Groundwater-dependency and water relations of four Myrtaceae shrub species during a prolonged summer drought

P K Groom

Centre for Ecosystem Management, School of Natural Sciences, Edith Cowan University,
100 Joondalup Drive, Joondalup, WA 6027: current address, Centre for Horticulture and Plant Sciences,
University of Western Sydney, Locked Bag 1797, Penrith South DC, NSW 1797   p.groom@uws.edu.au

Abstract

Seasonal water relations and water source (δ^2H analysis) data were examined for four Myrtaceae shrub species inhabiting a winter-wet depression (dampland) and surrounding landscape on Perth's coastal sandplain. Data were collected during an exceptionally dry spring-autumn period in 2000/2001. The two species occurring within the dampland, *Astartea fascicularis* and *Pericalymma ellipticum*, were probably accessing shallow soil moisture or groundwater (at a depth of 0.35 m) during October 2000 (spring), but were not accessing groundwater (at a depth of 1.45 m) during the summer drought (March 2001). Species occurring on the dampland embankment (*Hypocalymma angustifolium, Eremaea pauciflora*) and at a site further upslope (*E. pauciflora* only) had a significant reduction in predawn xylem water potential and morning stomatal conductance in response to the summer drought, with neither species accessing groundwater during summer. The dampland species were able to maintain summer morning stomatal conductances similar or greater than the conductance measured during the previous spring, implying that shallow soil moisture (gravimetric content of 10–20%) was sufficient to sustain their summer water-use requirements. δ^2H data suggests that *P. ellipticum* may have been utilising groundwater in early winter (July 2001), implying that the minimum accessible groundwater depth for this species at the study dampland is approximately 1.4 m.

Keywords: dampland, groundwater, sandplain, seasonal water relations, summer drought, winter-wet depression, Myrtaceae

Introduction

Plants occurring above a shallow aquifer may be dependent on groundwater as a regular source of moisture, with the degree of dependency depending on seasonal groundwater and depth, and the species' rooting pattern. Some species only occur where groundwater is at a particular depth, with their loss or decline indicative of an altered hydrological regime caused by a natural decline in water table levels or groundwater extraction (Stromberg *et al.* 1996; Wierda *et al.* 1997). The capacity to exploit an underground water source, or soil moisture at depth, makes it possible for some species to survive long periods without rain (Cramer *et al.* 1999; Williams & Ehleringer 2000).

Perth is on the northern section of a coastal sandplain, under which lies a large, shallow unconfined aquifer (total superficial aquifer groundwater storage of 18 700 x 10^6 m³; Davidson 1995). This coastal plain consists of urban development, extensive areas of native *Banksia* and other woodlands, introduced pine plantations, and numerous wetlands. Over 50% of the latter have been lost to landfill or drainage (Arnold & Sanders 1981). Shrub species from the family Myrtaceae are a major component of the coastal plain vegetation. The many winter-wet depressions are often dominated by a shrub stratum of shallow-rooted *Astartea fascicularis* (Labill) DC and *Pericalymma ellipticum* (Endl) Schauer. Species such

as *Hypocalymma angustifolium* (Endl) Schauer are dominant along the upper edges of these depressions where the soil is rarely waterlogged (Muir 1983; Farrington *et al.* 1990). In more elevated positions deeper-rooted species, *e.g. Eremaea pauciflora* (Endl) Druce, are common.

Populations of myrtaceous shrub species inhabiting low-lying, winter-wet depressions on Perth's sandplains have declined in size since 1966 (Groom *et al.* 2000a). This has been attributed to the gradual decline in groundwater and soil moisture levels in most areas of this aquifer since the 1970s (Heddle 1980; Davidson 1995), resulting from the combined effects of below average rainfall (the sole source of groundwater recharge on the sandplain) and increased regional groundwater abstraction.

Perth experienced its driest spring to autumn period between September 2000 and April 2001 (Bureau of Meteorology, Perth, WA). During this period, the seasonal water relations and groundwater-dependency (by δ^2H analysis) of the abovementioned myrtaceous shrub species were monitored at sites within and adjacent to a winter-wet depression (part of the Lexia wetlands) on the eastern edge of the coastal plain. This study examines how species from different topographical positions within a sandplain landscape sustain their water requirements during periods of drought. It is expected that during times of drought, plants overlying shallow aquifers may rely more on groundwater resources (*i.e.* less on soil moisture reserves) or may be

entirely dependent on groundwater. A species' ability to access groundwater during a summer drought may ultimately influence it's distribution within the landscape (Zencich *et al.* 2002).

Materials and Methods

Study site

The Lexia wetlands are a chain of wetlands on the eastern edge of the Gnangara Groundwater Mound, a large, shallow unconfined aquifer on the coastal sandplain north-east of Perth, Western Australia. The Lexia wetlands are unique when compared to other wetlands on Perth's coastal sandplain as they have remained undisturbed from human impact. The majority of the Lexia wetlands are damplands (seasonally waterlogged basins; Semeniuk 1987), which may have surface water depending on the amount of winter rainfall received and regional groundwater levels. A study on the hydrology and stratigraphy of these wetlands indicated that many of the Lexia wetlands may be perched at a soil depth of 2–3 m (Semeniuk & Semeniuk 1993).

The vegetation surrounding these damplands is dominated by an evergreen *Banksia* (Proteaceae)
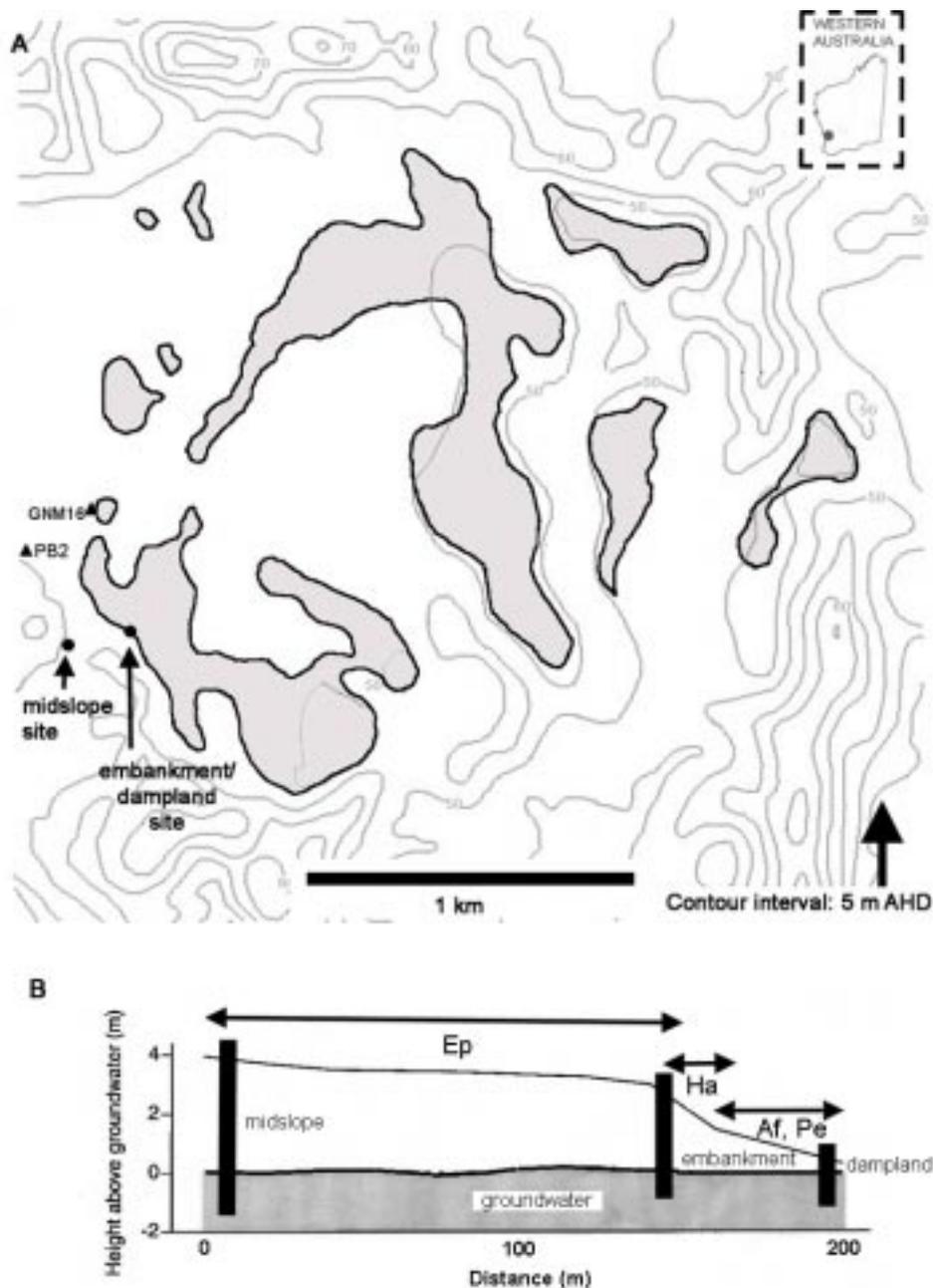
Figure 1. A: Location of study sites and two permanent groundwater monitoring bores (triangles) within the Lexia chain of wetlands (shaded areas), 25 km NE of Perth, Western Australia. **B:** Distribution of target species and position of sites (thick black lines represent groundwater monitoring piezometers) in the study area. Groundwater profile represents a typical spring (October) water table. Species abbreviations: Af = *Astartea fascicularis*; Pe = *Pericalymma ellipticum*; Ha = *Hypocalymma angustifolium*; Ep = *Eremaea pauciflora*.

overstorey with an understorey of low shrubs from the families Myrtaceae, Proteaceae and Fabaceae (Heddle *et al.* 1980). As groundwater becomes shallower, species tolerant of waterlogging dominate, specifically *Melaleuca preissiana* (Myrtaceae) trees and some myrtaceous shrub species (Farrington *et al.* 1990). Perth's coastal sandplain experiences a dry mediterranean-type climate (Beard 1984) of hot dry summers (December–March) and cool wet winters (June–August), with a long-term average of 870 mm annual rainfall recorded at the Perth meteorological station.

The sites chosen for this study were on the western edge of Lexia wetland number 84 and consisted of dampland, embankment and lower slope sites (Fig 1A). The dampland site (< 1 m depth to groundwater; Fig 1B) at 31°45'23" S 115°57'39" E was dominated by the myrtaceous target species *Astartea fascicularis* and *Pericalymma ellipticum*. The embankment site (2–3 m depth to groundwater) was on the edge of the dampland and had the target species *Hypocalymma angustifolium* (lower section) and *Eremaea pauciflora* (upper section) (Fig 1B). *E. pauciflora* also occurred at the midslope site (3–4 m depth to groundwater) at 31°45'27" S 115°57'26" E, which was located approximately 200 m from the dampland site. Groundwater access tubes were installed at all sites to a depth of approximately 1 m below maximum (spring) groundwater levels.

Seasonal water relations

Water relations of the target species were measured three times during 2000–2001 at dates that reflected seasonal hydrological differences. Data were collected on 31 October 2000 (spring, representing maximum groundwater levels), 19 March 2001 (late summer, representing minimum groundwater levels) and 24 July 2001 (winter, representing the beginning of groundwater recharge). July measurements were taken during the driest start of winter (June–August) that Perth has recorded. Each set of measurements was collected on a cloud-free, sunny day, at least 2 days after the last rainfall event.

Xylem water potentials were measured predawn (0300–0500 h local time; WP_{pd}) and midday (1200–1330 h; WP_{md}) for 3–4 leafy stems per species using a pressure chamber (Model 3005, Soil Moisture Equipment Co., Santa Barbara, CA). Predawn values indicate the maximum water potential, reflecting the degree of overnight recovery of water balance following water deficit incurred during transpiration the previous day. Midday water potential represents the minimum daily value and therefore the maximum stress.

Transpiration and stomatal conductance were measured mid-morning (0930–1030 h) and midday (1230–1330 h) using a portable infra-red gas analyser (LCi, ADC Bioscientific Ltd, Hoddesdon, England) for leaves produced in the previous year of three different plants per species. Afternoon measurements were not conducted as the equipment overheated (and malfunctioned) when the leaf chamber temperature was greater than 35 °C, a common occurrence during the afternoons of spring and summer measurements. Measurements were taken at ambient humidity and CO_2 concentrations, and recorded within 1 min of enclosing the leaf within the chamber. All gas exchange data were collected when light intensity (PAR) was > 1000 μmol m^{-2} s^{-1}. Transpiration and stomatal conductance data were expressed on an area basis, with leaf area measured in the laboratory with a digital image analyser (WinDIAS, Delta-T Devices, Cambridge, UK). Ventilated leaf chambers may alter boundary layer conductance and leaf temperatures (McDermitt 1990) and hence gas exchange parameters. These errors were relatively minor in the context of this investigation because leaves of the study species are small (0.025 – 1.5 cm^2) resulting in a large boundary layer conductance relative to stomatal conductance. Soil-to-leaf hydraulic conductance (K_L), was calculated after Hubbard *et al.* (1999) as midday transpiration/(WP_{pd} – WP_{md}).

Soil moisture

Soil samples were collected every 0.1 m (dampland) or 0.2 m (other sites) depth and stored in air tight containers. For spring and winter measurements soil samples were collected using a hand-held auger. Augering was not possible for the summer measurement because the soil was too dry. Instead, pits were hand dug until groundwater was reached or augering was possible. Due to safety concerns regarding the stability of the sandy pit walls at the midslope site, soil samples were only collected from the top 2 m of the soil profile. July soil samples were not collected for depths >3 m at the midslope site as winter rainfall had not penetrated below this depth. Soil samples were dried at 100 °C for 24 h and soil moisture was calculated gravimetrically (%) as (fresh weight – dry weight)/dry weight × 100.

Samples for deuterium analysis

Twig samples 5–10 cm in length were collected from three different shrubs per species, and their leaves immediately removed. Twigs were then wrapped in plastic cling wrap to prevent isotopic fractionation by evaporation and placed in an airtight container (see Turner *et al.* 2001). Groundwater samples and data of groundwater depth were collected from groundwater access tubes installed at each site. Soil samples for deuterium analysis were collected at the same time as samples for soil moisture. All samples were stored in airtight containers and kept at ~ 5 °C in the field until transported to the laboratory. Samples were then transferred to a freezer where they remained until the water was extracted. Bark was removed from twig samples prior to water extraction.

Water was extracted from soil and twig samples by cryogenic vacuum distillation (Ehleringer & Osmond 1989). Two Vycor glass tubes were attached to a vacuum pump in a Y-shape configuration. Twig samples or approximately 15 g of soil was placed in one tube and frozen by submerging the tube in liquid nitrogen. Both tubes were evacuated and then isolated from the vacuum line to create a closed U-shape configuration. The tube containing the sample was placed in boiling water, whilst the second tube was placed in liquid nitrogen to 'trap' water evaporating from the heated sample. After 1 h, the collection tube was removed and sealed. After thawing, the collected water was decanted into an airtight vessel.

Extracted water samples and free water samples (groundwater) were reduced to hydrogen gas for

analysis using a gas phase mass spectrometer (VG Isogas SIRA 10), and were analysed using the procedure outlined by Coleman *et al.* (1982). Hydrogen/deuterium ratios (δ^2H) were expressed according to standard notation in parts per thousand (‰) relative to the V-SMOW (Vienna Standard Mean Ocean Water) standard as δ^2H $=((R_{sample}/R_{standard})-1) \times 1000$, where R_{sample} and $R_{standard}$ are the ratios of the heavy to light isotope of the sample and standard water respectively.

δ^2H was only measured once for all water samples, except for free water samples where duplicate samples were analysed. For soil water δ^2H, soil samples collected at 0.4 m intervals were analysed.

Data analysis

Analyses of variance were calculated using the SuperANOVA (Abacus Concepts, Berkeley, CA) computer package. Homogeneity of variances was checked by residual plots and data were transformed as necessary by log or square roots, with data presented as untransformed means. Tukey's HSD test was used for comparisons between means at the 0.05 significance level.
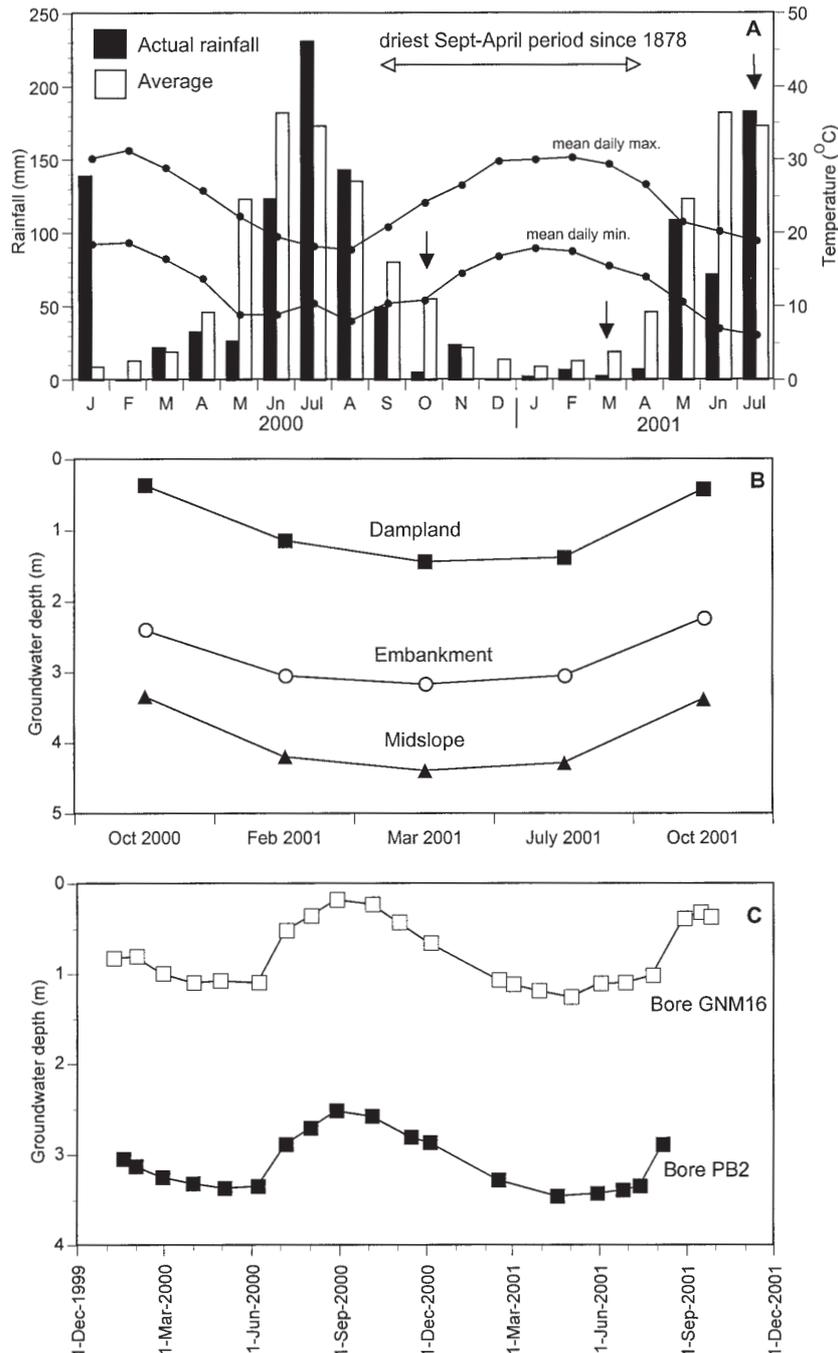
Figure 2. Climate and groundwater data for Perth and Lexia wetlands. **A:** Rainfall and temperature data for Perth meteorological station from Jan 2000 – July 2001. Arrows represent sampling times for plant water relations; **B:** groundwater levels *in situ* at the three study sites from Oct 2000 to Oct 2001; **C:** monthly variation in groundwater levels (Jan 2000 – Sept 2001) from two permanent monitoring bores near the Lexia wetlands (see Fig 1). Bores chosen were those that had similar October 2000 (spring) and March 2001 (summer) groundwater depths to the dampland and midslope study sites.

Results

Climate and groundwater levels

Perth and the surrounding environs (including the Lexia chain of wetlands) experienced an exceptionally dry spring to autumn period (Sept 2000–April 2001) with only 98 mm of rainfall, compared to the long-term average of 258 mm (Fig 2A). In comparison, the previous spring to autumn period was exceptionally wet, with 139 mm of rain recorded in January 2000 (average is 9 mm). Between October 2000 and July 2001 mean daily maximum temperatures peaked during February (30.2 °C) with the lowest maximum temperatures recorded in July (18.8 °C; Fig 2A). Highest (17.4 °C) and lowest (6.0 °C) mean daily minimum temperatures were also recorded in February and July respectively.

At all three topographical positions, groundwater levels were at their lowest by March 2001 and remained so when remeasured in July 2001 (Fig 2B), representing a decrease in groundwater levels ranging from 0.77 m (embankment) to 1.08 m (dampland) compared to October 2000 levels. At permanent monitoring bores situated within close proximity to the study sites (Fig 1A), groundwater levels did not increase until September 2001 (Fig 2C). In 2000 (a year of near-average rainfall) groundwater levels in these bores began to rise in June, as a result of April–May rainfall. By October 2001, groundwater levels at all sites had recovered to October 2000 levels.
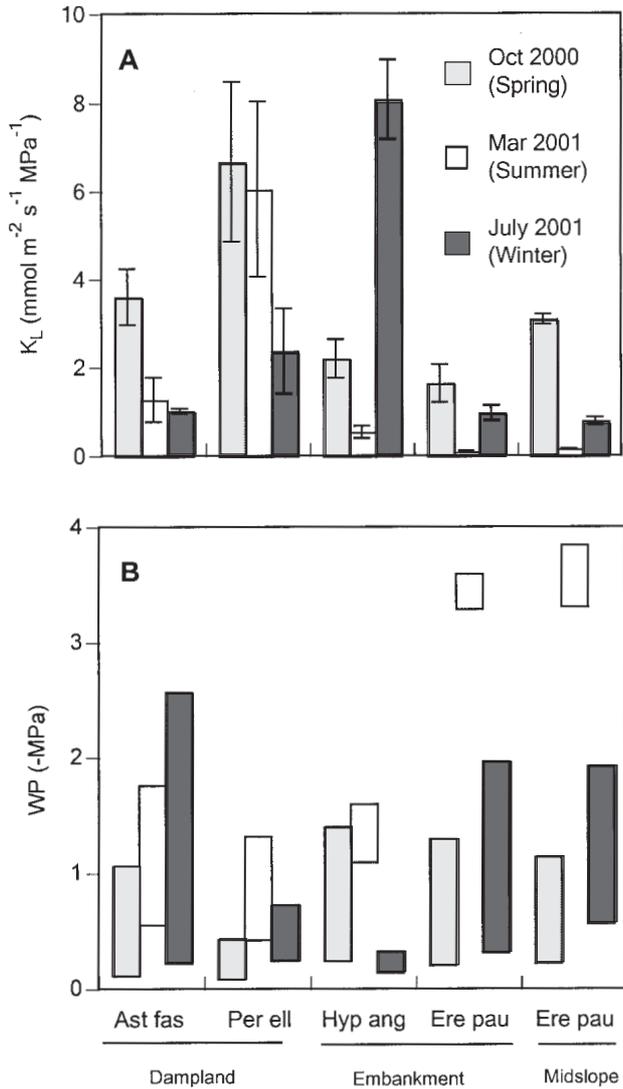
Seasonal water relations

There was no significant difference in morning stomatal conductance or transpiration data between species in either spring or winter (Fig 3A, B). Both dampland species (*A. fascicularis* and *P. ellipticum*) had significantly higher ($P < 0.001$) transpiration and stomatal conductance values (transpiration: 1.5–5.3 mmol m^{-2} s^{-1}; conductance: 0.09–0.23 mol m^{-2} s^{-1}) than the other species in summer. *E. pauciflora* at both the embankment and midslope sites had the lowest values of transpiration and stomatal conductance (transpiration: ~0.1 mmol m^{-2} s^{-1}; conductance: < 0.01 mol m^{-2} s^{-1}). *A. fascicularis* transpired at the same rate (~ 2 mmol m^{-2} s^{-1}) and had the same seasonal stomatal conductance (~ 0.1 mol m^{-2} s^{-1}) throughout the study (Fig 3A, B). For *H. angustifolium* and *E. pauciflora* occurring on the embankment and midslope (*E. pauciflora* only) sites, there was a significant decrease in transpiration and stomatal conductance between spring and summer. In *H. angustifolium* there was no significant difference between summer and winter transpiration and stomatal conductance data. Winter stomatal conductance values were similar to those recorded pre-drought in spring for both the embankment and midslope *E. pauciflora*, in contrast to transpiration values (Fig 3B).

Comparison of WP$_{pd}$ data between species for a given season showed that there was no significant differences between the two dampland species or between the embankment and midslope stands of *E. pauciflora*. Spring data varied from –0.09 (*P. ellipticum*) to –0.26 (*H. angustifolium*) MPa (Fig 3C); winter data varied from –0.15 (*H. angustifolium*) to –0.57 MPa (*E. pauciflora*; midslope). *E. pauciflora* had significantly lower (P=0.0001) summer WP$_{pd}$ (of around –3.3 MPa) in relation to the

other species, with *H. angustifolium* the next lowest WP$_{pd}$ (-1.1 MPa). The two dampland species had summer WP$_{pd}$ > -1 MPa (Fig 3C). Summer WP$_{pd}$ was always significantly more negative than spring and winter data (Fig 3C). There was no significant difference between
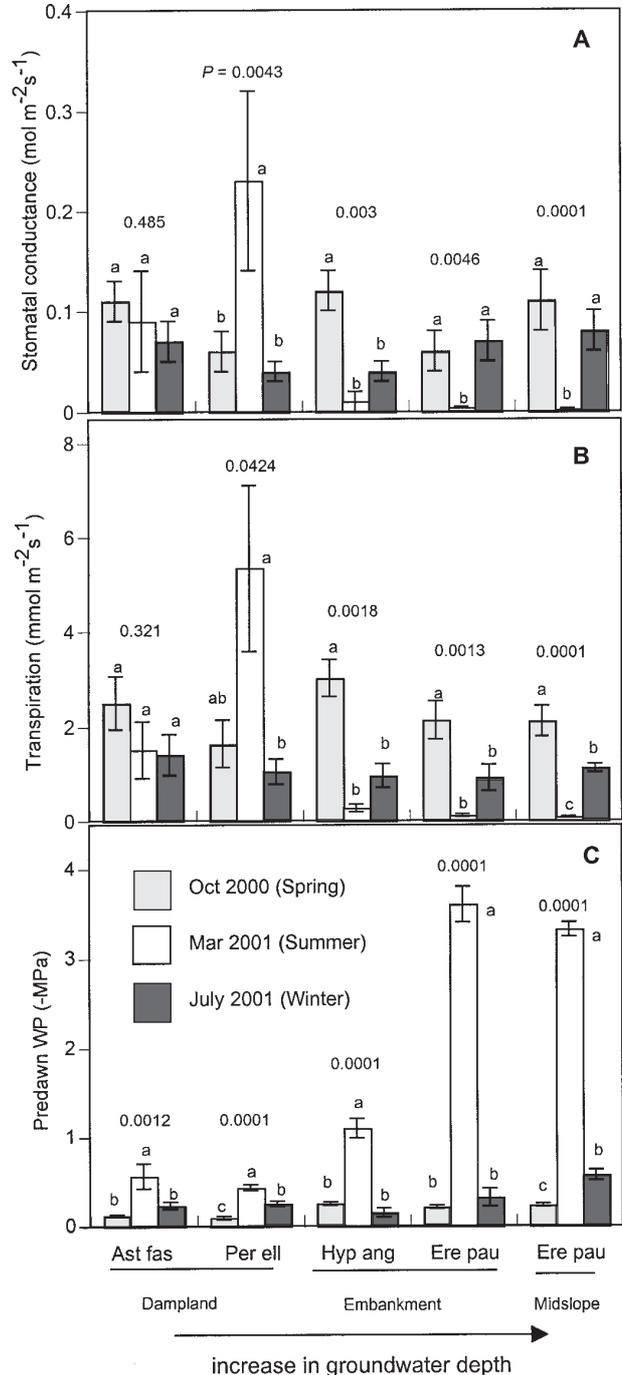
Figure 3. Seasonal water relations patterns. **A:** morning stomatal conductance, **B:** morning transpiration and **C:** predawn xylem water potential, for four myrtaceous shrub species occurring at three positions differing in groundwater depth. Morning data combines mid-morning and midday data (n = 6); predawn data were obtained from 3 individuals per species; values are mean ± se. Probability values are presented from a one-way ANOVA comparing seasonal differences within a species. Similar letters indicate no significant difference between means (Tukey's HSD test, *P*<0.05).

Figure 4. Seasonal water relations patterns for four myrtaceous shrub species occurring at three positions differing in groundwater depth. Values are mean ± se. **A:** soil-to-leaf hydraulic conductance (K_L). K_L values and se were calculated from the mean and se of transpiration, WP_{pd} and WP_{md} data; **B:** range of xylem water potential (WP). Lower end of bar is mean WP_{pd}, and the upper end is mean WP_{md}.

Soil moisture

Gravimetric soil moisture contents decreased from spring to summer and increased from summer to winter at all sites, with winter data greater than for the previous spring at the embankment and midslope sites (Fig 5). Soil moisture content within the dampland site varied from 8–20% during summer to 20–80% in winter. The soil moisture profiles at the midslope site were the driest of
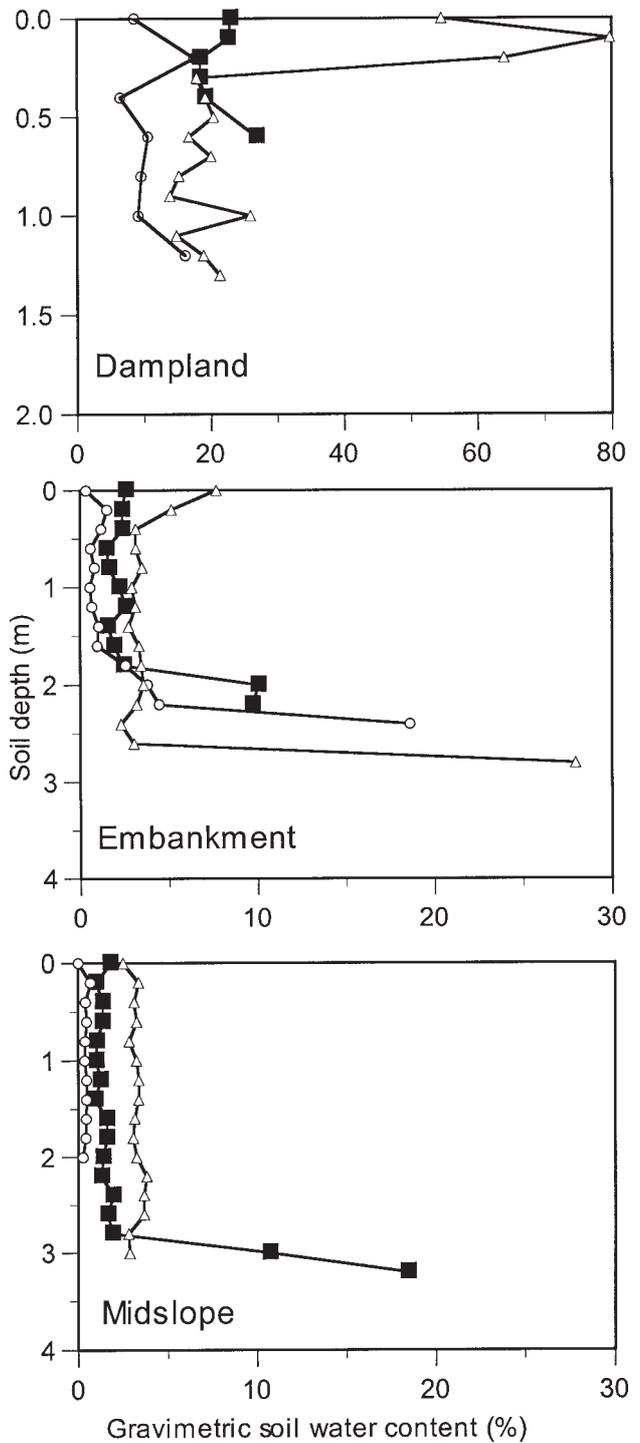
Figure 5. Gravimetric soil moisture profiles at the three topographical locations for spring 2000 (squares), summer 2001 (circles) and winter 2001 (triangles).

winter and spring WP_{pd} data for *A. fascicularis, H. angustifolium* and *E. pauciflora* (embankment).

For almost all species, soil-to-leaf hydraulic conductivity (K_L) decreased by 65–95% from spring to summer, except for *P. ellipticum* where K_L remained the same (Fig 4A). Summer K_L was highest for the two dampland species (1.3–6.0 mmol m^{-2} s^{-1} MPa^{-1}) and lowest for both stands of *E. pauciflora* (< 0.2 mmol m^{-2} s^{-1} MPa^{-1}), the latter due to low summer transpiration (Fig 3A) and a relatively small difference (< 0.5 MPa) between WP_{pd} and WP_{md} (Fig 4B). Overall, winter K_L was lower than spring K_L, with the exception of *H. angustifolium. H. angustifolium* had the highest winter K_L (8.1 mmol m^{-2} s^{-1} MPa^{-1}), reflecting a relatively large midday transpiration and a difference of only 0.03 MPa between WP_{pd} and WP_{md}.

all the sites with summer soil moisture content < 0.5% down to 2 m depth (Fig 5). Substantial increases in gravimetric soil moisture contents at depth for the embankment and midslope sites indicate the presence of the capillary fringe, a zone of saturated soil just above the water table.

Deuterium analysis

Groundwater δ^2H was generally less negative than δ^2H in the soil profile (see Fig 6 for exceptions) and became less negative as the seasons progressed, with summer and winter data displaying minimal variation between sites (Fig 7). Dampland spring groundwater δ^2H varied from -16.25 to –21.78 ‰ compared with –16.52 to –19.20 ‰ at the embankment/midslope sites.

For spring and winter data, species with lowest WP_{pd} had the lowest xylem δ^2H (*A. fascicularis* in spring and *H. angustifolium* in winter were the exceptions) (Fig 7). This

was not the case in summer, where xylem δ^2H became less negative as WP_{pd} decreased, with the three shallow rooted species (*A. fascicularis*, *P. ellipticum*, *H. angustifolium*; all < 1 m rooting depth; Dodd *et al.* 1984) having more negative δ^2H values than *E. pauciflora* (> 2 m rooting depth).

Comparing xylem water δ^2H with soil water and groundwater δ^2H data (Fig 6) it appears that *P. ellipticum* was utilising surface soil moisture (<0.2 m) in spring and soil moisture at relative depth (0.8–1.0 m) in winter. Spring xylem water δ^2H for *A. fascicularis* (-25.29 ± 0.90 ‰; mean ± SD) was less than that of groundwater (-16.25 to -21.78 ‰) and soil moisture (-4.50 to –21.82 ‰). Summer data suggest that both *A. fascicularis* and *P. ellipticum* were accessing soil moisture throughout the profile, although soil water δ^2H at 0.8 m was more negative than the xylem water. Summer xylem water δ^2H of *P. ellipticum* (-29.15 ± 4.62 ‰) was more negative than
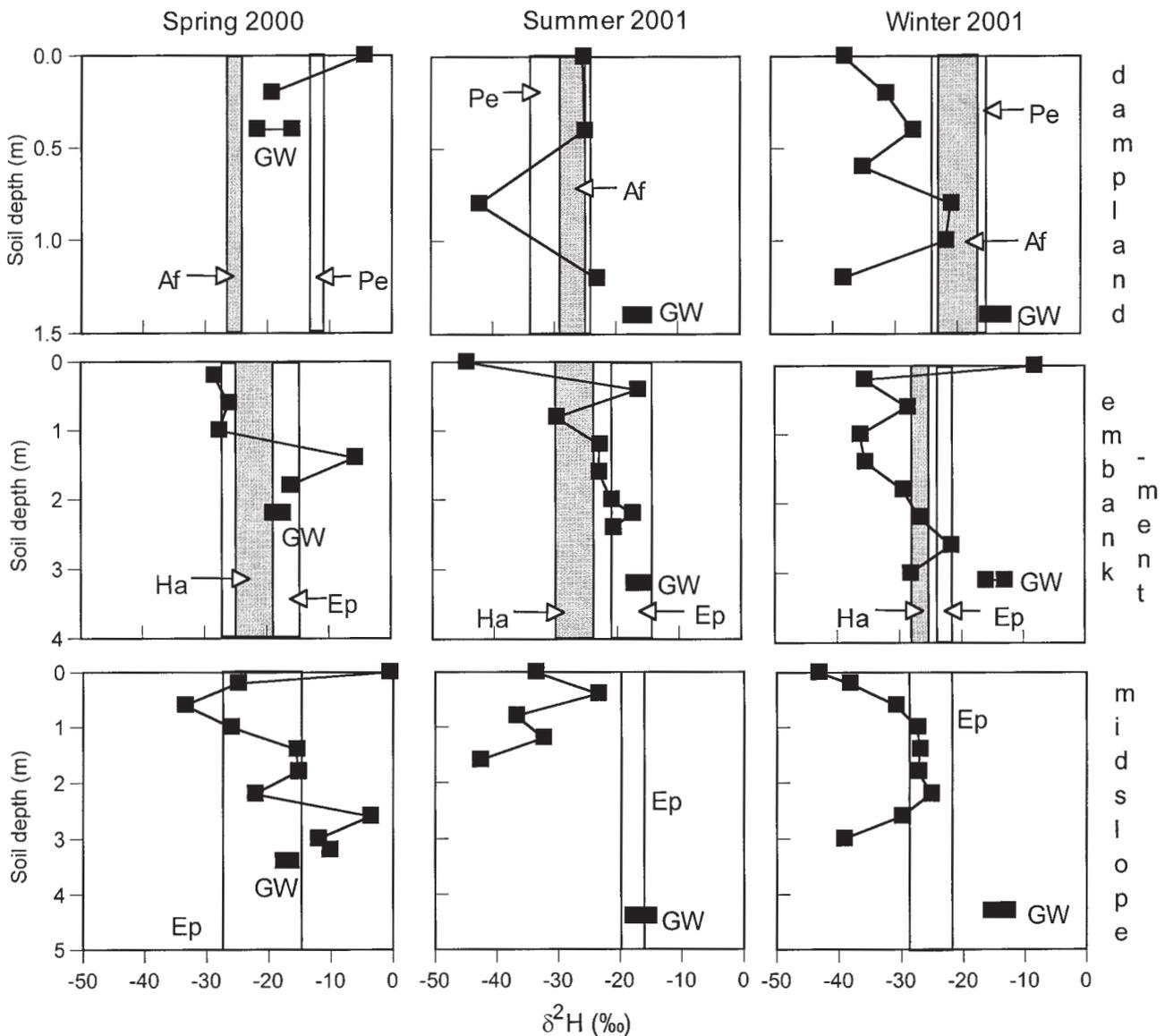
Figure 6. Seasonal profiles of soil δ^2H at the three topographical locations including groundwater (GW) values. Bars represent the range of xylem water δ^2H for the study species at each site. Shaded and unshaded bars are displayed to distinguish between different species at the same site. Summer and winter midslope profiles did not extend below 2 and 3 m respectively. Species abbreviations are provided in Fig 1. The values represent a single analysis from one sample per soil depth.
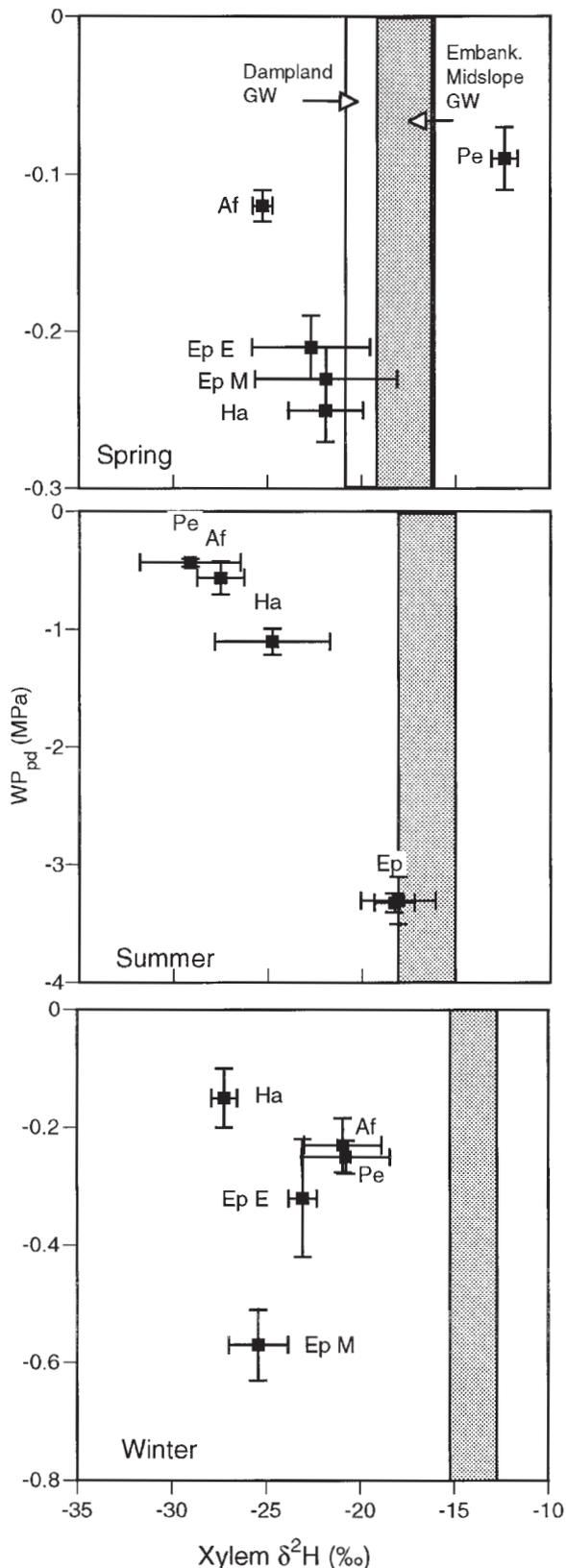
Figure 7. Predawn water potential (WP_{pd}) in relation to xylem water δ^2H on a seasonal basis. Shaded bars represent the range of groundwater δ^2H for the three sites, except for spring data where dampland and embankment/midslope sites are represented by different bars (unshaded and shaded respectively). Species abbreviations are provided in Fig 1. Values are mean ± se for 3 different individuals per species.

that of *A. fascicularis* (-27.54 ± 2.16 ‰). *A. fascicularis* was utilising the same soil moisture source (0.8–1.0 m) as *P. ellipticum* in winter.

At the embankment site, *H. angustifolium* was accessing soil moisture in the top 1 m of the soil profile in spring and summer (Fig 6) and probably in winter. Winter soil water δ^2H data coincided with xylem water δ^2H at 0.6, 2.2 and 3.0 m; however, *H. angustifolium* was unlikely to be accessing soil moisture at depths > 1 m, due to its shallow-rooted nature (Dodd *et al.* 1984). *E. pauciflora* was accessing moisture from both shallow (< 1 m) and deeper (< 2 m) soil depths in spring and summer at the embankment site, and possibly groundwater. Xylem water δ^2H data suggest that *E. pauciflora* was not accessing groundwater when winter data was collected.

It appears that at the midslope site *E. pauciflora* accessed groundwater during spring and summer, but not in winter. *E. pauciflora* was also accessing moisture from depths up to 2 m in the soil profile in summer and between 1–2 m in winter.

Discussion

Summer drought is one of the major environmental factors affecting species survival in south-western Australia (Hnatiuk & Hopkins 1980), with severe or prolonged drought periods considered an extension of the normal summer drought scenario (Hobbs & Mooney 1995). Past studies on plant water relations of Perth's sandplain species have shown that shallow rooted (< 1 m rooting depth) species tend to display more negative water potentials and have substantially lower transpiration rates than co-occurring deeper rooted shrub species during mid-late summer (Grieve 1956; Dodd *et al.* 1984; Dodd & Bell 1993). On the other hand, the present study shows that shallow-rooted species were the least water stressed, compared with the deeper rooted *E. pauciflora* species. The difference between these results is because none of the earlier studies included wetland sites, or sites where summer groundwater depth was < 3 m, whereas all the shallow-rooted species in this study occurred within or fringing a wetland.

The response of myrtaceous shrub species to the extended summer drought of 2000/2001 differed according to their location within the sandplain landscape, as shown by an overall decline in WP_{pd} with increased groundwater depth. A decline in water potential and stomatal conductance was expected during mid-late summer, as species respond to increasing soil moisture deficits. This was the case for *H. angustifolium* and *E. pauciflora* occupying the embankment and midslope sites, and resulted in substantial decreases in soil-leaf hydraulic conductivity, but not for the dampland species. For *H. angustifolium* and *E. pauciflora* the seasonal trends between stomatal conductance and WP_{pd} or hydraulic conductivity suggests a close association between the root/soil system and stomatal response, but does not explain *H. angustifolium*'s relatively large hydraulic conductance in winter. Differences in stomatal responses to soil and atmospheric water deficits between species may be explained by differences in soil-leaf hydraulic conductance and a species threshold water potential (Bond & Kavanagh 1999), the latter being a minimum water potential beyond which the chance of

xylem cavitation is greatly increased. Based on the data presented in this paper, it would be expected that the threshold water potential of *E. pauciflora* would be more negative than that of *H. angustifolium*.

The relatively low (approximately -3.3 MPa) WP_{pd} of *E. pauciflora* at the embankment and midslope sites suggests that this species did not have access to groundwater sources by late summer, and is in contrast to the interpretation obtained from comparing xylem δ^2H with that of groundwater and soil water δ^2H data. A lack of discrimination between groundwater δ^2H and soil water δ^2H, as occurred at both *E. pauciflora* sites in spring and the embankment site in summer, makes it difficult to ascertain the main sources of water used (see Burgess *et al.* 2000). In the present study, water potential data suggest that *E. pauciflora* had access to groundwater in October (spring), when groundwater levels were at their highest (2.40 and 3.34 m respectively for the embankment and midslope sites), but did not have access to groundwater in July (mid-winter) when groundwater levels were approximately 0.1 m higher than in March (late summer). It is therefore unlikely that *E. pauciflora* had direct access to groundwater in summer at either site, and this is supported by WP_{pd} data. This suggests that the minimum accessible groundwater depth for *E. pauciflora* at the embankment and midslope sites is between 2.4–3.0 m and 3.4–4.2 m respectively. Based on water potential data, Dodd & Bell (1993) showed that *E. pauciflora* was unable to access groundwater during summer at a depth of 7.2 m, but accessed groundwater during the spring months when the water depth was 6.3 m.

If *E. pauciflora* is not accessing groundwater during the summer period at the embankment site, then it stands to reason that *H. angustifolium* with its shallower root system is also not accessing groundwater. So why is it that *H. angustifolium* had a less negative WP_{pd}? *H. angustifolium* is restricted to and often fringes winter-wet depressions (Marchant *et al.* 1987), and is reliant on shallow soil moisture or groundwater sources when available. Differences in WP_{pd} may be a result of *E. pauciflora* being restricted to the top end of the embankment near where the piezometer was installed (Fig 1), whereas *H. angustifolium* was sampled from the lower edge of the embankment where groundwater levels would have been < 3 m in summer. The negative correlation of summer WP_{pd} with xylem water δ^2H between species (Fig 7) suggests that species reliant on shallow soil moisture sources (< 1 m soil depth) were less water stressed than those utilising deeper soil moisture reserves (*i.e. E. pauciflora*).

Of ten myrtaceous shrub species examined for their long-term (30 years) response to decreasing groundwater levels on Perth's Swan Coastal Plain, the species 'tolerant of excessive wetness' (see Havel 1968) displayed the greatest reduction in population size (Groom *et al.* 2000a). This included *A. fascicularis*, *P. ellipticum* and *H. angustifolium*. It was expected that as *A. fascicularis* and *P. ellipticum* are species restricted to winter-wet depressions (Marchant *et al.* 1987) such as damplands, they would be dependent on groundwater all year round, particularly during the dry summer period.

This study suggests that during a prolonged summer drought, neither *A. fascicularis* or *P. ellipticum* were accessing groundwater but were relying on soil moisture reserves. This also suggests that shallow soil moisture reserves (gravimetric content of 10–20%) were sufficient to sustain their summer water-use requirements, as both species were able to maintain summer stomatal conductances similar or greater than values obtained during the previous spring. The stable hydrogen isotope data show that *P. ellipticum* may have had access to groundwater in July 2001 (early winter) as a result of a small rise in winter groundwater levels, implying that the minimum accessible groundwater depth for *P. ellipticum* occurs between 1.39 to 1.45 m at this dampland.

Wetland water levels on Perth's coastal plain fluctuate seasonally, and some wetlands, including damplands, dry out by the end of summer. Damplands by definition are seasonally waterlogged basins (Semeniuk 1987); however, Perth's damplands do not always retain surface water, and was the case in 2000/2001 for the dampland studied in this paper. This may be due to below-average winter rainfall, reduced seasonal recharge and/or declining trends in regional groundwater level (Muir 1983; Townley *et al.* 1993). The trend for decreasing average rainfall currently being experienced by Perth may be part of a longer cycle (Davidson 1995). It has been predicted that by 2030 Perth may experience up to 10% less winter rainfall, and 5% more, or less, summer rainfall; by 2070, winter rainfall may decrease by 20% with summer rainfall increasing/decreasing by 10% (Anon 1996). Consecutive years of summer drought/poor winter rainfall can trigger extensive mortality of sandplain vegetation (Hnatiuk & Hopkins 1980; Groom *et al.* 2000b). If reduced winter rainfall translates into a lowering of summer groundwater levels and soil moisture content, then shallow-rooted species occurring in low-lying areas (*e.g. A. fascicularis, P. ellipticum*) will be particularly susceptible.

References

Anon 1996 Climate Change Scenarios for the Australian Region. Climatic Impact Group, CSIRO Division of Atmospheric Research, Aspendale, Victoria.

Arnold JA & Sanders CS 1981 Wetlands of the Swan Coastal Plain. In: Groundwater Resources of the Swan Coastal Plain (ed BA Carbon). CSIRO, Perth, 126–137.

Beard JS 1984 Biogeography of the Kwongan. In: Kwongan: Plant Life of the Sandplain (eds JS Pate & JS Beard). University of Western Australia Press, Perth, 1–26.

Bond BJ & Kavanagh KL 1999 Stomatal behaviour of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. Tree Physiology 19:503–510.

Burgess SSO, Adams MA, Turner NC & Ward B 2000 Characterisation of hydrogen isotope profiles in an agroforestry system: implications for tracing water sources of trees. Agricultural Water Management 45:229–241.

Coleman MC, Shepherd TJ, Durham JJ, Rouse JD & Moore GR

1982 Reduction of water with zinc for hydrogen isotope analysis. Analytical Chemistry 54:993–995.

Cramer VA, Thorburn PJ & Fraser GW 1999 Transpiration and groundwater uptake from farm forest plots of *Casuarina glauca* and *Eucalyptus camaldulensis* in saline areas of southeastern Queensland, Australia. Agricultural Water Management 39:187–204.

Davidson WA 1995 Hydrogeology and Groundwater Resources of the Perth Region, Western Australia. Bulletin 142. Western Australian Geological Survey, Perth.

Dodd J & Bell DT 1993 Water relations of understorey shrubs in a *Banksia* woodland, Swan Coastal Plain, Western Australia. Australian Journal of Ecology 18:295–305.

Dodd J, Heddle EM, Pate JS & Dixon KW 1984 Rooting patterns of sandplain plants and their functional significance. In: Kwongan. Plant Life of the Sandplain (eds JS Pate & JS Beard). University of Western Australia Press, Nedlands, 146–177.

Ehleringer JR & Osmond CB 1989 Stable isotopes. In: Plant Physiological Ecology: Field Methods and Instrumentation (eds RW Pearcy, JR Ehleringer, HA Mooney & PR Rundell). Chapman & Hall, London, 281–300.

Farrington P, Watson GD, Bartle GA & Greenwood EAN 1990 Evaporation from dampland vegetation on a groundwater mound. Journal of Hydrology 115:65–75.

Grieve BJ 1956 Studies in the water relations of plants. 1. Transpiration of Western Australian (Swan Plain) sclerophylls. Journal of the Royal Society of Western Australia 40:15–30.

Groom PK, Froend RH, Mattiske EM & Koch B 2000a Myrtaceous shrub species respond to long-term decreasing groundwater levels on the Gnangara Groundwater Mound, northern Swan Coastal Plain. Journal of the Royal Society of Western Australia 83:75–82.

Groom PK, Froend RH & Mattiske EM 2000b Impact of groundwater abstraction on a Banksia woodland, Swan Coastal Plain, Western Australia. Ecological Management and Restoration 1:117–124.

Havel JJ 1968 The potential of the northern Swan Coastal Plain for *Pinus pinaster* Ait. plantations. Bulletin 76. Forest Department of Western Australia, Perth.

Heddle EM 1980 Effects of changes in soil moisture on the native vegetation of the northern Swan Coastal Plain, Western Australia. Bulletin 92. Forests Department of Western Australia, Perth.

Heddle EM, Loneragan OW & Havel JJ 1980 Vegetation complexes of the Darling System, Western Australia. In: Atlas of Natural Resources, Darling System, Western Australia. Department of Conservation and Environment, Perth, 37–72.

Hnatiuk RJ & Hopkins AJM 1980 Western Australian species-rich kwongan (sclerophyllous shrubland) affected by drought. Australian Journal of Botany 28:423–438.

Hubbard RM, Bond BJ & Ryan MG 1999 Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiology 19:165–172.

Hobbs RJ & Mooney HA 1995 Effects of episodic rain events on mediterranean-climate ecosystems. In: Time Scales of Biological Responses to Water Constraint (eds J Roy, J Aronson & F di Castri). SPB Academic Publishing, Amsterdam, 71–85.

Marchant NG, Wheeler JR, Rye BL, Bennett EM, Lander NS & Macfarlane TD 1987 Flora of the Perth Region. Western Australian Herbarium, Department of Agriculture, Perth.

McDermitt DK 1990 Sources of error in the estimation of stomatal conductance and transpiration from porometer data. HortScience 25:1538–1548.

Muir BG 1983 Drainage, swamp structure and vegetation succession at Melaleuca Park, northern Swan Coastal Plain. Western Australian Herbarium Research Notes 9:27–39.

Semeniuk CA 1987 Wetlands of the Darling system – a geomorphic approach to habitat classification. Journal of the Royal Society of Western Australia 69:95–112.

Semeniuk V & Semeniuk C 1993 Investigations of stratigraphy and groundwater in four selected areas of the northeast corridor, Perth metropolitan area. V & C Semeniuk Research Group, Perth.

Stromberg JC, Tiller R & Richter B 1996 Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. Ecological Applications 6:113–131.

Townley LR, Turner JV, Barr AD, Trefry MG, Wright KD, Gailitis V, Harris CJ & Johnston CD 1993 Interactions between lakes, wetlands and unconfined aquifers. Wetlands of the Swan Coastal Plain, Vol 3. Water Authority of Western Australia and the Environmental Protection Authority, Perth.

Turner JV, Farrington P & Gailitis V 2001 Extraction and analysis of plant water for deuterium isotope measurement and application to field experiments. In: Stable Isotope Techniques in the Study of Biological Processes and Functioning of Ecosystems (eds M Unkovich, J Pate, A McNeill & DJ Gibbs). Kluwer Academic Publishers, Dordrecht, 37–55.

Wierda A, Fresco, LFM, Grootjans AP & van Diggelen R. 1997 Numerical assessment of plant species as indicators of the groundwater regime. Journal of Vegetation Science 8:707–716.

Williams DG & Ehleringer JR 2000 Carbon isotope discrimination and water relations of oak hybrid populations in southwestern Utah. Western North American Naturalist 60:121–129.

Zencich SJ, Froend RH, Turner JV & Gailitis V 2002 Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow, sandy coastal aquifer. Oecologia 131:8–19.