2009; Roberts et al. 2001; Yunusa et al. 2010) and a study of an old plantation of *Eucalyptus* stand transpiration (Macfarlane et al. 2010; Roberts et al. 2001) in Australia. Similarly, stand transpiration rates in the current study are comparable to a temperate woodland receiving high annual rainfall (3482 mm) in New Zealand, which reached a maximum of 1.7 mm per day (Barbour et al. 2005). Low daily and annual transpiration rates have also been recorded in European studies (Wullschleger et al. 2001). The effect of high precipitation (Schuur and Matson 2001) and its combination with shallow groundwater on forest function is poorly studied in humid ecosystems. The present study demonstrates that, given that annual stand water-use was much smaller than rainfall, groundwater-use was unlikely, which contrasts with patterns of water-use in GDEs of arid and semi-arid regions (Benyon et al. 2006; Lamontagne et al. 2005; Scott et al. 2000b). It remains to be determined whether a prolonged drought (such as that observed in the eastern coast of Australia, 2001 – 2007), will significantly increase the uptake of groundwater resources. It is possible, however, that the larger BA observed at the three shallowest sites reflects the past input of groundwater to the growth and structure of the woodland at the shallowest site during dry periods, especially during the prolonged drought experienced in eastern Australia in 2001- 2007 (see below for further discussion of this point.

The deepest and shallowest depth-to-groundwater sites had very similar transpiration rates (per unit ground area), despite the shallowest site maintaining a much larger leaf area index (LAI of 3.7 compared to 0.8) and basal area (BA of 82 compared to 32 m^2 ha^{-1}) than the deepest water table site. Leaf area index has been considered to be one of the most important factors in determining differences in transpiration between stands (Bréda and Granier 1996; O'Grady et al. 1999; Schipka et al. 2005), although Moore et al. (2004) recorded a larger rate of transpiration in stands with low LAI than high LAI in a riparian forest in Western Oregon, USA (maritime climate). Similarly, stands with high basal area are intuitively expected to transpire more water than stands with a low basal area (Marshall and Chester. 1992), although examples to the contrary can be found. One such example was identified by Macfarlane et al. (2010), who compared old and regrowth *Eucalyptus* forests and found smaller transpiration rates in the older forest despite their larger basal area.

Preceding the present study described in this chapter, a prolonged drought was experienced across the eastern coast of Australia (2001–2007). Even though groundwater-use had not been explicitly demonstrated in the present study, groundwater access during drought was inferred because of the observed longer-term accumulation of biomass and leaf area (see chapter 3) at the shallower sites than the deeper site. Thus, it is postulated that the larger basal area and leaf area index of the two shallowest sites were supported in the past by access to shallow groundwater, especially during relatively dry periods prior to the start of this study, whilst the lower basal area and leaf area index of the two deeper groundwater sites (9.9 and 37.6 DGW) reflects minimal or zero access to groundwater. However, with the abundant rainfall during the 2011–2012 study period, the limitation imposed by the lack of groundwater at the deepest site (37.6 m) was removed by an abundant supply of soil moisture in the upper soil profile.

Transpiration was largest at site 4.3 m depth-to-groundwater during the study period. At this site leaf area index and basal area was comparable with site 2.4 m DGW (shallowest groundwater site). These two sites are assumed to have access to shallow groundwater, given the known rooting depth of *Eucalyptus* in Australia (10 m; Canadell et al. (1996); 8 m Cook et al. (1998)). Considering the similarity in structure (basal area and LAI) of the two stands at the two shallowest sites and assuming similar access to groundwater, what might explain the significantly larger rate of transpiration for the 4.3 m site compared to that of the 2.4 m site? I suggest that this can be explained by differences in total rooting volume available at the two shallowest sites. At the shallowest site flooding of the upper 2 m of the soil profile was evident for many months of 2011 and 2012. This is likely to result in oxygen deficits (anoxia) for roots. Oxygen stress during flooding is the result of reduced oxygen conductivity in saturated soil and has been extensively documented (Brolsma and Bierkens 2007; Rodriguez-Iturbe et al. 2007; Schuur and Matson 2001). Oxygen deficits inhibit water uptake by roots, often causing reduced stomatal opening similar to the effect of water deficits (McAinsh et al. 1996; Sojka 1992). Such impacts result in reduced rates of transpiration (Baird et al. 2005; Cleverly 2013). At the site 4.3 m DGW site, flooding was not observed because the water table was deeper than at the shallowest site and consequently anoxia, reduced water uptake and reduced stomatal aperture were presumably not evident in the trees. Consequently rates of transpiration at the site 4.3 DGW exceeded those of the shallowest site.

Finally, I hypothesis that for the 9.9 m and 37.6 m sites, stand transpiration was low (compared to the 4.3 m site) through a combination of low basal area and LAI (arising from the absence of access to groundwater) and a low vapour pressure deficit and solar radiation receipt, arising from the cooler and cloudier weather conditions prevalent during the study. Low VPD and solar radiation reduce stomatal aperture and reduce transpiration and this can also mask the differences in leaf area index across these sites.

Low transpiration (especially in the shallowest site) may not necessarily be associated with low productivity, as evident at the two shallowest sites, which maintained a larger BA and LAI than the deeper sites. Having access to groundwater at 2.4 and 4.3 m means that there is likely to be a lower demand for investment in below-ground biomass in these trees. This may partially explain why there was a larger above-ground biomass at the two shallow water table sites compared to the two deepest groundwater sites. Lower investment in below-ground biomass can result in larger above-ground biomass (Comeau and Kimmins 1989).

Monthly stand transpiration rates *versus* depth-to-groundwater showed a peak in transpiration at 4.3 m depth-to-groundwater. Thus, the shallowest water table coupled to abundant rainfall was as limiting to transpiration as the presumed lack of groundwater at the deepest site. This observation is consistent with Baird et al. (2005) who also found this pattern. Similarly, Schipka et al. (2005) found the same pattern in the response of transpiration from a mature stands of *Fagus sylvatica* of a European temperate forest. Indeed they found a negative relationship between rainfall and transpiration when rainfall was larger than or smaller than an optimum. From the current study it can be seen that in high rainfall years (as observed in the present study), the optimal depth for maximum rates of stand water-use (and therefore, possibly, maximal productivity given the exchange of water for carbon through stomata), is not the shallowest nor the deepest depth-to-groundwater, rather there is an optimal depth-to- groundwater, which in this study was approximately 4 m.

The effect of abundant rainfall and shallow groundwater on vegetation structure and function in humid ecosystems is relatively poorly understood. In such an environment it is likely that excessive accumulation of water in the upper soil profile exceeds vegetation demand and constrains plant growth and productivity. Further investigation is required to substantiate this hypothesis, including investigations of relationships amongst root growth, anoxia and water uptake.

Water balance

The distribution of the four sites on the Budyko-curve clearly showed that evapotranspiration (ET) at these sites was limited by energy and atmospheric demand (Fig. 4-11), rather than water supply. This conclusion is supported by the observed small VPD and net radiation during the study period (Chapter 2). The absence of any evidence of moisture availability (either from soil or groundwater supplies) limiting ET in this study is in contrast to observations in arid or semi-arid regions where water supply limits ET and neither sunlight nor atmospheric demand limit ET and ET_{act} is typically 34–66% of ET_p (Devitt et al. 1998; Kalthoff et al. 2006). In the general complementary relationship between ET_{act} and ET_p, this study is placed well within the bounds of a "wet environment" where ET_{act} and ET_p converge on the wet environment ET rate (Jaksa et al. 2013). Results of the current research where all four sites were located close to the 1:1 energy limited line, are comparable to a Budyko curve analyses of 35 sites that were evaluated by Jones et al. (2012) in which all of the mesic ecosystems fell near the 1:1 energy limitation line.

In 2012, total stand transpiration was 21–43% of ET_0, which differed between sites as a function of LAI (cf. Chapter 7). Although it was assumed that overstorey transpiration would be a major component of the water balance, total tree transpiration from canopies was as small as 8% of annual rainfall (site 37.5 m DGW) rising only to 15% at site 4.3 m DGW. The small contribution of overstorey transpiration to the water balance indicates that 1) ET_0 was overestimated and 2) other pathways for discharge of rainfall (i.e., run-off, evaporation, or transpiration by the understorey) contributed significantly to the water balance of the sites. In the first case, computation of ET_0 assumes well-illuminated vegetation (Allen et al. 1998), which was often not the case in this study (Chapter 2) because of the large rates of rainfall and associated cloud cover. Over-estimation errors in ET_0 have been identified when ET is small (Cleverly et al. 2013; Steduto et al. 2003). Similarly in the current study, ET_0 (421–612 mm yr^{-1}, Table 2) was relatively low in comparison to neighbouring sites (within 100–150 km) where ET_0 was 914 mm (Castlereagh, NSW, Australia) and 1563 (Liverpool plains NSW, Australia) during drought (2003–

2007; Sun et al. 2011). Thus, some but not all of the difference between total stand transpiration and ET_0 were attributed to over-estimation of ET_0.

The remaining imbalance between total stand transpiration and ET_0 was attributable to run-off, groundwater recharge, evaporation, and the role of understorey transpiration (Baldocchi and Ryu 2011). The amount of run-off from the study area was measured in for this study. Using data from a comparable area in Illarwarra region, NSW, annual run-off was approximately 30% of total rainfall (Department of Environment 2010). Alternatively, mean annual runoff (RO) can be estimated as the residual of precipitation (P) and ET_p (Budyko 1974; Zhang and Chiew 2012) since:

$$RO = p - \left\{p\left[1 + \exp\left(-ET_P/P\right)ET_p \tanh\left(ET_p/p\right)\right]\right\}^{0.5}$$

In the present study, estimated values of RO using the Zhang and Chiew (2012) equation were 949–759 mm, or 63–59% of total rainfall. Thus, the small values of ET_p /P observed in the present study are related to large values of RO, which has been generally observed in south-eastern Australia across catchments where ET_p / P is less than 1.2 (Zhang and Chiew 2012).

In addition to run-off losses, several important forms of ET that were not measured directly contribute to the water balance: evaporation of intercepted rainfall, evaporation from wet surfaces, and understory transpiration (Baldocchi and Ryu 2011). Evaporation of intercepted rainfall can contribute significantly to the water balance of a site, ranging from 5% in a tropical savanna (Hutley et al. 2000), increasing to 10–15% in open canopy forests and woodlands (Mitchell et al. 2009; Zeppel et al. 2006), and up to 38% in closed forests and woodlands of similar structure to the current study (Feikema et al. 2010; Zeppel et al. 2006). In contrast to interception, understory transpiration increases with decreasing overstorey canopy LAI from as little as 10% in dense forests to as much as 80% in tropical savannas

(Baldocchi and Ryu 2011; Barbour et al. 2005; Hutley et al. 2000). Understorey transpiration from a nearby site (within 100 km) were shown to be approximately (30% of total ET; Zeppel et al. 2006). Large ecohydrological studies that are catchment-wide and interdisciplinary and which take into account the various forms of transpiration, evaporation, run-off and recharge are required to better understand the water balance of sites such as the Kangaloon bore-field. A summary of each site's water balance is presented in chapter 7 of this thesis.

Table 4-4: Values of average daily transpiration rate (T_{stand}; mm day^{-1}), LAI and annual rainfall (mm) of different sites taken from the literature.

Species	**Site location**	**Climate**	**Ecosystem type**	**LAI**	**Rainfall (mm)**	**T_{stand} (mm day^{-1})**	**Reference**
Eucalyptus globulus	VIC-Australia	Temperate	Plantation	1-3.5	700	0.4-1.9	(Forrester et al. 2010)
Eucalyptus capillosa	WA-Australia	Semi-arid	Native woodland	0.66	361	0.2-0.8	(Mitchell et al. 2009)
Eucalyptus miniata ***Eucalyptus tetrodonta***	NT-Australia	Wet-Dry tropics	Savanna	0.7-1	2815	0.87	(Kelley et al. 2007)
Coniferous Callitris ***Eucalyptus spp.***	NSW-Australia	Temperate	Open woodlands		554-1062	1.5	(Zeppel et al. 2006)
Eucalyptus sieberi	NSW-Australia	Temperate maritime	Forest	3.6 4 3.4	900	2.2 1.4 0.8	(Roberts et al. 2001)

Species	**Site location**	**Climate**	**Ecosystem type**	**LAI**	**Rainfall (mm)**	**T_{stand} (mm day^{-1})**	**Reference**
Eucalyptus marginata	WA-Australia	Mediterranean	Forest	0.88	1100	2.5-2.8	(Silberstein et al. 2001)
Mixed species	VIC-Australia	Temperate	Forest	0.8-1.3	1263	0.71	(Gharun et al. 2013)
Darcydium cupressinum	New Zealand	Temperate	Coniferous rainforest	2.9	3400	1.8	(Barbour et al. 2005)
Pseudotsuga menziesii ***Alnus rubra*** ***Tsuga heterophylla***	Oregon-USA	Maritime	riparian forest	12.1 10.6	2300	1 3.5	(Moore et al. 2004)
Taxodium distichum	Carolina-USA		Flooded forest	2.2	1140	1.3	(Oren et al. 1999)

Chapter 5 The hydraulic architecture of *Eucalyptus* trees growing across a gradient of depth-to-groundwater

Introduction

Heterogeneity in water resources is an important driver in causing variation in plant structure and function (Anderegg et al. 2013; Magnani et al. 2002; Williams et al. 1996). Plants use different strategies to adapt to their habitat and these strategies occur at different temporal scales as a result of phenotypic plasticity or genetic differentiation (Carter and White 2009; Choat et al. 2007). However, it is difficult to determine which of these adaptations have genetic or phenotypic origins as most comparative field studies on plant adaptations to environmental gradients compare different species and taxa or make comparison across different sites (Carter and White 2009; Lewis et al. 2011; Phillips et al. 2010).

In response to differing water availability, plants adapt a variety of strategies which can result in changes in their hydraulic architecture. Hydraulic architecture describes the structure and attributes of tissues engaged in uptake, conduction and loss of water in a plant (Cruiziat et al. 2002). The hydraulic architecture of a plant can control the rate of flow of water from roots to leaves and consequently has the potential to influence a plant's water potential, stomatal conductance, rate of photosynthesis, structure, growth, rate of water-use (Choat et al. 2007; Macinnis-Ng et al. 2004; Santiago et al. 2004b) and also their distribution across a landscape (Choat et al. 2012; Pockman and Sperry 2000; Willson et al. 2008). Differences in hydraulic architecture within and between species may vary across habitats having different water availabilities. Hydraulic architecture also varies seasonally (Zeppel and Eamus 2008)

Adjustments in hydraulic architecture can be made at many levels, from cellular to tissue, to whole tree, to stand level (Addington et al. 2006). The key components of hydraulic architecture are hydraulic conductance of xylem (defined as the relationship between flow rate (g s^{-1}) and driving force (MPa) for a plant organ e.g. root and stem), Huber value (defined as the ratio of sapwood area to leaf area), leaf area, sapwood density and sapwood area. Xylem embolism and the sensitivity to embolism are also aspects of hydraulic architecture of a plant. Environmental drivers such as water stress have strong impacts on hydraulic properties of plants. Strategies plants employ which adjust their hydraulic architecture in response to water stress are important in their growth and survival (Awad et al. 2010). Therefore understanding these strategies will help us to predict the response of plants to variations in water availability. Because the hydraulic conductance of xylem exerts a strong influence on stomatal conductance and as a result, photosynthesis and carbon economy (Hubbard et al. 1999; Hubbard et al. 2001; Nardini and Salleo 2000), understanding hydraulic properties of plants also helps to understand variation in leaf-level traits (Santiago et al. 2004b).

One of the components of the hydraulic architecture of plants, hydraulic conductivity (defined as hydraulic conductance per unit length of conducting pathway), depends greatly on xylem structure (Dettmann et al. 2013; Hacke et al. 2006; Sperry 2003). Changes in xylem conduit structure have the potential to alter hydraulic conductivity, Huber value, wood density and resistance to embolism (Hacke et al. 2006). Generally, xylem hydraulic conductivity of plants growing in mesic environments is larger than that of plants growing in xeric ones (Corcuera et al. 2011; Van der Willigen and Pammenter 1998), although contradictory trends have been observed in Australian temperate woodlands (Taylor and Eamus 2008) and *Pinus plaustris* Mill plantations in the USA (Addington et al. 2006). Drought tolerant plants also tend to exhibit lower branch conductivity per unit leaf area and sapwood area (Preston and Ackerly 2003; Van der Willigen and Pammenter 1998), lower transpiration rates (Grulke et al. 2003), larger Huber value and larger resistance to embolism (Canham et al. 2009) than plants intolerant to drought.

The Huber value of trees is possibly a plastic trait (Choat et al. 2005; Prior and Eamus 1999; Tyree et al. 1991) and it is closely correlated to xylem hydraulic conductivity. Decreases in sapwood-specific conductivity under water stress inversely correlate with the Huber value (Carter and White 2009; O'Grady et al. 2009). The balance between Huber value and sapwood-specific conductivity maintains the capacity of stems to transport water to leaves at a sufficient rate to ensure that leaf water potential, stomatal behaviour and leaf gas exchange are not greatly compromised (Carter and White 2009; Macinnis-Ng et al. 2004). Generally plants occupying drier habitats maintain a larger H_V than plants growing in wetter areas (Canham et al. 2009; Choat et al. 2007; Shumway et al. 1991).

During periods of transpiration water moves under negative pressure through the xylem and as a result the xylem is vulnerable to cavitation. Under high xylem tension, cavitation takes place as air infiltrates into water filled vessels (or tracheids) through inter-conduit pits (Ambrose et al. 2010; Cochard 2002; Sperry and Saliendra 1994). The negative pressure at which cavitation occurs is an indication of a plant's tolerance to drought stress (with plants highly drought tolerant experiencing cavitation at a more negative pressure value compared with drought sensitive plants; (Melcher et al. 2003)). The point at which xylem embolism occurs is a function of hydraulic architecture and soil and atmospheric water status. The occurrence of cavitation (embolism formation) reduces stem or branch hydraulic conductance, subsequently limiting plant water transport and carbon uptake (Awad et al. 2010; Cochard 2002; Sperry and Saliendra 1994; Taylor and Eamus 2008; Vogt 2001). Plants can recover from embolism by producing new xylem conduits, which is a relatively slow process, or by dissolving gas-filled conduits into the surrounding liquid phase (Franks et al. 2007; Hacke et al. 2001b; Holbrook and Zwieniecki 1999; Nardini et al. 2011), which is a faster process. However, whether recovered xylem is as functional as new xylem is still under debate (Hacke et al. 2001b). If a plant experiences water limitation for a prolonged period of time cavitation fatigue within the plant may occur and the plant is then more susceptible to drought-induced mortality, although more often, the embolism is repaired and plant death is avoided (Ambrose et al. 2010; Anderegg et al. 2013; Choat et al. 2007; Macinnis-Ng et al.

2004; Meinzer et al. 2009; Sack and Holbrook 2006; Sperry 2000). Regulation of stomatal conductance to avoid xylem cavitation results in a reduction in CO_2 supply to leaves and hence reduced rates of photosynthesis. This is a selective trade–off for plants (Ambrose et al. 2009).

Vulnerability to cavitation is an important parameter to consider in order to understand plant phenotypic plasticity (Cruiziat et al. 2002) and tolerance to drought stress (Cochard 2002; Sperry and Saliendra 1994). Vulnerability to xylem embolism varies significantly between plant species and within species across sites (Awad et al. 2010; Cruiziat et al. 2002; Kolb and Sperry 1999; Macinnis-Ng et al. 2004). Cavitation resistance increases with aridity (Maherali et al. 2004). Consequently plants growing in humid environments tend to experience a larger proportion of embolism per unit decline in leaf water potential than plants growing in arid and semi-arid environments (Alder et al. 1996; Choat et al. 2007; Cruiziat et al. 2002; Macinnis-Ng et al. 2004). However, xylem vulnerability is not always directly related to aridity, because plants exist on a spectrum of xylem efficiency and hydraulic safety (which is proportional to species-specific values of minimum daily stem water potential which is controlled by stomatal control of transpiration), regardless of aridity (Meinzer et al. 2009).

The relationship between xylem resistance to embolism and differences in availability of water indicates that plant hydraulic architecture plays a part in determining species ecological boundaries (by determining the adaptation ability of individuals) and consequently their habitat and survival (Cruiziat et al. 2002; Martínez-Vilalta and Piñol 2002; Tyree and Ewers 1991). Understanding the hydraulic adjustment of trees in response to differences in environmental factors such as water availability, will improve our ability to predict tree function, growth and survival under different environmental conditions. Although there have been many multi-species studies of hydraulic properties at a single site (Cochard 1992; Poorter et al. 2010; Zeppel and Eamus 2008), or studies of a single species across multiple sites, or studies of different species within different sites (Addington et al. 2006; Taylor and Eamus 2008), patterns in the responses of hydraulic traits to differences in water availability across sites within a single climatic envelope is less frequently examined.

Despite the importance of comparative studies in providing insight to plant adaptive strategies, few studies in Australia have focused on inter- and intra- species comparisons of hydraulic architecture in groundwater dependent ecosystems (Canham et al. 2009; Carter and White 2009; Froend and Drake 2006). The study presented in this chapter is one the few that compares closely related species from the same widespread genus, *Eucalyptus,* within a single climate regime and provides an opportunity to compare both within and between species across sites having different access to groundwater.

This study investigated intra-specific and inter-specific differences in hydraulic properties (branch hydraulic conductivity, Huber value, sapwood density and xylem embolism) in a mesic environment across a gradient of groundwater availability.

The aims of this study were to answer the following questions:

1- Are there differences in hydraulic properties within species across sites where depth-to-groundwater varies?
2- Are there significant seasonal differences in hydraulic properties of species across and within sites where depth-to-groundwater varies?
3- Are there significant differences in hydraulic properties between species within and across sites where depth-to-groundwater varies?

Methods

Maximum branch hydraulic conductivity and xylem vulnerability curves

1- Bench dehydration method

Maximum hydraulic conductivity of branches (K) and xylem vulnerability curves were measured on the dominant tree species from each of the four sites (sites with 2.4 m, 4.3 m, 9.8 m and 37.5 m DGW) during summer and winter. Measurements were conducted at sites where rates of tree water-use were measured (that is, sap flow sensors installed). For summer measurements the bench dehydration method was used (following the method of Sperry et al. (1988)) while winter measurements were completed using the air injection method. The reasons for this are given below.

Terminal branches (between 40-60 cm length and 3-5 mm diameter) were collected from three individual trees per species, re-cut immediately under water and placed up-right in water bottles (the basal end was submerged in water). Samples were covered with a black plastic bag to minimise transpiration until measurements started in the laboratory. Exposed (outer canopy) branches were collected from average sized trees in each site, from a mid-canopy height in December and January 2012/2013.

Maximum vessel lengths of four species were measured by passing low-pressure nitrogen gas through freshly cut branches. Nitrogen gas was forced through branches from the basal end while the distal end was held under water. The branch was gradually cut back until bubbles appeared from the distal end and then the length of the remaining branch was recorded as the maximum vessel length (5 branches per species).

Terminal branches for use in the determination of xylem vulnerability curves were selected to be at least 10% longer than the maximum vessel length, as suggested by Froend and Drake (2006). Two leaves from each fully rehydrated branch were cut and their water potential was immediately measured using a pressure chamber (Model 3000, Soil moisture Equipment Crop., Santa Barbara, CA). Both ends of all excised branches were trimmed with a fresh razor blade to remove superficial air blockages (about 0.5 cm). Next, all leaves were removed under water at the junction of the petiole and branch using a sharp razor blade and then leaf scars were sealed using glue and parafilm to stop water flow out through them. The basal end was fitted quickly through the seal in the vacuum chamber lid and attached to a graduated 1 mL pipette via flexible tubing. This pipette was filled with acidified filtered and degassed water (pH~ 2 HCl, 0.2µm). Conductance measurements were made using two custom made vacuum chambers. The vacuum chambers were constructed by PVC pipe (105 cm long and 26 cm diameter) and each could accommodate 3 branches (Fig. 5-1).

Figure 5-1: The vacuum chamber used for measurements of branch hydraulic conductance.

Six branches were inserted in the two chambers. Hydraulic conductance was measured by decreasing the pressure inside each vacuum chamber sequentially to four levels (ΔP = -20, -30, -40 and -50 kPa) and this was measured with a vacuum gauge. The acidified water was pulled through the branch in the same direction as the normal transpiration pathway by difference in pressure between inside and outside (atmospheric pressure) of the chamber. At each pressure level, the flow rate of acidified, filtered and degassed water through each branch (ml s^{-1}) was measured by recording the rate of change in the water column in each pipette with a stop watch. Branches were given 10 minutes to equilibrate to each pressure level following Taylor and Eamus (2008).

Hydraulic conductance (k) (kg s^{-1} MPa^{-1}) was calculated as the slope of the linear relationship between flow rate (kg s^{-1}) and pressure difference (MPa) using a linear regression. After the initial measurements of k, branches were flushed with acidified, filtered and degassed water at a positive pressure of 175 kPa for 30-40 minutes to remove any emboli in the branch. The pressure was then released and branches were given a further 15 minutes to allow tubing and xylem vessel to equilibrium before measurements of maximum conductance of each branch.

The remaining branch samples were removed from their plastic bag and allowed to dehydrate under laboratory conditions. The water potential of two leaves from each of 6 branches was measured (as described above). The branches were then covered in aluminium foil to equilibrate across the total branch for 30 minutes. For each new set (i.e species) of branches initial and maximum hydraulic conductance were measured as described above. Having calculated the maximum and initial conductance, percentage loss in conductance (PLC) was calculated using following equation (Froend and Drake 2006; Taylor and Eamus 2008):

$$\%PLC = \frac{k_{\max} - k}{k_{\max}} \times 100 \qquad \text{(Equation 1)}$$

Where k_{max} is the maximum conductance of the branch.

The percentage difference between the initial and maximum values was considered to represent the percentage loss in conductance due to embolism. Vulnerability to xylem embolism was determined as the relationship between percentage loss of hydraulic conductance and xylem water potential. The remaining branches were covered in aluminium foil, wrapped in dark plastic bags and kept at 4°C overnight. Measurements continued until 90% or more of branch conductance was lost.

Maximum hydraulic conductivity (K; kg m s^{-1} MPa^{-1}) was calculated by multiplying conductance (kg s^{-1} MPa^{-1}) by branch length. Conductivity was expressed on both a sapwood area (K_S; kg m m^{-2} s^{-1} MPa^{-1}) and leaf area (K_L; kg m m^{-2} s^{-1} MPa^{-1}) basis.

Sapwood area was measured after the maximum conductance measurements. Bark was removed from the basal end of branch and dye (Methylphenazin hydrochloride) was forced through the branch using a syringe. This allows easy differentiation of the active xylem (sapwood) and non-conductive tissues (pith). The diameter of sapwood and pith was measured with a digital caliper to calculate sapwood area. All the leaves excised from each branch were collected and leaf area was measured using a leaf area meter (WinDIAS, UK).

To confirm that the length of the branches used in these analyses were longer than the maximum vessel length a number of branches was randomly selected and their maximum vessel length was measured by passing nitrogen gas through the branch while the distal end of the branch was held under water and was cut back until bubbles were seen. Results confirmed that all measured branches were longer than maximum vessel length (data not shown). Branch length varied from 0.35 to 0.6 m and was species dependent.

2- Air injection method

For winter measurements of xylem vulnerability, branches from the dominant two species from each of two sites were measured by both the dehydration and air injection method. The air injection method used a commercially available Digital Cavitation Chamber Instrument (Model 1505D-EXP, PMS Company, Albany, USA) (Fig. 5-2). A comparison of both methods showed no statistically significant differences (consistent with Sperry and Saliendra (1994)) and because of the decreased measurement time using the air injection method, this method was used for winter measurements. The air injection method also makes it possible to measure the progressive loss of hydraulic conductance on a single stem, thereby reducing variability in the data.

Branches were collected and returned to the laboratory following the same procedure as described for the dehydration method for summer measurements. Once back at the laboratory, all leaves were excised from the branches and basal and distal ends were trimmed under water. A small length of bark was removed around the central part of the branch and the sapwood was lightly notched using sharp blade to facilitated air injection into the vascular system (Sperry and Saliendra 1994). The mid-region of a branch was then inserted into the chambers with both cut ends protruding outside of the chamber. Branches were flushed for 30-40 minutes with by acidified, filtered and degassed water which was forced through branches by compressed nitrogen (175 kPa). After this flush (to remove potential emboli) branches were given 15 minutes to relax, before measurement started. Maximum hydraulic conductance was determined by measuring the rate of flow of solution through the sapwood induced by a small (≈ 9.8 kPa) positive pressure generated from a 1 m hydraulic head. After the initial measurements of conductance, cavitation was induced by increasing the air pressure inside the chamber for 5 minutes after which time the pressure was released and the branches were allowed to equilibrium. Conductance was measured again following the same procedure as just described. After each measurement of conductance the pressure inside the chamber increased incrementally until 90% of initial conductance had been lost due to embolism. Percentage loss on conductance was calculated using Equation 1. Sapwood area, length of branches and total leaf area were also measured as described for the dehydration method. Vulnerability curve were plotted using xylem pressure *versus* percentage loss in conductance. Data were fitted with exponential-sigmoidal functions (Equation 2):

$$PLC = 100/\left(1+\exp\left[a\left(\psi_{\max} - b\right)\right]\right) \qquad \text{(Equation 2)}$$

Where a is the gradient of a linear transformation and b is the pressure at which PLC_{50} was reached (Froend and Drake 2006; Pammenter and Van der Willigen 1998).

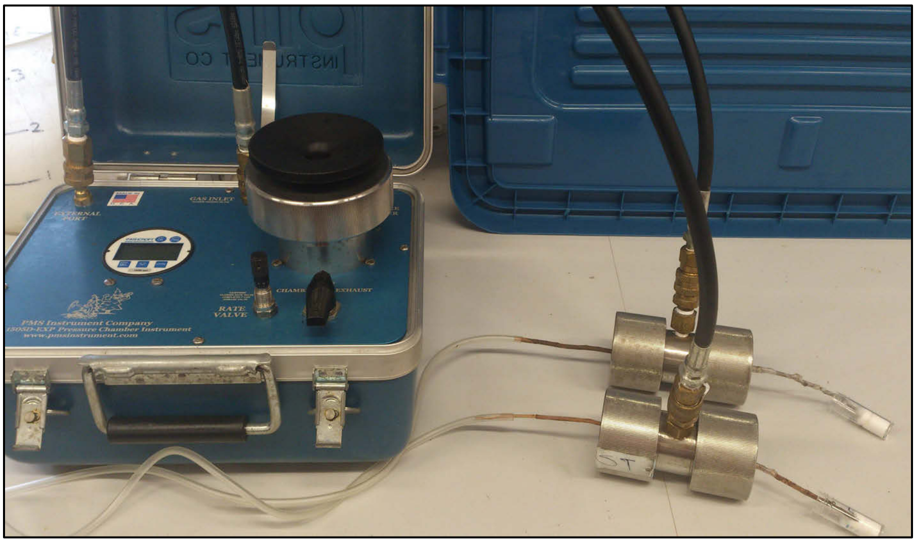


Figure 5-2: Digital Cavitation Chamber Instrument (Model 1505D-EXP, PMS Company, Albany, USA).

Huber value

The Huber value (H_V; $m^2\ m^{-2}$) is defined as the ratio of sapwood cross sectional area ($A_{sapwood}$) to leaf area (A_{leaf}). The H_V was measured for all branches used to determine hydraulic conductance. The Huber value was also calculated for five larger branches per tree and three trees per species. The dominant species from each site were measured.

$$H_V\ (m^2\ m^{-2}) = A_{sapwood} / A_{leaf} \qquad \text{(Equation 3)}$$

Sapwood density

Two sapwood samples were extracted (at a height of 1.3 m) from the stem of five trees per species from each site, using increment corers. Immediately after collection samples were sealed in plastic straws and returned to the laboratory in a cooler. Once in the laboratory each core was placed in water for half an hour to ensure full hydration. After removal from water, branches were surface dried and their fresh volume measured following method described by (Ilic 2000). The samples were then oven dried and the dry mass measured. Sapwood density (g cm^{-3}) was calculated as the ratio of dry weigh *versus* fresh volume.

Data analysis

Leaf specific and sapwood specific conductivity of branches, Huber value, sapwood density and vulnerability to xylem embolism were measured for four tree species across the four sites and comparisons were made between species within sites and also within species across sites. Differences between species and within species across sites were determined using two-way ANOVA. Normality of all data sets was confirmed using the Kolmogorov-Smirnov test. Where significant differences were identified *post hoc* Tukey-HSD tests were performed. The relationship between depth-to-groundwater and xylem sensitivity was determined using regression analysis. Analyses were performed using IBM SPSS STATISTICS version 19, Armonk, NY, USA. Significant differences at $P<0.05$ are reported.

Results

Between sites comparisons within a species

E. piperita

There was no significant seasonal change in the H_V of *E. piperita* within sites. However, H_V increased as depth-to-groundwater increased for this species (F= 7.96, df = 3,175; p< 0.001; Fig. 5-3a).

Leaf specific hydraulic conductivity (K_L) for *E. piperita* ranged between 2.9 to 4 $\times 10^{-4}$ kg m s^{-1} MPa^{-1} m^{-2} in summer and between 1.9 to 3 $\times 10^{-4}$ kg m s^{-1} MPa^{-1} m^{-2} in winter. Leaf specific hydraulic conductivity showed no significant differences across sites (F= 1.54, df = 2,145; p= 0.20). However, K_L decreased significantly in winter compared to summer within all sites for this species (F=11.94, df = 1,146; p=0.001; Fig. 5-4a). Sapwood specific conductivity (K_S) ranged between 1.7 to 2.33 kg m s^{-1} MPa^{-1} m^{-2} in summer and between 0.87 to 1.41 kg m s^{-1} MPa^{-1} m^{-2} in winter. There were no significant differences in sapwood specific conductivity (K_S) between sites (F= 0.59, df = 3,151; p= 0.61), however K_S was significantly smaller in winter than summer across all but the deepest depth-to-groundwater site (F=2.89, df = 1,40; p= 0.09; Fig. 5-5a). The maximum decline in conductivity for both K_L and K_S in winter was recorded at the shallowest groundwater site and the minimum seasonal decline recorded at the deepest water-table site (37.5 m DGW).

The xylem vulnerability curve of *E. piperita* showed no differences across sites in summer (Fig. 5-6a). However, during winter, trees at the shallowest groundwater site were more sensitive to cavitation than trees growing at the remaining three sites (Fig. 5-7a). During winter PLC_{50} significantly decreased as depth-to-groundwater increased (F=32.47, df = 1,3; p=0.02, r^2= 0.94) and the PLC_{50} ranged from -0.69 MPa at the 2.4 m DGW to -1.11 MPa at the 37.5 m DGW site. Consistent with the results of conductivity, both PLC_{50} and PLC_{88} were more negative in summer than in winter (Table 5-1).

E. globoidea

Depth-to-groundwater (F= 5.35, df = 3,173; p< 0.001,) and seasonality (F= 13.91, df = 1, 175; p= 0.001,) had significant impacts on H_V of *E. globoidea*. Huber value was significantly larger (26% on average) at the two deeper groundwater sites (9.8 m and 37.5 m DGW) during winter compared with summer (Fig. 5-3b). Huber value varied little across sites in summer.

Mean leaf specific hydraulic conductivity (K_L) ranged between 2.5 to 4.4 $\times 10^{-4}$ kg m s^{-1} MPa^{-1} m^{-2} in summer and between 1.9 to 2.9×10^{-4} kg m s^{-1} MPa^{-1} m^{-2} in winter. The minimum seasonal change occurred at the 37.5 m DGW while the largest seasonal decreases were observed at the two shallowest groundwater sites. Leaf specific hydraulic conductivity (K_L) was significantly smaller in winter than summer at three of the four sites 2.4, 4.3 and 9.8 m DGW (F=10.44, df = 1,126; p= 0.002, Fig. 5-4b). Average K_S of *E. globoidea* across sites ranged between 1.25 to 1.7 kg m s^{-1} MPa^{-1} m^{-2} in summer and between 0.67 to 1.23 kg m s^{-1} MPa^{-1} m^{-2} in winter. The K_S of *E. globoidea* was not significantly different between sites (F= 2.08, df = 3,133; p= 0.10, Fig. 5-5b). Seasonality had a significant impact on K_S (F= 20.02, df = 1, 135; p< 0.001) and at all sites K_S was lower during winter but was only statistically lower in winter at two sites; 4.3 m DGW (F= 20.14, df = 1, 35; p< 0.001) and 9.8 m DGW (F= 18.36, df = 1, 35; p<0.001; Fig. 5-5b).

Branches of *E. globoidea* growing at the 4.3 m DGW site were more vulnerable to embolism than the other three sites in summer (Fig. 5-6b) as reflected in a larger PLC_{50} and PLC_{88} (Table 5-1). There was no significant relationship between PLC_{88} with depth-to-groundwater during summer or winter for this species. However, the relationship between PLC_{50} and depth-to-groundwater was significantly different from 1:1 in summer (F=22.79, df = 1,3; p= 0.04; r^2= 0.91) and PLC_{50} decreased from -0.87 MPa to -1.52 MPa as depth-to-groundwater increased.

E. sieberi

The Huber value of *E. sieberi* did not show any significant difference across sites (F= 2.9, df= 2,58; p= 0.06). At the two deepest groundwater sites H_V increased significantly (16% at site 9.8 m DGW and 44% at site 37.5 m DGW respectively) in winter compared to summer (Fig. 5-3c).

Depth-to-groundwater did not have a significant impact on conductivity (either K_S or K_L) of *E. sieberi* but both K_S (F=14.01, df = 1,43; p=0.001) and K_L (F=10.36, df = 1,43; p=0.002) were significantly larger (about 3 fold) in summer than in winter at all sites (Fig. 5-4c and Fig. 5-5c). Species average across sites for K_L ranged from 5 to 5.6 kg m s^{-1} MPa^{-1} m^{-2} $\times 10^{-4}$ and K_S ranged between 2.6 to 2.79 kg m s^{-1} MPa^{-1} m^{-2} in summer.

The xylem vulnerability curve for this species showed that trees at the deepest groundwater site (37.5 m DGW) were more resistant to cavitation in both seasons than trees of the same species at shallower groundwater sites (Figs. 5-6c, 5-7c). Thus PLC_{50} and PLC_{88} occurred at a lower (more negative) pressure potential at the deepest groundwater site compared to the two shallower groundwater sites (4.3 m and 9.8 m DGW; this species was not available at 2.4 m site) (Table 5-1). There was a significant positive relationship between PLC_{50} and depth-to-groundwater for both winter (p=0.02) and summer (p=0.02). The PLC_{50} of *E. sieberi* decreased from -0.76 MPa to -1.42 MPa in summer and from -0.74 MPa to -1.57 MPa in winter as depth-to-groundwater increased (Table 5-1). Similarly PLC_{88} showed a positive relationship with depth-to-groundwater (p=0.04) in winter.

E. sclerophylla

Huber value of *E. sclerophylla* changed significantly as a function of depth-to-groundwater (F=4.55, df = 2,55; p=0.01) and seasonality (F=5.21, df = 1,56; p=0.02).

Within site comparisons showed in winter H_V was significantly larger for the two deepest groundwater sites (30% increase at 9.8 m and 40% increase at 37.5 m DGW) compared to the summer (Fig. 5-3d). Across sites comparisons showed in winter H_V was significantly larger at the deepest groundwater site (37.5 m DGW) than the two other sites (F=15.26, df = 2,55; $p<0.001$) and there was no difference between sites in summer.

Hydraulic conductivity of *E. sclerophylla* for both leaf specific (F=10.42, df=1,41; p=0.003) and sapwood specific (F=28.81, df = 1,41; $p<0.001$) was significantly larger in summer than winter (Figs 5-4d, 5-5d). Value of K_L ranged from 1.6 to 2.4 $\times 10^{-4}$ kg m s^{-1} MPa^{-1} m^{-2} in winter and was about 1.5 fold larger at all sites in summer. In summer K_S across sites ranged between 1.6 to 2.3 kg m s^{-1} MPa^{-1} m^{-2} in summer, which was 60% larger compared to the winter K_S at all sites. There was no significant difference between sites as a result of increase in depth-to-groundwater (p=0.52, F=0.64) (Figs. 5-4d & 5-5d).

There were no significant differences in PLC_{50} nor PLC_{88} across seasons for *E. sclerophylla* (Table 5-1). Site means for PLC_{50} ranged from -0.8 MPa to -1.33 MPa whilst site means for PLC_{88} ranged from -2.09 MPa to -2.95 MPa.

Within site comparisons

Huber value

The H_V ranged between 1.7-3.9 $\times 10^{-4}$ across all sites and species. At the two shallowest groundwater sites there was no significant seasonal change (2.4 m DGW (p = 0.05, F= 3.02) and 4.3 m DGW (p= 0.29, F= 1.08)), while at the two deepest water-table sites (9.8 m and 37.5 m DGW) there was a significant seasonal change in HV. At site 9.8 m DGW, all species except *E. piperita*, had significantly larger H_V (around 70% larger) in winter compared with summer ($p< 0.001$, F= 17.14). Similarly at the deepest groundwater site, there was a significant increase in H_V in winter compared with summer for all species ($p < 0.001$, $F = 14.88$) except *E. piperita.*

At all sites except the shallowest 2.4 m DGW ($p = 0.64$, $F = 0.29$) there were significant differences in H_V amongst the dominant tree species. At site 4.3 m DGW in both seasons *E. piperita* exhibited the smallest H_V while *E. globoidea* and *E. sclerophylla* had the largest H_V in summer and winter respectively. At the deepest water-table site (37.5 m), *E. sclerophylla* had a significantly ($p < 0.001$, $F = 8.26$) larger H_V than all other species in both seasons (1.5 fold larger than all other species).

Hydraulic conductivity

There were no significant differences between species for either K_L or K_S within sites except for the site 9.8 m DGW, where K_S but not K_L was significantly different between species ($p = 0.002$, $F = 5.20$). In winter *E. piperita* had significantly larger ($p=0.001$, $F=6.12$) K_S than other species.

Within all sites, both K_L and K_S decreased significantly in winter compared to summer except for *E. piperita* at site 4.3 m DGW and 37.5 m DGW and *E. globoidea* at the site 37.5 m DGW (Figs. 5-4 & 5-5).

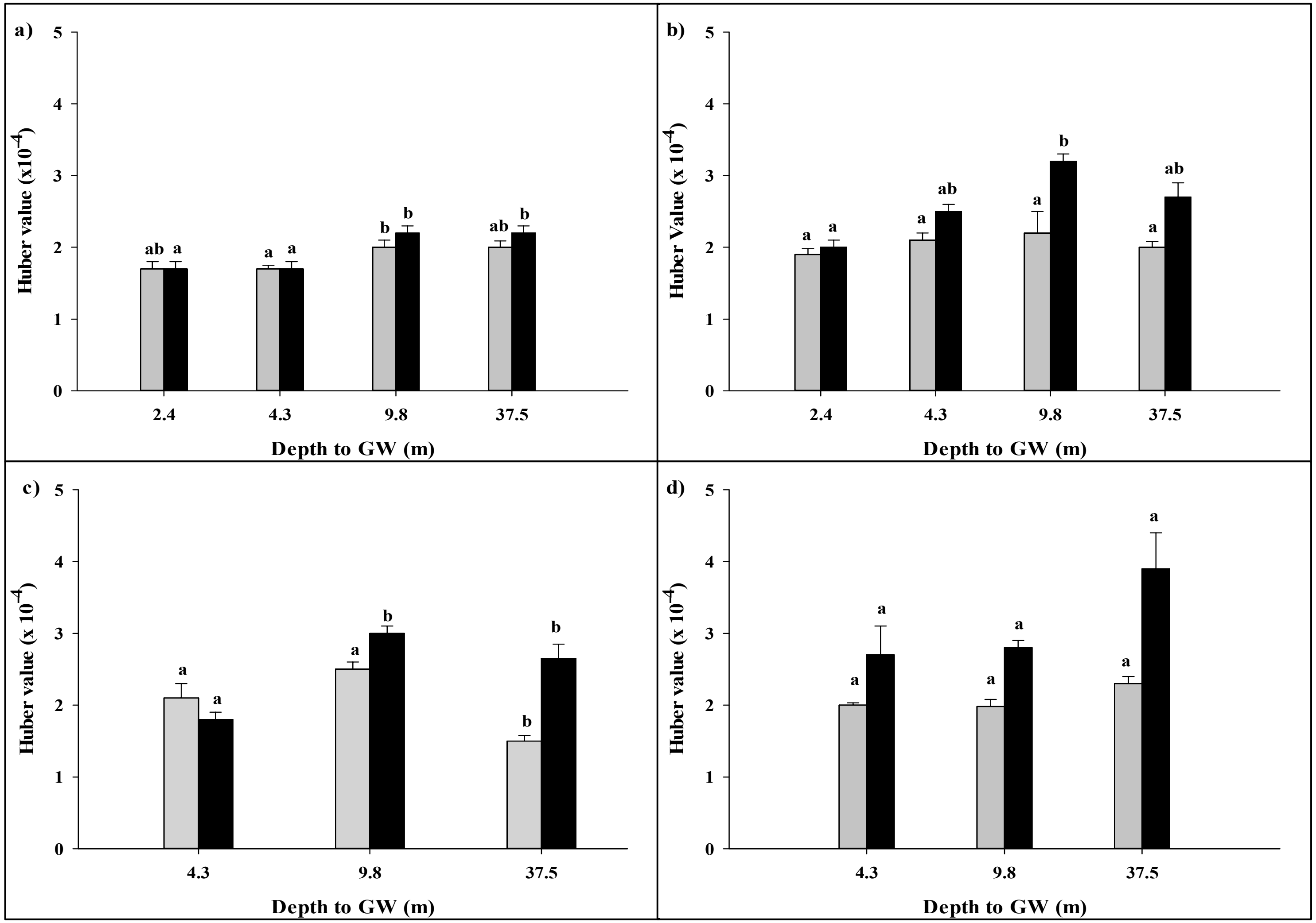


Figure 5-3: Huber value of four species across sites. Top panel includes a) *E. piperita* and b) *E. globoidea* and lower panel shows c) *E. sieberi* and d) *E. sclerophylla* for summer (gray) and winter (black). Letters above bars shows the differences between sites in each season.

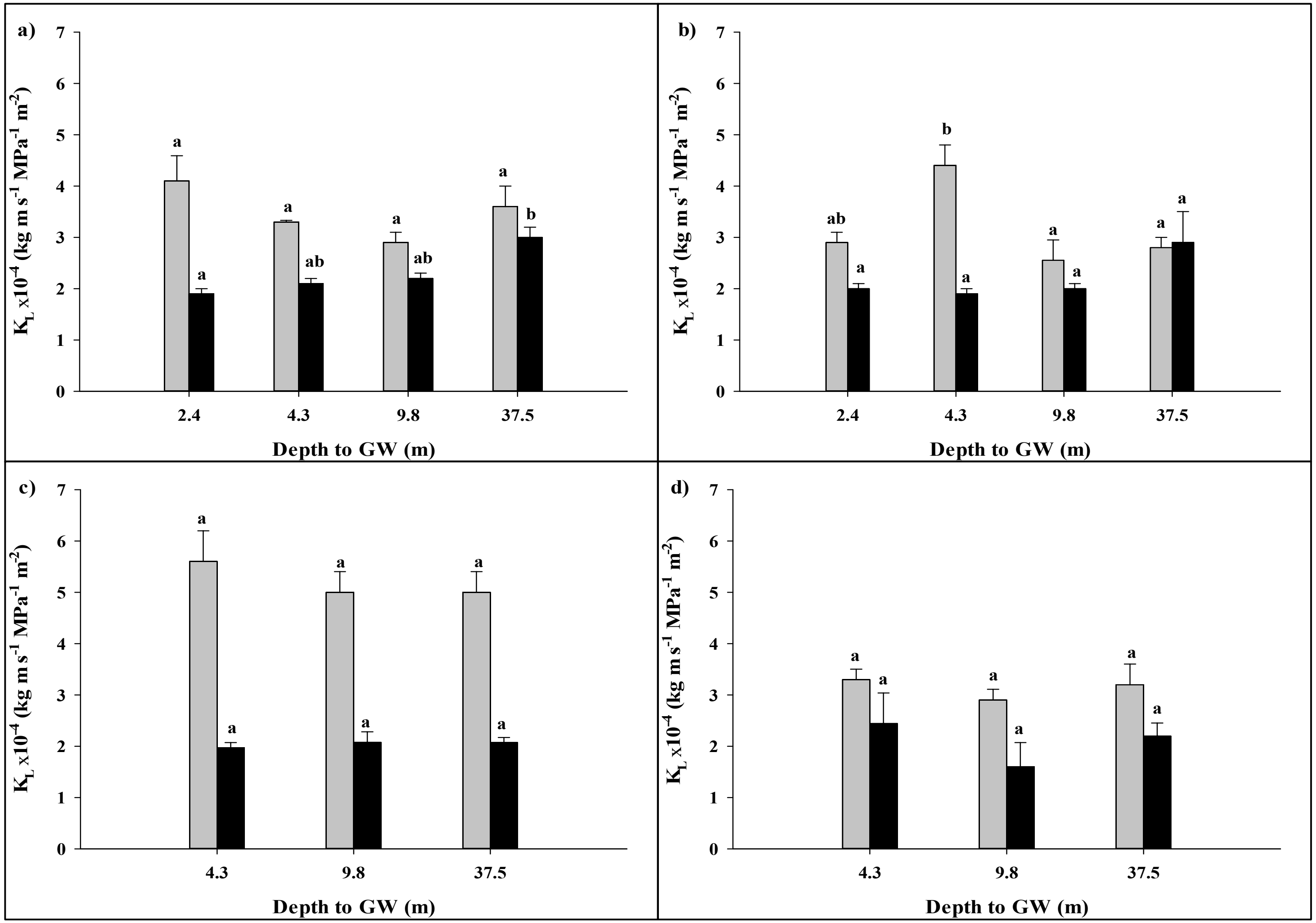


Figure 5-4: Leaf specific hydraulic conductivity of four species across sites. Top panel; a) *E. piperita* and b) *E. globoidea*. Lower panel; c) *E. sieberi* and d) *E. sclerophylla* for summer (grey) and winter (black).). Letters above bars show significant differences between sites in each season.

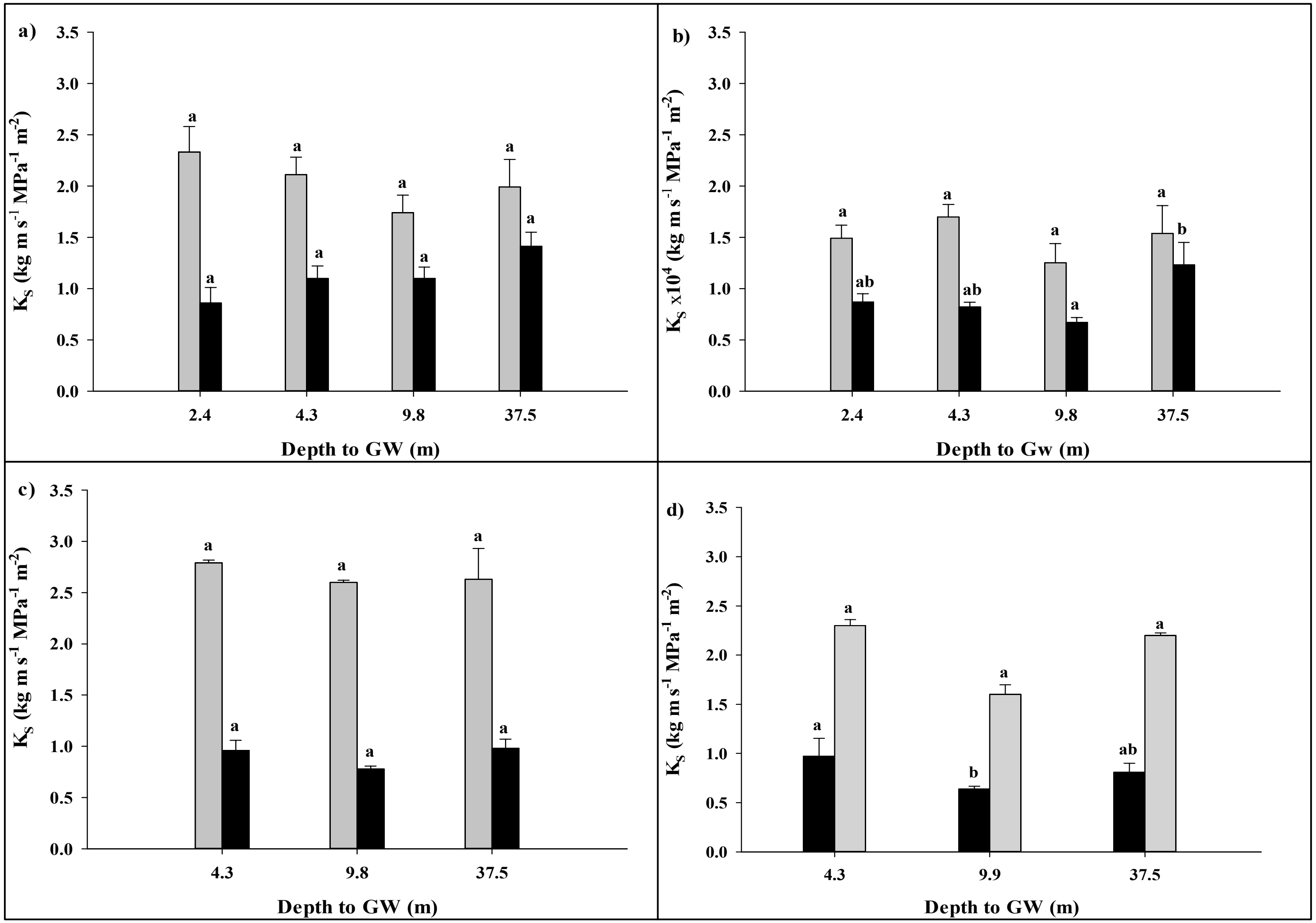


Figure 5-5: Sapwood specific hydraulic conductivity of four species across sites. Top panel; a) *E. piperita* and b) *E. globoidea* and lower panel; c) *E. sieberi* and d) *E. sclerophylla* for summer (grey) and winter (black). Letters above bars show significant differences between sites in each season.

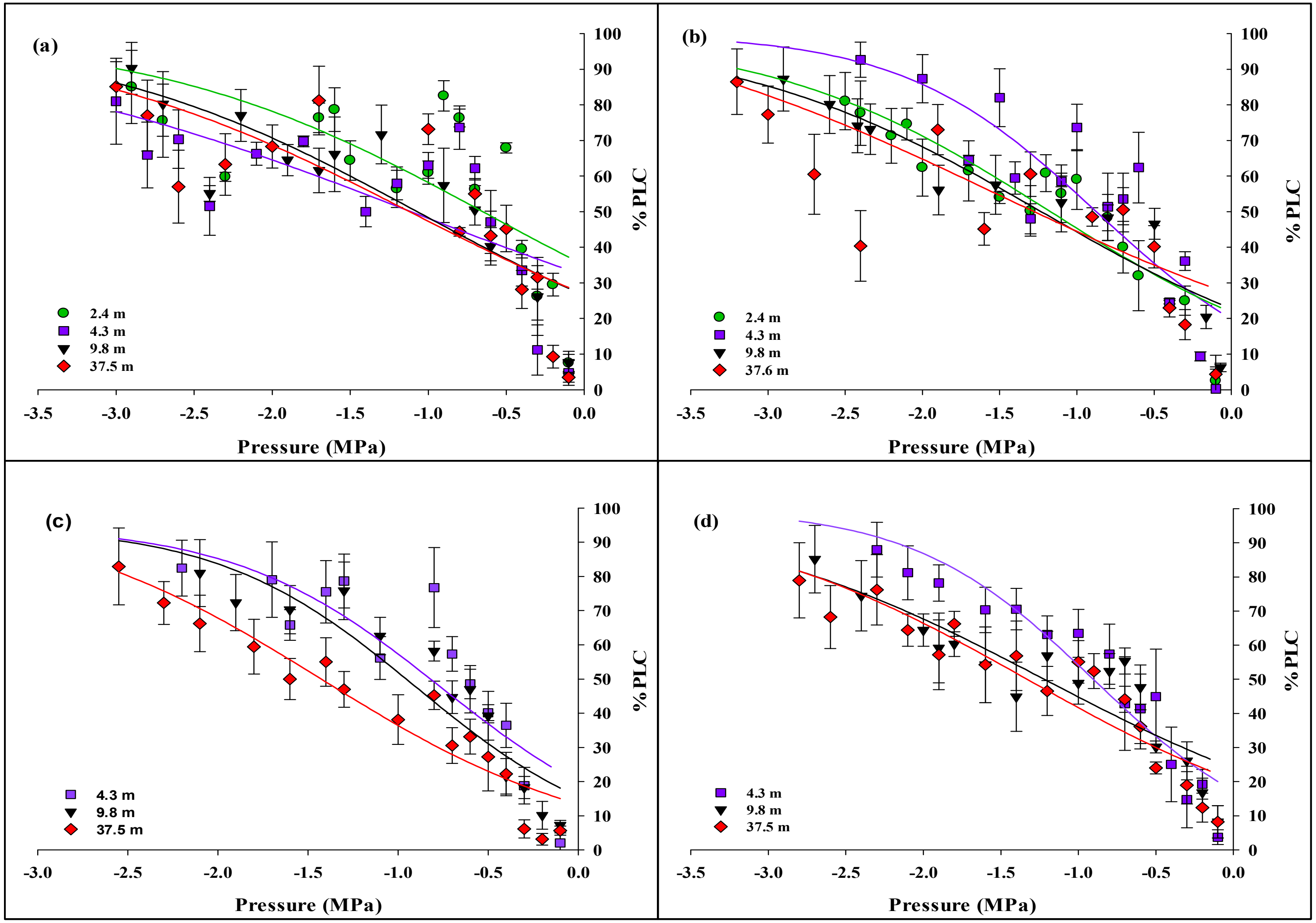


Figure 5-6: Summer measurement of xylem vulnerability of four species in four sites; a) *E. piperita* ,b) *E. globoidea* , c) *E. sieberi* and d) *E. sclerophylla*.

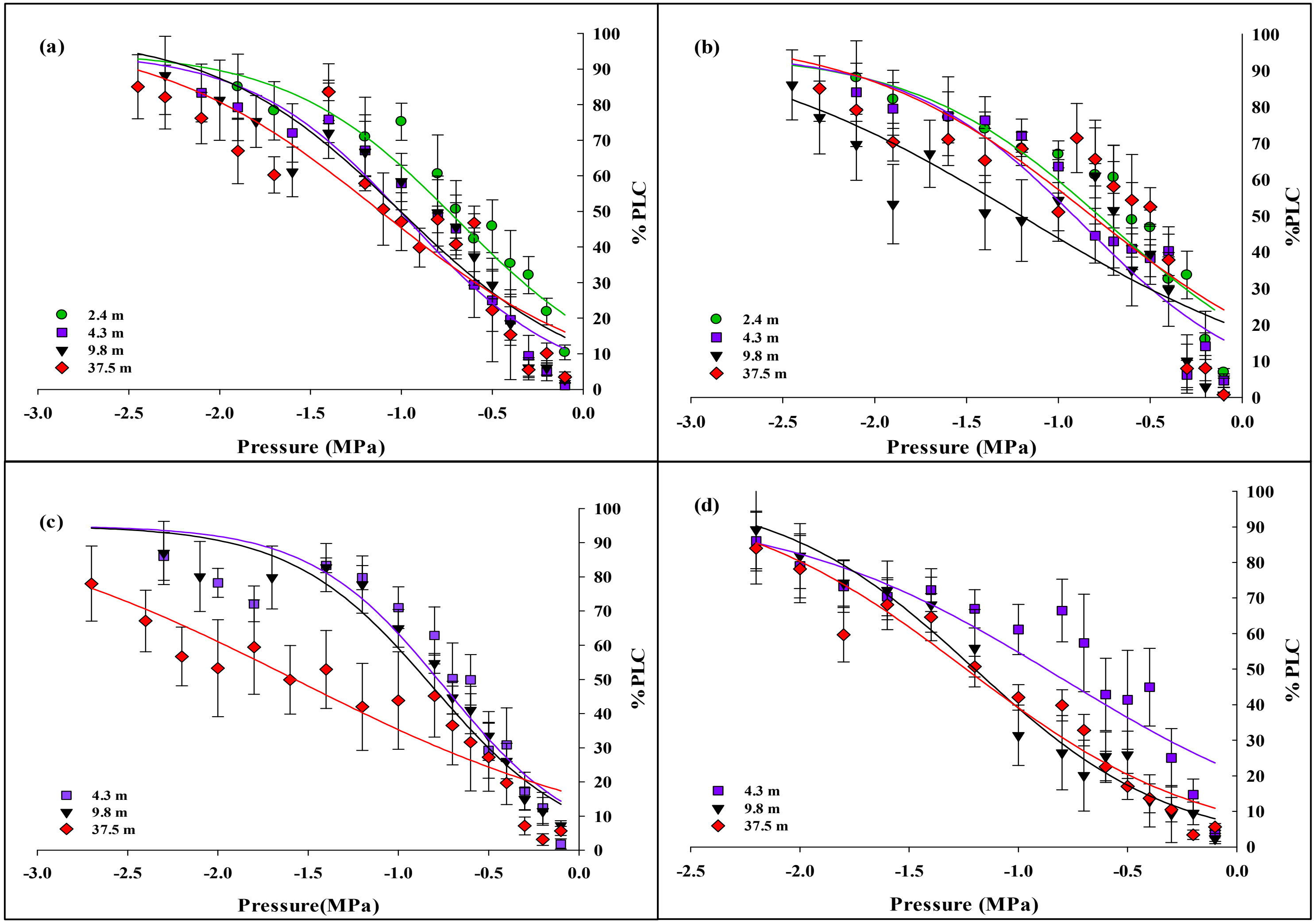


Figure 5-7: Winter measurement of xylem vulnerability curve of four species in four sites; a) *E. piperita*, b) *E. globoidea* , c) *E. sieberi* and d) *E. sclerophylla*.

Xylem embolism curves

Both PLC_{50} and PLC_{88} were significantly more negative at all sites and for all species in summer than in winter (Table 5-1). Results of all species within each site within each season were pooled together for further analysis. Regression analysis was used to examine the relationship between depth-to-groundwater and PLC_{50} and PLC_{88}. As depth-to-groundwater increased, PLC_{50} declined curvilinearly (Fig. 5-9). When depth-to-groundwater exceeded approximately 10 m, there was very little change in PLC_{50}, with the majority of the decline in PLC_{50} occurring across the three shallowest sites (< 10 m). There was no significant difference between the winter and summer trends in PLC_{50}. However, there was no significant relationship with PLC_{88} and depth-to-groundwater for any season.

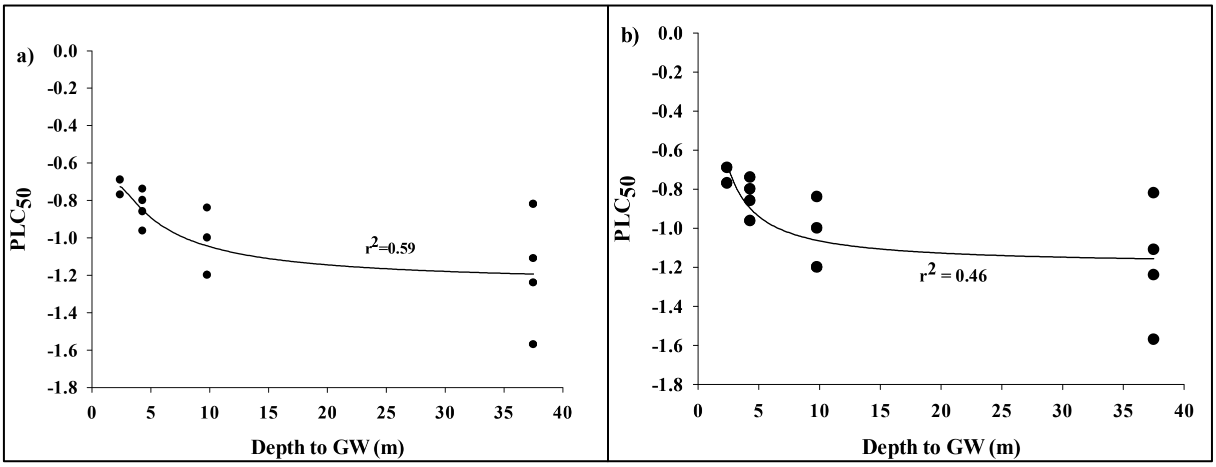


Figure 5-8: Pooled PLC_{50} of all species measured at each site as a function of depth-to-groundwater summer (a) and winter (b).

Table 5-1: Values for coefficients ***a*** (gradient) and ***b*** (PLC_{50}) of the vulnerability curves and PLC_{88} (pressure where PLC=88%) for stem for each species across sites in summer and winter.

Species	**DGW**	**Season**	***a***	***b***	**P_{88}**
E. piperita	**2.4 m**	Summer	0.94	-0.66	-2.75
		Winter	2.14	-0.69	-1.87
	4.3 m	Summer	0.67	-1.11	-3.10
		Winter	2.31	-0.963	-2.05
	9.8 m	Summer	0.94	-1.07	-3.00
		Winter	1.95	-1.00	-2.02
	37.5 m	Summer	0.89	-1.12	-3.10
		Winter	1.62	-1.11	-2.34
E. globoidea	**2.4 m**	Summer	1.59	-0.87	-2.12
		Winter	1.88	-0.77	-2.06
	4.3 m	Summer	1.09	-1.17	-2.99
		Winter	2.10	-0.86	-2.06
	9.8 m	Summer	0.993	-1.23	-3.19
		Winter	1.21	-1.20	-2.30
	37.5 m	Summer	0.74	-1.52	-3.23
		Winter	1.59	-0.82	-2.06
E. sieberi	**4.3 m**	Summer	1.74	-0.76	-1.99
		Winter	2.69	-0.74	-1.68
	9.8 m	Summer	1.81	-0.89	-2.29
		Winter	2.55	-0.84	-1.79
	37.5 m	Summer	1.30	-1.42	-2.75

Species	**DGW**	**Season**	***a***	***b***	**P_{88}**
		Winter	1.05	-1.57	-2.80
E. sclerophylla	**4.3 m**	Summer	1.72	-0.90	-2.09
		Winter	1.57	-0.80	-2.11
	9.8 m	Summer	0.94	-1.22	-2.85
		Winter	2.23	-1.20	-2.09
	37.5 m	Summer	1.02	-1.33	-2.95
		Winter	1.84	-1.24	-2.17

Sapwood density

There were no significant differences in sapwood density between sites for any species. Furthermore there were no significant differences between species within each site except for site 9.8 DGW (P= 0.20, F= 9.83) where *E. sieberi* had a significantly larger sapwood density compared with the other species (Table 5.2). Mean of the sapwood density of all species across all sites ranged between 0.45±0.01 to 0.58±0.01 g cm^{-3}.

Table 5-2: Sapwood density (g cm^{-3}) of species across sites with different depth-to-groundwater. Values presented as means followed by standard error. NA indicate that species was not measured at that site. The * symbol indicates a significant difference among sites for each species.

DGW / **Species**	**2.4 m**	**4.3 m**	**9.8 m**	**13.0 m**	**16.7 m**	**37.5 m**
E. piperita	0.54 ± 0.02	0.53 ± 0.01	0.52 ± 0.02	NA	NA	0.55 ± 0.01
E. globoidea	0.55 ± 0.02	0.54 ± 0.01	0.54 ± 0.01	NA	NA	0.56 ± 0.01
E. sieberi	NA	0.54 ± 0.03	0.58 ± 0.01*	NA	NA	0.53 ± 0.01
E. sclerophylla	NA	0.49 ± 0.01	0.52 ± 0.01	0.47 ± 0.02	0.45 ± 0.01	0.49 ± 0.02
E. radiate	0.53 ± 0.01	NA	NA	NA	NA	NA

Discussion

I hypothesized that despite occupying a mesic habitat, trees growing at sites with shallow groundwater will exhibit differences in their hydraulic architecture, compared with trees growing at sites with deeper groundwater (assumed to have a limited, or zero, access to groundwater) as a result of phenotypic plasticity. In this study I tested this hypothesis along with seasonal and intra-species differences in hydraulic properties of trees across sites with different depths-to-groundwater.

Figure 5-9 shows a conceptual model summarising the interactions amongst the traits examined in this chapter. Decline in water availability (increase in depth-to-groundwater) resulted in no change in sapwood density and branch hydraulic conductivity whilst H_V increased and xylem sensitivity to embolism declined. Sapwood density and branch hydraulic conductivity have been previously shown to be tightly coordinated whereby increasing sapwood density and conductivity are negatively correlated (Bucci et al. 2004b; McDowell et al. 2002b). Both traits are influenced by xylem structure and in particular by vessel diameter and the ratio of lumen area to wall thickness (Nijsse et al. 2001). Increased H_V is associated with decreased transpirational demand of the canopy and as a result tends to occur in dry environments (Mencuccini and Grace 1995). Similarly, a decline in xylem sensitivity to embolism results in increased in resistance to water stress and tends to occur in dry rather than wet environments (Awad et al. 2010; Choat et al. 2007).

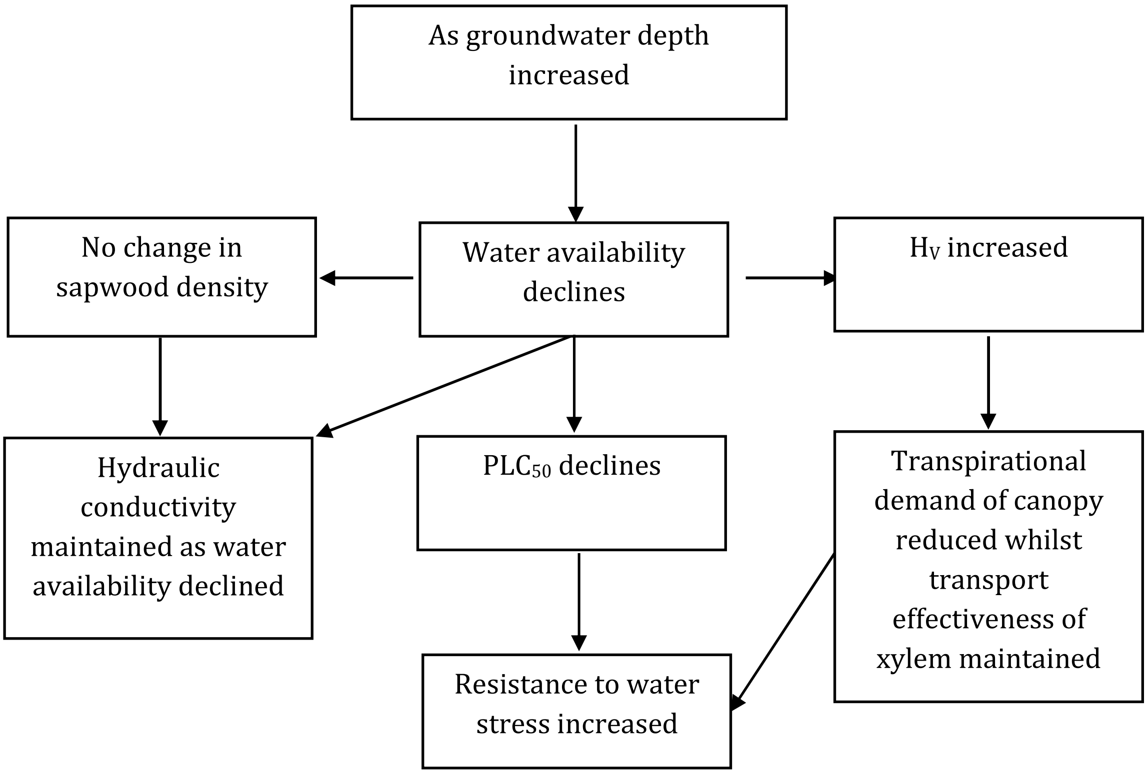


Figure 5-9: A conceptual model summarising the relation between the response of the principal trees hydraulic traits to increased depth-to-groundwater.

Whilst Huber values of trees are possibly a species specific trait (Choat et al. 2005; Prior and Eamus 1999; Tyree et al. 1991), significant variation within a species in response to differences in water supply and evaporative demand indicate a large degree of developmental plasticity (Mencuccini and Grace 1995). Huber values are also a function of tree height (Addington et al. 2006; Ambrose et al. 2010; Bucci et al. 2004b; McDowell et al. 2002a), water availability (both precipitation (Choat et al. 2005; Choat et al. 2007; Villar-Salvador et al. 1997) and groundwater resources (Carter and White 2009; Gazal et al. 2006), climatic conditions (Thomas et al. 2004) and seasonality (Macinnis-Ng et al. 2004; Zeppel and Eamus 2008). Generally plants occupying drier habitats maintain a larger Huber value than plants growing in wetter areas (Canham et al. 2009; Choat et al. 2007; Shumway et al. 1991). However, contrary to this general pattern, a seven species study of *Pereskia* (Cactaceae) did find that H_V varied independently of precipitation (Edwards 2006).

Huber values in the current study ranged between 1.7 and 3.9 $\times 10^{-4}$ which is comparable to values obtained from other woodlands in NSW (Macinnis-Ng et al. 2004; Mokany et al. 2003; Taylor 2008; Zeppel and Eamus 2008) and tropical forest in Central America (Choat et al. 2007). Huber values at the shallower groundwater sites were significantly smaller than those at the deeper sites (that is, trees at shallow sites maintained a larger leaf area per unit sapwood area) which is consistent with my initial hypothesis and also consistent with studies on *Eucalyptus kochii ssp.borealis* (Carter and White 2009) and *Populus fremontii* (Gazal et al. 2006). Smaller H_V at the wetter sites (shallower groundwater sites) indicates that these trees are able to sustain a larger leaf area and invest less in sapwood because of the more consistent and persistent supply of water at the shallower sites compared to the deeper sites (Carter and White 2009; Choat et al. 2005; Eamus 1999).

Huber value of all species across all sites was larger during the relatively drier winter than the wetter summer. Increased H_V for evergreen species in winter was also recorded in woodlands (*Eucalyptus haemostema*, *Angophora hispida* and *Banksia intregrifolia*) in the Sydney region (Macinnis-Ng et al. 2004; McClenahan et al. 2004) and *Eucalyptus crebra* and *Callitris glaucophylla* 200 km north-west of Sydney NSW (Zeppel and Eamus 2008). Increases in H_V in winter can be explained by one or more of the following processes: (i) some leaf loss during winter (Macinnis-Ng et al. 2004); (ii) increased production of new leaves during spring and summer (Hatton and Wu Hsin 1995); (iii) a response to seasonal changes in irradiance and temperature (Vertessy et al. 1995). However results from litter baskets in the present study (chapter 3) showed a decrease in litterfall during winter and this does not support this explanation. Seasonal differences in H_V were more pronounced at deeper groundwater sites compared to shallower sites for all species. The lack of seasonal changes in shallower sites coupled with their larger H_V may reflect groundwater-use at these sites because the additional supply of water may enable trees to produce more leaves for a given sapwood area all year around, whilst trees at the deeper sites alter their H_V value in response to the relatively drier winter compared to the summer.

Numerous studies support the premise that the ratio of sapwood area to leaf area (H_V) should increases as tree height increases to compensate for the increased path length of water flow in tall trees (Addington et al. 2006; Barnard and Ryan 2003; Magnani et al. 2000; McDowell et al. 2002a; Midgley 2003) as predicted from pipe model theory (Shinozaki et al. 1964). However, the results in the present study do not follow this general trend: trees growing at the shallower groundwater sites had smaller H_V despite being significantly taller (see chapter 3). Such contradictory results have also been observed for *Eucalyptus delegatensis* in NSW (Mokany et al. 2003); five Costa-Rican rainforest species (Calvo-Alvarado et al. 2008); *Quercus garryana* Dougl.ex in USA (Phillips et al. 2003) and *Picea* and *Abies* (McDowell et al. 2002a). These other studies that documented a decrease in H_V with tree height have also been from relatively wet environments where there is intense competition for light. It is possible; therefore, that H_V might decrease with increase in tree height if competition for light negates the requirement for a constant soil-to-leaf sapflow resistance which consequently results in reductions in g_s (McDowell et al. 2002a; Ryan et al. 2006) and K_S (McDowell et al. 2002a; Mokany et al. 2003). Reductions of stomatal conductance (g_s) may not necessarily be a disadvantage in a wet, cloudy environment where photosynthesis is constrained more by electron transport (that is, light supply) than by g_s (Calvo-Alvarado et al. 2008).

Water availability is a strong regulator of xylem structure and thus xylem structure differs across mesic and xeric environments (Pockman and Sperry 2000; Stevenson and Mauseth 2004). Consequently I hypothesized that the branch hydraulic conductivity of trees growing over shallow groundwater levels will be smaller than that of trees growing at sites with inaccessible groundwater. However, the results of the present study do not support this hypothesis because there was no significant difference in branch hydraulic conductivity across sites. This result suggests that trees at sites with deep groundwater are not significantly water stressed, or that the degree of water stress is too small to induce a response in hydraulic conductivity.

Since annual rainfall in the two years of study was larger than the long-term mean, it is unlikely that water stress was a significant factor for sites with a deep (37.5 m) water table.

I am not aware of any studies that have focused on the impact of groundwater depth on hydraulic architecture of trees in a mesic environment. However, there are comparisons of the hydraulic architecture of trees in mesic and xeric habitats (Van der Willigen and Pammenter 1998) or across a precipitation gradient (Choat et al. 2007; Taylor and Eamus 2008). Several such studies also found no difference in hydraulic conductivity in response to differences in water availability. Thus, a cross-species comparison along a 850 mm rainfall gradient in NSW, including *E. sclerophylla* (Taylor and Eamus 2008), a study of nine *Cordia* (Boraginaceae) species in tropical forests (Choat et al. 2007) and a study of six closely related species in California, USA (Bhaskar et al. 2007) found that the hydraulic conductivity (K_S and K_L) changed independently of differences in annual rainfall. Similarly in *Pereskia* (Cactaceae) (Edwards 2006) and *Pinus palustris* Mill. (longleaf *pine*) (Addington et al. 2006) there was no difference in K_L and K_S across xeric and mesic sites. In contrast, Van der Willigen and Pammenter (1998) compared hydraulic architecture of four closely related *Eucalyptus* species in mesic *versus* xeric sites and they found a larger conductivity at mesic sites compared to xeric sites whilst Carter and White (2009) found that sapwood specific conductivity was larger at shallow groundwater site compared with the deeper site, while leaf specific conductivity did not vary between sites. Clearly, there is not a universally observed trend in hydraulic conductivity as a function of water availability.

Seasonality was the most important factor in causing variation of hydraulic conductivity in this study for all species. Branch hydraulic conductivity was larger in summer than winter for all species and across all sites (both K_S and K_L), similar to a comparative study of *Eucalyptus haemostema*, *Angophora hispida* and *Banksia intregrifolia* in the Sydney region (McClenahan et al. 2004). Similarly branch conductivity decreased in the (winter) dry season compared to the (summer) wet season in northern Australia for *Eucalyptus tetrodonta* F.Muell and *Terminalia* *ferdinandiana* Excell (Prior and Eamus 1999). This seasonal pattern has been explained by the larger rainfall and higher temperature and solar radiation observed in the summer which results in large rates of growth which is associated with large rates of leaf production and new, larger diameter sapwood vessels and hence a larger conductivity (Macinnis-Ng et al. 2004). It is generally observed that xylem vessels in new growth (early season growth) have a larger diameter and a larger conductivity compared to the late and older xylem vessels (Domec and Gartner 2002). A larger conductivity is required to support the larger rates of transpiration that occur during the summer when VPD, temperature and solar radiation receipts are larger but photosynthetic rates are also larger because of reduced limitation imposed by low temperature and low light levels.

Xylem vulnerability to drought-induced cavitation is generally characterized by the pressure which reduces hydraulic conductance by 50% and 88% (PLC_{50}, PLC_{88}) (Awad et al. 2010; Meinzer et al. 2009; Meinzer and McCulloh 2013). Vulnerability curves differ largely in shape, slope and the values of $PLC_{50/88}$ both between species and within the same species growing in different environments (Melcher et al. 2003; Sperry et al. 1988).

Clearly, the vulnerability curves obtained in the current study across all sites for all species, have steep slopes during the transition from fully conductive xylem to a fully cavitated xylem. This shows high sensitivity of these trees to drought-induced embolism, that is, only a small decline in xylem water potential results in a large loss of conductance. Such steep slopes in vulnerability curves have been recorded for other species including *Acer saccharum Marsh* (Melcher et al. 2003), *Betula occidentalis* (Sperry and Saliendra 1994) and *Baccharis salicifolia* (Pockman and Sperry 2000). In contrast, some species have a much shallower slope between fully conductive to fully cavitated xylem including *Abies alba* and *Cedrus atlantica* (Cochard 1992) and *Quercus oleides and Hydmenaea courbril* (Brodribb et al. 2003).

Despite no significant differences in branch hydraulic conductivity across sites, the PLC_{50} measured in both winter and summer significantly decreased with increase in depth-to-groundwater. Thus, as depth-to-groundwater increased, the water potential that caused 50 % loss of conductance declined, indicating a larger resistance to embolism. Furthermore, these findings suggest that the development of cavitation resistance can be independent of any changes in hydraulic transport capacity (that is, K_S or K_L), a result in agreement with those of (Bhaskar et al. 2007; Maherali et al. 2004; Peguero-Pina et al. 2011).

These results of the embolism sensitivity analyses support the principal hypothesis of this chapter, namely, that trees growing over shallower groundwater sites are more sensitive to xylem cavitation and it is likely that this is a result of permanent access to groundwater. Similarly other comparative studies of xylem vulnerability to cavitation showed increased resistance to cavitation with xeric environments across and within species (Awad et al. 2010; Choat et al. 2007; Kolb and Sperry 1999; Maherali et al. 2004). Pockman and Sperry (2000) compared riparian with upland trees and attributed the limited distribution of most riparian species to their lower resistance to cavitation. However, such trends are not universally observed. Within tropical savanna woody species, sapwood and leaves were more vulnerable to caviation at xeric sites compared with mesic sites (Bucci et al. 2012). These contrary results were explained by suggesting that these species have mechanisms to maintain high water potentials despite inhabiting an environment with low water availability, including isohydric stomatal behaviour and a large intrinsic sapwood hydraulic conductivity and a large hydraulic capacitance.

There are studies where no significant differences in xylem sensitivity to drought induced cavitation were found across mesic and xeric sites (Maherali and DeLucia 2000; Van der Willigen and Pammenter 1998) and across a gradient of rainfall (Taylor and Eamus 2008). This independence of resistance to embolism from water availability suggests that the sensitivity to drought induced cavitation may be a genetically controlled trait that does not display a wide amplitude of plasticity in response to variations in environmental conditions (Kolb and Sperry 1999; Pockman and Sperry 2000; Takagi et al. 1998; Taylor and Eamus 2008; Van der Willigen and Pammenter 1998). Tight genetic controls may limit the capacity for plasticity in the responses of some traits in some species to environmental changes (Alder et al. 1996; Kolb and Sperry 1999). Indeed it has been recently suggested that adaptation to drier habitats may not necessarily result in high resistance to embolism (Choat et al. 2012; Miranda et al. 2010).

Sapwood density generally increases as the environment gets drier (Preston et al. 2006; Wright et al. 2006). As a general trend in xylem anatomy, vessels get larger in mesic environments to facilitate a larger conductivity of the sapwood, thereby supporting the larger stomatal conductance and rate of carbon gain that can be supported when water is abundantly available. However, this can make them more vulnerable to cavitation (Chen et al. 2009; Hacke et al. 2001a; Tyree and Zimmermann 2002; Wright et al. 2006). Larger vessels also tend to result in a lower sapwood density and consequently there is often a strong negative relationship between sapwood density and hydraulic conductivity (Meinzer et al. 2008a; Wright et al. 2006; Zhang et al. 2009). However, such relationships between sapwood density and hydraulic conductivity are not universally observed. Some studies have found no relationship between sapwood density and vulnerability to cavitation (Awad et al. 2010; Cochard et al. 2007). In these cases the lack of correlation may be explained by the Tyree and Zimmermann (2002) air seeding hypothesis. The air seeding hypothesis relates the vulnerability of xylem to embolism to the porosity of pit membranes rather than the diameter of xylem conduits. Contrary to our initial expectations, there was no difference in sapwood density of trees across the sites or species. However, despite this result being contrary to expectations, it is entirely consistent with the lack of response in hydraulic conductivity across sites.

There was a significant decrease in tree height from the shallowest groundwater site to the deepest site (see chapter 3). Tree height is an important factor in determining the hydraulic traits of trees (Zhang et al. 2009). For taller trees, maintaining the water column from roots to canopy is more difficult due to gravity (Franks 2004). Taller trees often, but not always, have lower K_L (Barnard and Ryan 2003; Phillips et al. 2003; Ryan et al. 2006) and K_S (McDowell et al. 2002a; Zhang et al. 2009), a lower sapwood density (Mokany et al. 2003; Poorter et al. 2010; Preston et al. 2006), a lower H_V (McDowell et al. 2002a; Zhang et al. 2009) and consequently can be more exposed to drought stress (Zhang et al. 2009). However, in the present study there was no significant decrease in wood density, K_L nor K_S and no significant increase in H_V as tree height increased or when depth-to- groundwater increased. Therefore there is a possibility that the differences in trees height among sites and differences in access to groundwater may negate the effect of one another. Finally, as previously noted, during the period of this study, annual rainfall was significantly larger than the long term average (see chapter 2). This too, may play a key role in masking the potential impact of depth-to-groundwater on tree hydraulic architecture.

In conclusion, the differences in hydraulic architecture observed across my four sites were not entirely as I originally hypothesized. I hypothesized that trees at the deeper groundwater sites would have lower branch hydraulic conductivity, larger Huber values, and more dense xylem vessels and as a result would be more resistant to drought induced cavitation. However, there were no differences in branch hydraulic conductivity (neither leaf specific nor sapwood specific) nor in sapwood density of trees across sites, despite finding a significant relationship between H_V and PLC_{50} with increase in depth-to-groundwater. H_V has previously been shown to exhibit greater variation than other traits with respect to environmental water stress (Edwards 2006). In the current study, although only water resource variability was hypothesized to cause changes in hydraulic attributes, it is known that there are other factors important in shaping hydraulic traits of trees which were not considered in this study, for example, soil nutrient content (Chandra Babu et al. 1999; Ewers et al. 2000). The responses of trees to habitat variability and the degree of plasticity of their traits are a combination of genetically determined traits and phenotypically plastic traits. Overall, a better understanding of genetic and environmental influences on hydraulic architecture is needed to fully elucidate the responses of trees to differences in groundwater depth. Finally, there is a possibility that the traits measured in this study were determined by the past three years of wet weather and that if I had measured them during a drought I may have found large differences amongst traits across sites.

Chapter 6 Leaf water relations and leaf structure of *Eucalyptus* trees growing along a gradient of depth-to-groundwater

Introduction

Water availability is one of the most important and primary abiotic factors in terrestrial ecosystems and has a major impact on the ecology and physiology of terrestrial vegetation (Taylor 2008; Xu et al. 2007). All plants respond to water deficit through biochemical, molecular, physiological and structural modifications or regulation which ultimately results in morphological and physiological adaptations (Niinemets 2001; Zhu et al. 2004). Vascular plants employ a range of mechanisms to withstand water stress (Atwell et al. 2003), including changes in leaf water relations (Ngugi et al. 2004), stomatal conductance (Lo Gullo et al. 2003) and Huber value (the ratio of leaf area to sapwood area) (Carter and White 2009). These adaptations are important because they affect plant growth, water-use and hydrological balance (Carter and White 2009). Understanding the adaptive mechanisms underlying vegetation responses to changes in water availability is important for predicting survival and growth of plants in different environments. Vegetation responses to abiotic factors can occur across different temporal scales (short, medium and long-term adaptations) and can be studied at different spatial scales (leaf, tree and stand). The research presented in this chapter is primarily focussed on medium term leaf-level adaptations of trees.

Leaves vary significantly in their morphology (area, shape, thickness), capacity for gas exchange and drought tolerance (Sack et al. 2003; Smith and Nobel 1977). Phylogeny and adaptation contribute to the formation of this diversity (Sack et al. 2003). In the medium term adaptations can occur in physiological traits such as water relations, (e.g. osmotic and elastic adjustment of leaf tissue) and structural traits (e.g. specific leaf area). The ability to perform such adjustments contributes to the maintenance of the gradients of water potential between roots and leaves that are required to maintain the flow of water from roots to leaves. This then allows maintenance of turgor when plants are experiencing water stress (Atwell et al. 2003; Carter and White 2009; Mitchell et al. 2008; Suarez 2011; Taiz and Zeiger 2010; Turner and Jones 1980; Uemura et al. 2004; White et al. 2000). The ability to maintain turgor in leaf cells is essential for leaf expansion, growth and gas exchange (White et al. 2000) and facilitates the movement of photosynthate through symplastic pathways (Mitchell et al. 2008).

Plants show considerable interspecific and intraspecific variation in their leaf water relations and leaf structure (Prior and Eamus 1999; Warren et al. 2005; White et al. 1996). Traits pertaining to leaf water relations (for example, ability to use osmotic or elastic adjustment) differ to some degree genetically between species (Abrams 1988; Lambers et al. 2008). Osmotic adjustment (accumulation of solutes in cells in order to reduce osmotic potential) is an important adaptive mechanism in response to declining water availability (Burgess and Oakley 2006; Ngugi et al. 2003) that result in enhanced capacity for turgor maintenance (Babu et al. 1999; Clifford et al. 1998).Similarly, adjustment of cell wall elasticity (Dreyer et al. 1990; Merchant et al. 2010; Pita and Pardos 2001) and other leaf structural adjustment including changes in specific leaf area (SLA) and stomatal density (Ngugi et al. 2004; Niinemets 2001; Turner et al. 2008) also occur in response to changes in water availability. Cell elasticity is a measure of the relationship between water potential and cell volume and influences the water potential at which turgor loss is reached(Lambers et al. 2008).

Trees of the genus *Eucalyptus* are the dominant tree species in most coastal Australian woodlands. They occupy a broad range of environmental condition from arid, semi-arid to mesic environments (Merchant et al. 2007; Tuomela 1997). Naturally occurring variation in the capacity to osmotically regulate may allow this trait to be used as a selection criteria for high performing individuals best adapted to drought conditions (Lemcoff et al. 1994). Osmotic and elasticity adjustments in combination with morphological adaptation enable *Eucalyptus* to better withstand water deficit (Merchant et al. 2007).

Groundwater, where accessible, is an important source of water for vegetation. Access and use of groundwater influences a plant's physiological and ecological function (Eamus and Froend 2006). This effect varies depending on the degree to which plants are dependent on groundwater (Canham et al. 2009; Nevill et al. 2010). There is an increasing awareness of the impact of groundwater supply on vegetation function and in order to better manage land and water resources sustainably (Eamus and Froend 2006) an understanding of the relationships amongst groundwater availability, plant physiology and ecophysiology is required.

Depth-to-groundwater can be an important factor that affects leaf water relations and transpiration rate. In areas where groundwater is within vegetation rooting depth, groundwater plays a key role in plant function and survival (Froend and Sommer 2010; Lamontagne et al. 2005; O'Grady et al. 2006c). Interactions between vegetation and groundwater tend to be more pronounced during dry seasons (Froend and Drake 2006; O'Grady et al. 2006c) or in arid rather than mesic environments. Consequently most of the research that has examined this topic has been focused on riparian, arid and semi-arid ecosystems. The work described in this chapter examined the influence of groundwater depth on leaf water relations, including osmotic and elastic regulation in a mesic environment with a relatively high annual rainfall.

In research presented in this chapter, pressure-volume analysis of leaves was used. Pressure-volume curves (P-V curves) summarize leaf-level responses to increasing water deficit (Schulte and Hinckley 1985). Pressure-volume (P-V) analysis has been successfully used in the past to explore differences in water relations between co-occurring species as well as seasonal changes between or within species (Sack et al. 2003; Suarez 2011; Tuomela 1997; Turner 1988; Tyree and Hammel 1972). Using P-V analyses it is possible to investigate several leaf water relations characteristics simultaneously. Leaf water relations characteristics refer to leaf traits which are important to maintain positive turgor pressure in leaf cells. These traits include maximum turgor potential, osmotic potential (at full and zero turgor), elasticity, relative water content (at zero turgor) and capacitance (at full and zero turgor). These characteristics determine how and if plants can maintain positive turgor pressure in leaf cells when exposed to water deficit. Understanding how these traits change in response to environmental condition can help in understanding which mechanisms (osmotic, elasticity or structural regulation) plants use to adapt to different environmental conditions.

The aim of this research was to assess inter-specific and intra-specific differences in leaf water relations and leaf structure as a function of depth-to-groundwater in a mesic environment. I hypothesised that:

1- Trees growing at sites with shallower groundwater depth are more sensitive to water stress and are not able to maintain their turgor pressure as effectively (defined by the relative water content at which zero turgor occurs) as trees growing at sites with deep groundwater.
2- Leaf structure (specific leaf area) varies as a function of depth-to-groundwater.
3- Seasonality influences leaf water relations and leaf structure.
4- Impacts of seasonality are more pronounced at sites with a deep water table.

Methods

Pressure-volume analyses

Pressure-volume analyses can be used for roots, twigs and leaves. In this study pressure-volume analyses of leaves were undertaken. Samples were collected from the most dominant tree species (defined as species with the largest contribution to total basal area of the site, these species accounted for more than 80 % of the total basal area) within each study area. Samples were collected from six sites. Within each of these six sites, a field survey was conducted to determine the basal area of all trees larger than one centimetre diameter, to allow determination of the contribution of all tree species present to total basal area of each site. The number of dominant tree species was different for each site, as was the total number of tree species present. The number of dominant tree species measured at each site varied from one species (sites with 13 m and 16.3 m depth), two species (site with 2.4 m depth), and four tree species (for site with 4.3 m, 9.8 m and 37.5 m) and all species were from the genus *Eucalyptus*.

Comparisons of P-V traits between sites and species as well as intra-specific comparisons were conducted across the summer (February and early March) and winter (August). Within each site three trees from each species were selected. From each selected tree, three terminal branches (from 10-15 m height, depending on tree height) were cut (leaves attached) and immediately recut under water to remove any possible air embolism. The newly recut end of the branch was placed in deionised water and the branch and water covered in black plastic bags to facilitate rehydration overnight in the laboratory. Following rehydration one mature fully expanded leaf per branch was selected and excised using a razor blade. Immediately after cutting leaf mass was measured using a three figure digital balance. Leaf water potential was measured using a Scholander-type pressure chamber (Model 3000, Soil moisture Equipment Corp., Santa Barbara, CA) which can reach to 100 bar. During measurements; the pressure inside the chamber was increased slowly to avoid damage to the leaf tissue. After each measurement of leaf water potential, the pressure inside the chamber was also released at a slow rate to avoid damage leaves (to prevent large changes in chamber temperature (Turner 1988). After each measurement leaves were allowed to dry on a bench top for a short period of time and measurements of leaf fresh weight and water potential repeated periodically (Hinckley et al. 1980; Turner 1988; Tyree and Hammel 1972).

Pressure-volume curves were established by plotting the inverse of leaf water potential ($-1/\psi$) of each sample *versus* relative water content (pressure-volume curve type II) (Eamus et al. 2006b). Measurements of leaf water potential were continued until at least 5 points were obtained on the linear part of the type II transform (i.e. five points beyond the point at which zero turgor was attained) (Fig. 6-1). After finishing the measurements of leaf water potential leaf area of each sample was measured using a leaf area meter (WinDAS 3.1). Samples were oven dried at 65^0 C for 72 h to obtain dry mass. Using the dry weight of each sample the relative water content (RWC) was calculated using the following equation:

$$RWC = \frac{(W_T - W_D) - (W_F - W_D)}{(W_F - W_D)} \times 100 \qquad \text{(Equation 1)}$$

Where W_T was fully rehydrated leaf weight, W_D was leaf dry weight and W_F was leaf fresh weight.

From the P-V curve several parameters were determined, including: leaf water potential at turgor loss point (Ψ_{TLP}), relative water content at turgor loss point (RWC_{TLP}), osmotic potential at full turgor (π_{100}), modulus of elasticity (ε) and saturated water content (SWC). Also leaf water content and specific leaf area (SLA) were calculated for each leaf. From each type II P-V curve, Höfler diagrams were established for each samples and leaf water potential at turgor loss point was determined from the intercept of turgor *versus* RWC line (Fig. 6-2). Leaf osmotic potential at full turgor was calculated by extending the regression of the linear portion of the type II transform back to the y-axis ($-1/\Psi$) using the equation of the linear part of the curve (Richter 1978; Schulte and Hinckley 1985). Bulk modulus of elasticity was calculated as the slope of turgor potential (full turgor to turgor loss point) *versus* relative water content changes (Schulte and Hinckley 1985; Sinclair and Venables 1983; Turner 1988). Type two pressure-volume curves were also used to calculate the relative capacitance at full turgor (C_{FT}), relative capacitance at turgor loss point (C_{TLP}) and absolute capacitance at full turgor (C_{FT}^{*}) using the method of (Lawren et al. 2010). Water capacitance of plant tissue has been defined as the change in volume per change in water potential for both above and below turgor loss point.

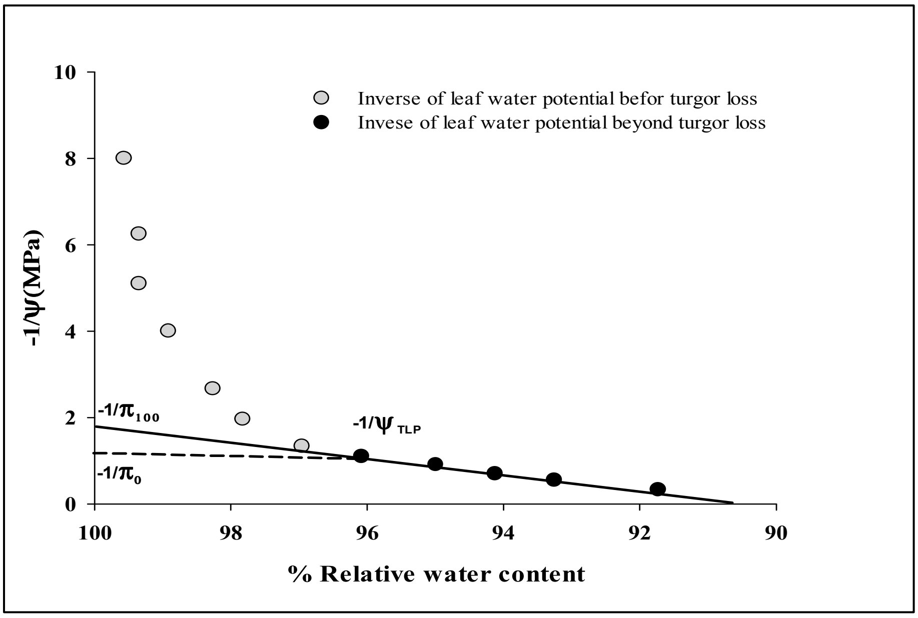


Figure 6-1: A typical type II pressure volume curve that shows the relationship between the inverse of the leaf water potential (-1/Ψ) and relative water content (%RWC). $-1/\Psi_{TLP}$, $11/\pi_{100}$ and $-1/\ \pi_0$ are the inverse of leaf water potential at turgor loss point, osmotic potential at full turgor and osmotic potential at turgor loss point respectively. (This P-V curve is a sample of one leaf of *E. piperita* in site 4.3 m DGW).

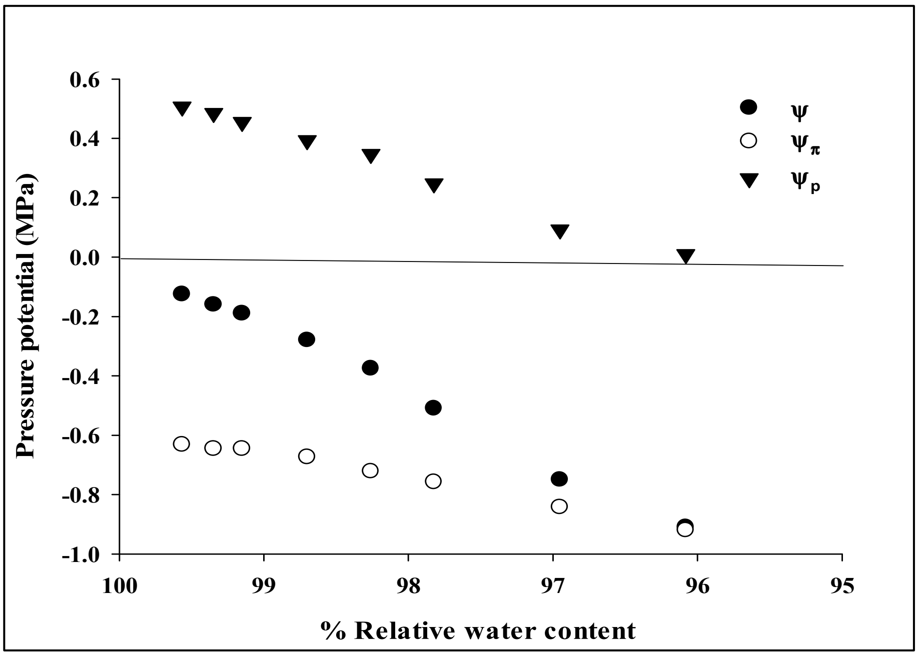


Figure 6-2: A Höfler diagram from one leaf sample of *E. piperita* from the 4.3 m DTG: this diagram is derived from the type II P-V curve (Fig. 6-1) and is used to determine the turgor loss point from the intercept by finding the intercept of turgor *versus* RWC line.

Specific leaf area

Specific lea area (SLA) was measured during summer and winter on all dominant species for which P-V analyses were performed. Six leaves per tree were sampled for each species. Three trees per species were sampled. The area of leaves was measured using a leaf area meter (WinDAS 3.1). Then samples were oven dried for 72-96 hours in oven 70 degrees. Mass of dry leaves was measured using a three digit electronic balance. SLA was calculated as the ratio of leaf area (cm^2) to dry mass of leaves (g).

Diurnal trends in leaf water potential

Pre-dawn and diurnal trends of leaf water potential were measured using a Scholander-type pressure chamber (Model 3000, Soil moisture Equipment Crop., Santa Barbara, CA). Measurements started before sunrise and continued every 90 minutes through the day. To avoid any nocturnal transpiration before pre-dawn measurements, three leaves per tree were wrapped in aluminium foil and covered in a ziplock plastic bag on the evening prior to measurement. At the time of measurements (pre-dawn) the wrapped leaves were sampled as well as adjacent leaves which were unenclosed to compare the results (no significant differences found between two groups of leaves). Leaves inside plastic bags are expected to show higher water potential and to more closely reflect soil water potential if night time transpiration was evident (Bucci et al. 2004a). Data presented here are from bagged leaves only. Also at the time of sampling leaves were cut using two different approaches to compare the outcomes. Three leaves were cut from their petiole using a sharp razor blade. From the same branches three small branches were cut using a pruner and then at the time of measurement one leaf was cut from each branch. This has been done to determine whether cutting the sample twice has any effect on the results (this has been done only in winter measurements- results are not shown in this chapter because there was no effect). One example of results is shown below (Fig. 6-3). Diurnal and pre-dawn measurements of leaf water potential were made at four sites: 2.4 m, 4.3 m, 9.8 m and 37.5 m. Three leaves per individual tree and three trees per species were sampled. To access the top canopy 16 m and 26 m hydraulic platforms were used. Measurements were conducted in late winter (early September) and summer (February). Due to large rainfall events in summer diurnal leaf water potential was not collected at all sites. Access to the study area was prohibited for a period of six weeks during the summer.

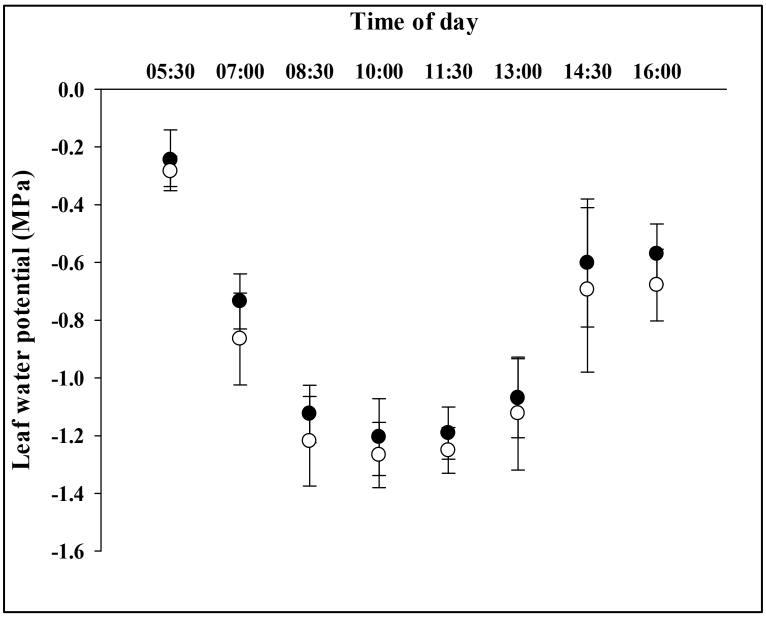


Figure 6-3: Diurnal leaf water potential comparing cutting single leaf (showed in white) with cutting a small twig first and cut off a leaf later at the time of measurements (shown in black). Results for *E. sclerophylla* from site with 4 m depth-to-groundwater.

Data analyses

All results were pooled and mean and standard error of means were calculated. Normal distribution of all data was tested using the Kolmogorov-Smirnov test. Homogeneity of variances was tested using Leven's test with the null hypothesis that all variances are equal across all groups.

Canonical correlation analysis (CCA) was used as one of the General Linear Model (GLM) methods to test the null hypothesis H_0: the measured environmental conditions had no effect on measured leaf traits. Measured variables were categorised into predictor or response groups. Predictor variables were depth-to-groundwater, species and season while response variables were measured leaf traits. Within CCA predictor and response groups, dependence between variables is identified through principal component analysis (PCA) of the correlation matrix (Sherry and Henson 2005). CCA determines the degree to which two sets of variables (predictors and responses) are related to each other and determine how specific variables function on this multivariate relationship. Through the use of CCA, I was able to determine which group of traits made the largest contribution to observed variation across sites.

The effects of groundwater depth, season and species on leaf water relations and leaf structure were assessed by multivariate analysis of covariance (MANOVA). For each species the impact of depth-to-groundwater and season on leaf water relations were investigated using two-way ANOVA. Multiple comparisons were made between groups using Tukey's *post-hoc* comparisons.

All statistical analyses were conducted using the built-in functions of the Statistical Package for the Social Sciences (SPSS; Version IBM SPSS statistics 19), with the exception of CCA, three-way ANOVA and two-way ANOVA, which were written using the SPSS syntax editor.

Results

A canonical correlation analysis (CCA) was conducted using three variables (depth-to-groundwater, species and season) as predictors of nine leaf water related traits to evaluate the shared relationship between two variable sets. The analysis yielded three functions with squared canonical correlations (R^2_C) of 0.37, 0.24 and 0.09 for each successive function. Collectively the full model across all functions was statistically significant using Wilk's $\lambda = 0.43$, F (3,27)=10.12, $p<0.001$. Because Wilk's represents the variance unexplained by the model, 1-λ yields full model effect size in a R^2 metric. Thus for a set of three canonical functions, the R^2_C type effect size was 0.57, which indicates that the full model explains a substantial portion, about 57%, of the variance shared between variable sets. As noted, the full model (function1 to 3) was statistically significant, functions 2 to 3 and 3 to 3 were also significant (F(3,16)=7.42, $p<0.001$ and F(3,7)=4.42, $p<0.001$) respectably. Given R^2_C effects for each function, only the first two functions were considered noteworthy in the context of this study (37% and 24% of shared variance). The last function only shared less than 10% of the remaining variance between two variable sets.

Table 6-1 presents standardized canonical function coefficients (*coef*) and structure coefficient (r_s) for functions 1 and 2. The squared structure coefficients are also given as well as communalities (h^2) across two functions for each variable. Looking at function 1 shows that the relevant criterion variables were primarily ε, SLA, Ψ_{TLP}, π100 and C_{FT}, with SWC having made a secondary contributions to the synthetic criterion variables. These water relation traits tended to have larger canonical function coefficients. An exception was SWC which had modest function coefficients but large structure coefficients. Elasticity was inversely related to other water related traits.

For function 2 (Table 6-1), variables of most importance were RWC_{TLP} and C_{TLP} with C_{FT}*, π_{100} and Ψ_{TLP} having less impact. With respect to the predictor variables set in function 1, site and species were most important but in function 2 DGW was the only primary contributor to the predictors synthetic variables. As a result depth-to-groundwater was the dominant predictor for all criteria. Results for commonality show that overall seasonality had the smallest effect in the model.

Table 6-1: Canonical solution for water related traits of leaves for function 1 and 2

	function 1:hydrated characteristics			Function 2: dehydrated characteristic			
Variables	***Coef***	r_s	r^2_s *(%)*	***Coef***	r_s	r^2_s *(%)*	h^2*(%)*
SWC	-0.08	0.58	34.22	-0.05	0.44	19.44	53.67
π_{100}	-0.54	0.61	38.19	0.54	-0.56	32.03	70.22
Ψ_{TLP}	0.65	0.64	41.86	-0.28	-0.55	30.25	72.11
RWC_{TLP}	-0.14	0.10	1.04	-0.77	-0.90	81.36	82.40
ε	-0.92	-0.73	54.64	-0.02	-0.27	7.56	62.06
C_{FT}	-0.50	0.60	36.24	-1.40	0.44	19.53	55.77
C_{TLP}	-0.01	-0.22	4.92	0.34	0.75	57.15	62.08
C_{FT}*	0.28	0.32	10.57	1.39	0.59	34.40	46.16
SLA	0.67	0.71	51.55	0.56	-0.003	0.0009	51.55
R^2			36.76			24.29	
Species	-0.78	-0.83	69.22	-0.41	-0.32	10.43	79.65
Depth to GW	-0.46	-0.55	30.58	0.86	0.81	65.28	95.86
Season	-0.30	-0.31	9.58	-0.41	-0.40	16.64	26.50

Note. Structure coefficients (r_s) greater than |0.45| are underlined. Communality coefficients (h^2) greater than 45% are underlined. *Coef*=standardized canonical function coefficient; r_s=structure coefficient; r^2_s= squared structure coefficient; h^2=communality coefficient.

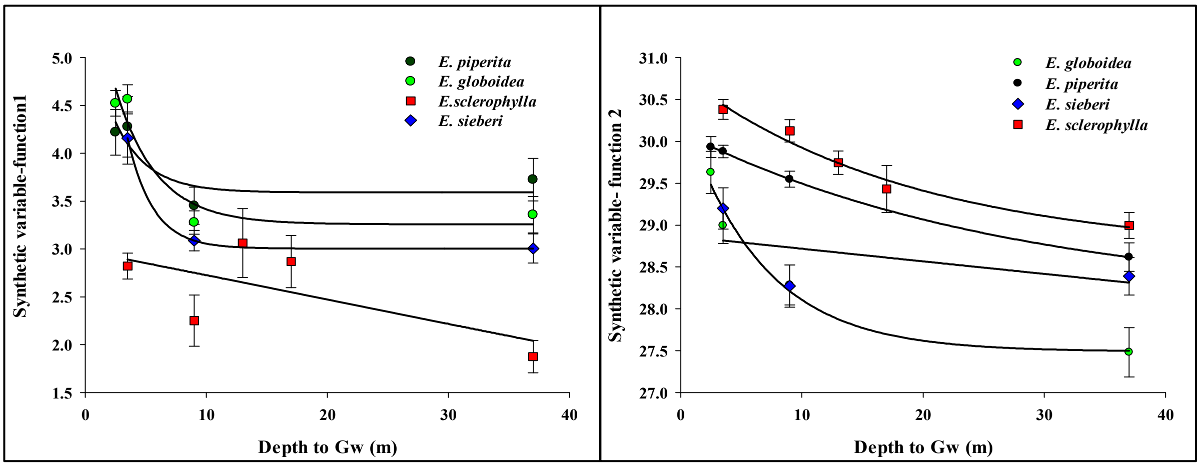


Figure 6-4: Response of synthetic variables (1 and 2) to a gradient of depth-to-groundwater for all four *Eucalyptus* species derived from first and second functions of CCA respectively.

Using the results from CCA analysis, the synthetic variables were calculated for each of the functions. Using the synthetic variables for both functions the response of each species to depth-to-groundwater was determined (Fig. 6-4). These synthetic variables show how leaf water relations overall responded to depth-to-groundwater for each species. Variable 1 and 2, which were derived from CCA analysis, can be called fully hydrated leaf water characteristics and de-hydrated leaf water characteristics respectively from a consideration of which leaf water traits made a significant contribution in them.

MANOVA analysis was conducted on the synthetic variable 1 (derived from function1 of the CCA outputs) and synthetic variable 2 (derived from function 2 of the CCA outputs) to determine whether there was any interaction of the three independent variables (depth-to- groundwater, species and season) on leaf water relations. Three-way ANOVA was also conducted to find the effect of independent variables (of depth-to-groundwater, season and species) on the most important leaf water relations (from table 6-2) π_{100}, Ψ_{TLP}, RWC_{TLP} and ε derived from P-V curve analysis to determine whether there was any interaction and whether interactions significantly contributed to the results. Three-way ANOVA was also used to assess the interaction between SLA and pre-dawn leaf water potential with the following independent variables: groundwater depth, season and species.

There was no significant three-way interaction between species, season and depth-to-groundwater for synthetic variable1. However, there were statistically significant two-way interactions between all independent variables ($p<0.05$). However, for the synthetic variable 2, the three-way interaction was significant ($p<0.001$). The only statistically two-way interaction for this variable was the interaction between species and season ($p<0.05$).

Three-way ANOVA was also used to assess the interaction of three variables on π_{100}, Ψ_{TLP} and ε . For π_{100} and Ψ_{TLP} there were no statistically significant interactions between the three factors ($p=0.06$, $F=1.95$,) and ($p=0.27$, $F=1.35$). The only interaction which had significant impact on both traits was depth-to-groundwater and season ($p<0.001$). Consequently further analyses focused on simple two-way interactions of site and season. This interaction was significant for all species except *E. piperita.* Depth-to-groundwater had the main effect on measured π_{100} and Ψ_{TLP} for all species during winter. Depth-to-groundwater did not have a significant impact on π_{100} of *E. sieberi* and *E. sclerophylla* during summer.

The results for MANOVA for elasticity showed no statistically significant interaction between depth-to-groundwater, species and season while the interaction for depth-to-groundwater and species ($p <0.05$, $F=3.39$,) and species and season ($p= 0.05$, $F= 5.00$) were significant. Simple two-way interaction results showed that the interaction of site and season were only significant for *E. piperita* and *E. sclerophylla.*

The interactions between depth-to-groundwater, season and species were tested for pre-dawn leaf water potential across sites where data were available for both seasons. The interaction of site and season as well as its interaction with site, season and species were not significant. Each variable individually had a significant effect on pre-dawn leaf water potential. The interaction between site and species was significant for both winter and summer ($p<0.001$).

A main aim of the research described in this chapter was to understand how inter-specific leaf water relations change across a gradient of groundwater depth. Consequently, for each species two-way ANOVA were conducted to determine the effect of depth-to-groundwater and seasonality as well as the interaction of these two factors. To assess the simple main effect a Bonferroni correction was performed. The following sections describe the results for each species.

E. piperita

This species was present at four sites (sites having 2.4 m, 4.3 m, 9.8 m and 37.5 m depth-to-groundwater).

Depth-to-groundwater was the only factor that had significant impact on variation of π_{100} (F= 9.46, $p<0.001$; df=3,69) and Ψ_{TLP} (F=13.56, $p<0.001$; df=3,72). Differences between sites were significant for both seasons, with π_{100} and Ψ_{TLP} declining significantly with increased depth-to-groundwater (Fig. 6-5a and Fig. 6-6a). However, the interaction between depth-to-groundwater and season was not statistically significant. In summer and winter both π_{100} and Ψ_{TLP} were significantly lower at the deepest (37.5 m) site compared to the site 2.4 m DGW. No seasonal changes for these two traits were observed within any sites. Leaf water potential at turgor loss point ranged from -1.02 MPa at site 2.4 m DGW to -1.60 MPa at site 37.5 m DGW in winter.

Relative water content at the turgor loss point declined significantly across sites in winter from 95.6% at site 2.4 m DGW to 92% at site 37.5 m DGW (Fig. 6-7a). However, decreases in RWC_{TLP} during summer were not statistically significant. *Post hoc* tests showed that leaves from trees on the sites 2.4 m and 4.3 m exhibited higher RWC_{TLP} than leaves from tress growing on the deepest water-table site (37.5

m; Table 6-2). Seasonality was a significant factor in explaining changes in bulk modulus of elasticity. Bulk modulus of elasticity was significantly smaller during summer measurements ($p<0.05$), with no site and site-by-season effects found (Fig. 6-8a).

Capacitance at full turgor (C_{FT}) and absolute capacitance (C_{FT}*) did not differ across sites along the depth-to-groundwater gradient, whereas seasonality had a significant effect on them; both were larger at all sites during summer (Table 6-2).

Specific leaf area for *E. piperita* was a function of seasonality, depth-to-groundwater and the interaction between these. Generally during winter SLA decreased with increase in depth-to- groundwater from 55.7 cm^2 g^{-1} at site 2.4 m DGW to 46.0 cm^2 g^{-1} at site 9.8 m DGW (Fig 6-9a).

Pre-dawn leaf water potential (Ψ_{pd}) for this species was significantly affected by DGW (F=16.68, $p<0.001$; df=3,51), season (F=12.3, $p<0.001$; df=1,53) and their interaction ($p<0.001$). In winter pre-dawn (Ψ_{pd}) did not differ significantly with increasing depth-to-groundwater between the three shallowest water-table (2.4 m, 4.3 m and 9.8 m) sites. However, Ψ_{pd} was significantly higher (closer to zero) at the 37.5 m DGW site compared to the other three shallowest sites. In summer, Ψ_{pd} was significantly lower at site 2.4 m (-0.22 MPa) compare to the other two sites 4.3 m, 37.5 m (-0.09 and -0.11 MPa). There was no difference in Ψ_{pd} between these two sites (Fig. 6-10a). No significant difference in minimum leaf water potential was found across sites and between two seasons (Fig. 6-11a).

E. globoidea

The distribution of this species was the same as that of *E. piperita*. Results of two-way ANOVA showed that for both π_{100} and Ψ_{TLP} seasonality did not have any influence. In contrast, depth-to-groundwater had significant influences on both π_{100} (F= 10.48, $p<0.001$; df=3, 69) and Ψ_{TLP} (F=12.27, $p<0.001$; df=3,69). In both seasons π_{100} and Ψ_{TLP} declined with increasing depth (Fig. 6-5b, Fig. 6-6b). *Post hoc* comparisons showed that sites 2.4 m and 37.5 m DGW were significantly different in both seasons (Table 6-2).

RWC_{TLP} varied across sites as a function of depth-to-groundwater only (F=11.77, $p<0.001$; df=3,69). Overall RWC_{TLP} decreased significantly from 94.2 % at site 2.4 m DGW to 91.2% at site 37.4 m DGW as depth increased from (Fig. 6-7b). As a result the deepest site had a significantly lower RWC_{TLP} compared with the other sites (Table 6-2). Depth was the only factor that affected bulk modulus of elasticity ($p<0.001$). In summer elasticity was significantly higher at the 9.9 m site (13.49 MPa) compared with the shallowest site (8.93 MPa). In winter, elasticity in site 9.8 m DGW was significantly larger than the site 4.3 m DGW. Furthermore, elasticity did not show any significant differences within each site between winter and summer.

Capacitance at full turgor and absolute capacitance changed significantly only as a function of depth-to-groundwater. There were no significant differences across sites during winter for either trait. In summer C_{FT}*, was significantly larger at the deepest site (37.5 m; 1.3 mol m^{-2} MPa^{-1}) compared to the three shallower sites. For both traits seasonal changes only occurred at the deepest site (37.5 m). Capacitance at turgor loss point (C_{TLP}) was a function of all three factors (depth-to-groundwater, seasonality and the interaction between those). Significant seasonal changes within site only occurred at the two deepest sites (9.8 m and 37.5 m DGW). There was no significant difference in winter across sites. However, in summer C_{TLP} at the two deepest (9.8 m, 37.5 m) sites were significantly higher than the shallowest sites and increased as depth t increased (Table 6-2).

SLA responded only to depth-to-groundwater. During winter SLA in two shallowest groundwater sites was significantly larger (≈ 30%) than the two other sites with deep water table (Fig. 6-9b).

Pre-dawn leaf water potential varied in response to seasonality and depth-to-groundwater. Pre-dawn leaf water potential was lower in winter than summer at all sites. In winter Ψ_{pd}, was significantly higher (closer to zero) in the shallowest site (2.4 m; -0.3 MPa) compared to all other sites. In summer the shallowest site (2.4 m) maintained a higher Ψ_{pd} but this was not statistically significant (Fig. 6-10b).

E. seiberi

This species was present at three sites: 4.3 m, 9.8 m and 37.5 m depth to GW. Seasonality did not affect π_{100} and Ψ_{TLP}; however, depth-to-groundwater had a significant impact on both π_{100} (F=8.31, p=0.001; df=2,52) and Ψ_{TLP} (F=12.65, p<0.001; df=2,52). During summer neither π_{100} nor Ψ_{TLP} showed any trend across sites. However, during winter π_{100} and Ψ_{TLP} declined significantly from -0.83 to -1.25 MPA for π_{100} and from -1.17 to -1.64 MPA for Ψ_{TLP} with increasing depth (Fig. 6-5c and Fig. 6-6c).

RWC_{TLP} was affected by all variables as well as their interaction. During summer there were no differences among sites but during winter the site with the shallowest depth-to-groundwater had a significantly larger RWC_{TLP} compared to the other 2 sites at which this species was found (Fig. 6-7c). Depth-to-groundwater and seasonality both contributed significantly in variation in bulk modulus of elasticity. Overall during summer there were no differences in ε between sites; however in winter significant reductions in ε with increasing depth were observed from 11.0 at site 4.3 m DGW to 13.7 MPa at site 37.5 m DGW (F=4.52, p=0.01; df=2,52) (Fig. 6-8c).

Neither absolute capacitance nor capacitance at full turgor changed significantly as depth-to-groundwater increased. However, season was a significant factor for both traits. Significant seasonal changes were observed across all sites for both traits which results in higher values during summer. In summer, C_{FT}* was significantly higher in deepest site (37.5 m) compared with shallowest sites.

Seasonality, depth-to-groundwater and the interaction between these two variables all had significant effects on SLA for *E. sieberi* (Fig. 6-9c). For both winter and summer, SLA declined with increase in depth-to-groundwater and SLA was consistently smaller in summer than in winter (Fig. 6-9c).

Depth and seasonality both had significant effects on pre-dawn leaf water potential (Fig. 6-10c). There were no differences among sites in summer but in winter the site with 9.9 m DGW had lowest Ψ_{pd} (-0.36 MPa) compared to the deepest site (-0.29 MPa) and the site with 4.3 m DGW (-0.3 MPa). Pre-dawn leaf water potential was significantly lower during winter compared with summer (Fig. 6-10c).

E. sclerophylla

E. sclerophylla was present at five sites. Depth-to-groundwater, seasonality and the interaction of depth and seasonality ($p<0.05$) all contributed significantly to variation of π_{100} and Ψ_{TLP} across sites (Fig 6-5d). Neither π_{100} nor Ψ_{TLP} varied across sites in summer for *E. sclerophylla* but in winter both π_{100} ($F=6.34$, $p<0.001$; df=4,42) and Ψ_{TLP} ($F=7.58$, $p<0.001$; df=4,42) decreased with increased depth (Figs. 6-5d & 6-6d). At the deepest site (37.5 m) π_{100} ($p<0.001$) and Ψ_{TLP} ($p<0.001$) were significantly lower in winter compared to summer (Fig 6-5d and Fig 6-6d).

Relative water content at turgor loss decreased significantly as a function of depth-to-groundwater in winter from 96.4% at site 2.4 m DGW to 92.4% at site 37.5 m DGW (Fig. 6-7d).Only the site with deepest groundwater depth (37.5 m) showed a seasonality effect with significant decrease ($p<0.001$) in RWC_{TLP} in winter.

Bulk modulus of elasticity did not differ as a function of depth-to-groundwater in either season. However, within sites, site 9.8 m ($p < 0.001$) and 16 m ($p < 0.05$) had significantly lower elasticity during winter than summer (Fig. 6-8d).

SLA tended to decrease with increase in depth-to-groundwater, with the exception of the 16.3 m site (Fig. 6-9d), where for both seasons, SLA was largest compared to all other sites. Within each site seasonal differences were not statistically significant.

For pre-dawn leaf water potential both season and depth had statistically significant effects (Fig. 6-10d). During summer the shallow site (4.3 m) had significantly lower Ψ_{pd} than the deepest site (37.5 m). In winter site with 9.8 m had significantly lower Ψ_{pd} compared with the other three sites (Fig. 6-10d).

All the means and standard errors of all measurements for all leaf water relations traits are presented in Table 6-2.

Table 6-2: Average of leaf relation traits for all four species in sites where there were measured. Data are mean ± SEM (n=9) shown together with the significance of differences between sites from Tukey's HSD test ($p<0.05$). Values followed by the same letter for each species are not significantly different. The results are presented for both summer (denoted as S) and winter (denoted as W). Shown in columns are groundwater depth at each site (DGW), osmotic potential at full turgor (π_{100}), leaf water potential at turgor loss point (Ψ_{TLP}), relative water content at turgor loss point (RWC_{TLP}), bulk modulus of elasticity (ε), capacitance at full turgor (C_{FT}), capacitance at turgor loss point (C_{TLP}), absolute capacitance (C_{FT}*), saturated water content (SWC) and specific leaf area (SLA).

Species	DGW (m)	π_{100} (MPa)	Ψ_{TLP} (MPa)	RWC_{TLP} (%)	ε (MPa)	C_{FT} (MPa^{-1})	C_{TLP} (MPa^{-1})	C_{FT}^{*} ($mol\ m^{-2}\ MPa^{-1}$)	SWC ($g\ g^{-1}$)	SLA (cm^2g^{-1})
E. globoidea	2.4	W -0.69±0.06 a	-1.03±0.07ab	94.20±0.182b	9.66±0.91ab	0.06±0.004ab	0.06±0.007a	0.93±0.05a	1.30±0.01ab	58.87±1.91 a
		S -0.58±0.05 a	-0.86±0.05a	94.33±0.57b	8.937±0.85a	0.07±0.005a	0.07±0.01a	0.95±0.08a	1.46±0.05ab	51.82±1.30a
	4.3	W -0.61±0.05 a	-0.94±0.06a	94.02±0.32b	8.43±0.98a	0.07±0.005b	0.06±0.004a	1.04±0.07a	1.35±0.02b	56.47±1.1a
		S -0.92±0.14 b	-1.29±0.13b	93.74±0.70b	10.79±1.01ab	0.06±0.004a	0.10±0.02ab	0.98±0.07a	1.32±0.02a	46.44±1.00b
	9.8	W -0.88±0.06 ab	-1.32±0.10bc	93.32±0.63ab	12.40±0.98b	0.05±0.002a	0.07±0.005a	1.04±0.05a	1.33±0.01b	41.01±0.53b
		S -1.03±0.08 b	-1.28±0.07b	93.02±0.52b	13.49±0.65b	0.06±0.002a	0.18±0.02c	1.00±0.04a	1.54±0.04b	50.79±1.01b
	37.5	W -1.13±0.13 b	-1.57±0.12c	91.27±0.84a	10.93±0.76ab	0.06±0.002ab	0.11±0.02b	1.11±0.03a	1.25±0.01a	39.62±1.15b
		S -1.02±0.05 b	-1.30±0.05b	92.85±0.36a	10.28±1.13ab	0.07±0.004a	0.17±0.01bc	1.31±0.08b	1.55±0.03b	48.68±1.23b
E.piperita	2.4	W -0.70±0.05 a	-1.03±0.05a	95.62±0176ab	14.73±1.14a	0.04±0.002a	0.05±0.004a	0.57±0.03a	1.26±0.04a	55.70±1.09a
		S -0.80±0.07 b	-1.16±0.07a	93.791±0.68a	12.91±1.332a	0.05±0.007a	0.09±0.02a	0.70±0.06a	1.55±0.08c	49.28±0.99a
	4.3	W -0.74±0.05a	-1.10±0.07ab	95.90±0.28a	15.72±1.59a	0.04±0.002a	0.04±0.002a	0.53±0.04a	1.30±0.03a	49.21±1.01b
		S -0.98±0.13 ab	-1.35±0.11ab	93.26±0.60a	13.19±1.66a	0.05±0.006a	0.11±0.03a	0.82±0.10a	1.22±0.02a	52.05±0.67a
	9.8	W -1.03±0.13 ab	-1.35±0.08bc	94.43±0.28b	16.22±1.33a	0.04±0.001a	0.10±0.02b	0.64±0.03a	1.24±0.01a	46.00±1.4b
		S -0.90±0.10 ab	-1.25±0.09ab	92.89±0.59a	11.60±1.45a	0.06±0.007a	0.12±0.03a	0.86±0.12a	1.49±0.06bc	63.33±1.81b
	37.5	W -1.28±0.11 b	-1.61±0.06c	91.95±0.49c	15.44±1.19a	0.05±0.002a	0.18±0.03b	0.66±0.03a	1.32±0.02a	46.47±0.7b
		S -1.25±0.14 a	-1.59±0.10b	91.97±0.58a	13.73±0.83a	0.05±0.001a	0.16±0.01a	0.83±0.03a	1.31±0.03ab	49.78±1a

Species	DGW (m)	π_{100} (MPa)	Ψ_{TLP} (MPa)	RWC_{TLP} (%)	ε (MPa)	C_{FT} (MPa^{-1})	C_{TLP} (MPa^{-1})	C_{FT}^{*} (mol m^{-2} MPa^{-1})	SWC (g g^{-1})	SLA (cm^2g^{-1})
E. sclerophylla	4.3	W -0.77±0.08 b S -0.86±0.07 a	-1.10±0.09 a -1.20±0.07 a	96.47±0.4 a 95.68±0.40 a	19.49±0.86a 18.52±0.73a	0.03±0.001a 0.03±0.001a	0.05±0.006a 0.06±0.007a	0.52±0.02a 0.56±0.02a	1.11±0.02a 1.18±0.02a	47.86±0.75b 46.39±0.84ab
	9.8	W -1.06±0.14ab S -1.10±0.12 a	-1.37±0.1 ab -1.41±0.11 a	95.63±0.42 ab 93.60±0.84 ab	21.80±1.14a 17.25±1.79a	0.03±0.001a 0.04±0.01ba	0.09±0.02ab 0.13±0.14ab	0.49±0.02a 0.66±0.09ab	1.11±0.02a 1.34±0.04ab	41.01±1.06a 43.13±1.64c
	13	W -1.13±0.10 ab S -0.92±0.04 a	-1.51±0.1 abc -1.28±0.05 a	94.34±0.57 bc 95.49±0.22a	18.42±1.81a 19.38±0.82a	0.04±0.003a 0.03±0.001a	0.07±0.01a 0.06±0.009a	0.52±0.04a 0.52±0.02a	1.18±0.01a 1.15±0.06a	42.94±1.72ab 39.51±1.03a
	16.3	W -1.22±0.13 ab S -1.09±0.07 a	-1.59±0.11bc -1.34±0.06 a	94.02±0.68 bc 93.03±0.43 b	19.36±1.18a 14.97±1.22a	0.03±0.001a 0.05±0.004b	0.10±0.02ab 0.18±0.02b	0.51±0.02a 0.76±0.05b	1.21±0.05a 1.51±0.08b	58.72±2.6c 53.37±2.4 ab
	37.5	W -1.59±0.08 a S -0.98±0.08 a	-1.91±0.07 c -1.30±0.08 a	92.44±0.46 c 94.48±0.63 ab	21.01±0.83a 19.57±0.92a	0.04±0.001a 0.03±0.002a	0.17±0.02b 0.10±0.02ab	0.65±0.02b 0.54±0.04a	1.18±0.01a 1.18±0.06a	38.76±0.68a 42.63±0.88 b
E.sieberi	4.3	W -0.83±0.11 a S -0.98±0.10 a	-1.17±0.10a -1.34±0.08a	93.76±0.47a 91.68±0.61a	11.00±0.82a 10.04±0.66a	0.062±0.002a 0.07±0.002a	0.09±0.02a 0.12±0.02a	0.096±0.04a 1.12±0.04a	1.37±0.03a 1.18±0.01ab	51.24±1.01a 44.37±0.91a
	9.8	W -1.37±0.09 b S -1.06±0.5 ab	-1.72±0.06b -1.53±0.04a	90.17±0.54b 91.21±0.22ab	13.20±0.56ab 10.21±0.48a	0.06±0.001a 0.067±0.001a	0.19±0.03b 0.09±0.01a	0.89±0.02a 1.12±0.05a	1.17±0.02b 1.06±0.03a	39.67±0.52b 35.06±1.09b
	37.5	W -1.25±0.12 b S -1.28±0.12ab	-1.64±0.10b -1.57±0.06a	91.55±0.63b 89.78±0.39b	13.78±0.84b 11.78±0.59a	0.054±0.001a 0.07±0.003a	0.15±0.02a 0.22±0.02b	0.88±0.02a 1.30±0.06a	1.21±0.03b 1.25±0.07b	38.77 ±1.31b 36.59±0.91b

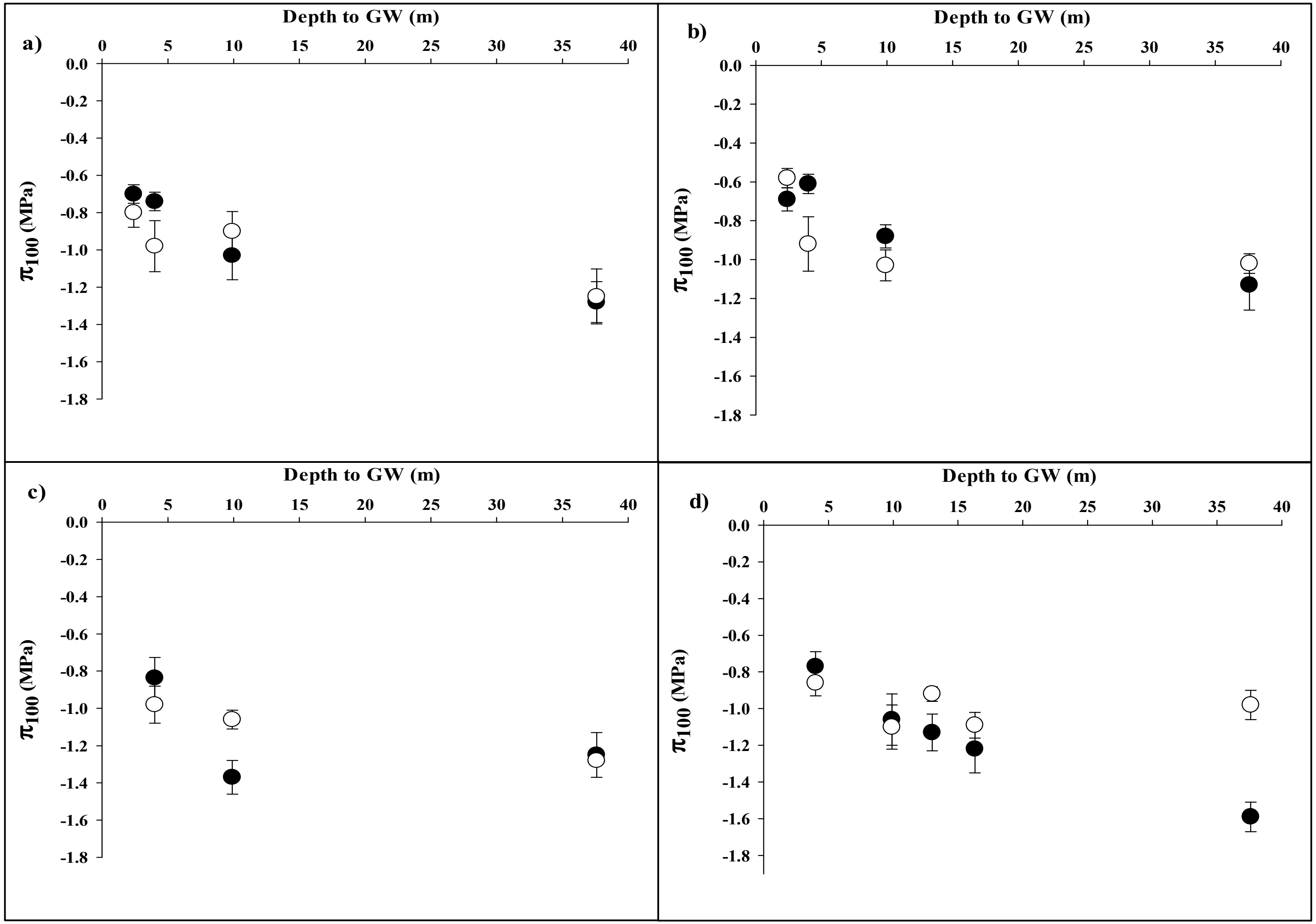


Figure 6-5: Osmotic potential at full turgor (π_{100}) for different species across sites that differ in depth-to-groundwater; a) *E. piperita* , b) *E. globoidea*, c) *E. sieberi* , d) *E. sclerophylla* for two seasons (winter shown in black and summer shown in hollow symbols).

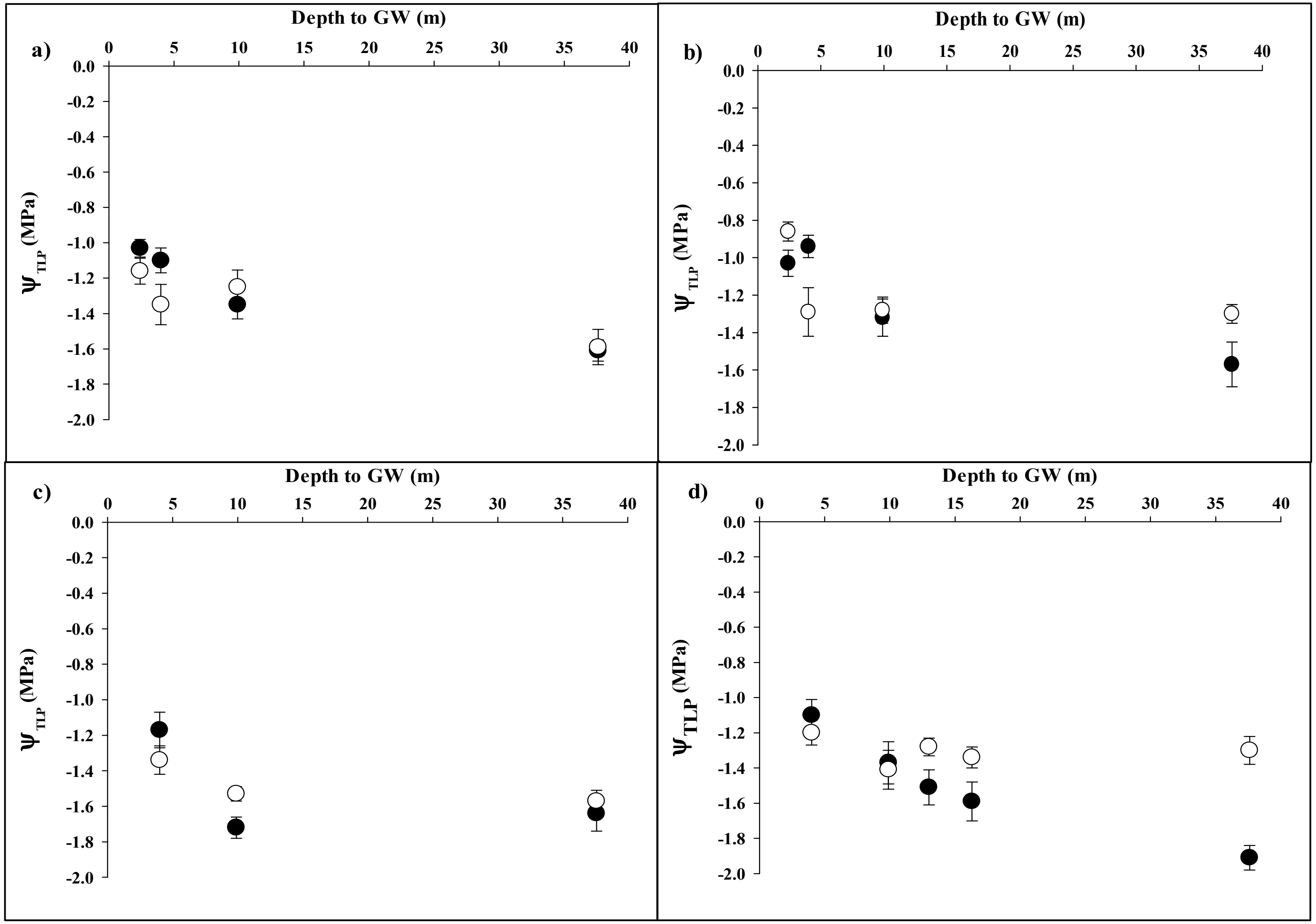


Figure 6-6: Leaf water potential at turgor loss point (MPa) for four species across sites differing in depth-to-groundwater: a) *E. piperita* , b) *E. globoidea*, c) *E. sieberi* , d) *E. sclerophylla* for two seasons (winter shown in black and summer shown in hollow symbols).

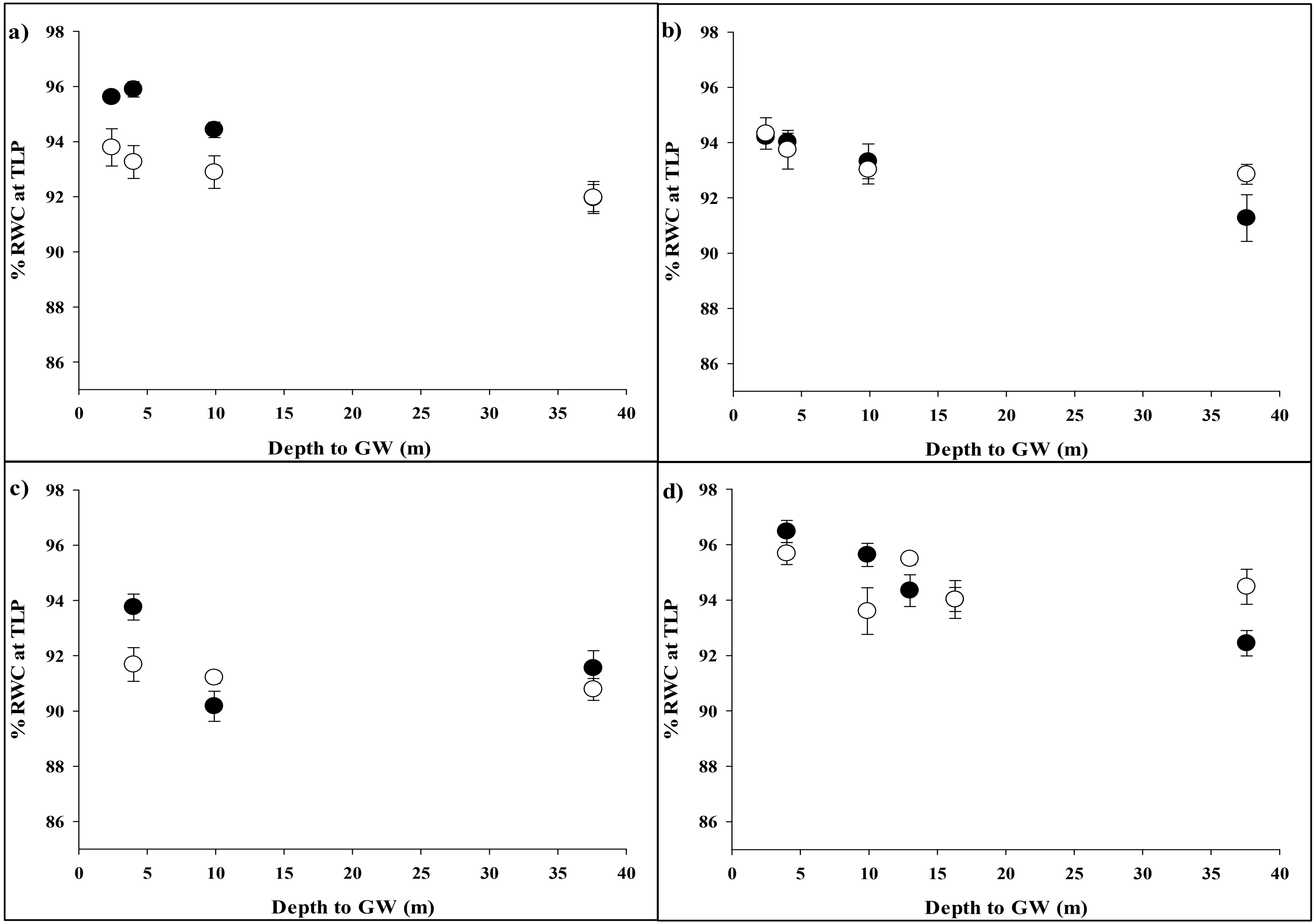


Figure 6-7: Relative water content at turgor loss point (% RWC $_{TLP}$) for four species across sites differing in depth-to-groundwater: a) *E. piperita* , b) *E. globoidea*, c) *E. sieberi* , d) *E. sclerophylla* for two seasons (winter shown in black and summer shown in hollow symbols.

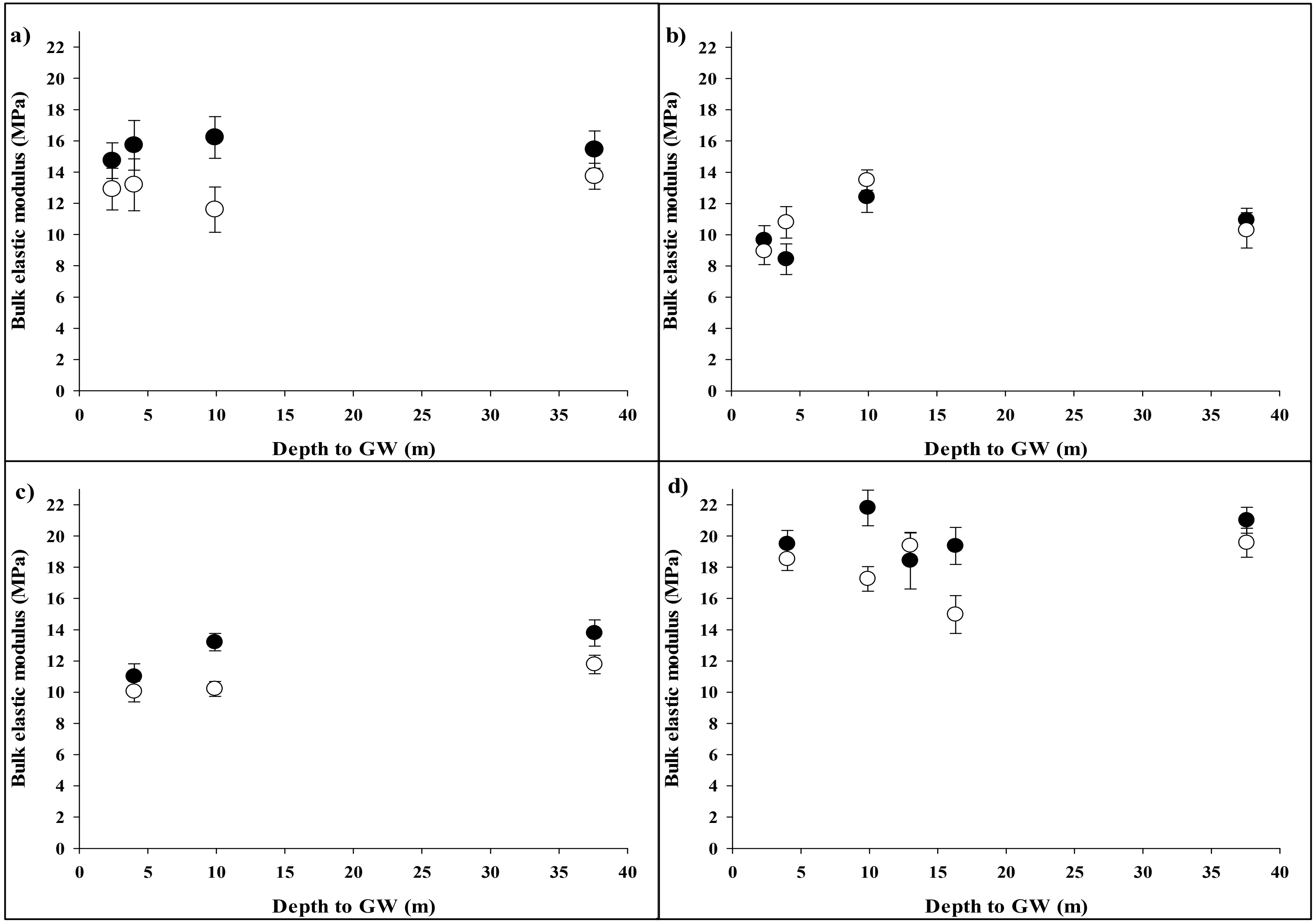


Figure 6-8: Bulk elastic modulus (ε) for four species across sites differing in depth-to-groundwater: a*) E. piperita* , b) *E. globoidea*, c) *E. sieberi* , d) *E. sclerophylla* for two seasons (winter shown in black and summer shown in hollow symbols).

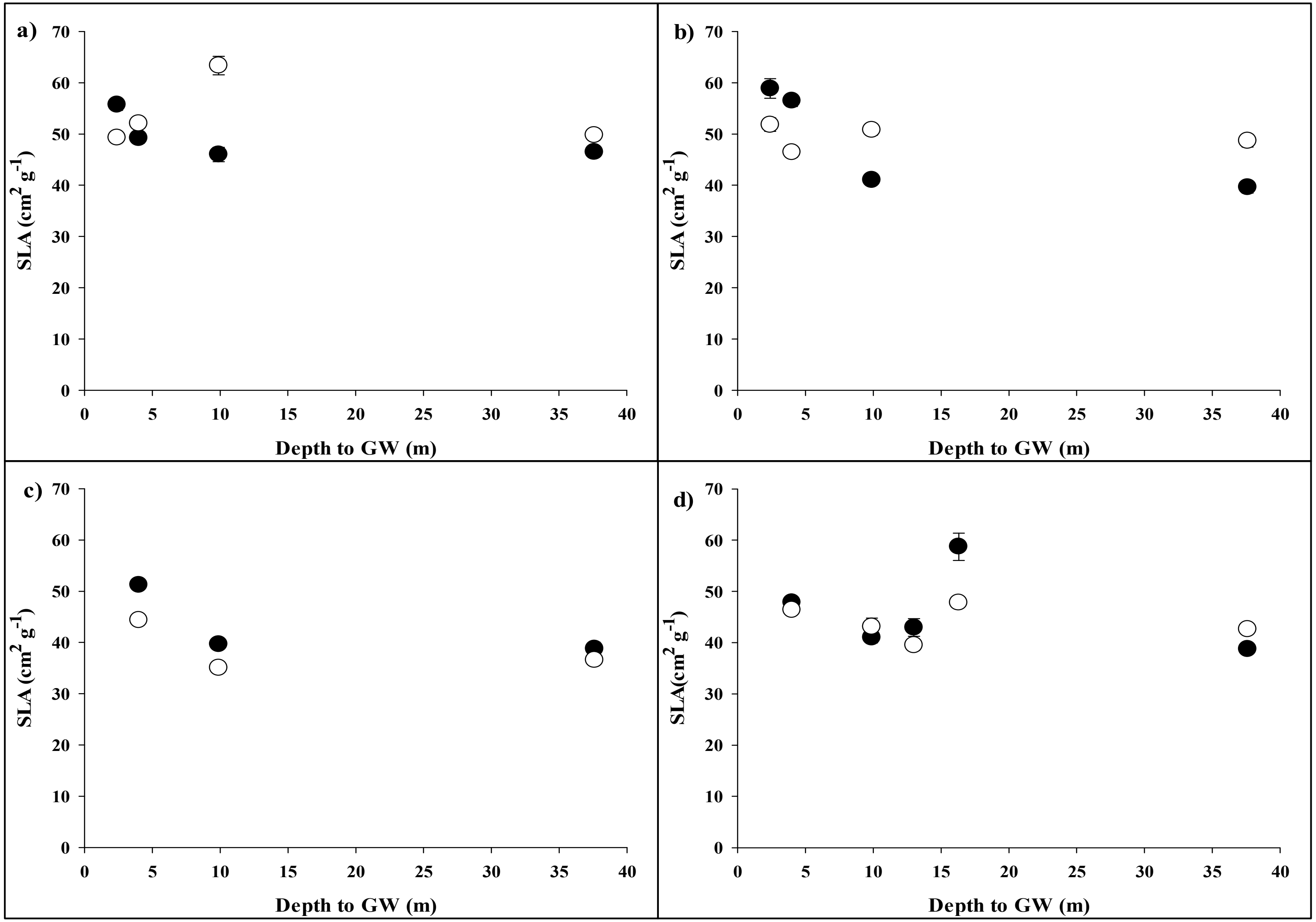


Figure 6-9: Specific leaf area of all four species across sites differing in depth-to-groundwater: a) *E. piperita* , b) *E. globoidea*, c) *E. sieberi* , d) *E. sclerophylla* for two seasons (winter shown in black and summer shown in hollow symbols).

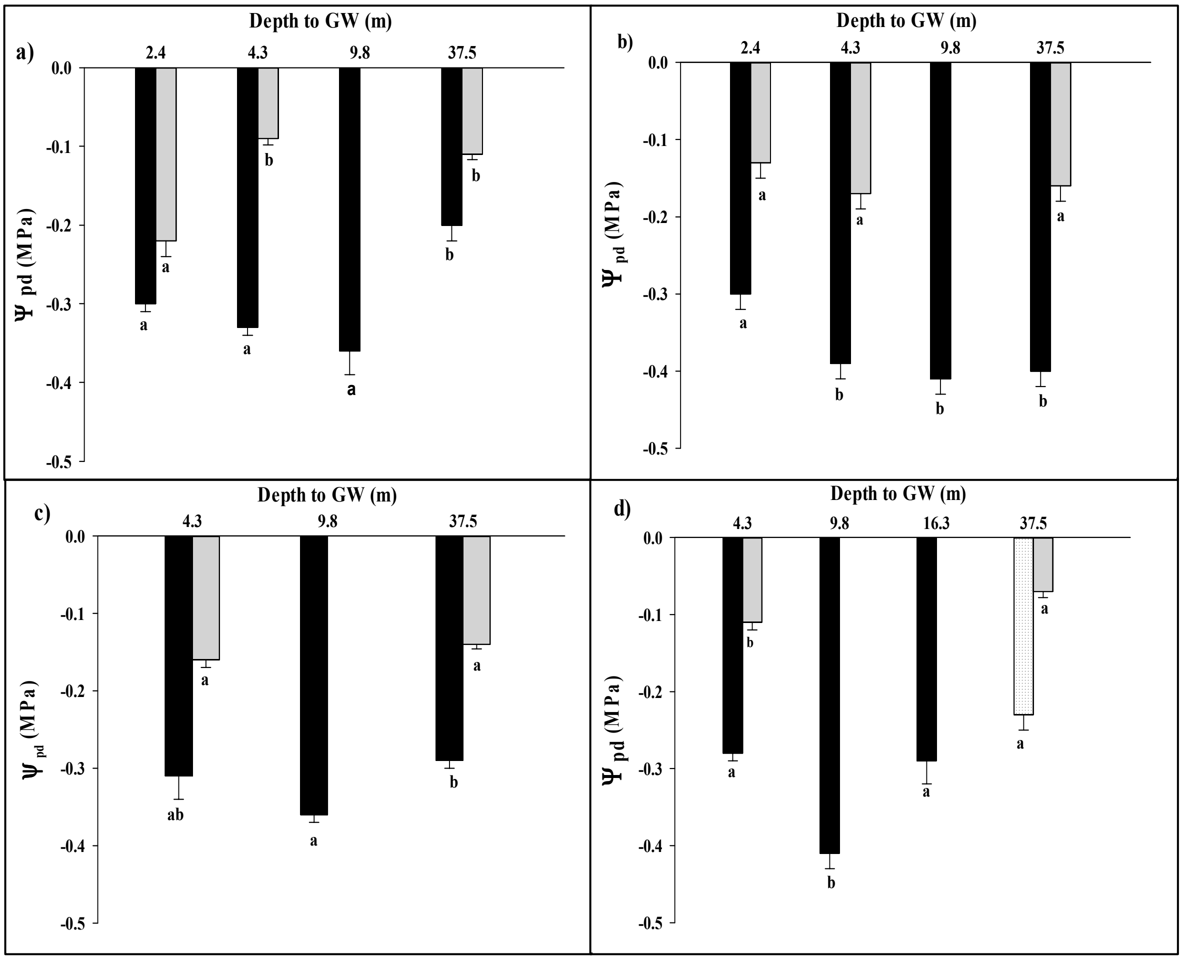


Figure 6-10: Pre-dawn leaf water potential of all four species across sites differing in depth-to-groundwater: a) *E. piperita* , b) *E. globoidea*, c) *E. sieberi* , d) *E. sclerophylla* for two seasons (winter shown in black and summer showed in grey). Columns labelled by the same letter for each species are not significantly different.

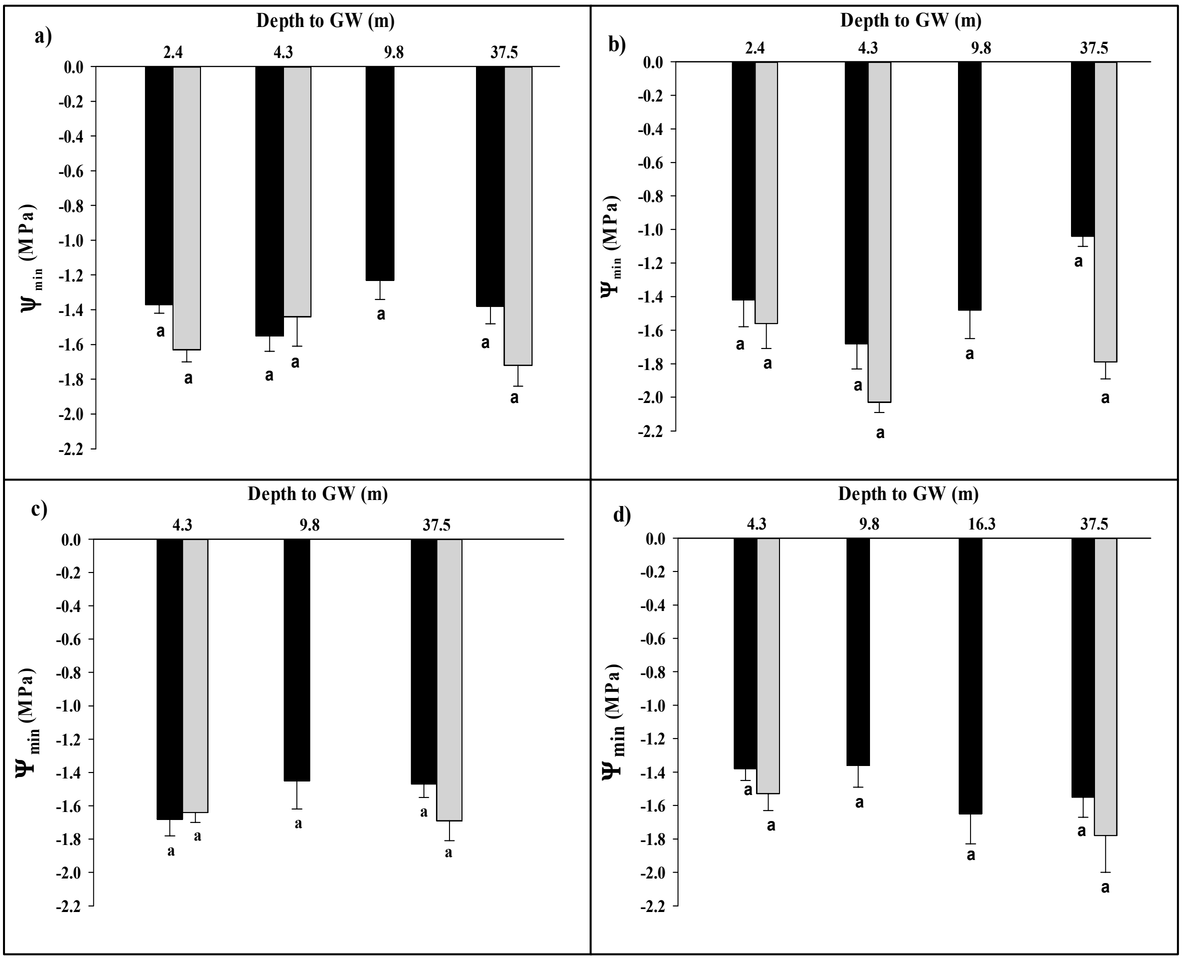


Figure 6-11: Minimum leaf water potential of all four species across sites differing in depth-to-groundwater: a) *E. piperita* , b) *E. globoidea*, c) *E. sieberi* , d) *E. sclerophylla* for two seasons (winter shown in black and summer showed in grey). Columns labelled by the same letter for each species are not significantly different.

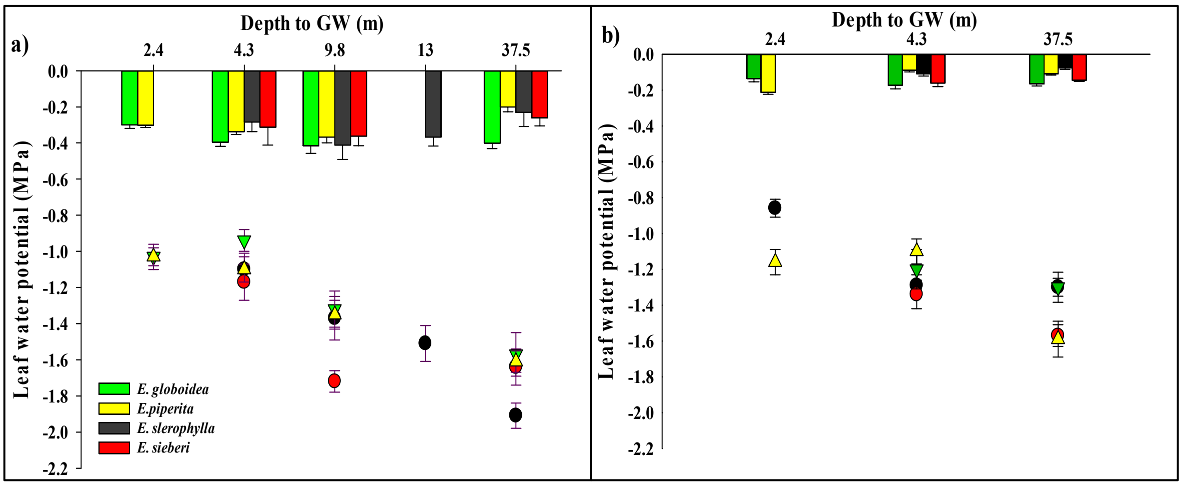


Figure 6-12: Pre-dawn leaf water potential (MPa; columns, n=9) and leaf water potential at turgor loss point (MPa; symbols) for winter (a) and summer (b) for all species growing across a depth-to-groundwater gradient.

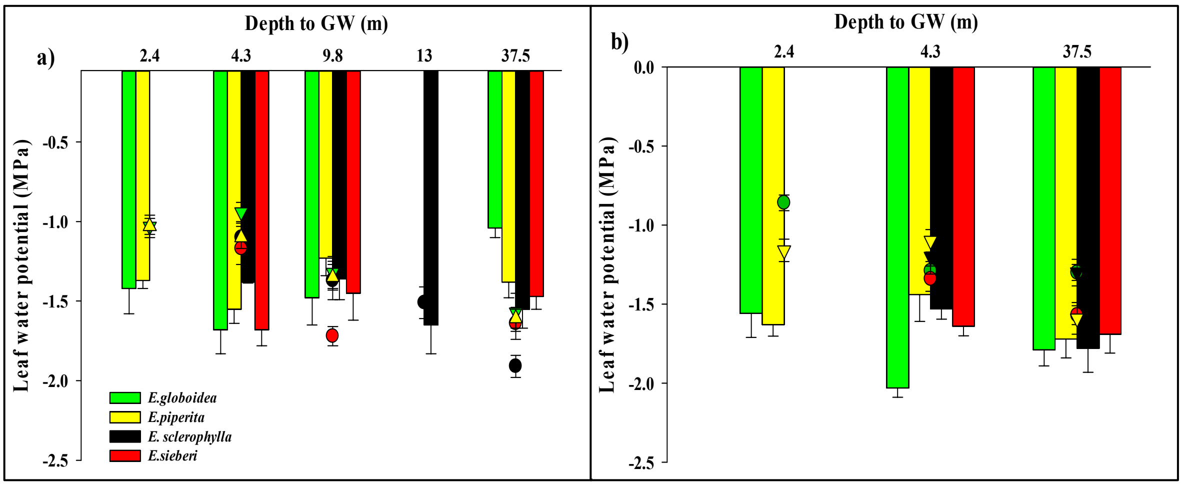


Figure 6-13: Minimum diurnal leaf water potential (MPa; columns n=9) and leaf water potential at turgor loss point (MPa- symbols, n=9) for winter (a) and summer (b) for all species growing across a depth-to-groundwater gradient.

As Ψ_{pd} did not show any significant relationship with depth-to-groundwater, results for all species within each site were pooled together to test whether any relationship existed in general between depth-to-groundwater and Ψ_{pd}. Results of ANOVA showed during summer the site with 2.4 m DGW was significantly different from site with 4.3 m and 37.6 m DGW, having a lower pre-dawn leaf water potential (p=0.003, F=6.16). In winter significant differences between sites were found, with the deepest site (37.6 m DGW) having a significantly higher Ψ_{pd} compared to all other shallower water-table sites (p<0.001, F=14.93). The same analysis performed for Ψ_{min} showed there was no significant difference in Ψ_{min} across sites in either summer (p=0.46, F= 0.78) or winter (p=0.08, F=2.22)

By comparing Ψ_{pd} and Ψ_{TLP} for all species across all sites showed that pre-dawn leaf water potentials were well above their turgor loss point in both winter and summer (Fig. 6-12). In contrast, minimum leaf water potentials measured during diurnal measurements of water potential, compared with leaf water potential at turgor loss derived from P-V analyses showed that during summer all species at all sites had minimum leaf water potentials that were lower than their turgor loss point (Fig. 6-12). However, during winter this was true only for the two sites having the shallowest depths-to-groundwater. In winter, there were several species that maintained minimum leaf water potentials that were lower than the water potential associated with zero turgor (Fig. 6-13a).

Discussion

Seasonality of leaf water potential and groundwater depth

I hypothesized that, despite having a relatively high (relative to much of Australia) annual rainfall (1067 mm), depth-to-groundwater may influence leaf water relations and leaf structure. Previously the impact of water deficit (Pita and Pardos 2001) or gradients of precipitation (Santiago et al. 2004a) on leaf structure and water relations has been examined in different biomes along a spatially extensive environmental gradient (e.g. from arid areas to a mesic rainforest), using saplings (Merchant et al. 2007) or woodlands (Mitchell et al. 2008), both within and between species. The potential impact of differences in depth-to-groundwater on leaf structure and leaf water relations in an environment with high annual precipitation has not, to my knowledge, been examined. In a recent study, Carter and White (2009) examined the impact of groundwater depth on water relations of an *E. kochii* plantation in Western Australia but this occurred at an arid site where average annual rainfall was 380 mm.

Across all species and all depth-to-groundwater, pre-dawn leaf water potential was significantly lower in winter than in summer. This was contrary to expectations given the fact that summer is generally much hotter than winter in the study region. However, during the period of summer sampling, there was a very high frequency of rainy days, with associated decrease in temperature and solar radiation, and increased soil moisture content, leading to Ψ_{pd} being higher in summer than winter.

In only one species (*E. globoidea*) in one season (winter) did Ψ_{pd} vary in accordance with the original hypothesis, namely that as depth-to-groundwater increased Ψ_{pd} declined. In all other species across all other sites, Ψ_{pd} either did not vary with depth-to-groundwater, or Ψ_{pd} was closer to zero at deep sites compared to the shallowest sites (*E. piperita*, summer and winter). These results can be explained by the unusually large amounts of summer rainfall across all sites before and during summer measurements.

There were no significant differences in minimum leaf water potential of all four species examined across all sites either during summer or during winter. This may also result from the wet conditions that were prevalent during the current study. As it was a very wet year and all soils were kept wet to the same extent, the availability of groundwater as a determinant of leaf water relations was unimportant. During summer measurements of diurnal leaf water potential sites with shallow groundwater experienced soil saturation and significant run-off was observed during measurement periods. The amount of rainfall in February 2012 (diurnal leaf water potential was conducted at the end of February) was more than 2 times higher than the long term average rainfall for this month. Furthermore, because leaves were sampled close to the top of the canopy at all sites and tree height increased as depth-to-groundwater (Chapter 3), and because leaf water potential declines with height (because of frictional effects of water transport through longer lengths of xylem (Bond and Kavanagh 1999; Chunxia et al. 2008) and given the abundant supply of water in the summer at all sites, leaf water potential at the shallowest sites (with the tallest trees) are likely to experience lower leaf water potentials than leaves taken from shorter trees growing at the deepest groundwater sites. This factor could potentially confound any influence of variation in depth-to-groundwater on leaf water potential during periods of high rainfall. A final factor to consider is the fact that at the two shallowest sites, root flooding and anoxia may have occurred (because depth to the water table was shallowest) and root anoxia causes reduced leaf water potential, compared to roots of trees growing at the deepest groundwater sites, where flooding was not observed and anoxia is likely to have been absent.

Leaf water relations across a depth-to-groundwater gradient

Changes in leaf water relations traits were consistent with the principle hypothesis that trees growing on sites with larger depths-to-groundwater were less sensitive to water deficit. A shallower depth-to-groundwater means trees have ready access to more water all year around. Consequently trees over shallow groundwater tend not to experience water stress, or experience it less often or less severely, than trees growing at sites where groundwater was inaccessible. Thus, trees growing at shallow sites were hypothesized to be more sensitive to water deficit and to not develop any mechanisms to tolerate drought. This synoptic conclusion is now discussed in detail.

Osmotic adjustment

Osmotic adjustment was evident by shifts in π_{100} which occurred in all species across all sites and was significant in explaining variation in the turgor loss point (Ψ_{TLP} and RWC $_{TLP}$). The magnitude of these variations differed between species. Lower leaf water potential at turgor loss indicates a lower osmotic potential at turgor loss, which shows development of osmotic adjustment. This increases drought resistance in trees growing over deeper groundwater tables. These results are consistent with previously published studies Suarez (2011), Pita and Pardos (2001) and Tuomela (1997) but are in contrast with(Carter and White 2009). Carter and White (2009) did not find any differences in turgor loss point between sites over shallow and deep groundwater. However, in the present study a higher degree of turgor maintenance with increased in depth-to-groundwater was consistently observed. For all four species leaf water potential at zero turgor (Ψ_{TLP}) and osmotic potential at full turgor (π_{100}) declined as depth-to-groundwater increased. There were strong significant inverse correlations between depth-to-groundwater and π_{100} and π_0 ($R = -0.758$, $p<0.005$). *Post hoc* comparison showed that for all four species on both extremes (shallowest and deepest groundwater sites) differed significantly from each other (Table 6-3). Reductions in osmotic potential allows trees to extract water from soil with a lower water potential (Pita and Pardos 2001; Seyfried et al. 2005; Wright et al. 2004). Similarly, RWC_{TLP} declined with increased depth of groundwater for all species. This is further evidence of adaptation to reduced water supply at the deeper sites.

Differences across sites in these three traits (π_{100}, Ψ_{TLP} and RWC_{TLP}) were more significant and the trend was clearer in winter than summer. This may reflect the much wetter-than-average summers experienced at all sites during this study and the stronger trend observed in winter, when rainfall was lower-than-average-to-average further supports the conclusion that depth-to-groundwater does influence leaf water relation traits, but the effect is reduced when soil moisture supplies are sufficient to reduce the importance of the availability of groundwater.

Modulus of elasticity, specific leaf area and leaf capacitance

Generally, drought increases leaf elasticity and this is attributed to increased cell wall thickness, reduction in cell size or both (Pita and Pardos 2001). In the present study the bulk modulus of elasticity (ε) did not show a significant correlation with depth-to-groundwater except for *E.sieberi* during winter (R= 0.477, $p<0.05$), where an unexpected decrease in elasticity as depth-to-groundwater increased, was observed. Seasonal shifts in elasticity were significant in site 9.9 m depth-to-groundwater for all four species. None of the species show adjustment in elasticity across any sites. These results confirm those observed by Merchant et al. (2007) for *Eucalyptus* species. They concluded that *Ecalyptus* species tend to use osmoregulation to withstand drought, rather than changes in elasticity.

Decreases in water availability along aridity gradients can result in more dense leaves (Niinemets 2001; Pita and Pardos 2001; Santiago et al. 2004a) and hence an increase in SLA. Higher density leaves have thick cell walls and a low fraction of air spaces and this can be observed within species across sites and across species across sites (Taylor and Eamus 2008). Niinemets (2001) found intra-specific plasticity in leaf structure occurs in response to gradients in water availability. In the present study, trees at sites with shallower groundwater had a significantly larger SLA than trees growing at sites with deeper groundwater (Fig. 6-9). Decrease in SLA as an adaptation to water deficit has been found for *Eucalyptus* species (Merchant et al. 2007; Ngugi et al. 2004; Nouvellon et al. 2010; Turner et al. 2008) which is consistent with the current study. Species in high rainfall habitat shows greater plasticity of SLA with a decrease in SLA with increasing in aridity (Merchant et al. 2007; Ngugi et al. 2003) which is again consistent with the present study. This trend was more significant during winter than summer and again this may reflect the impact of the wetter-than-average summers that were recorded during the current study, and reinforces the conclusion that the impact of groundwater supply on leaf water relations is smaller in wet periods compared to dry periods.

The result of capacitance at turgor loss point can be attributed to the decrease in RWC of leaves at turgor loss as depth-to-groundwater increased. Absolute capacitance found to be affected by seasonality for *E. piperita* and depth-to-groundwater for *E. globidea*. Leaf capacitance can be a potential adaptation strategy to buffer the effect of the soil and atmospheric drought (Hao et al. 2008; Ogburn and Edwards 2010). However, Scoffoni et al. (2011) found species in moist habitat had a larger capacitance for both before and after turgor loss compared with species growing in dry habitats.

Canonical correlation analysis

Results from CCA showed that depth-to-groundwater was the most important independent variable controlling leaf water relation characteristic and leaf structural traits. Also, the produced synthetic variables from CCA for both functions showed that all species, except *E. sclerophylla* for synthetic variable 1, showed the same response to increase in depth. The response of different species showed that leaf water relations of all species had larger variation up to 9.9 m depth-to-groundwater and beyond that they showed more constant responses with minimum changes. The slope of variation was different for each species but they followed the same pattern.

Water deficit appears to be the main factor driving variation in leaf traits on community wide precipitation gradients below 2500 mm (Santiago et al. 2004a). In the present study, the contribution made by osmotic adjustment was larger than that made by adjustment of elasticity. On a global scale Niinemets (2010) found increase in bulk modulus of elasticity via changes in internal leaf structure to be the most significant leaf-level adaptation to water deficit. In contrast, Scoffoni et al. (2011) concluded that osmotic potential at turgor loss point is the most reliable single predictor of species drought resistance. Although both elastic and osmotic adjustment are important for plant adaptation to water deficit, their contribution may be different for different species (Mitchell et al. 2008). Specific leaf area shows considerable phenotypic plasticity in *Eucalyptus* species and decreases as a response to water limitation (Nouvellon et al. 2010; Turner et al. 2008).

Conclusion

It was hypothesized leaf water relations vary as a function of depth-to-groundwater. Despite occupying a mesic habitat, the four *Eucalyptus* species examined here showed some adjustment to variation in groundwater availability. Trees at sites with shallower groundwater were more sensitive to water deficit (reached zero turgor at a higher leaf water potential compared to trees growing at sites having deeper groundwater). However, adjustment of bulk volumetric elastic modulus was not as significant as osmotic adjustment in these species. Specific leaf area tended to decline with increasing depth-to-groundwater. Impact of seasonality on each trait within sites was different for each species. During the very wet summer season, differences across sites diminished. It is expected that in drier years, differences across sites would become more pronounced.

Chapter 7 General discussion

A clear challenge to future development and management of groundwater resources is to consider ecosystem requirements for groundwater in addition to human needs for groundwater. Sustainable groundwater management requires extraction of groundwater at rates that do not have adverse effects on ecosystems. A key question, therefore, is what is the safe limit for groundwater draw dawn? The relationship between ecosystem (structure and function) and groundwater depth is complex. In this thesis the focus has been on trees because (a) they are deep rooted and may be able to access groundwater more readily than understory herbs and forbs; and (b) trees constitute a major pathway for groundwater discharge (Eamus et al. 2006b). Sustainable land and water management needs to understand the complex relationships amongst climate, groundwater depth and vegetation to determine the safe limits for groundwater extraction. A related question is: to what degree are trees affected if these safe limits are exceeded? Plants are adapted to natural fluctuations of groundwater within a certain range (Sommer and Froend 2011). When groundwater depth increases above a safe limit, there will be a change in functional and structural attributes of vegetation as groundwater is no longer accessible (Elmore et al. 2006; Sommer and Froend 2011). However, the sensitivity and response to groundwater draw dawn is likely to be species specific.

The work described in this thesis aimed to provide a detailed understanding of the impact of groundwater depth on functional and structural characteristics of native woodlands. To address the aim of this thesis a study area was selected where depth-to-groundwater ranged from 2.4 m to 37.5 m DGW; with relatively high annual rainfall (1067 mm - high compared to other parts of Australia). The impact of depth-to-groundwater on functional and structural attributes of trees was studied at three different scales (leaf, tree and stand-scales) across two seasons (winter and summer). The research described here addressed three principle questions:

1- **Are there any differences in structural and functional attributes in native woodlands across a gradient of depth-to-groundwater?**
2- **What should be measured to monitor tree responses to groundwater availability?**
3- **Can response functions to differences in depth-to-groundwater be identified across a range of traits?**

I now address these questions in turn.

1- Are these any differences in structural and functional attributes in native woodlands across a gradient of depth-to-groundwater?

To answer this question water-related traits of trees were divided into four groups: structural attributes (chapter 3), tree and stand-scale water-use (chapter 4), hydraulic architecture of trees (chapter 5) and leaf characteristics (chapter 6). The results obtained indicated that each group of characteristics showed different responses to variation in access to groundwater.

Consistent with current knowledge about GDEs and non GDEs (Eamus et al. 2006a; Ford et al. 2008; Naumburg et al. 2005; O'Grady et al. 2010) and my initial hypothesis that access to groundwater will result in larger productivity, the current study has illustrated the importance of groundwater depth in determining woodland structural attributes and hence ANPP (reflected in taller trees, larger leaf area index (LAI), larger stem density, larger basal area (BA), and larger above-ground biomass (AGB) as depth-to-groundwater decreased; Fig. 7-1). The three sites with the shallowest water-table depths (2.4 m, 4.3 m and 5.5 m DGW) had significantly larger above-ground biomass and productivity than sites with deeper water tables (9.8 m, 13 m, 16.3 m and 37.6m DGW). Similarity was found in the four sites with the deepest water-table in structural attributes (BA, height, LAI) and ANPP. A significant shift occurred in all measured variables when depth-to-groundwater increased from 5.5 m to 9.8 m. This result was found consistently for each trait examined in this group (LAI, tree height, BA, ANPP, AGB, stem density). Each trait displayed an exponential decay response to increase in depth-to-groundwater. Similarly, for monthly litter fall over the two year study period the same response curve was observed. Considering the shift in traits across sites, it may be concluded that somewhere between 5.5 to 9.8 m depth-to-groundwater trees loose access to groundwater. As the water table declines below the rooting depth and is not accessible, trees become insensitive to further increase in depth of the water table (Elmore et al. 2006) and this explains the plateau in the response of the large number of traits measured in the present study when depth-groundwater is larger than 9.8 m. Beyond this depth, the structure and function of the woodlands examined in this study are controlled by factors other than groundwater supply (Elmore et al. 2006; McLendon et al. 2008).

Initially I hypothesised that stand transpiration will be larger at sites having a shallower water-table because at these sites trees have access to permanent groundwater resources. The assumption that trees have access to groundwater at shallow depths is supported by the observation that at these sites a significantly larger basal area, leaf area index, AGB and ANPP was maintained. However, measurements of rates of tree water-use did not support the hypothesis (that rates of tree water-use are larger at shallow depth-to-groundwater). Total stand transpiration was significantly smaller at the shallowest site (2.4 m) than at the two intermediate depth-to-groundwater sites (4.3 m and 9.8 m). Thus the differences between sites did not follow the expected trend. Furthermore trees at the shallowest water-table site (2.4 m) transpired the same amount of water (mm d^{-1} per unit ground area) as trees at the sites with deepest groundwater site (37.5 m) despite significantly larger tree density, BA, and LAI at the shallowest site. Sites with intermediate depth-to-groundwater transpired larger rates of water than the shallowest and deepest sites (chapter 4).

Prior to the start of the present study, a prolonged drought was experienced across the eastern coast of Australia (2001–2007). Even though groundwater-use had not been explicitly demonstrated in this study, groundwater access during drought may be inferred because of the observed longer-term accumulation of biomass and leaf area at the three shallower sites compared to the four deeper sites. However, with the abundant rainfall during the study period (2011–2012), the limitation imposed by the lack of groundwater at the four deepest sites was absent because of the abundant supply of soil moisture in the upper soil profile.

The rate of transpiration was largest at the site with a 4.3 m depth-to-groundwater during the study period. At this site leaf area index and basal area were comparable with the site having a 2.4 m DGW (shallowest groundwater site). These two sites are assumed to have access to shallow groundwater, given the known rooting depth of *Eucalyptus* in Australia (10 m; Canadell et al. (1996); 8 m Cook et al. (1998) and because the BA, tree height and LAI were largest at these sites compared to sites with larger depth-to-groundwater. Considering the similarity in structure (basal area and LAI) of the two sites with the shallowest depth-to-groundwater and assuming similar access to groundwater for these two sites, the significantly larger rate of transpiration for the 4.3 m site compared to that of the 2.4 m site may be explained by differences in total rooting volume available at these two shallow sites and also a potential effect of oxygen deficits (anoxia) for roots as a result of flooding which was observed for many months in 2011 and 2012 at the shallowest (2.4 m) site. Oxygen deficits prevent water uptake by roots, often causing reduced stomatal opening similar to the effect of water deficits (McAinsh et al. 1996; Sojka 1992) which result in reduced rates of transpiration (Baird et al. 2005; Cleverly 2013). Consequently rates of transpiration at the site 4.3 DGW exceeded those of the shallowest site. However, it is likely that during the drought period (2001 – 2007) access to groundwater at the two shallowest sites gave rise to the larger BA and LAI observed at the two shallowest sites compared to the deeper sites.

Stand transpiration rates showed a peak in transpiration at 4.3 m depth-to-groundwater. Thus, the shallowest water table coupled to abundant rainfall was as limiting to transpiration as the presumed lack of groundwater at the deepest (37.6 m) site. From the current study it can be seen that during high rainfall years (as observed in the present study), the optimal depth for maximum rates of stand water-use (and therefore, possibly, maximal productivity given the exchange of water for carbon through stomata), is not the shallowest nor the deepest depth-to-groundwater, rather there is an optimal depth-to-groundwater, which in this study was approximately 4 m.

Low transpiration (especially in the shallowest site) may not necessarily be associated with a long-term low productivity, as evident at the two shallowest sites, which maintained a larger BA and LAI than the deeper sites. Water-use-efficiency is an important attribute of vegetation: almost all terrestrial ecosystems plants experience some limitation in growth and productivity at some time by reduced water availability (Huxman et al. 2004). Generally trees at sites with limited water resources have higher water-use-efficiency (WUE; ANPP (Mg ha^{-1})/ T (mm year^{-1}) where T is rate of stand water-use (Ford et al. 2008). At sites with abundant water resources plants with high growth rate are at a competitive advantage over plants with larger WUE as competition for other resources can have a large impact on ANPP (Huxman et al. 2004). The results of chapter 3 and 4 were combined to test whether trees at the deepest groundwater site were more efficient in water-use than those occupying shallower groundwater sites. Surprisingly the site 2.4 m DGW (shallowest site) had the largest WUE compared to all other sites (Table 7-1 and Figure 7-1). Thus trees at the shallowest groundwater site had a larger yield per unit of water consumed and this is reflected in the larger LAI, BA, stem density and taller trees at the site having the shallowest groundwater. Whether this is a result of the anoxia and flooding at this site in the past two years is unknown. The lower WUE at the deepest groundwater sites is not necessarily a measure of relative drought resistance because WUE and drought resistance are often not related (Hsiao and Acevedo 1974).

Table 7-1: Annual water-use-efficiency (ANPP/T) across sites for 2012, calculated as the ratio of annual ANPP to annual stand water-use (Chapters 3 and 4, this thesis).

DGW (m)	ANPP ($Mg\ C\ ha^{-1}$)	T ($mm\ day^{-1}$)	WUE ($Mg\ ha^{-1}\ mm^{-1}$)
2.4	6.08	105.04	0.0580
4.3	5.36	188.77	0.0284
9.8	3.05	117.06	0.0261
37.5	2.65	95.67	0.0277

1.1 Application of the Budyko framework to the Kangaloon study sites and a site-specific estimate of water budgets

The distribution of the four sites used to determine rates of stand water-use on the Budyko-curve indicates that evapotranspiration (ET) of woodlands across the Kangaloon bore-field was limited by energy supply and atmospheric demand (small VPD, and low levels of net radiation) rather than water supply. In 2012, total stand transpiration was 21–43% of ET_0, which differed between sites as a function of LAI (Table 7-2). Although it was assumed at the start of this study that overstorey transpiration would be a major component of the water balance, total transpiration from the tree canopy was as small as 8% of annual rainfall (site 37.5 m DGW) rising only to 15% at site 4.3 m DGW. The small contribution of overstorey transpiration to the water balance indicates that other components of the water budget (i.e., run-off, evaporation, and transpiration by the understorey) contributed significantly to the water balance of each site. In the current study, ET_0 (421–612 mm yr^{-1}) was relatively low in comparison to neighbouring sites (within 100–150 km) where ET_0 was 914 mm (Castlereagh, NSW, Australia) and 1563 (Liverpool plains NSW, Australia) during years with below-average rainfall (2003–2007; Sun et al. 2011). The low ET_0 reflects the fact that during this two year study the weather was very wet, with low energy input and low VPD. The remaining imbalance between total stand transpiration and ET_0 was attributable to run-off, groundwater recharge, evaporation and understorey transpiration (Baldocchi and Ryu 2011).

The rate of run-off from the study area was not measured in this study but an estimate of mean annual runoff (RO) of 28% of total rainfall from the Illawarra regions, NSW, which encompasses my study sites is likely to be a reasonable estimate across my study region (Table 7-2). In addition to run-off losses, evaporation of intercepted rainfall, evaporation from wet surfaces, and understory transpiration contribute significantly to the water balance of the site and these were not measured. Using published literature the contribution of these components was estimated for my study area (Table 7.2), although it is acknowledged that these values are subject to variation as a function of forest type, local topography and climate variables. Using average values for the components of the water budget that were not measured, I describe an estimate of the water budgets of the four sites at Kangaloon bore-field (Tables 7-2, 7-3). Table 7.2 and 7.3 reveal the importance of the other components of the water balance, including understory transpiration (356 mm year^{-1}) and run-off (332 mm year^{-1}) in the water balance of my sites. It is concluded that these components can greatly exceed the amount of total tree transpiration from the overstorey (95-188 mm year^{-1}). This estimate is in agreement with several other published water budgets where the importance of understory transpiration, interception loss and run-off have been identified (Baldocchi and Ryu 2011; Mitchell et al. 2012; Zeppel et al. 2006). It is clear that additional research is required to provide site-specific estimates of these additional components of the water budget.

Table 7-2: Estimates of the contribution of the major components of water budgets of (predominantly) Eucalypt woodlands in Australia. There is a high degree of uncertainty associated with these estimate because of large differences in species composition, soil, climate and topography across all studies.

Component	Estimate	Location of study	Reference
Annual rainfall (ARF)	1188	Kangaloon	This study, chapter 2
Annual stand water-use (% of ARF)	7-15%	Kangaloon	This study, chapter 5
Annual interception (% of ARF)	8-15%	Western Australia	(Mitchell et al. 2009)
	10-15%	Castlereagh; 100 km NW	(Zeppel et al. 2006)
	10-30%	Combined several studies	(Liu 2001)
	21-30%	VIC-Australia	(Mitchell et al. 2012)
	9.9-17%	ACT-Australia	(Crockford and Richardson 1990)
	11%	NSW, Australia	(Smith et al. 1974)

Component	Estimate	Location of study	Reference
Annual understory Et (% of ARF)	30-50%	Castlereagh; 100 km NW	(Zeppel et al. 2006)
	10-50%	Globally	(Baldocchi and Ryu 2011)
	35%	Westland, New Zealand	(Barbour et al. 2005)
	15%	VIC-Australia	(Mitchell et al. 2012)
Annual Run-off (% of ARF)	28%	Illawara region, NSW	(Department of Environment 2010)

Table 7-3: Estimates of the water budget of the four study sites at the Kangaloon bore-field based on the average values of the information from table 7-2. There is a high degree of uncertainty associated with these estimate because of large differences in species composition, soil, climate and topography across all studies.

DGW (m)	**2.4**	**4.3**	**9.8**	**37.5**
Annual rainfall, 2012 (mm)	1188	1188	1188	1188
Annual stand water-use (mm y^{-1})	105	188	117	95
Annual interception (mm)	225	225	225	225
Annual understory Et (mm)	356	356	356	356
Annual Run-off (mm)	332	332	332	332
Estimated annual GW recharge (mm)	**169**	**86**	**157**	**179**

1.2 Hydraulic architecture, relationships amongst traits and drought resistance

Tree hydraulic architecture was the least affected by depth-to-groundwater. The differences in hydraulic architecture observed across my four sites were not as I originally hypothesized. I hypothesized that trees at the deeper groundwater sites would have lower branch hydraulic conductivity, larger Huber values, more dense xylem vessels and hence a larger sapwood density. These traits were expected to result in more drought resistant trees as groundwater depth increased. In the present study, different hydraulic traits showed different responses to increase in depth-to-groundwater. Huber value significantly increased as depth-to-groundwater increased. Smaller H_V at the shallow groundwater sites indicates that these trees are able to sustain a larger leaf area and invest less in sapwood because of the larger and more consistent supply of water (Carter and White 2009; Choat et al. 2005; Eamus 1999;

Edwards 2006). Neither sapwood density nor branch hydraulic conductivity (sapwood and leaf area specific) varied significantly across the four sites. However, these two results were mutually consistent, suggesting that this represents a true representation of these traits. Branch hydraulic conductivity is highly dependent on xylem structure and vessel diameter, as is sapwood density. Larger vessels also tend to result in a lower sapwood density and consequently there is often a strong negative relationship between sapwood density and hydraulic conductivity (Meinzer et al. 2008a; Wright et al. 2006; Zhang et al. 2009). Differences in xylem structure are also often reflected in differences in xylem vulnerability to embolism (Sperry et al. 2008). Xylem vulnerability to embolism was assessed by determining PLC_{50} and PLC_{88}. PLC_{50} in both seasons (summer and winter) was significantly negatively correlated with depth-to-groundwater. Decrease in PLC_{50} as depth-to-groundwater increased suggests that drought resistance in trees at deeper groundwater sites increased because xylem function was maintained to lower values of xylem water potential.

In the current study, although only water resource variability was hypothesized to cause changes in hydraulic attributes, it is known that there are other factors important in shaping hydraulic traits of trees which were not considered. For example, soil nutrient content can alter hydraulic traits (Chandra Babu et al. 1999; Eamus et al. 2006b). The responses of trees to habitat variability and the degree of plasticity of their traits are a combination of genetically determined traits and phenotypically plastic traits. Overall, a better understanding of genetic and environmental influences on hydraulic architecture is needed to fully elucidate the responses of trees to differences in groundwater depth.

Leaf-scale measurements showed that trees occupying sites with shallow water-tables were more sensitive to drought stress than those growing at sites with deeper water-tables (Fig. 7-1). Several leaf characteristics (leaf turgor loss point, osmotic potential at full turgor and RWC_{TLP}) all decreased significantly as depth-to-groundwater increased. Decrease in these traits indicates that trees were more resistance to drought as depth-to-groundwater increased (Fig. 7-1). In contrast, leaf elasticity was independent of increase in depth-to-groundwater. Such a result has been recorded previously for *Eucalyptus* species, which tend to use osmoregulation to withstand drought, rather than changes in elasticity (Merchant et al. 2007). Specific leaf area declines as an adaptation to water deficit (Merchant et al. 2007; Ngugi et al. 2003) which is consistent with the results of the current study, where SLA decreased as depth-to-groundwater increased.

Impact of seasonality on each trait within sites was different for each species. During the very wet summer season, differences in leaf characteristics (leaf turgor loss point, osmotic potential at full turgor and RWC_{TLP}) across sites diminished. It is expected that in drier years, differences in leaf-scale traits across sites would become more pronounced.

Leaf traits (leaf turgor loss point, osmotic potential at full turgor and RWC_{TLP}) and structural properties (BA, LAI, AGB, stem density and ANPP) were responsive to increase in depth-to-groundwater; however the form of the relationship differed between these two groups (negative linear relationship for leaf-scale traits and an exponential decay response in the structural properties).

Some traits showed significant changes with increased depth-to-groundwater, whilst others showed no significant response. Thus plants are able to adopt a range of different strategies in response to variation in water supply. Some species are capable of wide physiological plasticity in response to a varying environmental condition while others show only a small degree of plasticity (Abrams 1988; Corcuera et al. 2011; Grime and Mackey 2002; Schlichting 1986). Physiological and morphological adaptations through genetic and plastic changes facilitate survival of species in contrasting environment. Identifying traits which are plastic and responsive to environmental conditions and how these traits respond to environmental changes such as groundwater availability will help us to better predict the survival and growth of vegetation.

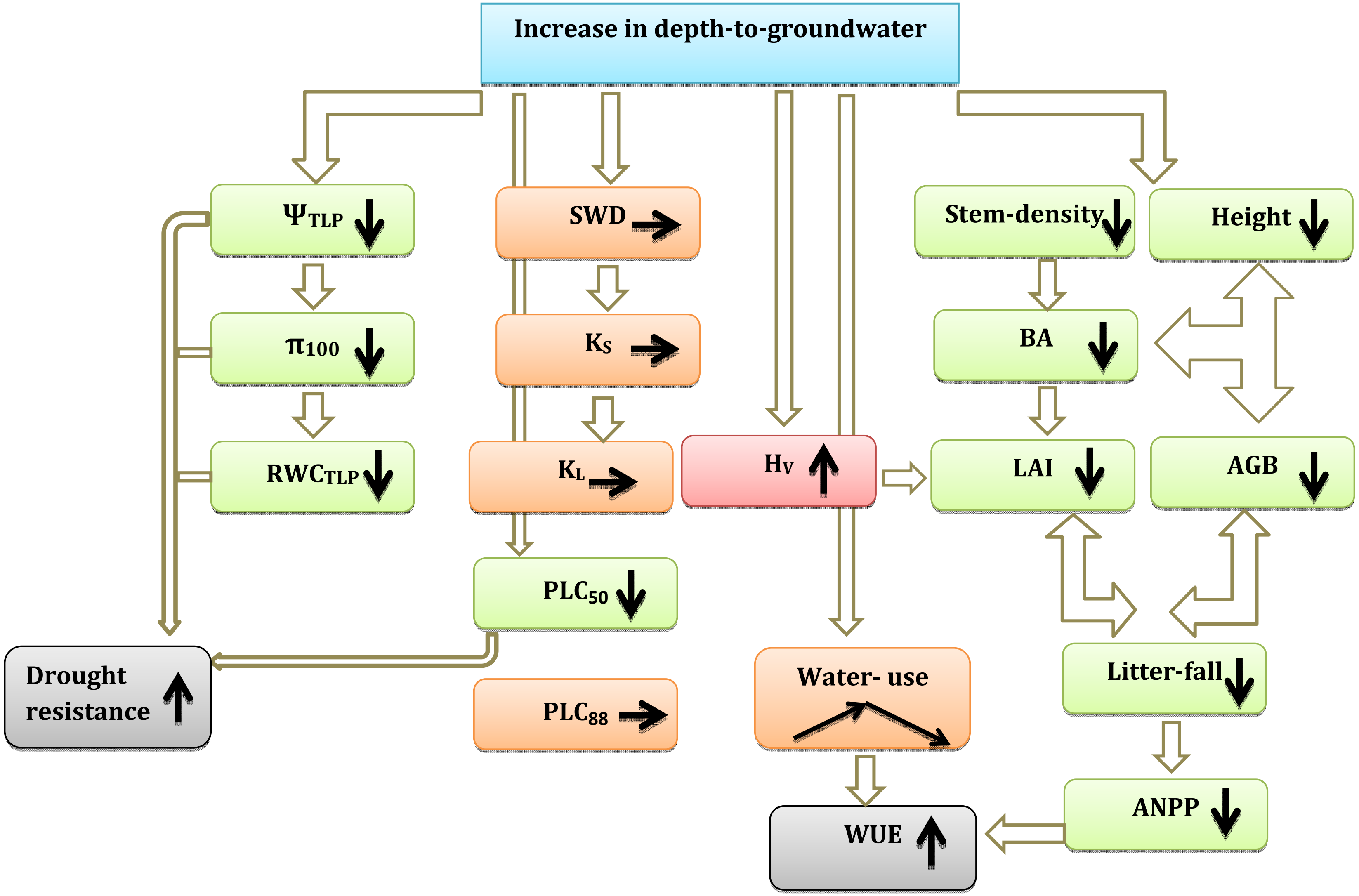


Figure 7-1: A summary of the response of each trait to increase in depth-to-groundwater. Colours denote direction of change in response to increase in depth-to-groundwater.

2- Co-ordination in the response of a leaf-scale and branch-scale trait and drought sensitivity

Some plant traits are a better indicator of plant sensitivity to water stress than others. Leaf water potential at turgor loss is recognised as a physiological measure of plant sensitivity to water stress (McDowell et al. 2008). Similarly, vulnerability to xylem cavitation and safety margins are critical determinants of drought tolerance (Markesteijn et al. 2011; Sperry et al. 2008). Safety margins are equal to the difference between minimum daily branch water potential and PLC_{50}; (Meinzer et al. 2008b; Sperry et al. 2008). A strong linear correlation between these two traits (Fig. 7-2) in the present study shows a co-ordination in the response of leaf (cell traits) and xylem (branch trait) anatomy (Aasamaa et al. 2001; Brodribb et al. 2003) as has been observed previously in a study of eight tropical dry forest species (Brodribb et al. 2003). This relationship indicates that as depth-to-groundwater increased, sensitivity to drought at both leaf cell and branch-scale decreased (lower leaf water potential is needed to reach turgor loss point and PLC_{50} declined).

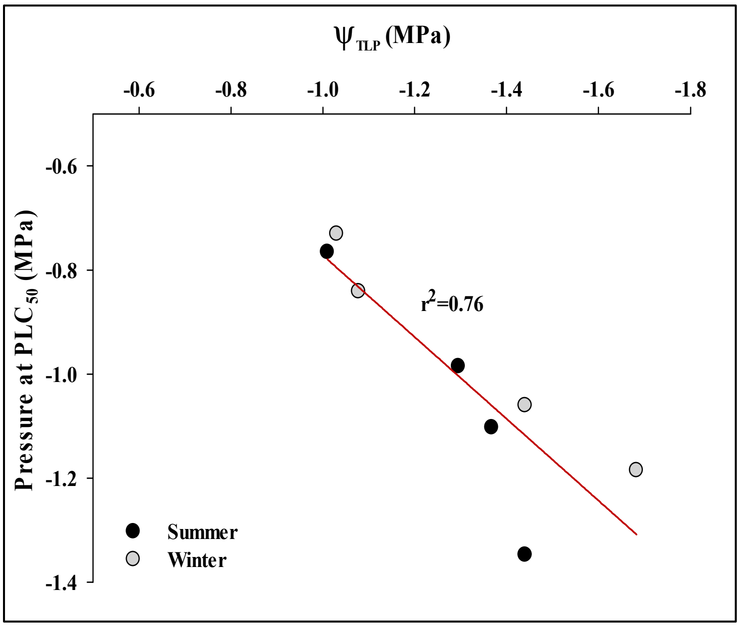


Figure 7-2: The relationship between leaf water potential at turgor loss point (Ψ_{TLP}) and pressure at which branches lost 50 % of their conductivity. Each point is the mean of all species at a single site; winter black circles and summer grey circles.

3- Can response functions to differences in depth-to-groundwater be identified across a range of traits?

Understanding how trees in groundwater dependent ecosystems respond to changes in groundwater availability is a crucial knowledge gap in our current understanding of GDEs. Determining the response function is likely to have management and conservation applications because such information may reveal how trees within an ecosystem may respond to changes in groundwater availability and thereby indicate possible changes in ecosystem function, structure, growth and ultimately, survival. It can also potentially determine the safe limit threshold for groundwater drawdown.

In an attempt to identify average site-scale responses of all measured traits all the trait results were normalized from zero to one by expressing the maximum trait value as 1 (i.e. 100 %) and all other values observed for that trait as a fraction of the maximum. The average normalized value for each site was plotted *versus* depth-to-groundwater (Fig. 7-3) to determine whether there was a consistent relationship in average trait values as a function of depth-to-groundwater. Analysis of variance showed there were significant differences across sites ($p<0.001$, $F=-7.75$) and *post hoc* tests revealed that the three shallowest sites (2.4 m, 4.3 m and 5.5 m) maintained average trait values that were significantly closer to one (larger values) than the remaining four sites with deeper water-table (9.8 m, 13 m, 16 m and 37.5 m). Results of regression analysis revealed that the slope of the regression line is significantly different from one ($p=0.03$, $F= 12.26$) and a significant negative sigmoidal response to increase in depth-to-groundwater provided a good fit to the data (Fig. 7-3). The fitted line clearly shows two plateaus in the response of average trait values to increase in depth-to-groundwater. These two plateaus are consistent with the finding of *post hoc* test of ANOVA which indicated that the three shallower groundwater sites showed similar responses to increase in depth-to-groundwater, whilst the average trait values of the four deeper groundwater sites were significantly smaller to the three shallowest sites, but not different across the four deep sites.

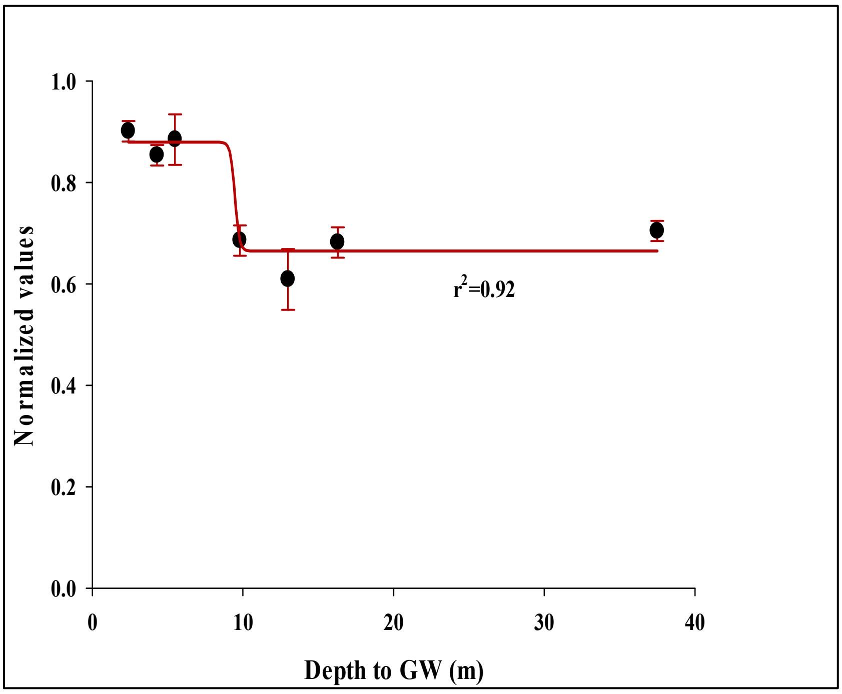


Figure 7-3: Average site trait responses to increase in depth-to-groundwater, fitted with a 4 parameter sigmoidal function. Twenty one leaf, branch and ecosystem-scale traits were used to calculate the average value for each site. These traits are: Ψ_{TLP}(summer and winter), π_{100}(summer and winter), RWC_{TLP} (summer and winter), ε (summer and winter), SLA (summer and winter), H_V (summer and winter), K_L (summer and winter), K_S (summer and winter), PLC_{50}(summer and winter), PLC_{88} (summer and winter), sapwood density, T_{stand}, LAI (average of two years), stem density, maximum tree height, BA, ANPP (two years), AGB, litterfall (two years), $\Psi_{pre\text{-}dawn}$ (summer and winter) and $\Psi_{minimum}$(summer and winter).

Eamus et al. (2006b) suggested several hypothetical ecosystem response curves as a function of groundwater availability (Fig 7-4) and one of the suggested response function was a curvilinear response with minimum change in ecosystem function until a threshold was reached and beyond that point there will be a significant change in ecosystem health or ecosystem function. This is consistent with the response curve obtained in this thesis (Fig. 7-3).

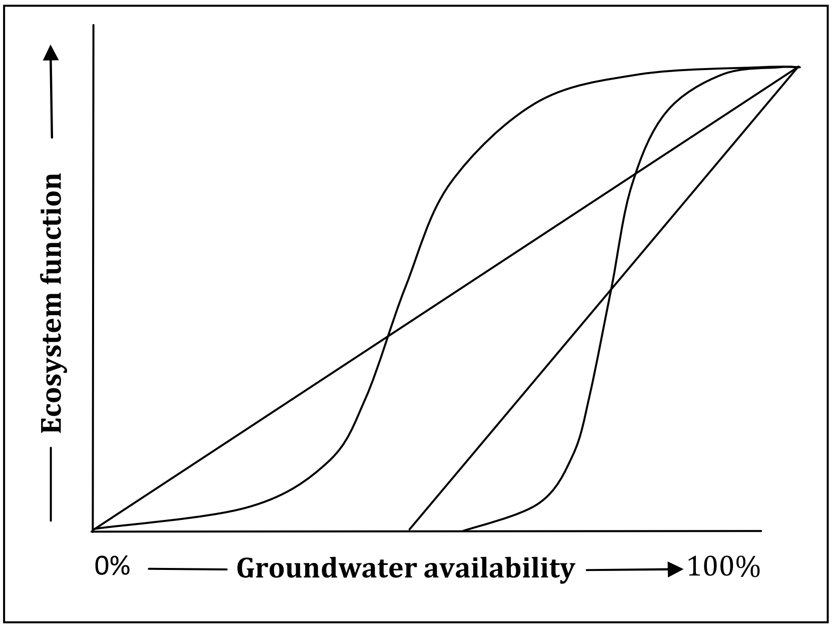


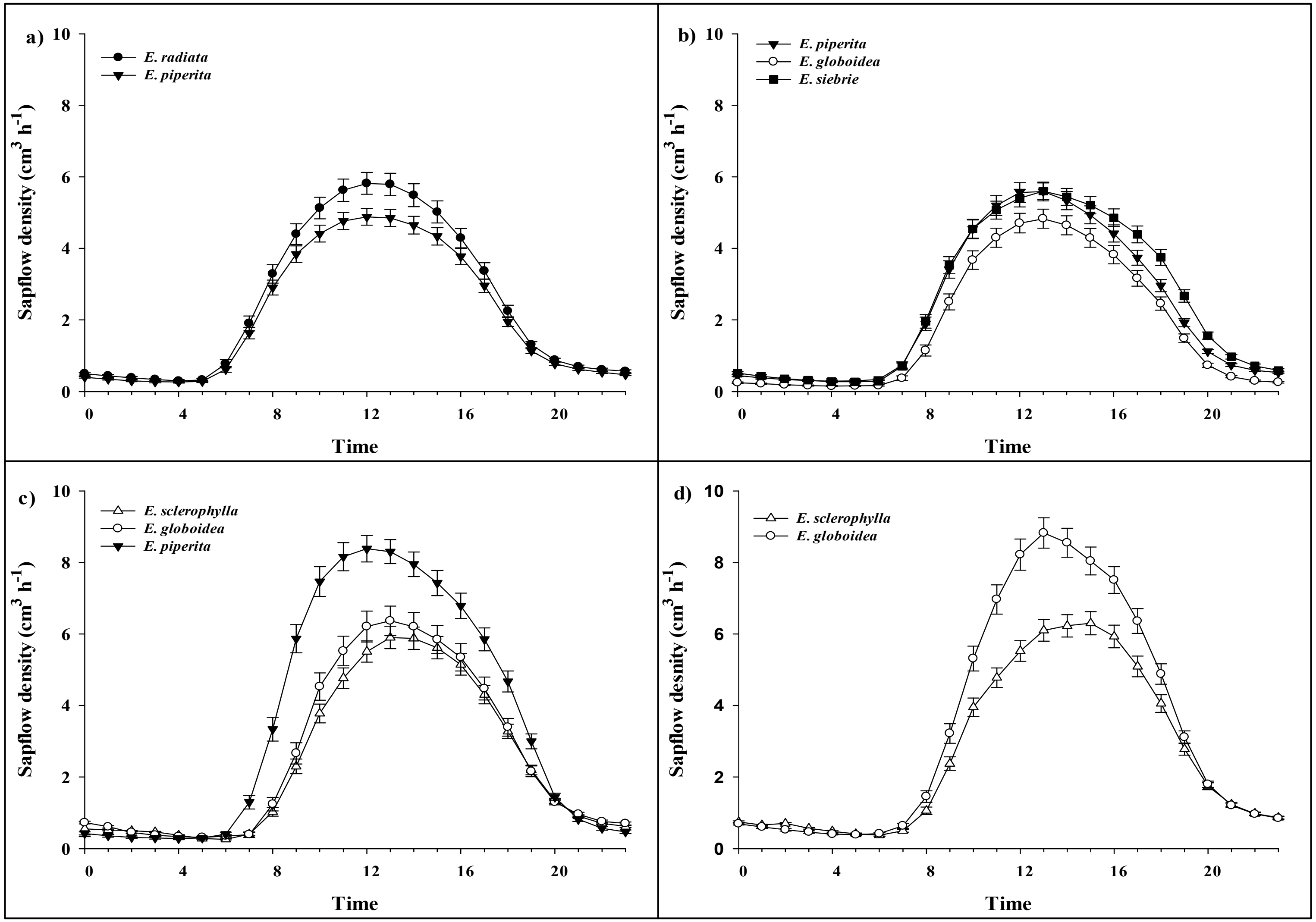
Figure 7-4: Theorical ecosystem response function to changes in groundwater availability (Eamus et al. 2006b).

From a consideration of the two plateaus observed in Figure 7-3, it can be see that a threshold in groundwater depth lies somewhere between 5.5 m and 9.8 m DGW. For these sites, at least, it is suggested that abstraction of groundwater beyond this depth range is likely to cause site-scale changes in ecosystem function. I am not aware of any similar study of multiple leaf-, branch-, or ecosystem traits that has identified a single, uniform, average site response curve to differences in groundwater depth.

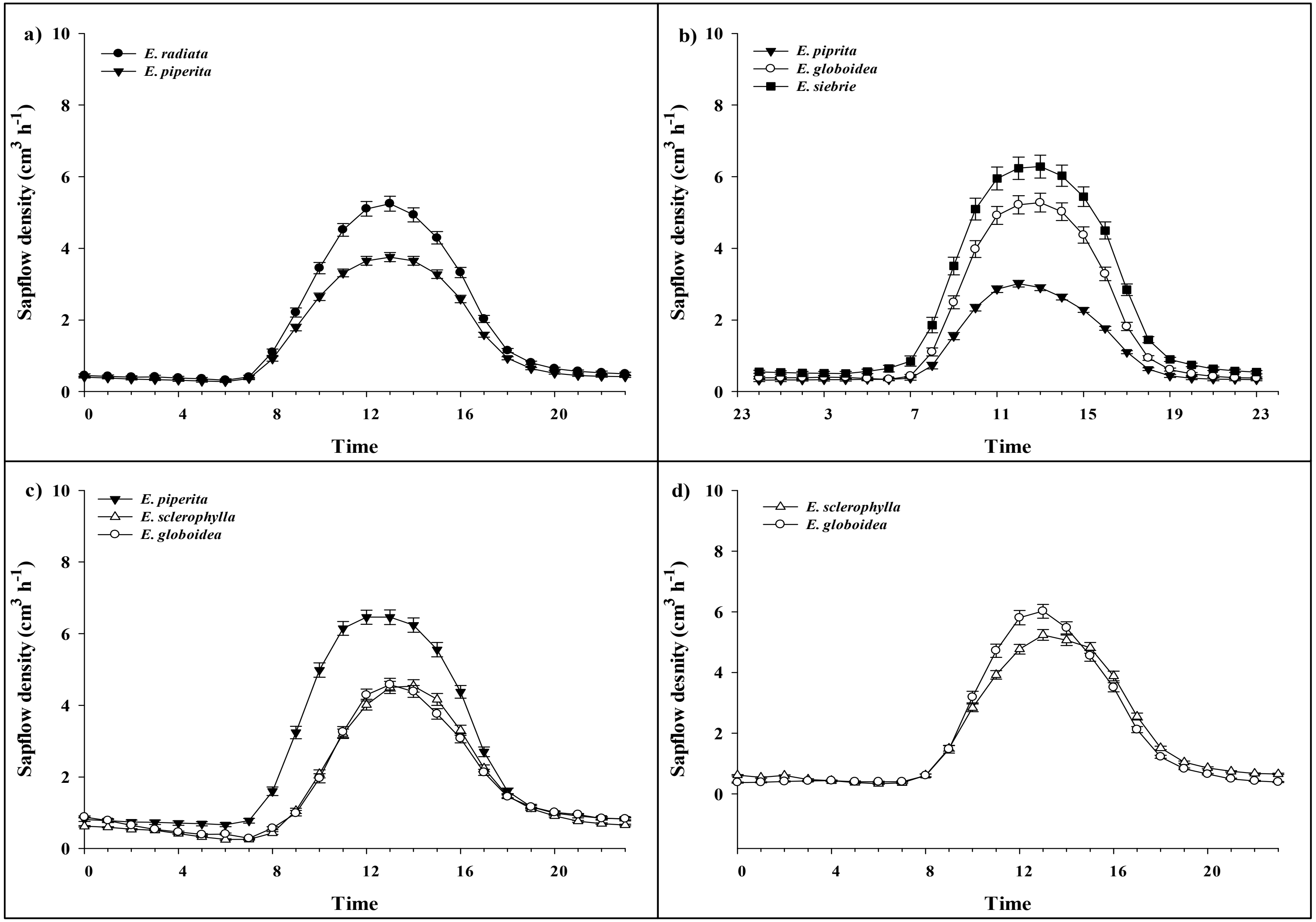
Vegetation access to groundwater depends on depth-to-groundwater, rooting depth and height of the capillary fringe in the soil (Mata-González et al. 2012; McLendon et al. 2008). The critical depth-to-groundwater for protecting ecosystem functionality and wellbeing is dependent on the vegetation type and their maximum rooting depth. The rooting depth for *Eucalyptus* trees in Australia is suggested to be approximately ≥10 m (Canadell et al. 1996; Cook et al. 1998). Generally trees growing at drier sites have deeper rooting depths than the same species growing at wetter sites. Considering the relatively abundant annual precipitation received by the study area, it is reasonable to assume that trees at site with 9.8 m DGW have a very limited access to groundwater as these trees have very similar structural attributes (e.g. BA, LAI, ANPP) and rates of water-use as trees at the deepest groundwater site. In a similar study in south-eastern Australia on *Eucalyptus camaldulensis*, it was shown that when groundwater depth increased there was a large increase in mortality (Horner et al. 2009) and the effective root zone of *Eucalyptus camaldulensis* in this study was concluded to be 9 m.

In summary; this study compared and contrasted ecophysiological, structural and functional attributes of trees of the same genus and in some cases, the same species across a natural gradient of depth-to-groundwater within a single climate envelope. Comparisons of individuals from the same species across sites differing in groundwater depth leads me to conclude that observed differences in such traits are most likely the result of differences in depth-to-groundwater. However, the current study did not include investigations of below-ground biomass and root distribution nor an examination of the understory components of the sites. These remain a priority for future studies.

Appendix A: supplementary figures for chapter 4



Chapter 4; Figure A 1: Diurnal pattern of water-use of each tree species for 4 sites: a) 2.4 m, b) 4.3 m , c) 9.8 m and d) 37.5 depth-to-groundwater; average for summer 2012.



Chapter 4; Figure A 2: Diurnal pattern of water-use of each tree species for 4 sites: a) 2.4 m, b) 4.3 m , c) 9.8 m and d) 37.5 depth-to-groundwater; average for winter 2012.

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