

## Maximising the use of soil water by herbaceous species in the high rainfall zone of southern Australia: a review

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*Abstract.* The planting of deep-rooted pasture species, herbaceous shrubs, and trees has been widely recommended to reduce deep drainage and recharge to the groundwater in the high rainfall zone (HRZ). However, in more recent years, the value of perennial pastures to reduce recharge has been questioned in areas with >600 mm annual rainfall. Currently, pastures dominated by annual species with relatively low productivity occur across much of the HRZ where deep drainage is most likely contributing to recharge. This review outlines our current understanding of water use by various herbaceous species, and indicates ways in which their water use may be increased in the HRZ of southern Australia.

To reduce deep drainage in the HRZ, the soil water deficit must be increased prior to the opening autumn rains. This will allow a greater storage of water before any potential deep drainage occurs. There are two ways that this can be achieved with the use of herbaceous species. Firstly, change to or encourage species that use more water annually. Although plants with deeper root systems including lucerne have the ability to dry the soil to depth, a combination of winter- and summer-active species, rotational grazing, and pasture spelling would extend the active growing season and soil water use of annual and perennial species. A second option is to increase the productivity of the pasture, as there is a direct link between growth and water use. For example, improving pasture productivity by 50%, say from 8 to 12 t dry matter/ha, could use (transpire) approximately 160 mm more water annually by a C<sub>3</sub> species, irrespective of evaporation from the soil surface or evaporative demand factors. This is supported by strong correlations between plant dry mass and water use among a wide range of C<sub>3</sub> and C<sub>4</sub> plants of diverse growth form and habitat. This relationship appears to have been overlooked in recent studies of various components of the soil water balance model, possibly due to limited and unreliable estimates of evapotranspiration (ET). An improved relationship between 'estimated' ET and measured dry matter production should improve the capability of the soil water balance model to predict deep drainage, which is primarily dependent on the ET. Ways to increase pasture productivity and soil water use include regular applications of fertiliser and lime, and better management of waterlogged and acidic soils in the HRZ. Summer-active native species may also be useful on soils where the persistence of other deep-rooted perennials is poor; however, little is known about their productivity and persistence when heavily grazed.

We believe that the relationship between water use and pasture production needs to be reassessed to improve the predictability of the soil water balance approach and recommend further research in both the field and under controlled conditions to determine the potential for increased water use in the HRZ of southern Australia by combinations of plant species and greater pasture productivity.

*Additional keywords:* deep drainage, WUE, ET, grazing management, plant nutrition.

### Introduction

There has been an increase in deep drainage and recharge to groundwater as a consequence of tree clearing and the replacement of native grasses and shrubs by introduced pastures and crop species (Dunin 1970; Sedgley *et al.* 1981; McFarlane and George 1992; White *et al.* 2000). This is a major environmental concern, particularly in many parts of

the high rainfall zone (HRZ) of southern Australia, which receive 500–800 mm of rain per annum. Inefficient use of available soil water by shallow-rooted annual species has been highlighted as the primary cause for deep drainage, which in some cases can be up to 30% of annual rainfall (Ferdowsian and Greenham 1992; Simpson *et al.* 1998). Re-establishment of deep-rooted plants, such as perennial

pasture species and trees, has therefore been recommended (George 1992; Williamson *et al.* 1997; Bolger and Turner 1999; Lefroy and Stirzaker 1999; White *et al.* 2000).

Increased water use by perennials, together with greater herbage production of these species, could help sustainability and productivity in the HRZ. However, changing herbaceous vegetation in the HRZ of southern Australia would have long-term effects on the hydrological cycle and livestock productivity and these effects are not clearly understood. A better understanding of soil water use and the productivity of alternative herbaceous species is needed before they are recommended for adoption in the landscape.

The primary components of the hydrological cycle in the HRZ can be well described through the soil water balance model below:

$$RF = I + R + E + T + L + \Delta S + D$$

where RF is rainfall, I is interception by the plant canopy and litter, R is surface runoff, E is evaporation from the soil surface, T is the transpiration, L is lateral movement from the root-zone,  $\Delta S$  is the change in soil water storage, and D is vertical drainage out of the root-zone. This review focusses on the herbaceous species and on key agro-climatic, biological, and management factors in the existing landscape (topography, soil type, and climate) of the HRZ (500–800 mm/year) in southern Australia.

### Factors influencing soil water use in the HRZ

#### *Agro-climatic factors*

##### *Evapotranspiration*

Evapotranspiration (ET) is the sum of evaporation (E) of water from the soil surface and transpiration (T) by the plant. ET is primarily influenced by ground cover, seasonal plant growth, and seasonal evaporative demand. Evaporative demand is a combined function of microclimatic parameters such as atmospheric temperature, leaf temperature, solar radiation, light intensity, and relative humidity. Measurement of actual ET under field conditions is highly complex; therefore, ET (actual) is mostly estimated as the potential ET or derived from the ET reference value using the modified Penman equation (Doorenbos and Pruitt 1984; Ridley *et al.* 1997; White *et al.* 2000). Large variations can occur in the estimates of ET from different methods such as the Bowen ratio method through continuous measurement of micrometeorological parameters, long-term weather data, and changes in soil water content. For a more accurate estimation of ET, inclusion of locally modified crop coefficients has been suggested (Meyer 1999).

Ward *et al.* (2001) and Angus and Watts (1984) reported the unreliability of the Bowen ratio method for predicting ET under conditions of low vapour flux and high available energy, particularly during the late spring and summer. Any

determination of ET, either by direct measurement or estimation from weather data, carries a minimum uncertainty of at least 10% (Angus and Watt 1984). Stewart (1984) and Gregory *et al.* (1992) noted that accurate measurement of ET under field conditions is very difficult and is seldom measured directly to an accuracy of >20% with flux-gradient, ventilated chambers, or porometry. This was in agreement with other studies, and the large uncertainty associated with ET estimation, up to 20% of rainfall, can contribute significant errors to estimates of drainage (Ward *et al.* 1998). If the determination of ET is in error by as little as 5%, deep drainage could be over or underestimated by as much as 32 mm per year (Murphy and Lodge 2001).

Ward *et al.* (2002) found no differences in ET measured by the Bowen ratio energy balance between wheat grown after lucerne (*Medicago sativa*) and after subterranean clover (*Trifolium subterraneum*), despite differences in soil water content detected by both neutron moisture meter (NMM) and time domain reflectometry (TDR). Under dry conditions, ET was estimated from changes in soil water storage using TDR and NMM (Ward *et al.* 2002). Dunin *et al.* (2001) reported that TDR records contain flawed information and adjustment was necessary to allow for an unexplained oscillation in TDR values for soil water content. They explained that systematic drifts in TDR values, both diurnally and seasonally, are likely to be due to thermal gradients occurring during drier periods. The estimation of ET through the energy balance technique is also likely to have some degree of error diurnally, due to low vapour flux, high available energy, and leaf stress in the crop canopy when transpiration demand exceeds water uptake by plant roots, particularly around midday.

##### *Rainfall*

There could be considerable differences in the rainfall actually reaching the ground in plant communities because of interception of rainfall by the canopies (Eidmann 1959; Penman 1963; Slatyer 1967). Intercepted water could be transferred to the soil through stem flow, dripping from the branches, or be lost by evaporation. Annual intercepted loss of rainfall from evergreen spruce and deciduous beech forest was 26% and 8%, respectively (Eidmann 1959). However, measurement of intercepted loss and lateral flow is complex, but together can account for up to 10–40% of the annual rainfall in the HRZ (Smith 1974; White *et al.* 2000; Lodge *et al.* 2001). The amount of intercepted rainfall returned directly to the atmosphere could be up to 5 times greater than that of potential evaporation during and following rainfall (Sharma 1984; Nulsen 1993) and can account for 10–20% of the annual rainfall (Smith 1974; Dunin and Mackay 1982; Greenwood *et al.* 1985). Ground cover, canopy structure, height, and litter can influence the intercepted loss, albedo values, and estimation of ET for pastures. For example, the intercepted evaporation from crop canopies was 166 and

**Table 1. Distribution of annual rainfall (RF, mm) and evapotranspiration (ET, mm) in May–August in four regions of southern Australia (from Passioura and Ridley 1998)**

Location	Annual rainfall	RF	ET	RF–ET
Albany, WA	808	436	148	288
Corryong, Vic.	825	325	111	214
Hamilton, Vic.	695	298	113	185
Tamworth, NSW	674	185	184	0

60 mm for high ground cover–herbage mass and low ground cover–herbage mass, respectively (Lodge *et al.* 2001). However, the amount of rainfall during summer and evaporative demand during winter are the key agro-climatic factors governing seasonal water use and biomass production by various plant species in the HRZ.

Rainfall received during autumn–winter in the HRZ of southern Australia is usually in excess of potential ET (Table 1), which is the primary cause of deep drainage and recharge. After estimating a soil water storage capacity of 135 mm at the beginning of winter, drainage at Hamilton was estimated to be 50 mm/year (Passioura and Ridley 1998).

Simpson *et al.* (1998) provided a different estimate of likely deep drainage at Hamilton. They predicted ET and other components of the soil water balance from modelling 20 years of data for various grazing and pasture management options (Table 2). On average, there was 484 mm of ET and 150 mm of deep drainage annually. In this study there was an estimated 130 mm of ‘excess’ rainfall at Hamilton, which the vegetation could not use even if actual transpiration were to approach potential ET. For drainage to be prevented in ‘average’ years at Hamilton, it was estimated that at least 1.8 m of soil would need to be dried to wilting point before the onset of autumn rain.

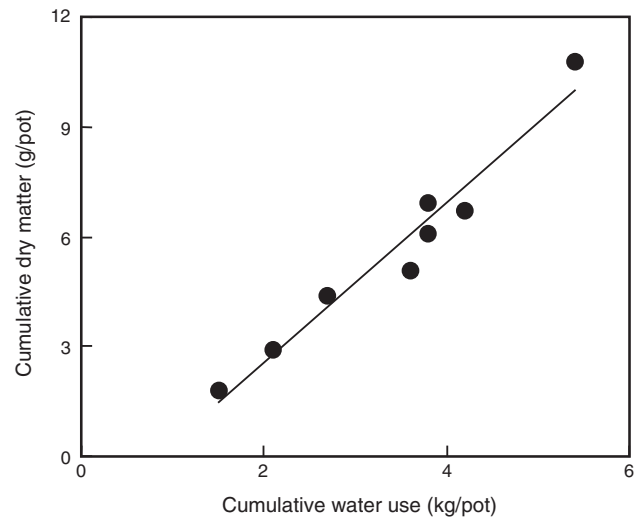
### Biological factors

#### Relationship between biomass and water use

It is now widely accepted that regardless of any strategy, dry matter production is primarily a function of water use

**Table 2. Simulated effects of various management options on average annual water balance (mm) at Hamilton 1970–90 (rainfall 639 mm) (from Simpson *et al.* 1998)**

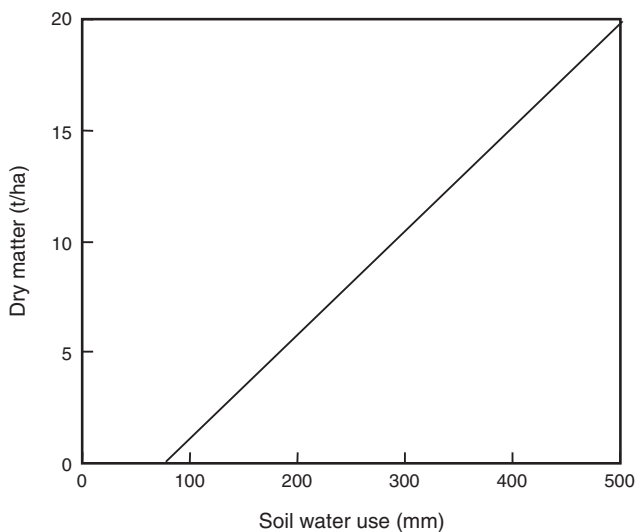
Management option	ET	D	R
Annual pasture (annual grass–subterranean clover), low fertility	425	209	7
Annual pasture (annual grass–subterranean clover), high fertility	454	181	6
Perennial pasture (phalaris–subterranean clover), continuous grazing	529	108	5
Perennial pasture (phalaris–subterranean clover), rotational grazing	529	108	5
Perennial pasture (phalaris–subterranean clover), complex rotational grazing with pasture rested in April (1–30 Apr.)	525	112	5



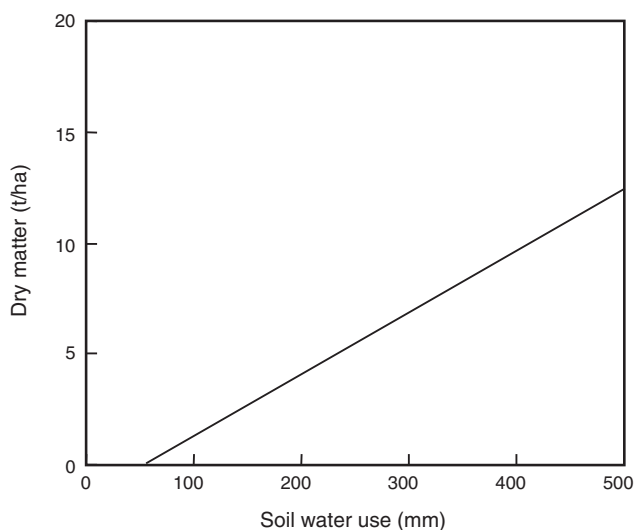
**Fig. 1.** Relationship between cumulative dry matter and plant water use of white clover grown under glasshouse conditions (from Singh and Sale 2000; Singh *et al.* 2000).

(de Wit 1958; Bierhuizen and Slatyer 1965; Tanner and Sinclair 1983). Leaf water (stomatal) conductance is correlated with photosynthetic capacity of leaves and carbon dioxide exchange for various plant species. von Caemmerer *et al.* (2001) showed this relationship for the C<sub>3</sub> pasture species, subterranean clover and perennial ryegrass (*Lolium perenne*), grown under different environmental conditions. Ghannoum *et al.* (2001) highlighted the strong correlations between plant biomass and water use, and between photosynthetic capacity and stomatal conductance for C<sub>4</sub> grasses of diverse growth, form, and habitat. Data reported by Singh and Sale (2000) and Singh *et al.* (2000) show a similar strong correlation between biomass production and soil water use for the C<sub>3</sub> species white clover (*Trifolium repens*) across a range of fertility, defoliation, and soil water contents (Fig. 1). French (1992) and Bolger *et al.* (1993) also reported a positive linear relationship between water used in the growing season and pasture dry matter production at a paddock level in South Australia and Western Australia, respectively (Figs 2, 3). Singh and Misra (1985) reported that one C<sub>3</sub> and two C<sub>4</sub> grasses exhibited similar positive relationships across 9 treatments. Water uptake was related to plant production, despite differences in photosynthetic type, growing season, and growth stages of the grasses.

Crop water production functions further describe the relationship of crop yield response to varying levels of water input (after Liu *et al.* 2002). Vaux and Pruitt (1983) found the yield of various agricultural crops as a linear function of cumulative ET. However, a non-linear response may also result due to the availability of excessive water, resulting in an increased E without a corresponding increase in the yield (Vaux and Pruitt 1983; Liu *et al.* 2002). In contrast, Dunin (2002) suggested that there was no relationship between net



**Fig. 2.** Relationship between pasture dry matter and soil water use in the field in South Australia (from French 1992).



**Fig. 3.** Relationship between pasture dry matter and soil water use in the field in Western Australia (from Bolger *et al.* 1993).

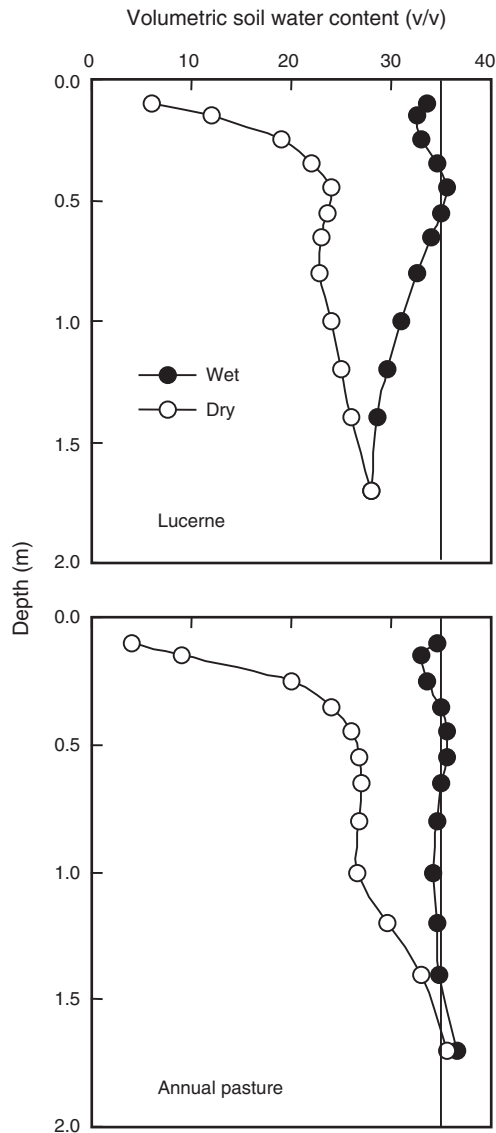
primary productivity and annual water use. This conclusion was based on derived inverse relationships between maximum leaf area and water use, from comparative measurements of annual ET for tree strips, crops, subterranean clover, and lucerne, while assuming that ET follows that of Ritchie (1981) with an approximated upper boundary (ET, Priestley Taylor) without any requirement for specifying leaf canopy conditions.

Dunin (2002) argued that differences in seasonal plant water uptake and growth patterns between natural ecosystems and introduced species of crops and pastures indicated a poor relationship between primary productivity and annual water use. He suggested that the natural

ecosystems conserve water during periods of high soil water availability with low evaporative demand and high water use efficiency (WUE), so that they can use this stored water in the dry periods, when water use is critical for survival of perennial species. There will be a loss in primary productivity due to the reduced WUE in the dry summer compared with winter, but the natural ecosystem with a lower LAI (leaf area per unit land area) should be able to use more stored water during summer, thus reducing deep drainage (Dunin 2002). On the other hand, although annual crops and pastures have greater productivity and LAIs than natural ecosystems, they would not be able to control deep drainage due to a lack of summer function and deep roots to utilize the excess rainfall stored below the roots-zone (Dunin 2002).

It can be suggested that productive crops and pastures with greater LAIs are more likely to use more water during the growing season in both winter- and summer-dominant rainfall regions. Consequently, less water would be stored in the soil profile compared with natural ecosystems in winter-dominant rainfall regions as suggested by Dunin (2002). Our view is strongly supported by the large amount of evidence that suggests a close relationship between productivity and water use (see previous sections). Importantly, uptake of water by any  $C_3$  or  $C_4$  plant species (whether native or exotic) is primarily governed by stomatal conductance, which is largely dependent on the photosynthetic capacity of the leaves and rates of  $CO_2$  exchange (von Caemmerer *et al.* 2001; Ghannoum *et al.* 2001) in any given condition of water availability or evaporative demand. This means that a productive species in a given environment with whatever evaporative demand would use more water than the non-productive species, whether annuals or perennials. A combination of highly productive winter- and summer-active crops and pasture species can be grown with better management practices to maximise water use, thus reducing deep drainage.

There is much evidence of drier soil profiles under natural ecosystems and well established deep-rooted perennials such as lucerne (Dunin *et al.* 2001; Ridley *et al.* 2001; Ward *et al.* 2001, 2002). The drier profiles under such species can be attributed to both intercepted losses of water by dense canopies and litter layers, and the drying of soil profiles by deep roots. It can be argued that intercepted losses of water are more likely to prevent greater amounts of water from entering the soil than those taken up by perennial species when there are no comparative increases in productivity. This process might further explain why soils under perennials such as lucerne have been found to be mostly dry or appear to have been rapidly dried, particularly under wet conditions, compared with continuously grazed annual pastures. This 'classic' pattern of soil drying under wet conditions can be seen in most studies, as illustrated in Fig. 4. Lightly grazed lucerne pastures with tall and dense



**Fig. 4.** Changes in soil water content with depth under lucerne and annual pasture at Tatura. Closed and open symbols refer to measurements made in winter and autumn, respectively. The vertical line indicates field capacity of the soil (from Whitfield 1996).

canopies might also intercept more water during any rainfall event. Furthermore, the perception of substantial extraction of water from below 1 m depth by a 'negligible' amount of deep roots may prove to be confounded, if the relationship between intercepted loss and reduced wetting of soil under these conditions could be quantified. Unfortunately, intercepted loss has been ignored in most soil water balance studies due to the complexities involved with its measurement (Ridley *et al.* 1997; Dunin *et al.* 2001; Ward *et al.* 2001, 2002; Dunin 2002).

The wide variations in how well the reported data describe the relationship between water use and biomass production could be largely due to variation in the estimates

of ET obtained from different indirect methods such as the Bowen ratio, soil water change, long-term weather data, and simulations, compared with more reliable direct measurements from weighing lysimeters. Although Dunin *et al.* (2001) used weighing lysimeters and showed a close agreement between ET values obtained from lysimeters and the Bowen ratio energy balance technique through a 1:1 regression relationship, a variation of around 12% occurred within a season for a wheat crop in 1993. The regression line drawn for lucerne was based on 4 seasons of data and was in good agreement, but large variations were apparent if the relationship was drawn for each individual season, except for 1995, which involved unreplicated lysimeter values. The authors acknowledged that there were significant interruptions to the lysimeter measurements during the study period and interpolation of data from micrometeorological measurements was necessary to recover the values (Dunin *et al.* 2001).

Furthermore, WUEs (un-normalised) of wheat and lucerne were 3.0 and 2.0 g dry matter (DM)/kg water, respectively, where the water use value (ET) included a high (>50%) soil evaporation (Dunin *et al.* 2001). After accounting for the seasonal soil evaporation, further calculations indicated WUEs of 6.0 g and 4.0 g DM/kg of 'transpired' water, for wheat and lucerne, respectively. These values are very high compared with the range of WUEs reported for C<sub>3</sub> plants, particularly for lucerne (Briggs and Shantz 1914; Asseng and Hsiao 2000) (see section on WUE below). An overestimated value of WUE or transpiration efficiency is more likely to result in poor correlations between water use and dry matter production and may also overestimate the deep drainage component in the soil water balance model.

#### *WUE and implications for soil water use*

The tight relationship between water use and dry matter reflects the very narrow range of WUEs. For the purpose of this review, we have defined the WUE of a plant as the amount of dry matter accumulated per unit of water 'transpired'. It has been widely used as a measure of how efficiently crops and (to a lesser extent) pastures acquire and transpire available water (Reuter *et al.* 1996). A greater evaporative demand or vapour pressure deficit (VPD) would decrease the boundary layer and stomatal resistances to gas exchange and increase transpiration with a reduction in WUE. VPD is primarily a difference between saturated and ambient concentrations of atmospheric water vapour. Bierhuizen and Slatyer (1965), Tanner and Sinclair (1983), and Leuning *et al.* (1994) reported that plant growth was directly proportional to transpirational water use, but inversely dependent on atmospheric VPD. Relative annual water requirements and plant yields for numerous C<sub>3</sub> and C<sub>4</sub> plants were determined earlier last century with large lysimeters, and averaged over a number of years and varieties

**Table 3. Water use efficiency (WUE, g/kg of transpired water) of C<sub>3</sub> and C<sub>4</sub> plants, determined by lysimeters in field studies conducted by Briggs and Shantz (1914) at Akron, Colorado, USA, and summarised from Stanhill (1986)**

Plant species C <sub>3</sub>	WUE	Plant species C <sub>4</sub>	WUE
Lucerne ( <i>Medicago sativa</i> )	1.2	Maize ( <i>Zea mays</i> )	2.9
Red clover ( <i>Trifolium pratense</i> )	1.3	Sudan grass ( <i>Sorghum sudanense</i> )	2.6
Sweet clover ( <i>Melilotus officinalis</i> )	1.4	Sorghum ( <i>Sorghum bicolor</i> )	3.3
Turnip ( <i>Brassica napus</i> )	1.6	Teosinte ( <i>Zea mexicana</i> )	2.7
Desert wheat grass ( <i>Agropyron desertorum</i> )	1.5	Pigweed ( <i>Amaranthus alba</i> )	3.8
Smooth brome grass ( <i>Bromus inermis</i> )	1.0	Russian thistle ( <i>Salsola kali</i> )	3.2
Barley ( <i>Hordeum vulgare</i> )	1.9		
Wheat ( <i>Triticum aestivum</i> )	1.8		
Rye ( <i>Secale cereale</i> )	1.6		
Oats ( <i>Avena sativa</i> )	1.7		
Rice ( <i>Oryza sativa</i> )	1.5		
Navy bean ( <i>Phaseolus</i> )	1.5		
Horse bean ( <i>Vicia faba</i> )	1.3		
Soybean ( <i>Glycine max</i> )	1.4		
Chickpea ( <i>Cicer arietinum</i> )	1.6		
Winter vetch ( <i>Vicia vilosa</i> )	1.8		
Lambs quarters ( <i>Chenopodium album</i> )	1.5		
Cocklebur ( <i>Xanthium spinosum</i> )	2.4		
Curlycup gumweed ( <i>Grindelia squarrosa</i> )	1.7		
Sunflower ( <i>Helianthus annuus</i> )	1.8		

(Briggs and Shantz 1914; de Wit 1958). WUE of selected species has been summarised in Table 3.

To compare WUE under different climatic conditions, normalisation of WUE for the evaporative demand of the atmosphere has been the preferred approach (de Wit 1958; Tanner and Sinclair 1983; Asseng and Hsiao 2000). However, the preference in evaporative demand factor, which can be expressed as pan evaporation, cumulative ET relative to the mean daily pan evaporation (de Wit 1958; Asseng and Hsiao 2000), or air vapour saturation deficit (Tanner and Sinclair 1983), can be contentious. Most studies use the mean value of the evaporative data collected during the entire crop growth period, whereas evaporative demand varies diurnally with the crop growth stage and season. Unless normalisation is done on a daily basis, evaluation and comparison of WUEs normalised with only mean values of evaporative demand are likely to be confounded (Asseng and Hsiao 2000). We have focussed on un-normalised WUEs in this review for simplicity and to avoid any confounding effect due to variation in the measurement of evaporative demand. However, it is the differences in the abilities of the plant species, such as those between C<sub>3</sub> and C<sub>4</sub> plants, to use soil water and produce dry matter that can be exploited by better management practices and improved soil fertility for particular climatic conditions. Both cultivar selection and nutrient management have an effect on water use by altering photosynthetic rates, yields, rooting characteristics, transpiration, and soil evaporation (Davis and Quick 1998).

The following un-normalised WUEs have been reported for lucerne: 2.3 g DM/kg water (Grimes *et al.* 1992), 1.8 g

DM/kg water (Smeal *et al.* 1992), 1.7 g DM/kg water (Wright 1988), and 2.1 g DM/kg water (Asseng and Hsiao 2000). These values equate to requirements of 43.5–58.8 mm of water for each tonne of lucerne dry matter. Shih and Snyder (1984) noted that average daily ET varied from 2.0 to 7.3 mm/day, and 86–94 mm of water was required to produce each tonne of dry biomass of pasture, corresponding to a WUE of 1.1 g DM/ kg water. It has been shown that an increase of 3.9 g cumulative dry matter yield of a C<sub>3</sub> plant (white clover) resulted in 1.6 kg more water being transpired when the soil supply of phosphorus increased from 50 to 150 mg/kg soil (Table 4). This indicates a WUE of 2.4 g DM/kg of transpired water. On average, WUE varied between 1.2 and 2.0 g DM/kg of transpired water (Table 4).

The measured range of WUEs from these studies indicates that the C<sub>3</sub> herbaceous plant with the high WUE of 2.4 g DM/kg of transpired water will require 417 t or 41.7 mm of water (10 t water = 1 mm water) to produce each tonne of dry matter. Therefore, a 50% improvement in the net pasture production, say from 8 t to 12 t, through improved agronomic practices and/or use of higher yielding varieties would use approximately 160 mm more water, irrespective of the water lost through soil evaporation or evaporative demand. Studies by Ridley *et al.* (1997) and Clifton and Taylor (1995) reported that increased yields through better agronomic management practices resulted in higher soil water use. Clifton and Taylor (1995) reported that swards of both phalaris (*Phalaris aquatica*) and cocksfoot (*Dactylis glomerata*) that were allowed to grow to higher herbage mass were able to transpire more water than swards that were kept

**Table 4. Main effect treatment means for P supply (mg/kg soil), defoliation frequency (days), and soil water regime for cumulative yield (g), cumulative water use (g), and WUE per pot (g/kg water) over 56 days (from Singh and Sale 2000; Singh *et al.* 2000)**

Treatments/rates	Cumulative yield	Cumulative water use	WUE
<i>P supply</i>			
0	1.8	1500	1.2
17	2.9	2071	1.4
50	6.9	3833	1.8
150	10.8	5400	2.0
<i>Defoliation frequency</i>			
2	6.7	4187	1.6
4	4.4	2750	1.6
<i>Soil water regime</i>			
Wet (100–50% FC)	6.1	3812	1.6
Dry (40–0% FC)	5.1	3643	1.4

**Table 5. Summary of total dry matter production (t/ha), evapotranspiration (mm/year), and WUE (g/kg water) from 1992 to 1994 for annual and perennial pastures with medium cutting height at Axe Creek (from Clifton and Taylor 1995)**

Pasture type	Dry matter	Evapotranspiration	WUE
Phalaris	7.77	525	1.5
Cocksfoot	6.48	435	1.5
Annual	6.61	395	1.7

short. Phalaris transpired 130 mm more water (33% increase) and produced 17% more dry matter than annual pasture under a medium cutting height (Table 5). Similarly, in the study of Ridley *et al.* (1997), the yield of phalaris + N treatment increased from around 8 t to more than 16 t/ha between 1992 and 1993, despite similar pan evaporation in both years and higher April–October rainfall in 1992 (580 mm) than in 1993 (368 mm). The increased yield was more likely due to increased soil fertility, as these pastures received 400 kg N in 1992 and 500 kg N in 1993. Importantly, estimated ET in 1993 was 131 mm higher than in 1992, indicating the influence of increased yield, rather than evaporative demand.

### Maximising soil water use in the HRZ

The key agronomic and biological factors influencing soil water use in the HRZ suggest that there are two major ways of increasing plant water use: firstly, to change or encourage perennial species that use more water on an annual basis; and secondly, to increase the productivity of the existing pastures.

#### Changing the plant species

##### *Annual v. perennials*

Perennial pastures such as lucerne and phalaris have high water use relative to annual species, largely because they

actively transpire for longer than the annuals (Nulsen 1993), and their roots are deeper. However, a survey of the botanical composition of 286 pastures across major grazing industries (dairy, sheep, and beef), rainfall zones (500–800 mm annual rainfall), and soil types (Ordovician, basalt, and mixed coastal soil) in south-western Victoria (Quigley *et al.* 1992) revealed a very small proportion of perennial species. Undesirable, volunteer annual grass species, especially *Vulpia* spp., dominated the pastures in this survey.

Deep drainage has been reported to be greater under annual than under perennial pastures in southern Australia (Ferdowsian and Greenham 1992; Whitfield *et al.* 1993; Ridley *et al.* 1997; White *et al.* 2000). Clifton and Johnston (1997) used a 1-dimensional model (WAVES) to estimate deep drainage for perennial and annual winter-active pastures, 228 and 314 mm/year, respectively. They suggested that there was minimal lateral flow for rainfall up to 900 mm/year. However, White *et al.* (2000) reported that combined lateral flow and deep drainage was 40 mm less for perennial pastures than for annual pastures and that, at times, lateral flow exceeded the deep drainage. They suggested that Clifton and Johnston (1997) overestimated deep drainage with the 1-dimensional model. Similarly, Ridley *et al.* (1997) estimated that deep drainage below 1.1 m depth was only 50–55 mm under a phalaris pasture, and 80–85 mm under annual ryegrass.

Lucerne, phalaris, and cocksfoot have been the most commonly studied perennial species in pasture improvement programs for HRZ (Clifton and Taylor 1995; Ridley *et al.* 1997; Lolicato 2000). Lucerne was the most vigorous and persistent species among 100 perennial legume cultivars, representing 45 diverse species in a 2-year study, in central Victoria (Lolicato 1993). The ability of lucerne to dry the soil to a greater depth, particularly during the spring–summer, has been highlighted by Humphries and Auricht (2001) and Ridley *et al.* (2001). Lolicato (2000) reported that the maximum amounts of extracted water were

230 mm by lucerne, 210 mm by phalaris, 200 mm by lotus, and 170 mm by cocksfoot, with the driest soils associated with greater herbage growth and greater depths of water extraction.

Ridley *et al.* (1997) suggested that phalaris had the highest ET, followed by cocksfoot and annual ryegrass pastures. The patterns of seasonal dry matter production and ET were similar for these 3 pasture types. Similarly, established lucerne pastures have been reported to have both increased biomass production and soil water use compared with an annual pastures, by 2 times and 51 mm, respectively (Lyons and Latta 2001).

### *C<sub>3</sub> and C<sub>4</sub> plants*

Potential dry matter yield and WUE are usually greater in C<sub>4</sub> than in C<sub>3</sub> plants because the biochemical pathways for carbon assimilation during photosynthesis are different. Tropical C<sub>4</sub> species such as sugar cane (*Saccharum officinarum*), sorghum (*Sorghum bicolor*), maize (*Zea mays*), and *Panicum* have greater carbon assimilation rates per unit leaf area than temperate C<sub>3</sub> species such as ryegrass, cocksfoot, and tall fescue (*Festuca arundinacea*). In C<sub>4</sub> species, the internal resistance to CO<sub>2</sub> diffusion is normally about half that in C<sub>3</sub> species, and their stomatal resistance is generally higher (Gifford 1974; Rawson *et al.* 1977).

Low yielding C<sub>3</sub> and C<sub>4</sub> plant species have low evapotranspirational water use, due to low leaf areas as influenced by root growth, and water and nutrient supply (Schenk and Barber 1979; Faraquhar and Richards 1984). Direct comparisons between C<sub>4</sub> (consol lovegrass) and C<sub>3</sub> plants (phalaris and lucerne) were made for dry matter production and total water use under varying water and nutrient levels (Johnston and Shoemark 1993). Total dry matter (shoot + root) for consol lovegrass (18.2 g per pot) was twice that of Sirosa phalaris (9.5 g) and Pioneer lucerne (9.8 g), and the total water use per pot was 4.1, 3.9, and 4.3 L respectively. Johnston *et al.* (1999) indicated that summer-active C<sub>4</sub> grasses are likely to reduce deep drainage to a greater extent than C<sub>3</sub> grasses as they can use water during summer; this warrants further investigation in southern Australia.

Kawamitsu *et al.* (1987) compared 4 C<sub>3</sub> and 14 C<sub>4</sub> grass species for vapour pressure deficit (VPD), net CO<sub>2</sub> assimilation, and leaf water conductance. Photosynthesis and transpiration were measured under different conditions of VPD and irradiance using a climate-controlled assimilation chamber. All species showed a decrease in leaf water conductance and CO<sub>2</sub> assimilation rate with increasing VPD, but the rate of decrease of the C<sub>3</sub> species was greater than that of the C<sub>4</sub> species. This indicates that C<sub>4</sub> grasses are able to use greater amounts of water under increasing VPD conditions, which are experienced during the spring and summer seasons of the HRZ.

Ghannoum *et al.* (2001) reported on the carbon and water economy of 17 Australian C<sub>4</sub> grasses in a glasshouse study. Cumulative water use was strongly related to plant dry matter in both winter and summer. On average, during winter the grasses used only 20% of the water they used under summer conditions, which was associated with an 87% decrease in leaf area, relative to that grown in summer. The WUE in winter was half that achieved under summer conditions for these C<sub>4</sub> grasses.

### *Root activity and rooting depth*

Taylor and Clifton (1993) noted that shallow-rooted annual pastures did not take up water from below about 0.6 m, whereas phalaris-based perennial pastures extracted water to at least 1.2 m. Cocksfoot pasture was unable to dry the soil sufficiently to prevent saturation to 1.2 m by mid-August, whereas phalaris plants were more effective in drying out the soil. Similarly, White *et al.* (2000) reported that annual pasture extracted water to between 0.9 and 1.2 m, whereas phalaris extracted water to 1.5 m. Lucerne has been reported to extract soil water from below 1.5 m depth (Fig. 4) to about 3 m depth (Ridley *et al.* 2001). However, the roots of perennial grasses and subterranean clover grown on basalt soils occur mostly in the top 0.8 m, with only a small proportion extending to 1.3 m (Clark *et al.* 2000).

Plants with deep tap roots should be able to dry soils to a considerable depth and survive droughts. For example, tall fescue, lucerne, and phalaris are better able to survive drought than other cool-season turf grasses such as perennial ryegrass or Kentucky blue grass (*Poa pratensis*) (Sheffer *et al.* 1987). An understanding of the anatomical and physiological mechanisms of water uptake by these species might indicate the presence of novel traits that could be incorporated into breeding programs to improve water uptake. Both intraspecific and interspecific variations in turf grass drought resistance have been attributed mainly to differences in total root density and rooting depth (Carrow 1996; Huang and Fry 1998). Roots that have greater xylem densities and diameters will have greater hydraulic conductivities, which will lead to improved water uptake, use, and tolerance to environmental stresses (Sharp and Davies 1985; Gallardo *et al.* 1996; Huang *et al.* 1997; Singh and Sale 2000).

Understanding root morphology is also critical for interpreting soil water use as a function of rooting volume and depth of rooting. Ward *et al.* (2001, 2002) reported that lucerne produced 1.7 times more root mass than subterranean clover. However, the total root mass to a depth of 2.0 m was less than 1.0 t/ha, and there was negligible root mass below 1.0 m depth for both the lucerne and clover, which may have reflected the root recovery technique of washing over a 2.0-mm sieve. This could have resulted in significant losses of fine clover roots, as more than 50% of roots could be less than 2.0 mm in diameter, as reported for



white clover (Singh and Sale 2000), which has similar rooting characteristics to those of subterranean clover. This contrasts with the thicker roots of lucerne (being a tap-rooted crop), more of which would have been retained on a 2.0-mm sieve during washing. Any comparisons between plant species with different rooting habits could be biased and ambiguous if root morphology is not considered in the techniques used to recover roots from soil. Nevertheless, it is unclear if a small proportion of deeper roots has any real effect on water use. For example, in a recent study, it was noted that the lucerne roots >2.5 m deep failed to take up and use water from a subsurface watertable that was maintained at 2.5 m depth (Hoffmann *et al.* 2003).

#### *Native species*

Historically, there is evidence that native grasslands grazed by marsupials had either the capacity to use sufficient water, or the mechanisms to prevent the development of dryland salinity, before they were overgrazed and eliminated by sheep in Western Victoria (Mitchell 1838; Bride 1898; Pressland 1980). Dense tussocks of kangaroo grass (*Themeda triandra*) and other native species may have provided effective water-trapping features, thus reducing run off and allowing greater direct evaporation of water from the foliage. Evaporation and transpiration from a pasture in a weighing lysimeter containing 50% kangaroo grass accounted for about 20% and 80% of the annual water loss, respectively, in a 3-year study in a subhumid region of New South Wales (Dunin and Reyenga 1978).

Dunin *et al.* (1999) suggested that the loss of native grasses from the basalt plains of western Victoria, as a result of overgrazing, was the reason for the appearance of secondary salinity. Garden *et al.* (2000, 2001) also noted that increasing stocking rates decreased kangaroo grass populations in NSW pastures, whereas wallaby grass (*Austrodanthonia* spp.) appeared to be more persistent under sheep grazing, and kangaroo grass under cattle grazing (Garden *et al.* 2000).

Native pastures have been generally considered to be slow in growth and not as productive as improved pastures. However, native pastures that have been fertilised, and to which legumes have been added, may be quite productive. For example, applying superphosphate to native grass pastures in Tasmania increased the carrying capacity from 2.9 to 6.0 DSE/ha over 5 years (Friend *et al.* 2001). Garden *et al.* (2000) noted greater proportions of wallaby grass and microlaena (*Microlaena stipoides*) in pasture that had received more superphosphate.

Kangaroo grass pastures may be less productive than wire grass (*Aristida*), microlaena, and wallaby grass pasture (Garden *et al.* 2000). Growth rate was 19 kg DM/ha.day for the kangaroo grass pasture, but was 35, 50, and 80 kg/ha.day for microlaena, wire grass, and wallaby grass respectively. The rates of growth of these latter native species were similar

to those of several other exotic perennial and annual pasture species used in commercial production.

The use of native perennial species under appropriate management might be crucial in areas where the persistence of lucerne and phalaris is poor. For example, both of these introduced species establish and persist poorly in acidic soils with high levels of toxic aluminium (Crawford and Ransom 1993). The native grasses wallaby grass, microlaena, and kangaroo grass are tolerant of acidic soil conditions, including tolerance to toxic levels of aluminium and manganese (Johnston 1993); however, their use for difficult environments in southern Australia needs further investigation.

#### *Growing more pasture*

##### *Grazing management*

Grazing management is a key issue for the productivity and sustainability of pasture and livestock enterprises. The most efficient grazing system will probably involve a combination of set-stocking and some form of rotational grazing during the year, as both have advantages under certain growing conditions, and for specific feeding purposes (Saul *et al.* 2000). Modelling studies conducted for the Sustainable Grazing Systems project indicated that calculated drainage beneath all grazing systems was excessive and deep-rooted species, such as lucerne, will need to be included if such systems are to be sustainable (Bond *et al.* 1997). However, rotationally grazed or infrequently defoliated and summer-spelled pastures were more likely to dry soil profiles compared with frequently grazed pastures (Clifton *et al.* 1997).

It has been shown that a rotationally grazed pasture had a greater soil water deficit to 80 cm depth than a set-stocked pasture (Lisa Warn, pers. comm.). Rotational grazing generally favours an increased proportion of perennial grasses, compared with set stocking (Barker *et al.* 1991; Culvenor 2000; Virgona *et al.* 2000); this might translate into increased soil water use because of the greater rooting depths and longer period of active growth of the perennial grasses.

The influence of grazing management practices on soil water use and pasture production may also interact with other factors such as the growing season, availability of soil water, plant species and variety, and other agronomic factors. The effects of these interactions on the soil water use have been found to be variable, and fairly complex to understand. For example, Ward *et al.* (2001, 2002) reported that there was no difference in the estimated ET or above-ground yields between lucerne and subterranean clover pastures, despite large variations in rainfall, soil water deficits, and grazing management. The subterranean clover pasture was severely grazed, being set-stocked with 12 dry sheep equivalents (DSE)/ha, compared with the lucerne that was rotationally grazed. The lucerne was grazed for 1 week with about

50 DSE/ha followed by a 6-week spell, which equates to a grazing pressure of about 7 DSE per day over 7 weeks. It was therefore not surprising that rotationally grazed lucerne was able to grow more roots and appeared to extract more water from deeper depths than the set-stocked subterranean clover (Ward *et al.* 2001). The repeated removal of leaf canopy with set-stocking results in a reduced photosynthate supply and translocation to the roots (Chapman *et al.* 1992), which in turn leads to a decline in root elongation (Chapman and Robson 1992).

Dunin *et al.* (2001) also reported similar ET values for wheat in 1993 and lucerne in 1995, although the wheat yielded 50% greater dry matter and had 25% greater leaf area index than the lucerne, despite a shorter growing season of approximately 8 months. Furthermore, Cox *et al.* (1988) reported that infrequent cutting, which led to higher yields and higher water use efficiencies than the frequent cutting, did not affect total water use or the shape of the soil water extraction profile. Sowing density influenced sward composition and the pattern of water use, but not total water use (Cox *et al.* 1988). The swards from the low sowing density had a lower stubble mass and tiller density, and extracted relatively more water at depths of 75 and 85 cm and less at depths of 15 and 35 cm, than the swards derived from the high sowing density. The ratio of actual/potential evapotranspiration was reduced as the soil-water deficit increased and was lowest in the summer after a dry spring (Cox *et al.* 1988). Neither cutting height nor frequency during summer was shown to be an effective method of either conserving water or manipulating the effective rooting depth of an established sward (Cox *et al.* 1988). Inconsistencies in the results of these studies on grazing management and its influence on dry matter yield, soil water use, and ET are apparent, that might be due to the confounding effects of likely errors associated with the estimation of ET and/or soil water, as discussed above. Otherwise, pastures under different grazing pressures would have different defoliation stresses, heights, canopy structures, herbage masses, litter, and ground covers and so would be expected to have different net radiation, albedo values, ET and soil water use (Meyer 1999; Lodge *et al.* 2001).

In other physiological studies on grazing management, Singh and Misra (1985) simulated the effect of stocking rate through the use of clipping frequency when comparing the C<sub>3</sub> winter annual *Polypogon monspeliensis*, the C<sub>4</sub> perennial *Dichanthium annulatum*, and the C<sub>4</sub> warm-season annual *Echinochloa colona* during summer and winter under different regimes of soil moisture. Leaf water status and transpiration rate decreased with increasing soil moisture stress, but the opposite effect occurred with increased clipping frequency. During winter, the transpiration rate of the C<sub>4</sub> perennial was much lower than that of the C<sub>3</sub> winter annual, as well as its own rate in summer. An increase in the

transpiration rate per unit leaf area was also noted for the frequently defoliated white clover plants, but the total water use per pot was much greater for the infrequently defoliated plants due to their larger canopies (Singh *et al.* 2000). Asseng and Hsiao (2000) similarly reported that immediately after cutting, the total water use by lucerne through transpiration was reduced markedly, increasing to about 85% of the initial value about 3 weeks after cutting. Before cutting, the photosynthetic rate of the canopy was similar to that for other high-yielding crop species and ET was very close to the reference ET rate. These physiological studies further indicate that the frequent removal of canopy under set-stocking would result in reduced soil water use, compared with the rotationally grazed swards.

### *Waterlogging*

Soil waterlogging during autumn and winter is a major environmental constraint to the survival of sensitive plant species in the HRZ (McDonald and Gardner 1987; Stephens and Lyons 1998). Seasonal production of pasture can be generally about 10% less on waterlogged soils than on well-drained soils (McFarlane *et al.* 1992). The low concentration of oxygen in the rooting zone, caused by saturation or near saturation of the soil with water (Kozłowski 1984; Drew 1992; Drew *et al.* 1994), is the key factor in the decreased growth of waterlogging-sensitive species. For example, Rogers and Davies (1973) found that the yield of cocksfoot was most severely restrained by waterlogged conditions when compared with timothy grass (*Phleum pratense*), perennial ryegrass, or tall fescue. Relative yields of the 4 species varied during the season; at wet sites, timothy grass proved to be the best yielding species followed by tall fescue.

Donohue *et al.* (1985) reported that the cumulative yield of flooded perennial ryegrass decreased by 25% relative to the non-waterlogged control. However, the waterlogged plants partially acclimatised by growing new roots close to the soil surface as there was no difference between the effects of the shorter (24 h) and longer (48 h) periods of waterlogging. These results suggest that the drainage of surface water after irrigation is necessary to avoid significant yield losses in irrigated perennial pastures.

Rubio and Lavado (1999) reported that waterlogging significantly decreased root:shoot ratios in 2 waterlogging-tolerant grasses (*Paspalum dilatatum*, *Danthonia montevidensis*). Resource partitioning within above-ground parts was less sensitive to waterlogging than partitioning between roots and shoots. Waterlogged plants allocated more resources to stems, contributing to increased plant height, and less to the submerged tissues. Watt and Haggard (1980) reported similar decreases in shoot dry weight for perennial ryegrass and fog grass (*Holcus lanatus*), but the plants later responded to waterlogging by producing large numbers of

nodal roots and fine surface roots that may have enabled them to survive such conditions.

Nevertheless, where waterlogging has reduced the size of root systems or decreased the efficiency of water and nutrient uptake by roots, chlorosis, senescence, stunted growth, and death of various plant parts result (Troughton and Drew 1980; Belford 1981). Davidson *et al.* (1989) reviewed the adverse effects of prolonged waterlogging on the macrostructure of fragile duplex soils, denitrification, and root growth for southern Australia. However, they suggested that the deleterious effects of waterlogging can be ameliorated through the adoption of tolerant varieties, improved drainage, and agronomic practices such as raised beds, early planting, higher seeding rates, and maintenance of higher levels of nutrients using split-fertiliser applications.

#### *Soil acidity*

Acidic and acidifying soils generally occur in areas where rainfall exceeds 450 mm/year (Scott *et al.* 2000). A decrease in soil pH increases Al and Mn availability, and as a result, the production and persistence of most pasture species are decreased, resulting in decreased water use.

The application of lime to an acidic soil ( $\text{pH}_{\text{Ca}} = 4.4$ ), high in aluminium (82 mg/kg; KCl extract), in south-western Victoria reduced the detrimental effect of soil acidity on pasture growth (Quigley *et al.* 2001). Where Al was low (26 mg/kg), DM production was affected by an interaction between lime and superphosphate. At lower rates of lime, DM production increased with increasing rates of superphosphate. Similarly, on dairy pastures in southern Victoria, after 5 years of lime application, soil pH had been increased, and soil aluminium decreased, but pasture responses were highly variable and not economic (Crawford and Gourley 2001). Scott *et al.* (2000) reviewed the responsiveness of subterranean clover, phalaris, lucerne, and cocksfoot to the liming of acidic soils, but the magnitude of responses varied under different conditions, with most responses occurring in the autumn–winter period. They concluded that the use of lime is the major solution to acidification if agricultural production is to continue in much of the HRZ. They also recommended sowing perennial pasture species and reduced stocking rates in a system based on native perennial pasture species.

#### *Plant nutrition*

Nutrient supply strongly affects soil water use through its effect on plant productivity. The opportunity for unused soil water to become recharge can be minimised by growing crops and pastures at their potential production levels (Nulsen 1993). Angus *et al.* (2001) and Dalal *et al.* (1998) reported that management practices that optimise crop vigour also maximise water removal by a crop and improve the WUE. Similar responses in crop growth and soil water

use to improved nutrient supplies were also noted in the studies of Ridley *et al.* (1997) and Singh and Sale (2000). This is consistent with the close relationship between productivity and soil water use, although there are inconsistencies in the reported water-use data between fertilised and unfertilised crops. For example, despite large increases in pasture production following additional fertiliser, water use was generally similar or only slightly greater for the fertilised plots compared with control plots (Bolger and Turner 1999). Similarly, Simpson *et al.* (1998) (see Table 2 in this review) and Tennant and Hall (2001) reported no differences in water use by pastures fertilised with low and high rates of fertilisers.

Asseng *et al.* (2001) reported a minimal impact on crop transpiration when wheat crops were fertilised with nitrogen in long-term simulation studies using the Agricultural Production Systems Simulator (APSIM). In particular, they found that when the rate of nitrogen fertiliser was increased from 30 to 210 kg/ha, grain yield increased from 3.5 to 7.5 t/ha, with a corresponding increase in crop transpiration of 54.5 mm, from 63.0 mm to 117.5 mm (Asseng *et al.* 2001). This corresponded to an increase in WUE from 5.4 to 6.4 g/kg of transpired water, both of which appear to be overestimates when compared with the measured values reported for C<sub>3</sub> plants (Table 3). It is, though, possible to increase the WUE of C<sub>3</sub> plants by up to 70%, and C<sub>4</sub> plants by up to 200%, by modifying varieties, soil, and nutrient management practices (Singh *et al.* 2000; Ghannoum *et al.* 2001; Hatfield *et al.* 2001); significant increases in WUE outside the reported range of lysimeter-measured values for C<sub>3</sub> and C<sub>4</sub> plants would be questionable. Nevertheless, an increase in the WUE from low-fertility growing conditions to high-fertility growing conditions is mostly associated with simultaneous increases in productivity and total soil water use, although increases in the productivity are relatively greater than the increases in soil water use between the two growing conditions (Singh *et al.* 2000; Ghannoum *et al.* 2001; Hatfield *et al.* 2001).

On the other hand, Dalal *et al.* (1998), Singh and Sale (1998), Bruck *et al.* (2000), and Angus *et al.* (2001) reported increased water use and biomass production in response to enhanced plant nutrition. Bruck *et al.* (2000) reported that pearl millet [*Pennisetum glaucum* (L.)], a C<sub>4</sub> plant, had an increased shoot dry matter production in response to high water and phosphate supplies. Similar increases in water uptake and WUE with increasing dry matter production were reported by Singh and Sale (1998) for white clover, a C<sub>3</sub> plant, in response to increased water and phosphorus supply (also see Table 4).

Although numerous studies have shown a positive relationship between soil water use and biomass production from well-managed studies in the field and under controlled conditions (Tanner and Sinclair 1983; Singh and Misra 1985; Leuning *et al.* 1994; Ghannoum *et al.* 2001), the potential to

use this relationship to minimise deep drainage needs to be explored further under different farming systems.

## Conclusions

Maximising the potential use of soil water by herbaceous species in the HRZ would be achieved in two ways. The first option is to encourage management practices that increase plant water use. Plants with deeper roots, including lucerne, phalaris, and cocksfoot, have the ability to dry the soil to depth. A combination of winter- and summer-active species, rotational grazing, and pasture spelling would also extend the active growing season and soil water use of pastures. Rotational grazing would favour the proportion of perennial grasses, relative to set-stocked pastures, which then might translate into increased soil water use due to greater rooting depths and extended growing seasons. There is a need for more work on deep-rooted native species that appear to be suited to areas of the HRZ affected by waterlogging and soil acidity. There is also a need to collect evidence on the relative abilities of native and exotic perennial pastures to control deep drainage and recharge under conditions of heavy grazing. Under light grazing, however, it is possible that dense tussocks of native species could effectively trap rainfall in their canopies, enabling greater direct evaporation of water from the soil surface and foliage. This needs to be investigated further.

The second option is to increase the productivity of existing pastures, as there is strong evidence of a direct link between growth and water use among a wide range of C<sub>3</sub> and C<sub>4</sub> plants of diverse growth form and habitat. This relationship appears to have been overlooked in recent studies of the various components of the soil water balance model and their effects on soil water use, although the issue has not been clarified because of limited or inaccurate field data sets for validation. In particular, the measurement of intercepted loss of water needs to be included in the soil water balance model for quantifying and predicting ET and deep drainage more accurately in future studies.

Evidence presented in this review suggests that incorporation of WUE in the soil water balance model might improve the reliability of the prediction for deep drainage, while considering the closeness of the relationship between biomass and water use and a greater reliability of the 'measured' WUE compared with the 'estimated' ET. It should also be noted that leaf water conductance is correlated with photosynthetic capacity and carbon dioxide exchange for various plant species. A significant increase in water use is more likely to be correlated with greater carbon assimilation and increased dry matter production and WUE, and vice-versa. However, further study is warranted under both controlled and field conditions to address the fundamental issue: do more productive pastures use more water?

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