Structural characteristics of banksia woodland along an ecohydrological gradient, Western Australia

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Structural characteristics of *Banksia* woodland along an ecohydrological gradient, Western Australia

Rebecca Thomas

A thesis submitted in partial fulfilment of the requirements for the award of Bachelor of Science (Environmental Management) Honours

At the School of Natural Sciences

Edith Cowan University

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Supervisors: Associate Professor Ray Froend and Professor Will Stock
Abstract

Water availability (the defining feature of a ‘hydrological habitat’) has a major effect on plant growth, and the physiological and structural characteristics of plants often reflect the availability of this resource. In relation to development of vegetation structural characteristics as a consequence of a given hydrological habitat, it is important to understand whether self-organisation of plant cover (productivity, structure and function) interacts with water availability and if adjustment to water limitation exists (‘ecohydrological optimization’ or establishment of a ‘hydrological equilibrium’). This study tested, through three hypotheses, whether structural and functional attributes of *Banksia* woodland vary with water availability, i.e. whether stand-level productivity and capacity to transpire is optimised under the prevailing hydrological conditions. The hypotheses are that *Banksia* woodland i) leaf area, ii) density, and iii) sapwood area (of the dominant overstorey species) are greatest where water availability is highest.

The study used spatial variation in groundwater availability (defined by depth to groundwater and phreatophyte water source partitioning) in the Gnangara Groundwater System on the Swan Coastal Plain, Western Australia, to select sites from three contrasting hydrological habitats across which comparisons of *Banksia* woodland structural characteristics were made. To quantify differences in leaf area associated with water availability, Foliage Projective Cover (of the understorey and overstorey) and leaf age (of the dominant overstorey species *B. attenuata*) were measured. To quantify differences in spatial distributions of plants, the density and distances to nearest overstorey, conspecific and similar aged neighbour were calculated for the same overstorey species. *B. attenuata* sapwood area per basal area and sapwood area per hectare were calculated to assess the transpirational capacity of each habitat. All of these variables were statistically tested for significant difference between hydrological habitats.

It was found that significant differences occur in the structural characteristics of *Banksia* woodland in contrasting hydrological habitats along an ecohydrological gradient. These findings support the hypotheses that leaf area and sapwood area are greatest where water availability is highest, but do not support the same pattern for
density. As water availability increased, growth per overstorey individual (*B. attenuata*, including tree size and amount of foliage) was maximised, with a trade off reflected in decreased plant densities. In more xeric hydrological habitats, increased plant densities were observed, with smaller individual tree sizes and leaf area. The more mesic habitats also have a taller overstorey stratum, with a canopy of increased leaf area and longer foliage retention times. This in-turn is correlated with increased total habitat sapwood area (despite lower plant densities) and increased individual tree sapwood area. The nature of Banksia woodland structural adjustments to water availability seen involve processes of hydrological optimisation to achieve vegetative equilibrium with the hydrologic environment. These are habitat-specific and occur over different time scales. These mechanisms reflect *Banksia* woodland’s adaptive capacity to respond to variability in water availability and have impacts on NPP, ecosystem function, habitat and environmental water requirements. This study enables the prediction of vegetation responses to changes in water availability (climatic or anthropogenic) and can also aid in formulating better informed objectives for vegetation rehabilitation.
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“The man who has no tincture of philosophy goes through life imprisoned in the prejudices derived from common sense, from the habitual beliefs of his age or his nation, and from convictions which have grown up in his mind without the co-operation or consent of his deliberate reason.”

Bertrand Russell
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1. Introduction

1.1 Introduction

The distribution of plants and the structure of vegetation at a site is a consequence of adjustment to long-term environmental conditions. The environmental factor thought to cause most of the variation in distribution and structure is water availability. This has a major effect on plant growth and the physiological and structural characteristics of plants often reflect the availability of this resource. Water availability or a plant’s hydrological habitat can be partly defined by rainfall, recharge sources, depth to groundwater and soil water potential (Eamus, Hatton, Cook & Colvin, 2006). The water available within a habitat can vary from a readily available supply of water over most of the year (for example, shallow groundwater), through to a strong seasonal variability in availability (for example, predominantly rainfall-driven, and greater depth to groundwater). The ecohydrology of a site is further modified by the composition and structure of the vegetation present which is supported by and influences hydrology. Hydrological habitats differ along gradients of water availability (or ‘ecohydrological gradients’) within landscapes, and as a consequence vegetation characteristics are thought to develop in equilibrium with spatial patterns in water availability.

Plant species are spatially distributed across ecohydrological gradients according to competitive displacement processes and plant traits associated with water acquisition (Austin, 1985; Florence, 1996; Oliver & Larson, 1996; Jackson, Sperry & Dawson, 2000; Westoby, Falster, Moles, Vesk & Wright, 2002; Groom, 2004). Therefore structural differences are likely to occur in vegetation at different habitats on ecohydrological gradients due to the variable physiognomy of different species. Also,
for species that exist over the entire ecohydrological gradient it would follow that intraspecific structural differences may occur resulting from different growth characteristics in response to different habitats.

The structural attributes of vegetation that vary (at the intraspecific level) with water availability include size-frequency distributions (e.g. Denslow & Battaglia, 2002), densities and spatial arrangement (e.g. Toft & Frazier, 2003; Naumburg, Mata-Gonzalez, Hunter, McLendon & Martin, 2005; Perry, Enright, Miller & Lamont, 2009), plant height, basal areas, and crown dimensions (Ferreira, Bustamante, Garcia-Montiel, Caylor & Davidson, 2007; Merchant, Callister, Arndt, Tausz & Adams, 2007; Saha, Strazisar, Menges, Ellsworth & Sternberg, 2008). Differences in these stand and individual level structural characteristics are coupled with and reflected in leaf area, through their effects on physiological functions such as transpiration and photosynthesis. Consequently, leaf area has been shown to decrease along ecohydrological gradients with decreasing water availability (e.g. Scholes, Frost & Tian, 2004; Merchant et al., 2007). All of the above characteristics represent integral measurements of vegetation structure and (implied) functional responses to a hydrological habitat (refer to conceptual framework in Figure 1.1).

1.2 Hydrological equilibrium/ecohydrological optimization

In relation to the development of vegetation structural characteristics as a consequence of a given hydrological habitat, it is important to understand whether self-organisation of plant cover with water availability and adjustment to water limitation exists. This has been theorised as ‘ecohydrological optimization’ or
establishment of a ‘hydrological equilibrium’ (sensu Eagleson, 1982; and further development by Eagleson & Segarra, 1985; Nemani & Running, 1989; Hatton, Salvucci & Wu, 1997; Kergoat, 1998; Caylor, Scanlon & Rodriguez-Iturbe, 2008; Troch et al., 2009). Eagleson et al. (1982) developed statistical models showing that water-limited natural vegetation systems are in stable equilibrium with

A schematic diagram of just some of the inter-relationships among processes that link declines in ecosystem water status to NPP. The same schema can be viewed as representing a comparison of two ecosystems differing in ecosystem water status by replacing ‘Rainfall declines’ with ‘Low ecosystem water status’.

**Figure 1.1** Summary of the pathways (mechanisms) by which declines in ecosystem water status might cause a reduction in above and below ground NPP and where structural characteristics play a role. Focus is at the individual tree scale. (Eamus, 2003).
their climatic and soil environments under three expected state of vegetation optimality constraints (hypotheses). These hypotheses (Eagleson cited in Hatton et al., 1997) are: a) over short time scales (one or a few generations) the vegetation canopy density will equilibrate with the climate and soil at a value where equilibrium soil moisture will be maximised; b) over longer time scales (a few generations), species will be selected whose potential transpiration efficiency results in the maximum equilibrium soil moisture; and c) over much longer time scales vegetation will alter soil physical properties toward equilibrium values at which the minimum stress canopy density of a given species is maximum under a given climate.

The ecohydrological optimisation concept is based on water limits to plant productivity. Optimal efficiency in water utilisation occurs (in both short term succession and long term evolution) (Hatton et al., 1997) so that above ground plant growth is maximized within the limits imposed by a habitat’s water constraints. Models have been developed to express how this ‘homeostasis’ in water support is achieved by a combination of stomatal regulation and the optimal allocation of resources between the area of transpiring foliage, conductive sapwood, tree height and absorbing roots (Magnani, Grace & Borghetti, 2002). This form of analysis assists in explaining commonly observed changes in tree structure as a function of the environment. In particular, water availability changes the ratio between foliage and conductive sapwood with a shift away from foliage production under xeric conditions and also affects the functional balance between transpiring foliage and absorbing roots (Magnani et al., 2002). In turn, this effect on transpiring foliage is reflected in other measures of productivity at the individual and stand level, such as foliage projected cover, sapwood area, height and density.
1.3 Significance of vegetation structure

Whilst a number of comprehensive theories on plant adjustment and coping mechanisms for water limitation remain in development (some of which remain contentious; Kerkhoff, Martens & Milne, 2004), quantitative information on the observed differences in native vegetation structure along hydrological gradients remains limited (Magnani, et al. 2002; Caylor et al., 2008). This paucity of information is evident not only for ecosystem (vegetation) response but also the vegetation functionality (largely determined by structural character) on water balance dynamics (e.g. Rodriguez-Iturbe, Porporato, Laio & Ridolfi, 2001; Troch et al., 2009).

The structural character of vegetation is not only important due to the previously stated relationship with ecosystem functionality, but it is also a defining character of 'habitat' and is of intrinsic ecosystem service value.

There is a need for research into hydrological equilibrium/ecohydrological optimisation processes. Quantifying vegetation structural changes along ecohydrological gradients provides information to better understand the ecology and ecohydrology of a system and to support improved modelling and management of ecosystems under various water regimes (MacKay, 2006). It also provides insight into the question of whether optimisation processes are occurring within ecosystems and at landscape scales. The importance of such research on ecosystems is further reinforced by the fact that many catchments are undergoing natural or anthropogenic changes in water availability.
1.3.1 Ecohydrological gradients of the Gnangara Groundwater System on the Swan Coastal Plain, Western Australia

A local example of an area exhibiting changes in water availability is the northern portion of the Swan Coastal Plain, Western Australia. Through connection with the underlying superficial aquifer (the 'Gnangara Mound'), a significant area and diversity of groundwater dependant ecosystems (GDEs) occur associated with riverine baseflow, shallow watertables and wetlands (Rutherford, Roy & Johnson, 2005). The terrestrial vegetation of this region is dominated by Banksia or Tuart woodlands located on sandy soils and a complex series of seasonal wetlands exist throughout the entire system in topographic and interdunal depressions (Mitchell, Williams & Desmond, 2002).

Spatial variation in water availability occurs on the Gnangara Mound through topographical changes in the landscape separating vegetation from the groundwater to varying degrees and leading to ecohydrological gradient from low to high points in the landscape. The majority of past research relevant to the identification of ecohydrological gradients in this region, has focussed on ecophysiological adaptations, including plant hydraulic architecture (Canham, Froend & Stock, 2009), phreatophyte water source partitioning (Zencich, Froend, Turner & Gailitis, 2002), and short term response of plant abundances and plant vigour to changes in groundwater availability (Groom, Froend & Mattiske, 2000a, 2000b; Groom, 2004). However, research has not quantified the relationship between vegetation function (relevant to stand-level water uptake) and differences in hydrological habitat along an ecohydrological gradient. Such a relationship is predicted to exist through observed differences in plant ecophysiological functioning in contrasting hydrological habitats.
on the Gnangara Mound (Zencich et al., 2002; Canham et al., 2009) and in other Australian ecosystems (e.g. Prior, Bowman & Eamus, 2005).

In addition to spatial gradients in water availability, natural or anthropogenic long-term change in water availability within a given habitat represents a temporal ecohydrological gradient (Snyder & Tartowski, 2006). Such temporal gradients have also been observed on the Gnangara Mound as a result of declining groundwater levels attributed to decreasing rainfall and increased groundwater discharge through abstraction (Yesertemer, 2003, 2008). This has resulted in the loss of environmental values in local areas of the Gnangara Mound, especially wetland ecosystems (Wilson & Valentine, 2009), although the threat of hydrological change extends over a large area of Banksia woodland habitats (Groom et al. 2000a, 2000b).

The extent of this hydrological change has led to the development of a whole-government initiative, the ‘Gnangara Sustainability Strategy’, which aims to develop an action plan for the coming decades that will ensure the sustainable use of groundwater whilst protecting groundwater dependant ecosystems (Government of Western Australia, 2009). Research into quantifying vegetation ecohydrological optimisation along spatial (and inferred temporal) gradients in water availability would give researchers and managers an insight into the response of phreatophytic vegetation as a result of continued groundwater drawdown from climatic change and water abstraction.
1.4 Aims of the study

This study aims to test whether structural and functional attributes of *Banksia* woodland vary with water availability, i.e. whether stand-level productivity and capacity to transpire is optimised under the prevailing hydrological conditions. If such a relationship (ecohydrological optimisation/hydrological equilibrium) were to hold true, it is expected that a decrease in stand level productivity and transpirational capacity would occur with decreasing water availability along an ecohydrological gradient.

This study aims to test the following three hypotheses:

Along an ecohydrological gradient

1. *Banksia* woodland leaf area is greatest where water availability is highest.

2. Density of the dominant overstorey species in *Banksia* woodland is greatest where water availability is highest.

3. Sapwood area of the dominant *Banksia* species is greatest where water availability is highest.
2. Methods

2.1 Study Design

2.1.1 Defining hydrological habitat and ecohydrological gradients in water availability

Phreatophytic *Banksia* woodland plant species of the northern Swan Coastal Plain, are 'groundwater dependent' to varying degrees and are distributed along an ecohydrological gradient of contrasting hydrological habitats, formed by topographical changes in the landscape and depth to accessible groundwater (DTW) (Zencich *et al*., 2002; Groom, 2004). This gradient occurs from interdunal depressions where there is shallow depth to the saturated groundwater zone (≤2 m), to dune crests (≈30 m DTW).

The annual cycle of groundwater use and inferred dependency varies between obligate and facultative phreatophytes (Zencich *et al*., 2002), with obligates such as *Banksia ilicifolia* limited to regions of higher water availability and shallow groundwater depth. The facultative phreatophyte *Banksia attenuata* is a dominant overstorey species of these woodlands which occurs within a greater topographical range. For this species it has been shown that on the lower slope (≈4 m DTW) both ground and subsurface water are used all through the winter-summer cycle. However, during autumn, the end of the dry season, reliance on groundwater increases to 85% of total water use (Figure 2.1, Zencich *et al*., 2002). In habitats with greater depth to groundwater such as upper slope (≈9 m DTW) sites, plant water partitioning shifts with subsurface soil being the dominant water source throughout the year and there is an absence of a peak in groundwater-reliance during the end of the dry season (Figure 2.1, Zencich *et al*., 2002). Representing the 'driest' habitat, dune crest sites (≈30 m DTW) plants have no reliance on groundwater at all, as all water is sourced from
surface and subsurface soils and with 80-100% of water sourced from deeper (>4 m) subsurface soils in summer (Figure 2.1, Zencich et al., 2002).

The present study used the spatial variations in groundwater availability (defined by depth to groundwater and phreatophyte water source partitioning demonstrated by Zencich et al., 2002) to select sites that represent a gradient of three contrasting hydrological habitats from which comparisons of Banksia woodland structural characteristics were made. This design, using spatial variability in water availability, can also represent a space-for-time design for inferring structural and functional changes in vegetation undergoing a temporal shift in water availability.

2.1.2 Site Selection and Sampling Design

Three hydrological habitats were selected at positions of 0-5 m DTW, 10-15 m DTW and 20 m+ DTW (Table 2.1), representing a gradient of decreasing access to groundwater by the dominant overstorey facultative phreatophyte species B. attenuata.
(sensu Zencich et al., 2002). The study sites were located in Banksia woodland north east of Perth (31°57'7" S 115°51'32" E), Western Australia, on the Swan Coastal Plain (Figure 2.2; Appendix 1). The region experiences a Mediterranean climate and the study sites were all located within one rainfall zone (Appendix 1), receiving ~700 mm mean annual rainfall (BoM, 2009; Appendix). The sites were restricted to the Bassandean dune system which has low water-holding capacity soils and overlies the unconfined Gnangara Mound aquifer. Soil moisture (up to 10m in depth) and groundwater levels at these sites are strongly in phase with the seasonal pattern of rainfall and the shallow soils (3-5 m) progressively dry out through summer to a minimum water content in autumn (Farrington & Bartle, 1991; Sharma, Bari & Byrne, 1991).

Table 2.1. Study Site Depth to Groundwater Ranges. Replicates Refer to Study Replicates as per Figure 2.3. Groundwater Level Data Sourced from the Department of Water, Western Australia.

<table>
<thead>
<tr>
<th>Ecohydrological Habitat/Gradient position</th>
<th>Nearby DoW monitoring bore</th>
<th>10yr mean minimum groundwater level (mAHED)</th>
<th>Replicate ground elevation range (mAHED)</th>
<th>Depth to groundwater (m) at replicate (based on 10yr mean minimum gw level)</th>
</tr>
</thead>
<tbody>
<tr>
<td>20m+ DTW</td>
<td>L120C</td>
<td>51.296</td>
<td>85 - 90</td>
<td>33.7 to 38.7</td>
</tr>
<tr>
<td></td>
<td>PM8</td>
<td>67.814</td>
<td>95 - 105</td>
<td>27.19 to 37.19</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-15m DTW</td>
<td>GG1(I)</td>
<td>68.943</td>
<td>-80</td>
<td>-11.96</td>
</tr>
<tr>
<td></td>
<td>PM4</td>
<td>56.708</td>
<td>-70</td>
<td>-13.29</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-5m DTW</td>
<td>L86</td>
<td>47.496</td>
<td>-50</td>
<td>-2.50</td>
</tr>
<tr>
<td></td>
<td>L186</td>
<td>47.006</td>
<td>-50</td>
<td>-2.99</td>
</tr>
<tr>
<td></td>
<td>1</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.2. Study site locations and surrounding land uses (Image courtesy Google Earth, 2008).
To minimise the effects on vegetation structure from variables other than water availability (including soil hydrological properties), such as fire and presence of dieback (*Phytophthora* sp.), sites were also restricted to those with a minimum post-fire age of 14 years and no recorded presence of *Phytophthora* sp. (Appendix 1). The minimum post-fire age used here is similar to the optimum fire interval (13 yrs) found for the resprouter *B. attenuata* (Enright, Marsula, Lamont & Wissel, 1998), which enables peak survivorship, resprouting of canopy and return to viable canopy seed store. Restriction of study sites to this age ensures the vegetation has sufficient time to return to a structural/functional equilibrium with the hydrological habitat (as per the hypothesis of Eagleson, 1982).

Each hydrological habitat was represented by three replicates (each comprised of three 30 m x 30 m subsample plots) (Figure 2.3). Replicates per habitat (ecohydrological gradient position) were spatially distinct from one another to avoid pseudoreplication (Hurlbert, 1984) and to enable statistical and qualitative structural comparisons between gradient positions. Three nested subsample quadrats within each replicate were included, to enable statistical and qualitative within-position analysis.
2.2 Sampling and data analysis

2.2.1 General stand characteristics

To assess the overall character of the vegetation stand within each hydrological habitat, several variables were measured. The size class frequency of the dominant overstorey species *B. attenuata* was assessed by measuring trunk diameter at breast height (DBH 1.3 m from ground height). Where an individual forked before this height, all trunks were measured and summed. Juveniles were not measured but
grouped within a 0-4.9 cm DBH size class. To plot the size class frequencies, the trunk sizes were classed in 5 cm categories and tallied.

Mean mature *B. attenuata* DBH was also calculated for each hydrological habitat and these were compared using the non-parametric Kruskal-Wallis and the Mann-Whitney post hoc tests, after failing to meet the assumptions of ANOVA. The height of every *B. attenuata* (excluding juveniles) was measured in all subsample plots, using a clinometer (or measuring tape if <2 m high). The mean height of mature *B. attenuata* was calculated for each hydrological habitat and these were compared using the Kruskal-Wallis and the Mann-Whitney post hoc tests, after failing to meet the assumptions of ANOVA.

2.2.2 Hypothesis one: *Banksia* woodland leaf area is greatest where water availability is highest.

As Foliage Projective Cover (FPC) (degree of canopy closure and a measure of the fraction of ground overlain by leaf) is inferred to be determined by water availability and has a significant impact on stand-level transpirational capacity (Specht & Specht, 1999; Eamus et al., 2006), this structural feature was measured in each hydrological habitat. To measure FPC, a cross-wire sighting tube (1” diameter, 8” in length) (sensu Winkworth & Goodall, 1962) was used to determine presence or absence of both the understorey (held above understorey and looking down) and the overstorey canopy (held above understorey and looking up) at 40 points on a grid overlaying each subsample plot. Instead of sampling a small portion of the plot, the 40 points were distributed on a quadrat along 7 lines (at 5 m intervals) covering the entire plot, to increase precision (Floyd & Anderson, 1987). For each stratum, in each subsample
plot, the number of points with foliage present was interpreted as a proportion of all the points in the grid (40).

Hydrological habitat mean FPC (%) for understorey and the overstorey canopy were then established using the subsample plots (n=9 per hydrological habitat) and compared using one-way ANOVA (providing data met the assumptions of normality and homogeneity of variance) and Tukey’s post hoc test, or the non-parametric Kruskal-Wallis and the Mann-Whitney post hoc tests. The mean proportional contribution of each stratum to a habitat’s total FPC was expressed as a percentage and visually compared on a bar graph.

The age of the leaf area present on a plant is representative of the amount of supportable foliage and is linked to site conditions. *B. attenuata* leaf ages were measured by counting the number of bud scars from the tip of a stem back up the branch until leaves were no longer present. As each bud scar represents one year of growth (Lamont, 1985; Figure 2.4) the number of bud scars was interpreted as years worth of leaf area held. Leaf ages were cross-referenced between several branches per tree to ensure the maximum age was the one recorded. This variable was measured on every *B. attenuata* present (excluding juveniles) per subsample plot. Hydrological habitat leaf age means were calculated from mature *B. attenuata* and compared using the Kruskal-Wallis and the Mann-Whitney post hoc tests due to data not conforming to the assumptions of ANOVA.
Figure 2.4. Annual incremental growth of stems in *Banksia menziesii*, representative of most *Banksias*. By counting the budscars, the age of the stems with leaves present can be determined. (Lamont, 1985).

2.2.3 *Hypothesis two*: *Density of the dominant overstorey species in *Banksia* woodland is greatest where water availability is highest.*

Greater water availability in a hydrological habitat has been shown to support greater densities of vegetation (Naumburg *et al.*, 2005) and density is an important characteristic of stand structure and function. To assess density per hydrological habitat, the habitat mean density (ha$^{-1}$) of the dominant overstorey species *B. attenuata* was calculated from the subsample plots and compared using one-way ANOVA and Tukey’s post hoc test.
To assess the spatial distribution of this woodland overstorey species, which can infer aspects of competition in water availability, all *B. attenuata* (excluding juveniles) were measured for the distance to their nearest overstorey (any species) neighbour, conspecific neighbour, and nearest similar aged tree. Similar age was inferred by trunk size and tree height. Distances were measured from outside of trunk to outside of trunk. Within each neighbour category the mean distance per hydrological habitat was calculated and compared using the Kruskal-Wallis and the Mann-Whitney post hoc tests, as the data did not conform to the assumptions of ANOVA.

2.2.4 **Hypothesis three:** Sapwood area of the dominant Banksia species is greatest where water availability is highest.

As individual and stand level sapwood area is linked to water availability (Specht & Specht, 1999; Eamus et al., 2006), leaf area and function, this study quantified the amount of sapwood area and therefore transpirational capacity, of the dominant overstorey species at each hydrological habitat. Twenty *B. attenuata* (except 20 m+ DTW *n*=11) were cored across the full existing range of trunk sizes per habitat type, using a 5.15 mm Hagløf increment borer. Cores were extracted and immediately measured for bark depth and the depth of sapwood (conducting tissue), based on colour and density differenced from the contrasting heartwood (non-conducting tissue) (Zencich, 2003, p. 275).

Each sapwood depth was converted to sapwood area per basal area by calculating:

1. bark area = difference between basal area [calculated using \( \pi r^2 \)] and the basal area without bark [calculated using \( \pi r^2 \) where bark depth subtracted from radius]
2. heartwood area, using \( \pi r^2 \) where [sapwood depth + bark depth] subtracted from radius

3. sapwood area = basal area – (bark area + heartwood area)

Regression analysis was used (and plotted using SigmaPlot v10.0) to establish the relationship of proportion of \( B.\ attenuata \) sapwood area per basal area, within each hydrological habitat and these relationships were tested for significance using the same software.

Relating the DBH of all measured \( B.\ attenuata \) (excluding juvenile size class 0-4.9cm) to sapwood area, regression equations were used to calculate total sapwood area (m\(^2\)ha\(^{-1}\)) for each replicate in each habitat. Hydrological habitat mean total sapwood area (m\(^2\)ha\(^{-1}\)) was calculated using these replicates and means were compared using one-way ANOVA and Tukey’s honestly significant difference post hoc test.

Regression analysis of \( B.\ attenuata \) sapwood area (m\(^2\)ha\(^{-1}\)) with FPC of the overstorey canopy and with leaf age were computed, plotted and tested for significance using SigmaPlot v10.0, with data based on replicate means. For the latter regressions, data were transformed appropriately and tested for normality to conform to the assumptions of a linear regression.
3. Results

3.1 General stand characteristics

Hydrological habitats differed in general stand characteristics. The range in size classes of the dominant overstorey species *B. attenuata* increased with habitat groundwater availability (Figure 3.1) with the 20 m+ DTW habitats having a maximum upper size class (trunk diameter) of 35.1-40 cm, whilst 10-15 m DTW habitats ranged up to 75.1-80 cm and 0-5 m DTW habitats to 90.1-95 cm. This pattern was reflected in a significantly different mature *B. attenuata* trunk diameter at breast height (DBH) between all hydrological habitats (Figure 3.2). The mean DBH was 13.12 cm (± 0.32) in the 20 m+ DTW habitat, 15.77 cm (± 0.45) in 10-15 m DTW habitat and 19.23 cm (± 0.77) in 0-5 m DTW habitat.

The overstorey stratum was significantly taller in habitats with increased groundwater availability (Figure 3.2). In the 20m+ DTW habitat mean, *B. attenuata* height was 3.40 m (± 0.12), 10-15 m DTW was 4.49 m (± 0.06) and 0-5 m DTW was 5.48 m (± 0.12). The maximum *B. attenuata* height was restricted to ~7 m at the 20 m+ DTW habitat but reached up to ~12.5 m at the 0-5 m DTW habitats.
Figure 3.1. *B. attenuata* size class (trunk Diameter at Breast Height [DBH] 1.3 m) frequencies, derived from the total in each hydrological habitat (where DTW= depth to watertable).
Figure 3.2. Mature *B. attenuata* trunk diameter at breast height (DBH) and height of mature *B. attenuata* along an ecohydrological gradient (where 20m+ Depth To Watertable $n=433$, 10-15m DTW $n=387$, and 0-5m DTW $n=311$). Statistical analysis was performed on transformed data (ln) and the Kruskal-Wallis test found significant differences between hydrological habitats (DBH: $d.f= 2$, $K=42.6$, sig.$= 0.000$ and Height: $d.f= 2$, $K= 297.51$, sig.$= 0.000$). Letters indicate significant differences identified by Mann-Whitney U post hoc test ($P < 0.05$).
3.2 Hypothesis one: Banksia woodland leaf area is greatest where water availability is highest.

3.2.1 Leaf age
The maximum leaf age supported by *B. attenuata* significantly increased with habitat water availability (Figure 3.3). Where 20 m+ DTW habitat had a leaf age of 1.93 yrs (± 0.03), 10-15 m DTW of 2.09 yrs (± 0.04) and 0-5 m DTW 2.38 yrs (± 0.05).

![Figure 3.3.](image)

*Figure 3.3. B. attenuata leaf age along an ecohydrological gradient (where 20m+ Depth To Watertable n=409, 10-15m DTW n=343, and 0-5m DTW n=245). Data plotted is the mean ± 1.S.E. Statistical analysis was performed on transformed data (ln) and the Kruskal-Wallis test found significant differences between hydrological habitats (d.f= 2, K= 59.08, sig.= 0.000). Different letters indicate significant differences identified by the Mann-Whitney U post hoc test (P < 0.05).*

3.2.2 Foliage Projective Cover
The proportion of total Foliage Projective Cover contributed by overstorey and understorey varied with water availability (Figure 3.4). The overstorey canopy increased with increasing groundwater availability, from 30.2% (± 3.62) in 20 m+ DTW habitat to 42.16% (± 2.07) in the 0-5 m DTW habitat. FPC of the
overstorey canopy was significantly higher in the 0-5 m DTW habitat (48.05% ± 2.91) compared to the other habitats with lower groundwater availability (Figure 3.5). The 10-15 m DTW and 20 m+ DTW habitats were not significantly different \((P=0.204)\), with 31.39% (± 5.12) and 21.7% (± 3.2) FPC respectively. FPC of the understorey also increased with groundwater availability (Figure 3.6), from 50% (± 3.7) in the 20 m+ DTW habitat to 66.3% (± 3.87) in the 0-5 m DTW habitat. This increase was only significant between 20 m+ DTW habitat and the other habitats \((P=0.012,\) Figure 3.6) and not between the 10-15 m and 0-5 m DTW habitats \((P=0.778)\).
Figure 3.5. Foliage Projective Cover (%) of the overstorey canopy in *Banksia* woodland (dominated/ co-dominated by *B. attenuata*) along an ecohydrological gradient (where *n*=9 per hydrological habitat and DTW: depth to watertable). Statistical analysis was performed on transformed data (arcsine) and one-way ANOVA found significant differences between habitats (*d.f*= 2, *MS*= 0.186, *F*= 12.01, *sig.* = 0.000). Different letters indicate significant differences determined by a Tukey's *post hoc* test (*P* < 0.05).

Figure 3.6. Foliage Projective Cover (%) of the understorey in *Banksia* woodland (dominated/ co-dominated by *B. attenuata*) along an ecohydrological gradient (where *n*=9 per hydrological habitat and DTW: depth to watertable). Statistical analysis was performed on transformed data (arcsine) and the Kruskal-Wallis test found significant differences between habitats (*d.f*=2, *K*= 8.847, *sig.* = 0.012). Different letters indicate significant differences identified by the Mann-Whitney *post hoc* test (*P* <0.05).
3.3 Hypothesis two: Density of the dominant overstorey species in Banksia woodland is greatest where water availability is highest.

3.3.1 Density

Density of the dominant overstorey species *B. attenuata* decreased with increasing groundwater availability (Figure 3.7). Significantly between the 20 m+ DTW habitat and both other habitats, but not significantly between 10-15 m and 0-5 m DTW habitats (*P*=0.692) (Figure 3.7). This density ranged from 1 148 (± 111) *B. attenuata* (ha⁻¹) in the 20 m+ DTW habitat, to 670 (± 94.7) *B. attenuata* (ha⁻¹) in the 0-5 m DTW habitat.

![Figure 3.7](image_url) Density of *B. attenuata* along an ecohydrological gradient (where n=9 per habitat and DTW: depth to watertable). One-way ANOVA found significant differences between hydrological habitats (d.f= 2, MS= 554444.4, *F*= 5.61, sig.= 0.01). Different letters indicate significant differences identified by Tukey's post hoc test (*P* < 0.05).
3.3.2 Nearest neighbour analysis

The hydrological habitats differed in their spatial distribution of the dominant overstorey species *B. attenuata* (Figure 3.8). The 10-15 m DTW habitat had the greatest distance to nearest neighbour in all categories of neighbour, and 20 m+ DTW habitat had the smallest distance. The trends in density (section 3.3.1) were reflected in distances to nearest conspecific neighbour which increased from 1.84 m (± 0.04) in 20 m+ DTW habitat to 2.04 m (± 0.07) in 0-5 m DTW habitat, though only the 20 m+ and 10-15 m DTW habitats were significantly different (Figure 3.8). Nearest overstorey neighbour (of any species) distances were not significantly different between habitats (Figure 3.8). Nearest similar aged neighbour distances were significantly larger in 10-15 m and 0-5 m DTW habitats compared to the 20 m+ DTW habitat (Figure 3.8).
Figure 3.8. *B. attenuata* distance to nearest overstorey, conspecific and similar aged (tree) neighbour, along an ecohydrological gradient (where 20m+ Depth To Watertable *n*=491, 10-15m DTW *n*=450, and 0-5m DTW *n*=372). Statistical analysis was performed on transformed data (ln) and the Kruskal-Wallis test found no significant differences between hydrological habitats for the overstorey neighbour category (d.f= 2, $K=1.16$, sig.= 0.281) but did for the conspecific neighbour (d.f= 2, $K=7.63$, sig.= 0.022) and similar aged tree (d.f= 2, $K=23.94$, sig.= 0.000). Different letters indicate significant differences identified by the Mann-Whitney *post hoc* test ($P<0.05$).
3.4 Hypothesis three: Sapwood area of the dominant Banksia species is greatest where water availability is highest.

Each hydrological habitat showed a unique and significant positive relationship for the proportion of sapwood area per B. attenuata basal area (Figure 3.9, Table 3.1). Once these regressions were employed to extrapolate sapwood area (m$^2$ ha$^{-1}$) per hydrological habitat, sapwood area was shown to significantly increase with increasing groundwater availability (Figure 3.10), from 1.62 m$^2$ (± 0.1) in the 20 m+ DTW habitat to 3.87 m$^2$ (± 0.4) in the 0-5 m DTW habitat. One-way ANOVA results showed a significantly different sapwood area between the 0-5 m DTW habitat and the other habitats ($P=0.01$, Figure 3.10) but not between the 10-15 m and 20 m+ DTW habitats ($P=0.35$).

The relationship between B. attenuata sapwood area and FPC of the overstorey canopy showed a positive regression ($r^2=0.54$, Figure 3.11) although this relationship was not significant (Table 3.2). There was a significant relationship between B. attenuata sapwood area and leaf age (Table 3.2), where sapwood area increased with leaf age (weak positive regression [$r^2=0.28$]; Figure 3.12).
Figure 3.9. Relationship between proportion of *B. attenuata* sapwood area in a given basal area, per hydrological habitat along an ecohydrological gradient. Fitted curves are logarithmic where a) is 20 m+ Depth To Watertable (n= 11) and $y = -97.3 + 27.48 \times \ln(x)$, b) is 10-15 m DTW (n= 20) and $y = -151.41 + 41.22 \times \ln(x)$, c) is 0-5 m DTW (n= 20) and $y = -325.93 + 81.13 \times \ln(x)$. 
Table 3.1. Significance of the Relationship Found Between Proportion of *B. attenuata* Sapwood Area per Basal Area (Relationships shown in Figure 3.9), in Contrasting Hydrological Habitats Along an Ecohydrological Gradient.

<table>
<thead>
<tr>
<th>Hydrological habitat</th>
<th>r</th>
<th>r²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>20m+ DTW</td>
<td>0.71</td>
<td>0.50</td>
<td>0.015 *</td>
</tr>
<tr>
<td>10-15m DTW</td>
<td>0.77</td>
<td>0.60</td>
<td>&lt;0.0001 *</td>
</tr>
<tr>
<td>0-5m DTW</td>
<td>0.86</td>
<td>0.74</td>
<td>&lt;0.0001 *</td>
</tr>
</tbody>
</table>

* significance with alpha: 0.05

Figure 3.10. Total *B. attenuata* sapwood area per hectare, along an ecohydrological gradient (where *n*=9 per hydrological habitat). One-way ANOVA found significant differences between habitats (d.f= 2, MS= 3.95, *F*= 10.96, sig. = 0.01) and different letters indicate significant differences identified by Tukey's *post hoc* test (*P* < 0.05).
Figure 3.11. Relationship between *B. attenuata* sapwood area per hectare and the Foliage Projective Cover of the overstorey canopy (arcsine transformed) in *Banksia* woodland (dominated/co-dominated by *B. attenuata*). Data used are replicate means of each hydrological habitat (n=3 per habitat), along an ecohydrological gradient (where DTW: depth to watertable). Relationship is polynomial – quadratic where $y=2.15+-4.7x+15.24x^2$.

Table 3.2. Significance of *B. attenuata*’s Sapwood Area Relationship to both Foliage Projective Cover of the Overstorey Canopy and to Maximum Leaf Age (Relationships shown in Figures 3.11, 3.12), in Contrasting Hydrological Habitats Along an Ecohydrological Gradient.

<table>
<thead>
<tr>
<th><em>B. attenuata</em> relationship</th>
<th>r</th>
<th>$r^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sapwood area (m² ha⁻¹) vs. FPC overstorey canopy</td>
<td>0.73</td>
<td>0.54</td>
<td>0.62</td>
</tr>
<tr>
<td>Sapwood area (m² ha⁻¹) vs. maximum leaf age (years)</td>
<td>0.53</td>
<td>0.28</td>
<td>0.004 *</td>
</tr>
</tbody>
</table>

* significance with alpha: 0.05
Figure 3.12. Relationship between *B. attenuata* sapwood area per hectare and *B. attenuata* leaf age. Data used are subsample plots of each hydrological habitat (*n* = 9 per habitat), along an ecohydrological gradient (where DTW: depth to watertable). Relationship is linear where $y=-2.46+2.4x$. 

$r^2=0.28$
4. Discussion

4.1 Functional relationships and evidence for ecohydrological optimisation in Banksia woodland

4.1.1 Hypothesis one: Banksia woodland leaf area is greatest where water availability is highest.

The results of this study show significant differences in Banksia woodland leaf area in contrasting hydrological habitats. Leaf area (represented by FPC and leaf age) significantly increases with increasing water availability along the ecohydrological gradient, supporting the first hypothesis of this study. The increase in leaf area associated with higher water availability observed in this study, parallels results of multiple studies on vegetation systems elsewhere. Canopy cover and leaf area have been shown to increase along water availability (precipitation) gradients in semi-arid and arid Kalahari woodland and savanna (Privette et al., 2004; Scholes et al., 2004); savanna tree species in the tropics of Australia (Prior et al., 2005); and wide-ranging Eucalyptus species in Australia (Merchant et al., 2007).

Decreasing leaf area associated with lower water availability in this study can be explained through several different mechanisms. Whole plant carbon gain would increase with greater photosynthetic leaf area however this would incur a greater cost through increased transpirational water loss (Nemani & Running, 1989). Thus, water availability has been shown to induce changes in the ratio between production of sapwood area and leaf area (Magnani et al., 2002) and below-ground to above-ground biomass ratios (Barton & Montagu, 2006). Plants often reduce foliage production under xeric conditions (such as those in the 20 m+ DTW habitat) as a mechanism to minimise transpirational water loss.
The reduction in leaf area observed in Banksia woodland overstorey and understorey FPC and overstorey leaf age in the more xeric habitats (10-15m DTW and 20m+ DTW), implies a reduction in leaf production and/or maintenance processes to minimise water loss. Although not demonstrating cause and effect, this result does suggest optimisation of water use is occurring along the ecohydrological gradient. The demonstration of stand level structural optimisation in this study concurs with and expands on previous studies that have shown stomatal regulation changes in Banksia woodland to cope with water deficits (e.g. Groom, 2004). Stomatal conductance (and therefore assimilation and transpiration) are coordinated with vascular conductance and the risk of cavitation (Westoby et al., 2002). Canham et al. (2009) have shown that facultative Banksia phreatophytes have an increased resistance to xylem cavitation in xeric sites as opposed to more mesic sites. This mechanism, coupled with stomatal control and leaf area reduction, would aid these plants in surviving in xeric sites. This synthesis suggests ecohydrological optimisation is occurring. That is, development of a safe or efficient hydraulic architecture and establishment of a proportional allocation of growth in plant parts is linked to water availability, therefore representing functional and structural adjustment in plants and equilibrium with the hydrological habitat.

The mesic sites have higher overstorey FPC and leaf age despite smaller overstorey plant densities. This indicates that at an individual tree scale there is maximisation of foliage production within the crown. This increase in foliage in mesic sites is facilitated by a greater transpirational support to the leaf area by larger sapwood areas (Figure 3.10). Synergistically, this sapwood area increase in mesic sites is supported by increased allocation of growth to non-leaf tissues through the larger, longer retained, leaf area which has greater photosynthetic capacity (Figures 3.11, 3.12). The
increased allocation of growth to non-leaf tissues (through having increased leaf area and photosynthetic capacity) in mesic sites is also evident in other structural attributes, such as the increased tree heights in more mesic habitats. Allocation of growth to non-leaf tissues increases with the height of a tree (Westoby et al., 2002) which explains the larger trunk diameters in the 10-15m DTW habitat and even larger in the 0-5m DTW habitat. These results are supported by studies of height and diameter increasing with water availability in other native Australian species (Merchant et al., 2007) and in species of semi-arid systems (e.g. Ferreira et al., 2007; Saha et al., 2008). Within the present study, Banksia attenuata height and trunk size were probably smaller in the xeric habitat due to lower photosynthetic capacity of the smaller leaf area causing reduced allocation of growth to non-leaf tissues per plant. Reduced tree height in the 20m+ DTW xeric habitat could also be related to the ‘hydraulic limitation to tree height’ theory (Ryan & Yoder, 1997; Sperry, Meinzer & McCulloh, 2008). This theory suggests that the taller the tree, the lower the whole tree hydraulic conductance, and so it is possible the trees in the xeric habitat where water availability is reduced allocate less energy to height growth, to reduce gravitational potential on sapflow and therefore avoid lower levels of hydraulic conductivity. This would represent another mechanism of hydrological optimisation. The reduced heights may also be the result of reduced productivity (due to reduced leaf area) and enhanced water conservation previously discussed.

Leaf Area Index (LAI) provides another useful structural variable for quantifying the energy and mass exchange characteristics of a terrestrial ecosystem and for estimating net primary productivity and evapotranspiration (Nemani & Running, 1989; Eamus, 2003). Therefore any further research on these woodlands should measure LAI as another attribute indicative of ecohydrological optimisation. LAI was not determined
in this study due to time constraints and the lack of consensus (in the literature) on the best methods of measuring LAI in these particular systems which have highly heterogeneous canopies (Wilson & Valentine, 2009).

4.1.2 Hypothesis two: Density of the dominant overstorey species in Banksia woodland is greatest where water availability is highest.

The results of this study show significant reductions \( (P<0.05) \) in Banksia woodland overstorey densities in contrasting hydrological habitats along an ecohydrological gradient of increasing water availability. These findings do not support the second hypothesis of this study. The density results were surprising given previous research showing increased densities along gradients of increasing water availability (Naumburg et al., 2005; Prior et al., 2005).

Despite lower than expected densities at mesic habitats, the larger individual \( B. \) attenuata tree sizes in mesic habitats are probably responsible for the decreased overstorey densities and increased conspecific neighbour distances observed, through increased competition for site resources, namely light, water and root space. However, the low densities of larger individuals may well represent a higher productivity (standing biomass in this case) per unit area in habitats with greater water availability. Furthermore, competition in the more mesic habitat may not just be between the overstorey species but also the understorey as evidenced by the largest understorey FPC in this habitat. In the 10-15m DTW habitat, water seems to be more limiting for overstorey species than in the more mesic 0-5m DTW habitat, as greater neighbour distances are seen despite similar levels of understorey FPC to the mesic habitat.
This difference between hydrological habitats can be further explained by Grimean theory which addresses the interaction between stress, disturbance and competition (Grime, 1974, 1977). The mesic sites have greater resource availability (in this case water), supporting higher productivity (represented here as an interaction between size of individuals, density and foliage cover) as well as competition. In the more xeric 10-15m DTW habitat with reduced water availability, productivity decreases, stress increases (inferred as greater drought stress through reduced water availability) and competition remains high resulting in less overstorey individuals with increased neighbour distances. In the most xeric habitat, (20m+ DTW) drought is suggested as the dominant mechanism through which productivity is limited. This is reflected in the xeric habitats of this study where productivity (smaller individuals and reduced leaf area) is decreased, but densities are high. The higher overstorey (B. attenuata) densities seen in the xeric 20m+ DTW habitat are also supported by the dimorphic rooting patterns of these species that have been shown to enable toleration of surface soil water deficits through allocating increased root growth either to greater depth to access the watertable, or to a breadth of shallower roots to maximise use of upper soil moisture (Dodd, Heddle, Pate & Dixon, 1984; Schenk & Jackson, 2002; Groom, 2004).

In addition to the inferences above, there may also be population level patterns in competition which determine the density and spatial dispersion found in this study. Long-standing theories on spatial dispersion of shrubs in water-limited systems predict uniform dispersion through the process of self thinning caused by competition for water (Toft & Fraizer, 2003). The overstorey plants in the xeric habitat (20m+ DTW) of this study are more uniform than the more mesic sites (less variation in conspecific nearest neighbour distances). Spatial dispersion also has implications for
tree growth through competition and plants in a similar sandplain system to this study have shown smaller plant sizes in more dense aggregations of seedlings (Toft & Fraizer, 2003).

Density-dependant effects on tree size and mortality have been shown to be prevalent in the pre-phreatophytic stage (juveniles yet to produce a deep root profile and are reliant on depleteable upper soil moisture) as opposed to the later phreatophytic stage in tree development (Toft & Fraizer, 2003). B. attenuata would be competing for shallow soil water with the understorey species during their young pre-phreatophytic stage. Therefore in the more mesic sites the reduced sapling and juvenile counts seen in this study can be explained by increased resource competition from a higher understorey density (reflected in higher understorey FPC). This interpretation however, contrasts with the findings of Enright and Lamont (1992) that showed greater survival rates in B. attenuata in mesic sites compared to dune crests. This difference may be accounted for by different overstorey and understorey characteristics of the sites, or different hydrological attributes used to define the sites.

Fire regimes can have major effects on plant recruitment however this factor is not likely to be the cause of significant differences in seedling counts between the hydrological habitats of this study. This is due to the minimum fire disturbance age used in selecting the sites being close to the fire interval deemed to be optimal for the resprouter B. attenuata (~14yrs sensu Enright et al., 1998), which enables peak survivorship, resprouting of canopy and return to viable canopy seed store. Furthermore, it has been shown that resprouters (i.e. B. attenuata) are well represented and maintain their presence in the community after a fire event (Lamont & Markey, 1995) with the rapid restoration of reproduction capacity of resprouters enabling seedling recruitment (Lamont & Markey, 1995).
This study quantified the density and spatial distribution of the dominant overstorey species, but to improve understanding of the woodland’s structure and function at a stand level, these variables could also be measured in future studies on multiple species of both the understorey and overstorey. For example, Perry et al. (2009) have highlighted the importance of species interactions along gradients of water availability, the consequences of which would have implications on competition and use of resources.

4.1.3 Hypothesis three: Sapwood area of the dominant Banksia species is greatest where water availability is highest.

This study aimed to determine the difference in sapwood area of contrasting hydrological habitats of Banksia woodland, as it represents the capacity of vegetation to conduct water which feeds back on leaf area. Sapwood cross-sectional area was coordinated with total leaf area (the ratio of the two being adjusted to the evaporative climate) (Westoby et al., 2002), with total habitat sapwood area (m$^2$ ha$^{-1}$) increasing with greater water availability. The results of this study support the hypothesis that sapwood area of Banksia woodland is greatest where water availability is highest, and this has significant implications for the transpirational capacity of each hydrological habitat.

The unique relationship between the proportion of B. attenuata sapwood area and basal area in each hydrological habitat conforms to general theory that sapwood area is highly site-specific due to climatic and plant functional variables (e.g. Specht & Specht, 1999; Eamus et al., 2006). At an individual plant level this proportion of sapwood area per basal area decreased with lower water availability, therefore these
individuals have lower capacity to conduct water. This supports the previously discussed notions that productivity is reduced in xeric habitats (limited allocation of growth to non-leaf tissues) and that water use is also constrained, representing vegetation adjustment to available water. Despite the xeric sites having much higher plant densities, the total habitat sapwood area ($m^2\ ha^{-1}$) was smaller than the more mesic habitats due to this reduced proportion of sapwood area per basal area and smaller trunk sizes.

4.2 Consequences for management and future research

It has been demonstrated in this study that structural characteristics of Banksia woodland reflect the outcome of plant adjustments to water availability in a hydrological habitat. The different structural characteristics of Banksia woodland found in each type of hydrological habitat shows that this vegetation responds to decreasing groundwater availability by reducing leaf area, leaf retention time, tree sizes and sapwood area. The hydrological habitats also vary in densities and spatial arrangement of overstorey trees. These structural differences have significant implications on ecosystem function, net primary productivity, environmental water requirements and available habitat for biodiversity. By quantifying the relationships between vegetation structural attributes and water availability, we can enable the prediction of vegetation responses to changes in water availability as well as formulate objectives for vegetation rehabilitation.

About 22 000 ha of land across the Gnangara Groundwater Mound will need to be rehabilitated to Banksia woodland following pine plantation removal over the next 10 to 15 years (Government of Western Australia, 2009; Maher, 2009). The results of
this study showing the hydrological habitat-specific structural optimisation of *Banksia* woodland will aid in producing better informed targets for rehabilitation in a region of spatially and temporally variable groundwater availability.

The ability of these ecosystems to tolerate natural and anthropogenic temporal shifts in water availability, through structural and functional optimisation, is fundamental to their future (Fitzpatrick, Gove, Sanders & Dunn, 2008). Complexities arise when using the different structural characteristics found in contrasting hydrological habitats in this study as ‘reference states’ for the trajectory of vegetation undergoing a temporal shift in hydrology. The structural attributes of hydrological habitats represent long-term vegetation adjustment to environmental conditions, i.e. they need to attain equilibrium with resource availability and this takes time, particularly at the stand-level.

It is not necessarily correct to assume that vegetation would develop the exact same structural attributes in all cases, or do so through the same mechanisms, in response to a temporal shift in water availability. This is because it is unclear as to whether the structural changes seen are a product of phenotypic plasticity or genetic adaptation under long-term pressure of natural selection (sensu Eagleson, 1982; Magnani *et al.*, 2002). Plant structural and functional adjustments would also vary between species making up the woodland. The structural changes seen appear to play a central role in the adjustment of vegetation to a hydrological regime, but the following must be considered: which aspects of these structural changes become important to an individual tree over a single generation? Therefore, the question of what length of time would be adequate for assessing whether vegetation has structurally acclimatised
to its hydrologic environment, is also fundamental for predicting vegetation structural response to temporal variation in a hydrological regime.

Vegetal biomass (largely represented by leaf area) is the vegetation parameter capable of change on the shortest time scale, in response to attaining equilibrium with climatic variables of a habitat (Eagleson, 1982). Reducing leaf area and plant water use, as a minimisation of water demand stress, provides a short-term equilibrium condition (Eagleson, 1982). Therefore, the reductions in leaf area (and above ground biomass) associated with lower water availability seen in this study represent the initial Banksia woodland structural adjustment to low water availability. As the habitats in this study are ‘permanent’ in their hydrological attributes, the maintenance of the observed structural change to vegetal biomass (leaf area) is also sustained. Leaf area would also be the first structural attribute to respond and adjust into equilibrium with a temporal shift in water availability.

In the medium term (i.e. generations) it is possible for a habitat’s plant species to change through substitution of one species for another or through biological evolution, to select those who achieve transpirational efficiency resulting in maximum equilibrium soil moisture (Eagleson, 1982). This may be evident in this study not by species replacement, but by survival of B. attenuata with particular rooting patterns and traits of water acquisition that reflect a safer more efficient hydraulic architecture, in the xeric habitat. However, species replacement would occur in this particular system over generational time scales if a habitat was undergoing a temporal reduction in water availability, i.e. through facultative phreatophytes replacing obligate phreatophytes in mesic habitats that cannot adjust to or survive in the state of
decreased water availability. A resulting change in the structure of vegetation would follow, with its own trajectory towards achieving hydrologic optimisation.

Over longer time scales plants modify the soil by adding organic matter which changes the soil texture and thus soil moisture (in addition to providing increased nutrients), leading to a ‘climax’ system which is in equilibrium with its environment (Eagleson, 1982). The more mesic habitats in this study have higher productivity and therefore are more capable than the xeric habitats (dune crests) of sustaining an optimised soil moisture condition, at a higher level of productivity (in vegetative equilibrium).

To provide more site and species specific predictions of *Banksia* woodland structural acclimatisation to temporal shifts in water availability, research into within-hydrological habitat structural response (and associated plant functional mechanisms) should be conducted within similar study sites to provide a more accurate understanding of short-term and long-term vegetation adjustment to water availability. Ecophysiological traits of the overstorey and understorey species in *Banksia* woodlands should be further investigated for any mechanisms evident in their hydraulic architecture which point to evidence for hydrological optimisation (in habitats with decreased water availability). Further research into whole-tree scale vascular system efficiency of design (sensu Murray [1926] in Sperry *et al.*, 2008) differences between contrasting hydrological habitats, would provide a better insight into processes of hydrological optimisation in these species.
To improve understanding of leaf area optimisation within a hydrological habitat, spatial and temporal variability of LAI of the overstorey and understorey in Banksia woodlands needs to quantified. Secondly, it has been shown that leaf area equilibrium with water availability is more reliably predictable (smaller than catchment scales) when a spatial knowledge of soil (namely nitrogen limitations) can be obtained and integrated into any model (Mackay, 2001).

Understanding ecosystem water use is of increasingly high importance to environmental managers in light of competitive demands for water between humans and the environment, and the need for estimating and providing environmental water provisions. This study provides the first step towards understanding the capacity of Banksia woodland water use under different water availabilities, through quantifying overstorey species sapwood area for particular hydrological habitats.

4.3 Conclusions

The results of this study show significant differences in the structural character of Banksia woodland in contrasting hydrological habitats along an ecohydrological gradient. As water availability increased, growth per overstorey individual (B. attenuata, including tree size and amount of foliage) was maximised, with a trade off reflected in decreased plant densities. In more xeric hydrological habitats, increased plant densities were observed, with smaller individual tree sizes and leaf area. The more mesic habitats also have a taller overstorey stratum, with a canopy of increased leaf area and longer foliage retention times. This in-turn is correlated with increased
total habitat sapwood area (despite lower plant densities) and increased individual tree sapwood area.

The nature of *Banksia* woodland structural adjustments to water availability seen involve processes of hydrological optimisation to achieve vegetative equilibrium with the hydrologic environment. These mechanisms reflect *Banksia* woodland's adaptive capacity to respond to variability in water availability and have impacts on NPP, ecosystem function, habitat and environmental water requirements. These structural changes, including processes of ecohydrological optimisation, are habitat-specific and occur over different time scales. To improve our understanding of the structural characteristics of *Banksia* woodland hydrological habitats, further research should be conducted on i) the within-habitat effects of temporal shifts in water availability, ii) evidence of ecohydrological optimisation within plant hydraulic architecture, and iii) other stand level structural attributes which are indicative of ecohydrological optimisation, such as LAI.
5. Reference list


Location of study sites (ecohydrological gradient position, replicate number), including subsample plots, in a) Lexia and b) Pinjar, Western Australia (Images courtesy Google Earth, 2009).
Study site post fire age and status for presence of dieback (Phytophthora). Data sourced from Department of Environment and Conservation.

<table>
<thead>
<tr>
<th>Gradient position</th>
<th>Years Since Last Burn (DEC)</th>
<th>Phytophthora presence (DEC VHS)</th>
<th>Project Dieback</th>
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<tbody>
<tr>
<td>20m+ DTW</td>
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</tr>
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<td></td>
</tr>
<tr>
<td>2</td>
<td>14</td>
<td>-</td>
<td>uninfested (low confidence)</td>
</tr>
<tr>
<td>3</td>
<td>14</td>
<td>-</td>
<td>uninfested (low confidence)</td>
</tr>
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<td></td>
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</tr>
<tr>
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<td>-</td>
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<tr>
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<tr>
<td>0-5m DTW</td>
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<tr>
<td>3</td>
<td>20+</td>
<td>negative</td>
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</tbody>
</table>

Study site vegetation complexes (Mattiske, 2003), showing the key species present:

<table>
<thead>
<tr>
<th>Gradient position</th>
<th>Vegetation Complex (Mattiske, 2003)</th>
<th>Shared some understorey vegetation of neighbouring complex</th>
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<td>G1</td>
</tr>
<tr>
<td>1</td>
<td>II</td>
<td></td>
</tr>
<tr>
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<td>II</td>
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</tr>
<tr>
<td>3</td>
<td>II</td>
<td></td>
</tr>
<tr>
<td>10-15m DTW</td>
<td>I1</td>
<td>H1</td>
</tr>
<tr>
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<td>I1</td>
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<tr>
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<td>0-5m DTW</td>
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<tr>
<td>3</td>
<td>II</td>
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</tr>
</tbody>
</table>

I1: Low Open Woodland of Banksia attenuata - Banksia menziesii over Verticordia nitens, Dasypogon bromeliifolius, Melaleuca sericea and Patersonia occidentalis.

G1: Low Woodland to Low Open Woodland of Banksia attenuata - Banksia menziesii - Eucalyptus smithiana - Nuytsia floribunda with occasional Allocasuarina fraseriana and Banksia grandis (southern section only) over Leucopogon conostephioides, Scholtzia involucrata, Eremea pacifica var. pacifica, Melaleuca scalina, Boronia pteridifolia subsp. pteridifolia and Astroloma sericephyllum.

H1: Low Woodland to Low Open Woodland of Banksia attenuata - Banksia menziesii - Banksia ilicifolia - Nuytsia floribunda over Beaufortia elegans, Leucopogon polymorphus, Melaleuca synnema, Calytrix angulata, Calytrix flavescens, Strigilina lanigera, Dasypogon bromeliifolius, Leucopogon conostephioides, Lygina barbata, Macrozamia riedlei and Xanthorrhoea preissii.

K1: Open forest of Eucalyptus rudis subsp. rudis – Melaleuca preissiana – Banksia ilicifolia with occasional Banksia attenuata, Banksia menziesii, Nuytsia floribunda and Eucalyptus smithiana over Kennedia prostrata, Lygina barbata, Xanthorrhoea preissii, Hyocalycula angustifolia, Dasypogon bromeliifolius, Pypecyma ellipticum var. Ellipticum, Astretea scorpius, Leptosperma tenea, Jackinia furcellata, kunzea ericifolia subsp. Ericifolia and Bossiaea ericoides.
Showing all the study sites fall within the same rainfall zone (Australian Bureau of Meteorology, 2009).
Showing the mean annual rainfall of study sites, using closest weather station (Pearce) (Australian Bureau of meteorology, 2009).