

Impact of subsoil water use on wheat yield

J. A. Kirkegaard^{A,B}, J. M. Lilley^A, G. N. Howe^A, and J. M. Graham^A

^ACSIRO Plant Industry, GPO Box 1600, Canberra, ACT 2601, Australia.

^BCorresponding author. Email: john.kirkegaard@csiro.au

Abstract. Water stored deep in the soil profile is generally considered valuable to crop yield because it becomes available during grain filling, but the value of subsoil water for grain yield has not been isolated and quantified in the field. We used rainout shelters with irrigation to control the water supply to wheat crops that had different amounts of subsoil water available to isolate and quantify the efficiency with which the subsoil water was converted to grain yield. Under moderate post-anthesis stress, 10.5 mm of additional subsoil water used in the 1.35–1.85 m layer after anthesis increased grain yield by 0.62 t/ha, representing an efficiency of 59 kg/ha.mm. The additional yield resulted from a period of higher assimilation 12–27 days after anthesis and was related to an increase in grain size rather than other yield components. Under more severe stress with earlier onset, extra water use below 1.25 m was accompanied by additional water use in upper soil layers and it was more difficult to isolate and quantify the benefit of deep water to grain yield. The additional water used from all layers from the time the stress was imposed was converted to grain at 30–40 kg/ha.mm, but this increased to 60 kg/ha.mm for water used after anthesis. The high efficiency for subsoil water use is 3 times that typically expected for total seasonal water use, and twice that previously estimated for total post-anthesis water use in a similar environment. The results demonstrate that relatively small amounts of subsoil water can be highly valuable to grain yield.

Additional keywords: marginal water-use efficiency, drought, water-soluble carbohydrate, transpiration efficiency.

Introduction

The effective use of water stored deep in the soil profile by annual crops has important productivity and environmental implications. From a productivity perspective, such water is generally regarded as highly valuable to dryland crops as it becomes available to crops during the post-anthesis period when grain yield is particularly sensitive to water deficit (Fischer 1979; Passioura 1983). Failure to use such water at the bottom of the root zone increases the risk of subsequent leaching and the associated environmental consequences (Dunin and Passioura 2006). Several recent reviews consider strategies to improve subsoil water use using both genetic and agronomic approaches (Tennant and Hall 2001; Gregory 2006; Passioura 2006).

Despite the proposed benefits of deeper rooting or different root distribution to improve water use in particular environments, few studies have adequately isolated and quantified the value of subsoil water for crop yield. Typically, the maximum value of wheat grain produced per mm of water used throughout the season in southern Australia is estimated to be 20–25 kg/ha.mm (French and Schultz 1984). Notwithstanding the previously discussed simplifications inherent in this estimate (Connor and Loomis 1991) it is unclear whether such efficiency is achieved for water extracted by deep roots in the subsoil. Retrospective analysis of field experiments relating different amounts of water use from the subsoil to crop yield is often confounded because the treatments that generate such differences simultaneously influence water use in other soil layers, as well as nitrogen availability, disease levels, or the size and duration of the transpiring canopy. For example,

Kirkegaard *et al.* (2001) showed that the extra water available at sowing in wheat crops grown after a range of break crops during a drought increased grain yield by 18 kg/ha.mm, but the additional water was distributed throughout the profile and was accompanied by differences in N profiles, stubble loads, and disease levels. Angus and van Herwaarden (2001) estimated that the efficiency of water use after anthesis for grain yield of wheat crops grown under terminal stress was 33 kg/ha.mm, while the study reported by Condon *et al.* (1993), where transpiration was explicitly separated from evaporation after anthesis, indicated post-anthesis efficiency of water use for grain of 59 kg/ha.mm. Although water-use efficiency during the grain-filling period was higher than the commonly used maximum seasonal efficiency estimates (20–25 kg/ha.mm), the contribution of water used from different soil depths was not discriminated.

Crop simulation models have been used to predict the value of water used at different stages and from different depths to crop yield. A simulation study by Dreccer *et al.* (2002) suggested that small increases in rooting depth (2%) would increase wheat yield in the low-rainfall environments of southern Australia, and that preserving water in deeper layers during early growth increased yield by increasing the amount of water available at, and after anthesis. Manschadi *et al.* (2006) predicted that water extracted by wheat during the grain-filling stage in northern Australia is converted to grain at 55 kg/ha.mm, although the contribution of water from different depths was not reported. King *et al.* (2003) used a quantitative model to demonstrate significant production and economic benefits of deeper rooting for winter wheat crops in the UK. Simulation studies using crop models provide

valuable insights into crop response and seasonal interactions, but invariably involve assumptions, particularly with respect to the dynamics of water extraction and root growth in dense, structured subsoils during drying (Wang and Smith 2004). Water in the subsoil is generally used late in crop development when the efficiency of water use can be high due to reduced evaporation and allocation of assimilates directly to grain (Condon *et al.* 1993; Angus and van Herwaarden 2001). However, the deepest roots typically have very low density, are clumped into biopores and cracks that can restrict water uptake, and ironically leave significant amounts of subsoil water unused by water-stressed crops (Passioura 1991). The high vapour-pressure deficit late in the season when much of the upper soil may be dry can also induce physiological responses such as stomatal closure, leaf rolling, and senescence, which can reduce transpiration efficiency (Kemanian *et al.* 2005). Significant remobilisation of assimilate stored in the stems during this period further complicates predictions of yield response (Asseng and van Herwaarden 2003). The value of additional subsoil water to grain yield therefore remains uncertain.

In this paper we describe field experiments in which the water supply to wheat crops was carefully controlled to isolate and quantify the value of subsoil water to wheat grain yield under terminal stress. The effect of seasonal conditions on the value of subsoil water was investigated further in a subsequent paper (Lilley and Kirkegaard 2007).

Materials and methods

Site description and soil characterisation

The experiments were conducted in 2004 near Bethungra in southern NSW, Australia (34°43'S, 147°48'E), on a red Kandosol (Isbell 2002) typical of the red acidic loams in the wheatbelt of southern NSW. A rotation experiment conducted at the site from 1993 to 1996 (Kirkegaard *et al.* 2001) provided useful background data on wheat growth, root depth, and water use and was also used to validate the APSIM-Wheat model at the site (Lilley and Kirkegaard 2007). From 1998 the site was sown to a lucerne-based pasture that was renovated and maintained grass-free during 2003 and was maintained on the experimental area until autumn 2004 to ensure that experimental treatments could be imposed onto soil profiles that were dry to at least 2.5 m. Soil chemical and physical characterisation was conducted in a pit opened to a depth of 2 m at the site in April 2004 using techniques described in Geeves *et al.* (1995) (Table 1). An automatic weather station at the site recorded rainfall and temperature at 30-min intervals.

Irrigation system for controlled water supply and neutron-probe calibration

A drip-irrigation system designed to wet the soil to specified depths was designed and tested at the site during February 2004. Manifolds of 4 mm (i.d.) Drip-eze® polyethylene pipe with drippers spaced 300 mm along the pipes, and pipes spaced in 180-mm rows were constructed. Water was supplied to each dripper manifold from 500-L storage tanks via a small 5-L trough fitted with a float valve that provided a constant head of 300 mm. The resulting water application rate of 2 mm/h was well below the measured saturated hydraulic conductivity for these soils (Geeves *et al.* 1995) and prevented uneven profile wetting due

Table 1. Characteristics of the red Kandosol (Isbell 2002) at the experimental site

Horizon	Depth (m)	pH (CaCl ₂)	EC (1:5) dS/m	Texture ^A	Bulk density (g/cm ³)
A11	0–0.1	5.12	0.47	SL	1.45
A12	0.10–0.15	4.28	0.14	SL	1.50
B21	0.15–0.40	5.61	0.04	LC	1.65
B22	0.40–0.70	5.91	0.03	LMC	1.63
B31	0.70–1.10	5.55	0.03	LMC	1.63
B32	1.10–1.30	6.47	0.09	LMC	1.60
D1	1.30–1.70	7.28	0.15	LMC	1.66
D2	1.70–2.00	7.66	0.11	LMC	1.65

^ASL, Silty clay; LC, light clay; LMC, light medium clay.

to saturated flow down cracks and macropores. Repeated testing of 2 m by 2 m manifolds on areas with a centrally fitted neutron access tube was used to establish the relationship between added water and depth of soil wetting. These test areas were also used to improve the calibrations for the neutron moisture meter (Troxler 440) previously established at the site, and to determine the drained upper limit (field capacity) of the soil profile. Soil cores (42 mm diam.) were removed from the plots using a tractor-mounted hydraulic soil corer, sectioned, and oven-dried to determine gravimetric water content. These data together with bulk density measured in the pit at the site provided the necessary data for the neutron calibration. Analysis of individual 0.1-m depths revealed that a single calibration curve could be used for all depths at 0.2 m and below ($r^2 = 0.86$), and the error in estimation of volumetric water content for the calibration was 0.013 m³/m³.

Experiment 1. The value of subsoil water under moderate post-anthesis stress (automatic rainout shelter)

Experiment 1 was designed to isolate and quantify the value of subsoil water to wheat under post-anthesis stress. An automatic rainout shelter with the drip-irrigation system described above was used to establish 2 treatments that were wet to different depths (1.35 m and 1.85 m) (Fig. 1a). Wheat was grown on both treatments and the water supply controlled to ensure that stress developed during the post-anthesis period when rainfall and irrigation were excluded. As the 2 treatments had identical biomass at anthesis, but different amounts of water available in the subsoil during the grain-filling period, which are not subject to evaporation, the value of the additional subsoil water (1.35–1.85 m) to grain yield could be determined.

Rainout shelter design and operation

Eight individual rainout shelters that moved along metal tracks to cover the experimental plots during rainfall were constructed. Individual shelters comprised 3 m by 4.2 m rooves of corrugated Laserlite® on aluminium frames supported by 4 corner struts that were fitted with small side-mounted metal wheels at the base. The wheels were enclosed within metal tracks fixed 0.2 m above the ground, along which the shelters could move. The tracks were spaced 2.8 m apart and were 32 m long so that 4 shelters operated on 4 experimental areas spaced alternately with 4 parking areas along the tracks. The shelters were all fixed at the bottom of the track struts to a common

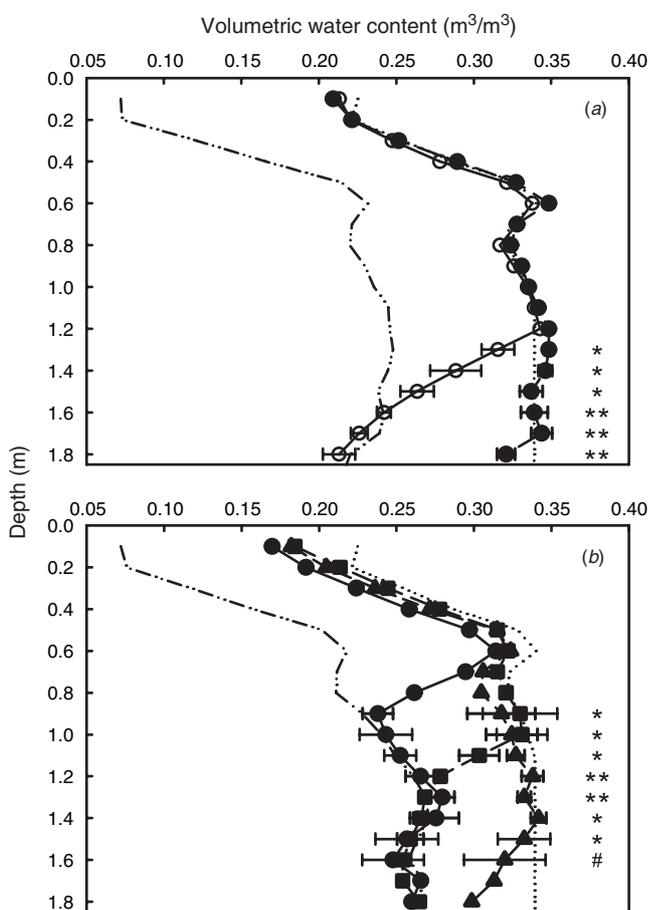


Fig. 1. Maximum volumetric water content established for the 1.35 (O) and 1.85 m (●) depth of wetting treatments in (a) Expt 1, and for the 0.85 (●), 1.25 (■), and 1.65 m (▲) depth of wetting treatments in (b) Expt 2. Horizontal bars are standard error of means where significant differences in water content between treatments exist as shown ([#] $P < 0.1$; * $P < 0.05$; ** $P < 0.001$). The dotted line is the drained upper limit of PAW and the dotted/dashed line is the lower limit of PAW.

wire cable allowing them to be moved simultaneously from their parked position over the experimental plots via an electric winch activated by a conical moisture sensor during rainfall. The electronic sensor and control system for the winch was designed to avoid activation by small rainfall events or dew (< 1 mm), and to return the rooves to the parked position only after the sensor had been dry for 20 min, to avoid excessive winching during intermittent rainfall. The rainout shelter successfully excluded rainfall for the required period after anthesis.

Crop establishment and management

The plots were irrigated (50 mm) on 3 April to encourage lucerne re-growth, which was removed by herbicide application on 30 April and 13 May. Neutron tubes were installed centrally in each 4 m by 2 m plot to a depth of 1.9 m (to permit readings at 1.8 m) in April using tractor-mounted equipment driven between the tracks following roof removal. Wheat (cv. Janz) was sown at 80 kg/ha on 13 May 2004 using an experimental plot seeder into 10 rows spaced 180 mm apart, and 120 kg/ha Granulok15 fertiliser (20 kg/ha N, 18 kg/ha P, and 16 kg/ha S) was applied

with the seed. The irrigation manifolds were immediately positioned onto each of the 8 plots and 15 mm of irrigation was applied to ensure even germination and emergence. The plots were subsequently wet up in stages to a depth of 1.2 m from May to July using the neutron access tubes to monitor soil water content. On 13 and 19 July, the 4 replicates of the 1.85-m treatment allocated randomly within the 8 plots received additional water (41 mm) to establish the desired differences in the depth of soil wetting (as shown in Fig. 1a). From 23 July until the final irrigation on 1 October (6 days before anthesis), all plots received the same amount of water (100 mm total in 3 applications) to avoid significant pre-anthesis stress while maintaining the differences in soil water established at depth. All rainfall and irrigation were excluded after 1 October to induce terminal stress. Nitrogen was managed using an N budget calculated from pre-sowing soil mineral N (from neutron access tube installation) and 24 kg of additional N was applied as urea through the irrigation system on 6 September. The plots were hand-weeded as required and prophylactic fungicide (Tilt®) was applied from booting to ensure that green leaf area was not affected by fungal disease.

Crop and soil measurements

Soil water content was monitored weekly in all plots using a neutron moisture meter that was calibrated at the site. The repeated-measurements at each depth in the plots provided a pattern of water depletion so that variable data points could be readily identified and if necessary re-measured. At anthesis and final harvest, each depth was measured twice (2 consecutive 15-s counts) to improve the accuracy of water content estimates. Soil water was also measured gravimetrically at 0.1-m increments from 42-mm-diameter soil cores (to 1.9-m depth) removed for neutron-tube installation before sowing, and immediately following harvest (1/plot). Three additional cores were also removed at harvest in each plot for measurement of root depth and density in 0.1-m increments to 1.9 m. The 0.1-m core segments were stored at 4°C before washing roots using the hydro-pneumatic root elutriation system with 0.5-mm sieves as described by Smucker *et al.* (1982). The washed root samples were sorted to retain only current wheat roots, and root length density (RLD) was calculated using a flat-bed scanner to capture digitised images that were analysed using WINRhizo® software.

Plant population was measured at the 2-leaf stage by counting plants along five 1-m row lengths selected randomly in each plot. Total and component above-ground biomass (including stem, head, and dead and green leaf), tiller and head numbers, and green leaf area index were measured at anthesis on plants removed at ground level from 3 by 0.5-m lengths of row in each plot. At 7–12-day intervals during the post-anthesis period the same measurements were made on grab samples of ~50 stems removed from random positions throughout the plot, avoiding the central 1-m² area surrounding the neutron tube, which was maintained for a maturity sample. At maturity, 6 by 1-m lengths of row (1.08 m²) surrounding the central neutron probe were removed for final grain yield, and a subsample of around 50 stems selected for yield component analysis. At each harvest, the separated plant samples were dried in an oven at 70°C and ground in a Wiley mill for analysis of tissue N (Kjeldahl) and water-soluble carbohydrate (WSC). WSC of the combined stem and leaf sheath tissue was analysed

by the anthrone method as described by van Herwaarden *et al.* (1998).

During the anthesis to maturity period the crops were frequently assessed and measured for the degree of water stress including the number of green leaves, degree of leaf rolling, wilting, and death. Physiological measurements included measurement of leaf conductance using a viscous-flow porometer (Rebetzke *et al.* 2000) during the early stages of stress development and canopy temperature using an infrared gun (Blum *et al.* 1989) as the stress became more severe.

These measurements were compared with those taken on duplicate well-watered plots of similar size grown adjacent to the rainout shelter as a guide to the timing and severity of stress.

Experiment 2. The value of subsoil water under severe terminal stress (permanent rainout shelter)

Experiment 2 was designed to investigate the value of subsoil water under more severe terminal stress with earlier onset than in Expt 1 (Fig. 2b). The experiment was a randomised

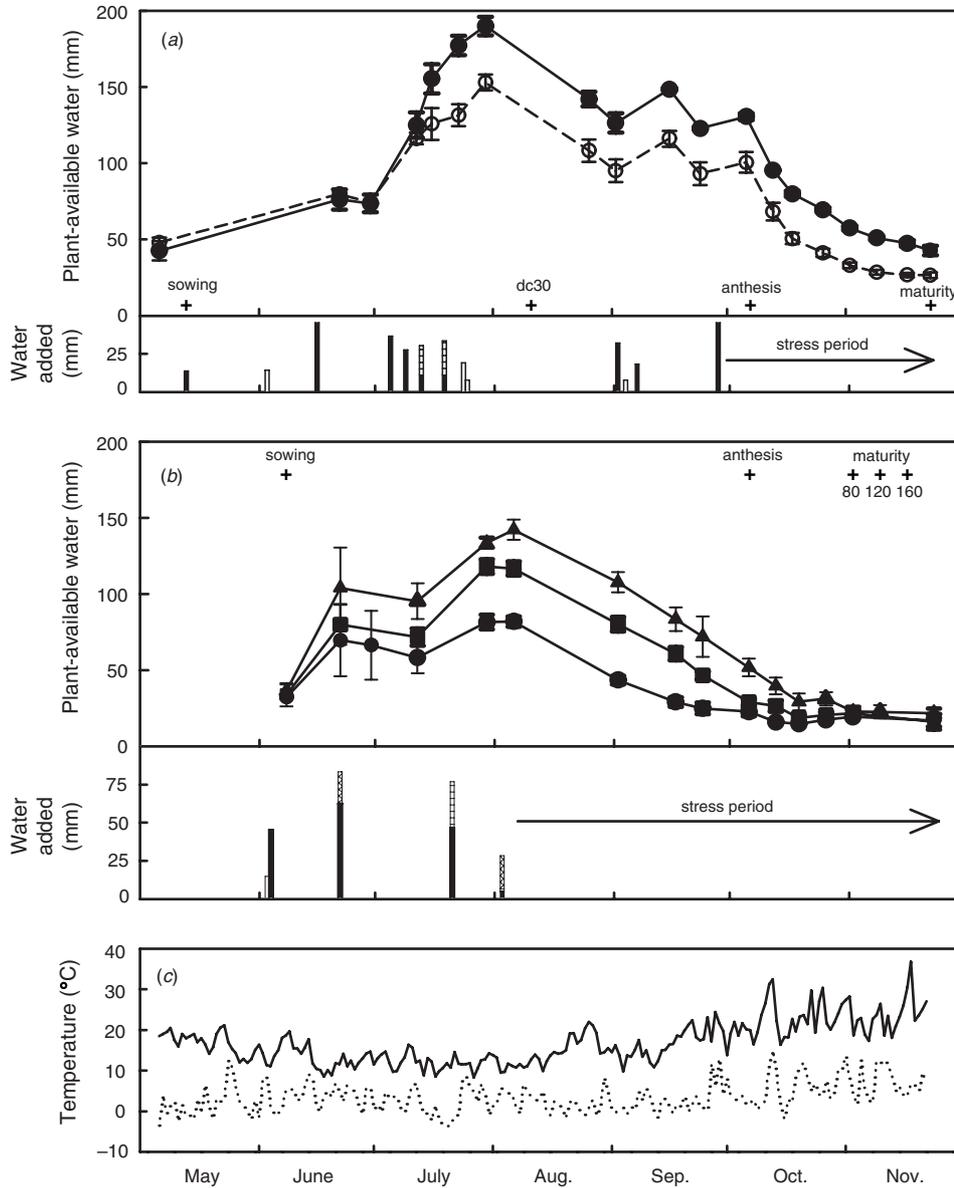


Fig. 2. Seasonal pattern in plant-available water for the 1.35 (O) and 1.85 m (●) depth of wetting treatments in (a) Expt 1, and for the 0.85 (●), 1.25 (■), and 1.65 m (▲) depth of wetting treatments in (b) Expt 2 in relation to the rainfall and irrigation applied to each treatment. Black and white columns indicate irrigation and rainfall, respectively, applied to all treatments; hatched columns indicate irrigation to produce treatment differences. Vertical bars represent standard error of mean. Key stages in crop development are indicated and the periods of terminal stress in which rainfall and irrigation were excluded are indicated with arrows. (c) The daily maximum and minimum temperature throughout the season.

design with 3 replicates and compared 3 depths of soil wetting (0.85 m, 1.25 m, and 1.65 m) (Fig. 1*b*). In common with Expt 1, the treatments were established using drip irrigation on plots established with a central neutron access tube to monitor soil water. The main difference was that the 9 experimental plots were smaller (2 m by 2 m), and the rainout shelters were permanent fixed rooves constructed over the plots after sowing.

Rainout shelter design and operation

The permanent rainout shelters were constructed from 8 individual 6 m by 3 m Laserlite® roof panels supported on metal piping legs and arranged together to cover a 12 m by 12 m area. The shelter was 1.5–2 m in height and open at the sides. When erected, the panels were pitched and rainfall was intercepted and removed via guttering and down-pipes, and the area was surrounded by large drains to prevent run-on. The 9 experimental plots (3 replicates × 3 treatments) were initially 4 m by 1.8 m and had a central neutron access tube installed on 8 June. The experimental plots were subsequently reduced to 2 m by 1.8 m, reflecting the size of the irrigation manifolds used to create the wetting treatments, and were positioned within the covered area so that rain did not reach the plots. Measurements using a ceptometer indicated that the Laserlite roof transmitted 80% PAR, and temperature loggers set at canopy height indicated that temperature did not differ significantly from that recorded by the weather station.

Crop establishment and management

The plots were initially wet to a depth of 0.4 m by application of 50 mm water using the drip-irrigation manifolds on 2 June, and were sown to wheat (cv. Janz) on 6 June at 80 kg/ha with 140 kg/ha Granulok 15 applied with the seed. After establishment, subsequent irrigation was applied using 2 m by 2 m manifolds placed so that the neutron probe was in the centre of the plots. All plots were irrigated during autumn and early winter to a depth of 0.85 m using the neutron access tubes to monitor soil water content. On 21 July and 3 August, the 3 replicates of the 1.25 and 1.65 m treatments received additional irrigation to establish the desired differences in the depth of soil wetting (Fig. 1*b*). From 3 August, all rainfall and irrigation were excluded. Agronomic management was similar to Expt 1, although no supplementary N was applied.

Crop and soil measurements

Soil water content, plant population, total and component biomass, and plant water stress observations were conducted as for Expt 1, with the following changes due to smaller plot size. Biomass measurements were conducted only at anthesis and maturity and from 4 by 0.5-m lengths of row. At maturity, 2 cores were removed in each plot for measurement of root depth and RLD.

Results

Seasonal conditions and plant-available water (PAW)

The lower limit of PAW to 1.85 m at the site was determined using a combination of pressure-plate measurements at –1500 kPa on intact soil cores removed from the soil pits (Geeves *et al.* 1995), and the driest soil profiles measured previously under lucerne at

the site. The lowest of the 2 measures was adopted and PAW was calculated as the water in the profile between this lower limit and the drained upper limit. The pattern of total PAW throughout the season in relation to the irrigation/rainfall supplied, the periods of stress imposed, and plant development in Expts 1 and 2 are shown in Fig. 2*a*, and *b*, respectively. In Expt 1, an additional 41 mm of irrigation supplied to the 1.85-m treatment on 13 and 19 July (61 and 67 DAS) resulted in an increase in PAW of 35 mm below 1.3 m on 20 July (Figs 1*a*, 2*a*). Roof failure on 24 July resulted in 27 mm of rain on both treatments, but the difference in subsoil water content between the treatments was retained. This additional rain resulted in some water (estimated 3 mm PAW) moving below the depth of subsequent measurement (assuming the soil below 1.85 m was initially at the same water content as the 1.75–1.85 m layer). The PAW in both treatments in Expt 1 was maintained at or above 100 mm up to 1 October by 3 irrigations in September (Fig. 2*a*). At anthesis (6 October), 6 days after the commencement of the terminal stress period, the 1.85-m treatment had an additional 30 mm of PAW, 24 mm of which was between 1.35 and 1.85 m.

In Expt 2, the additional 32 and 60 mm of water applied on 21 July and 3 August to the 1.25 and 1.65 m treatments, respectively, resulted in an additional 30 and 55 mm of PAW below 0.85 m in those treatments on 6 August (Figs 1*b*, 2*b*). The plots received no further rain or irrigation in order to induce a severe terminal stress.

An unusually warm period (max. 33°C) followed immediately by a mild frost in mid-October (Fig. 2*c*) did not damage the developing kernels in either experiment, and temperatures were otherwise close to the long-term average for the site.

Experiment 1. Automatic rainout shelter, moderate post-anthesis stress

Plant growth and stress development

Uniform, healthy plant stands were established in all plots (mean 170 plants/m²) and there was no significant difference in biomass (10.8 ± 0.3 t/ha) or tiller numbers (444 ± 18/m²) between the 1.35 m and 1.85 m treatments at anthesis [147 days after sowing (DAS)]. No symptoms of plant water stress were obvious before anthesis (7 October), but by 6 days after anthesis (DAA) the leaf porosity measurements indicated that both treatments were more stressed than well-watered plots (Table 2). Conductance was significantly lower in the 1.35-m treatment than in the 1.85-m treatment 12 DAA, although there were no visible differences in leaf symptoms or green leaf area between treatments at that stage. From 12 DAA to maturity, all plant symptoms of water stress including yellowing and death of lower leaves, flag leaf tip death and rolling, loss of green leaf area, and canopy temperature, were more severe in the 1.35-m treatment than in the 1.85-m treatment (Table 2) and the plants matured around 3–4 days earlier in the 1.35-m treatment.

Total plant biomass increased at the same rate in both treatments in the first 12 days after anthesis, but the rate of increase was reduced in the 1.35-m treatment over the subsequent 15 days and no increase in total biomass occurred in either treatment thereafter (Fig. 3*a*). Green leaf biomass was similar in both treatments and relatively constant in the first 12 days

Table 2. Observations and measurement of stress development in Expt 1

(C), Conductance measurements ($\text{mmol}/\text{m}^2 \cdot \text{s}$) using viscous-flow porometer (Rebetzke *et al.* 2000); CTD ($^{\circ}\text{C}$), difference in temperature between canopy and ambient (21°C); DAA, days after anthesis. Readings were conducted within 30 min of time shown. Within rows, numbers followed by the same letter are not significantly different

Date	1.35-m treatment	1.85-m treatment	Watered ^A
-2 DAA (C) 1300 hours	540	592	-
Anthesis (7 Oct.)	No stress symptoms obvious in canopy		
6 DAA (C) 1000 hours	118a	104a	748b
12 DAA (C) 0915 hours	8a	75b	301c
20 DAA	Lower leaves yellow/dying, flag rolling, heads turning	Lower leaf green, flag leaf tipping, awns tips brown	
27 DAA	Flag leaf dead/tightly rolled, 1/2 green leaf left	Flags green, rolled, some penultimate leaf, 1.5 green leaf left	
34 DAA	Flag leaf dead, peduncle yellow/green, head trace green	Minor flag left, peduncle yellow/green, head trace green	
CTD ($^{\circ}\text{C}$) 1000 hours	-1.1a	-1.6b	-3.1c
41 DAA	No green in head	Some green in head	
47 DAA	No green in stems	9% green stems	
		Harvest	

^APlots were grown adjacent to rainout shelters and received weekly irrigations throughout grain-filling.

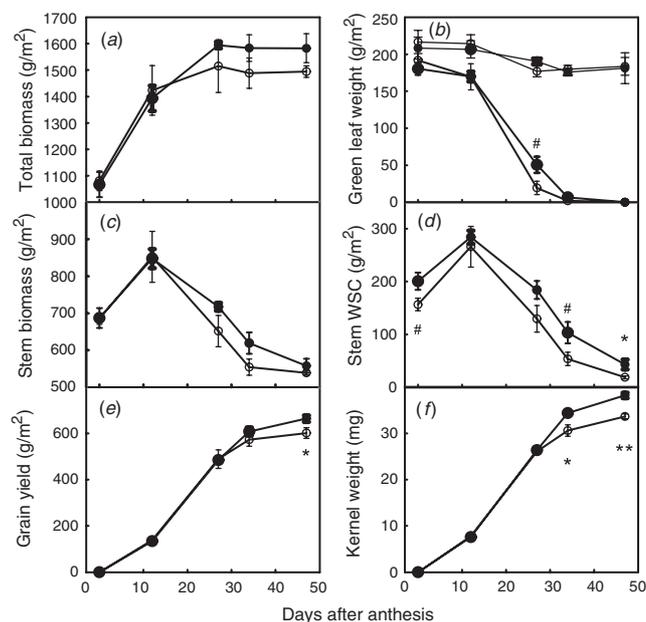


Fig. 3. Post-anthesis patterns of (a) total plant biomass, (b) green leaf and total leaf biomass, (c) stem biomass, (d) stem water-soluble carbohydrate, (e) grain yield, and (f) kernel weight for the 1.35 m (○) and 1.85 m (●) depth of wetting treatments in Expt 1. Vertical bars represent standard error of the mean and significant treatment differences are shown (# $P < 0.01$; * $P < 0.05$; ** $P < 0.001$).

after anthesis but declined rapidly in both treatments over the subsequent 15 days, although more rapidly in the 1.35-m treatment, which had significantly less green leaf weight 27 DAA (Fig. 3b). There was a small decline in total leaf weight but no difference between treatments throughout the grain-filling period. Stem biomass was similar in both treatments at anthesis and increased at a similar rate in both treatments during the first 12 days after anthesis (Fig. 3c). Stem biomass declined rapidly

in both treatments thereafter with a trend towards an earlier and more rapid rate of decline in the 1.35-m treatment, although stem biomass did not differ between the treatments at maturity. The WSC in the stem followed a generally similar pattern to stem biomass, and changes in stem biomass could be accounted for by the loss of WSC measured in the stems (cf. Fig. 3c and d). The WSC was similar in both treatments 12 DAA, but the levels fell more rapidly in the 1.35-m treatment thereafter and the amount of WSC was significantly lower in the 1.35-m treatment at maturity (Fig. 3d). The rate of decline in WSC in the period 12–35 DAA was significantly greater ($P < 0.05$) in the 1.35-m treatment than in the 1.85-m treatment (83 and 64% reduction, respectively). Grain yield increased at a similar rate in both treatments until 27 DAA, after which the 1.85-m treatment accumulated more grain yield (Fig. 3e). The increase in final grain yield from $602 \text{ g}/\text{m}^2$ in the 1.35-m treatment to $664 \text{ g}/\text{m}^2$ in the 1.85-m treatment (Table 3) was accounted for by an increase in kernel mass (Fig. 3f), with similar kernel number/head (mean 41), head density (mean $431/\text{m}^2$), and kernels/ m^2 (mean $17700/\text{m}^2$) in both treatments throughout the post-anthesis period.

Root depth and water use

At anthesis, when the stress was first imposed, the PAW remaining in the profile to 1.85 m in the 1.85 m and 1.35 m treatments was 131 and 101 mm, respectively, while at harvest the total remaining was 43 and 27 mm (Fig. 2a). At final harvest, both treatments had dried the profile to a similar extent to a depth of 1.25 m (Fig. 4a) and since the water content was similar initially, the water extracted from the 0–1.25 m layer was similar (Fig. 4b). The 1.35-m treatment extracted little water from below 1.4 m, reflecting the small amount of PAW initially present at those depths. The 1.85-m treatment extracted water from all depths to 1.8 m, and significantly more water from 1.5 m and below, although a significant amount of PAW remained below 1.5 m (Fig. 4a, b). The uptake of water below 1.85 m (an estimated 3 mm PAW was available for uptake) would presumably have been negligible given that only 2 mm of the

Table 3. Calculations of water-use efficiency (WUE) and marginal water-use efficiency (MWUE) (kg/ha.mm) of subsoil water in Expt 1
Numbers in parentheses are s.e.m.

Treatment	Anthesis biomass (g/m ²)	Grain yield (g/m ²)	HI	Water application ^A (mm)	F&S WUE ^B	Total water uptake (mm)	WUE Grain	Post-anthesis water extraction (mm)		MWUE of subsoil water
								0–1.35 m	1.35–1.85 m	
1.35 m	1081	602 (23)	0.40	337	26.7	306	19.7	70.2	4.8 (1.6)	–
1.85 m	1083	664 (14)	0.42	378	24.8	309	21.4	72.4	15.3 (1.7)	59
<i>F-value</i>	<i>n.s.</i>	<i>0.05</i>	<i>n.s.</i>	–	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>0.005</i>	–

n.s., Not significant.

^AApril–October water application.

^BF&S, French and Schultz (1984); calculated as $WUE = [\text{grain yield}]/[\text{April–October rainfall} - 110]$.

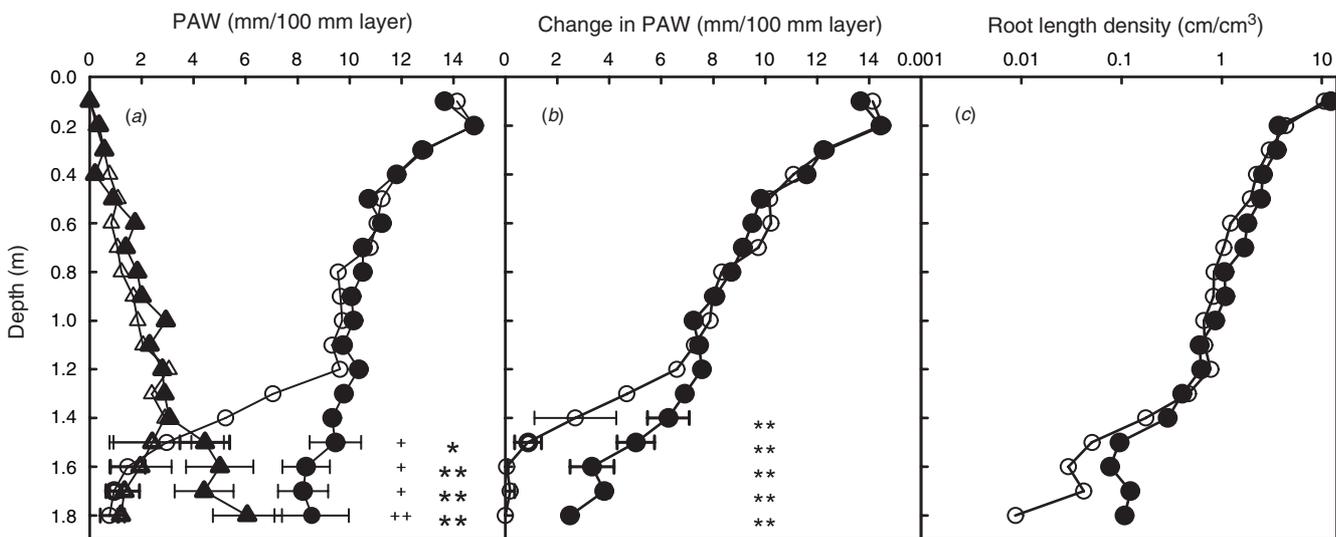


Fig. 4. Profiles of (a) plant-available water at the maximum soil water content (circles) and maturity (triangles), (b) changes in available water, and (c) root length density for the 1.35 m (open) and 1.85 m (closed) treatments in Expt 1. Horizontal bars show standard error of mean at depths where treatment differences are significant (**P* < 0.05; ***P* < 0.05; at maturity; +*P* < 0.05, ++*P* < 0.001 for maximum water content).

10 mm PAW was extracted from the 1.75–1.85 m layer and the uptake pattern declined with depth. There was no significant difference in the RLD measured at any depth (Fig. 4c). The RLD was low (<0.1 cm/cm³) and highly variable below 1.4 m and no statistical differences were apparent. However, it is relevant to note that the mean RLD was 2–3 times higher at all depths below 1.4 m in the 1.85-m treatment (0.06–0.1 cm/cm³) compared with the 1.35-m treatment (0–0.05 cm/cm³).

Water-use efficiency and marginal water-use efficiency

Conventional estimates of seasonal water-use efficiency for grain production such as those of French and Schultz (1984) based on April–October rainfall (plus irrigation), or those based on estimates of total water use (including the change in soil water content), show that the experimental treatments were at the high end of the range previously reported for well-managed crops (20–25 kg/ha.mm), and there was no significant difference between the treatments (Table 3). The value of the subsoil water to grain yield can be expressed as a marginal water-use efficiency (MWUE), the ratio of the additional yield (kg/ha) derived from the additional subsoil water use (mm). The MWUE calculated in

this way is shown in Table 3. The additional 620 kg/ha (62 g/m²) of grain yield achieved in the 1.85-m treatment was associated with an additional 10.5 mm of water use from below 1.35 m (*P* = 0.005), resulting in a MWUE of 59 kg/ha.mm of subsoil water used. Given that the difference in water use between the treatments above 1.35 m was small and not significant, and that the treatments had identical biomass at anthesis, all of the additional yield can be attributed to the additional subsoil water use in the post-anthesis period. Including the non-significant 2.2 mm difference in water use above 1.3 m as contributing to yield would reduce the MWUE to 49 kg/ha.mm. Regression analysis of the relationship between subsoil water use in the post-anthesis period and grain yield for individual plots revealed a significant relationship (*r*² = 0.79), the slope of which suggests a somewhat higher MWUE of around 67 kg/ha.mm for subsoil water used after anthesis.

Experiment 2. Fixed rainout shelter, severe terminal stress

Plant growth and stress development

Uniform, healthy plant stands were established in all plots (mean 140 plants/m² at anthesis) and there was no obvious

difference in shoot growth and biomass at the time the subsoil treatments were established on 3 August, 62 days before anthesis. However, by 2 September, 35 days before anthesis, visual differences were apparent among the treatments and subsequent measurements indicated increasing levels of water stress (Table 4) consistent with reduced PAW in drier treatments (Fig. 2*b*). In contrast to Expt 1, significant stress symptoms were apparent at anthesis, especially in the 0.85 m and 1.25 m treatments (Table 4). Despite these obvious symptoms of plant water stress and trends towards higher biomass, and tiller and head density as the depth of wet soil increased, differences in growth parameters were not significant at anthesis (Table 5). The amount of stem WSC was also similar among the treatments at anthesis, but was much less in absolute terms (6 times less) and relative terms (8.5% cf. 16% of biomass) than that measured in Expt 1 (cf. Fig. 3 and Table 5). By 20 DAA, the 0.85-m treatment had no green leaf left and all heads had begun to senesce, and the estimated physiological maturity dates (no green colour remaining in head or peduncle) were 3, 10, and 23 November (47 DAA) for the 0.85, 1.25, and 1.65 m treatments, respectively (Table 4).

At maturity, total biomass, grain yield, and harvest index increased as the depth of wet soil increased (Table 5). In contrast to Expt 1, the increase in yield was predominately associated with an increase in kernel number per m² due to increased kernel number per head, while head density and kernel weight were not

significantly affected by the treatments (Table 5). At maturity, the levels of WSC in the stem were very low (2–6 g/m²) compared with that remaining in Expt 1 (30–50 g/m²) and this was related to both reduced stem biomass and the WSC concentration of the stem.

Root depth and water use

On 3 August, at the point of maximum soil water content, the PAW remaining in the profile was 82, 117, and 142 mm in the 0.85, 1.25, and 1.65 m treatments, respectively, while at maturity the total remaining was 17, 16, and 22 mm (Fig. 2*b*). At maturity, all 3 treatments had extracted most of the PAW from the profile except for the 1.65-m treatment, which had significantly more PAW remaining in the 1.35–1.45 m layer (Fig. 5*a*). The pattern of water extraction reflected the initial water content, with significant uptake occurring to 0.8 m, 1.1 m, and 1.5 m, respectively, in the 0.85, 1.25, and 1.65 m treatments. Roots were measured to a depth of 1.15, 1.45, and 1.60 m in the 0.85, 1.25, and 1.65 m treatments, respectively. This reflected some variability in the depth of wetting among replicates, but also an apparent capacity for roots to grow beyond the depth of wetting of the bulk soil. There were no significant differences in the RLD above 0.9 m, but differences were apparent in the 1.0–1.2 m layers (Fig. 5*c*). In those layers the mean RLD was <0.05, 0.32, and 0.60 cm/cm³ in the 0.85, 1.25, and 1.65 m treatments, respectively.

Table 4. Observations and measurement of stress development in Expt 2

CTD (°C), Difference in temperature between canopy and ambient (21°C); DAA, days after anthesis. Within rows, numbers followed by the same letter are not significantly different ($P < 0.05$)

Date	0.85-m treatment	1.25-m treatment	1.65-m treatment
–62 DAA	Treatments established and rainfall excluded from this point		
–35 DAA	Differences in growth apparent		
Anthesis (7 Oct.)	Flag leaf curled, penultimate dying, 1–2 green leaves	No flag curling, lower leaves dying, 3 green leaves	No flag curling, little leaf death
20 DAA	No green leaf, heads 50% senescing	Half flag leaf green, heads just senescing	3/4 flag green, heads green
27 DAA	Plants mature	Head some green, peduncle yellow/green	1/2 flag green/rolled, peduncle yellow/green, head yellow/green
34 DAA	Plants mature	Trace green in few heads	Some green in peduncle and head
CTD (°C) 1010 hours	+ 1.9a	+ 0.7b	–1.3c
47 DAA	Final harvest		

Table 5. Biomass, yield, and yield components in Expt 2

Treatment	Anthesis				Maturity							
	Biomass (g/m ²)	Tillers (m ²)	Heads (m ²)	WSC ^A (g/m ²)	Biomass (g/m ²)	Yield (g/m ²)	Heads (m ²)	Grain (/head)	Grain (/m ²)	Grain wt (mg)	HI	WSC (g/m ²)
0.85 m	568	524	443	42	635	200	329	24.7	8180	25.3	0.31	2.3
1.25 m	600	551	551	59	850	322	367	33.1	12157	26.4	0.38	4.6
1.65 m	664	620	608	54	991	378	393	36.9	14445	26.3	0.38	6.0
<i>F</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	0.007	0.008	<i>n.s.</i>	0.05	0.02	<i>n.s.</i>	0.03	0.01
<i>l.s.d.</i>	–	–	–	–	176	90	–	9.7	4053	–	0.05	2.0

n.s., Not significant.

^AWater-soluble carbohydrate in the stem and leaf sheath.

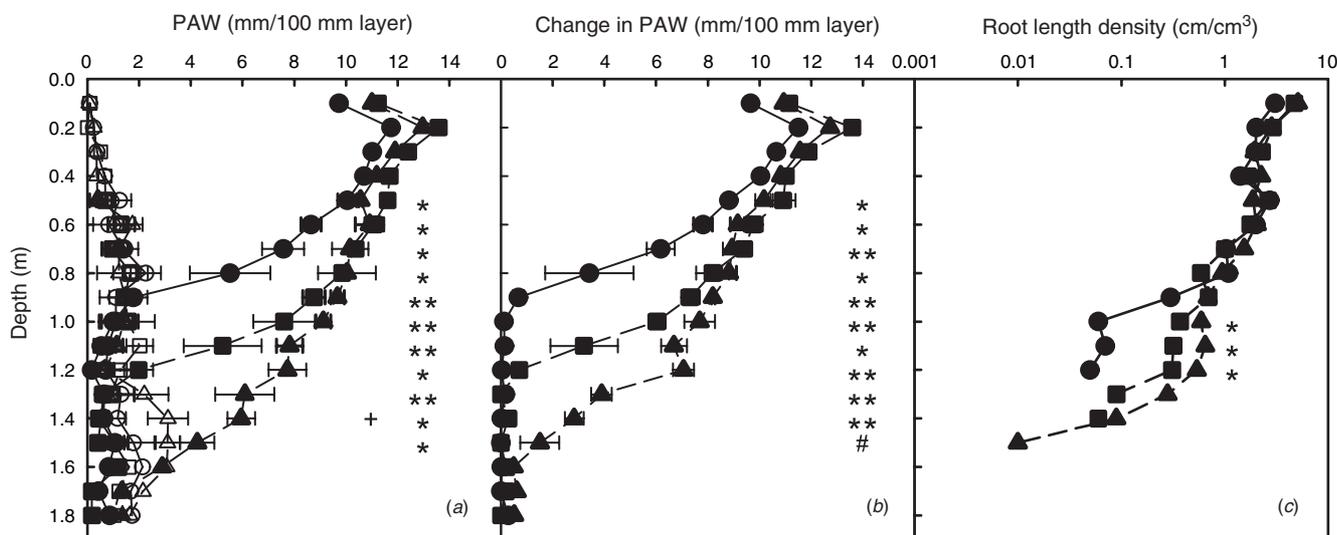


Fig. 5. Profiles of (a) plant-available water at the maximum soil water content (closed) and maturity (open), (b) changes in available water, and (c) root length density for the 0.85 (●), 1.25 (■), and 1.65 m (▲) depth of wetting treatments in Expt 2. Horizontal bars show standard error of mean at depths where treatment differences are significant (#*P* < 0.1; **P* < 0.05; ***P* < 0.001 at maturity; +*P* < 0.05 for maximum water content).

Water-use efficiency and marginal water-use efficiency

Estimates of WUE based on French and Schultz were high (>30 kg/ha.mm) presumably because the true evaporative loss was likely to have been less than the standard 110 mm estimate due to the mostly dry soil surface maintained from August under the fixed rooves. WUE based on total water use ranged from 14 to 21 kg/ha.mm, lower than in Expt 1, but within the range reported for well-managed crops. Isolating and quantifying the value of subsoil water was more difficult in Expt 2 because water use from the deeper soil layers was generally accompanied by significant uptake from upper soil layers during the stress period (Table 6). For example, the 1.65-m treatment used 7 mm more PAW from below 1.25 m than the 1.25-m treatment, but also used 8 mm more water from the 0.85–1.25 m layer during the stress period. Some differences in water use also reflected differences in the PAW at the onset of stress in upper soil layers rather than more complete soil drying (Fig. 5a). As a result, we estimated the MWUE based on the increase in yield associated with differences in the total water use from the time the stress was imposed. The values of MWUE calculated in this way varied

from 28 to 37 kg/ha.mm for comparisons among the treatments (Table 6). The MWUE based on total post-anthesis water use was 60 kg/ha.mm, similar to those in Expt 1, although differential water use in the upper 0.8 m, as well as treatment effects before anthesis may have contributed to these yield differences.

Discussion

Isolating and quantifying subsoil water use

The strategy adopted in Expt 1, based on experience gained previously at the site (Kirkegaard *et al.* 2001; Kirkegaard and Lilley 2007), was effective in isolating and quantifying the value of subsoil water under the conditions of terminal stress imposed. The elements of the strategy that made this possible included: (1) managing the water balance to avoid run-off or drainage losses by controlling water supply to a previously dry profile; (2) establishing the differences in subsoil water during the cooler winter months to avoid transient benefits when wetting up the soil profiles to different depths; (3) establishing and maintaining identical crop canopies in the treatments before the onset of the terminal stress; (4) managing the available soil water in the treatments to isolate a subsoil layer above which soil water

Table 6. Water-use efficiency (WUE) and marginal water-use efficiency (MWUE) (kg/ha.mm) for water used from different soil depths in Expt 2

Treatment	Water applied ^A (mm)	F&S WUE ^B	Total water uptake (mm)	WUE grain	Yield increase cf. 0.85 m (g/m ²)	Water extraction ^C (mm)			Total	MWUE of subsoil water	
						0–0.85 m	0.85–1.25 m	1.25–1.65 m		>0.85 m	>1.25 m
0.85 m	175	31.7	141	14.1	–	66	2	0	68		
1.25 m	206	34.3	171	19.2	122	82	21	0	101	37	
1.65 m	235	30.2	177	21.4	178	84	29	7	121	34	28
<i>F</i>	–	<i>n.s.</i>	<i>n.s.</i>	0.04	–	0.07	0.001	0.01	0.001	–	–
<i>l.s.d.</i>				5.5		16	4	4	15		

^AApril–October water applied.

^BF&S, French and Schultz (1984); calculated as WUE = [grain yield]/[April–October rainfall – 110].

^CFrom date of last water (6 Aug.) to maturity.

use was similar. Satisfying these conditions made it possible to attribute the additional yield produced in the 1.85-m treatment solely to the availability and use of subsoil water below 1.35 m. In Expt 2, the earlier onset and longer duration of the terminal stress created differences at anthesis in the size of the transpiring canopies and the yield potential developed (grain number) in the different treatments, as well as variation in the amount of water extracted from the soil profile above the subsoil treatment layers established. These effects, in common with most field experiments where crops are grown on different amounts of stored water under rainfed conditions, make it more difficult to isolate and quantify the value of the subsoil water to grain yield.

The value of subsoil water: marginal water-use efficiency (MWUE)

The value of the subsoil water to grain yield in Expt 1 was expressed as a marginal water-use efficiency (MWUE), the ratio of the additional yield (kg/ha) derived from the additional subsoil water use (mm). This value is an arithmetic construct developed primarily as a means of comparing the value of subsoil water with the widely used WUE value of 20–25 kg/ha.mm for whole-of-season water use developed by French and Schultz (1984). The French and Schultz WUE approach is itself a simplification and is variously criticised (Connor and Loomis 1991) or lauded (Passioura 2006), depending upon its application and the assumptions made regarding its use. Nevertheless the expected upper limit of 20–25 kg/ha.mm for total seasonal water use provides a useful benchmark with which to compare that achieved for subsoil water. Angus and van Herwaarden (2001) have pointed out that the assumption of an equal value of water supply throughout the season (implicit in French and Schultz 1984) is unjustified and provide retrospective analysis of their own field data for wheat under terminal stress, which suggests that the WUE for grain yield of wheat was 33 kg/ha.mm for the post-anthesis period. Condon *et al.* (1993) conducted a study of 8 wheat cultivars at Moombooldool, 100 km west of the present study, and separated the transpiration and evaporation components of water use. The mean transpiration efficiency for grain yield calculated from that study was 59 kg/ha.mm for post-anthesis transpiration. In a similar study reported by Condon and Richards (1993) and Condon *et al.* (2002), post-anthesis transpiration efficiency for grain averaged for 2 wheat varieties was 77 kg/ha.mm at Condobolin (1990) and 73 kg/ha.mm at Wagga Wagga (1989). A higher efficiency for water used after anthesis is not surprising because most of the post-anthesis assimilation is directed to the grain (Fischer 1979), and pre-anthesis assimilates stored in the stem and remobilised to the grain after anthesis can also contribute significantly to grain yield (Asseng and van Herwaarden 2003). In addition, under terminal stress, evaporation would constitute a smaller part of total water use after anthesis. As wheat roots reach their maximum depth at or around anthesis (Gregory 2006; Kirkegaard and Lilley 2007), subsoil water will inevitably be used later in the season, most probably after anthesis, potentially increasing the expected efficiency of conversion to grain compared with that for total seasonal water. The MWUE for subsoil water in Expt 1 was 59 kg/ha.mm if calculated on the basis of treatment means or 67 kg/ha.mm

based on regression analysis of individual replicates. This is 2–3 times higher than that expected for total seasonal water use in southern Australia (French and Schultz 1984), and double that previously reported for post-anthesis water use in the same region (Angus and van Herwaarden 2001), but falls within the range calculated from data by Condon and Richards (1993) and Condon *et al.* (1993, 2002), where transpiration was carefully partitioned from evaporation. Manschadi *et al.* (2006) predict an average WUE of 55 kg/ha.mm for post-anthesis water use in simulation studies of wheat crops in the northern wheatbelt.

The physiological measurements taken in the study provide a reasonable explanation as to how the additional subsoil water contributed to higher yield. In Expt 1, the differences between treatments were visually subtle but developed in the period 12–35 DAA. The 1.85-m treatment had a slower onset of water stress, maintained green leaf for longer (Fig. 3*b*), and maintained a higher assimilation rate for a short period during 12–27 DAA (Fig. 3*a*, Table 2), thus delaying and reducing the rate of decline in the soluble stem reserves during that period (Fig. 3*d*). Initially the combination of current assimilation and stem reserves was sufficient to satisfy the demand for grain growth in both treatments; however, from 35 DAA, kernel growth was restricted in the 1.35-m treatment (Fig. 3*f*). Presumably the short period of higher assimilation made possible by the subsoil water available at depth was sufficient to significantly increase the total assimilate available for grain growth in the 1.85-m treatment. At maturity, the potential contribution of stem reserves to yield ($\sim 300 \text{ g/m}^2$) was similar in both treatments (calculated as the change in stem weight or stem WSC; Fig. 3*c*, *d*), suggesting that the increased yield related to a period of higher assimilation, rather than to an increase in re-translocation. These observations are generally consistent with current understanding of the physiological processes of grain yield development under terminal stress (Richards *et al.* 2002). Calculated transpiration efficiency for biomass (biomass produced/mm water transpired) during the grain-filling stage (assuming that all water use was transpiration at that stage) in the 1.35 and 1.85 m treatment were 55 and 54 kg/ha.mm, respectively; very similar to the mean value of 55 kg/ha.mm that can be calculated for the data provided in Condon and Richards (1993) for an experiment at Condobolin, but higher than the 33 kg/ha.mm calculated from Condon *et al.* (1993). Part of the variation in post-anthesis transpiration efficiency for biomass results from differences in the vapour-pressure deficit (VPD) during the grain-filling stage, as reported for cereals by Kemanian *et al.* (2005). The transpiration efficiency for biomass in the experiments reported here (54–55 kg/ha.mm) is consistent with that reported by Kemanian *et al.* (2005) given that the average daily VPD measured at the site during grain filling was 1.14 kPa. The lower value of 33 kg/ha.mm reported by Condon and Richards (1993) is also consistent with the higher mean post-anthesis VPD of 2.0 kPa reported at the Moombooldool site post-anthesis.

In Expt 2, the earlier and more severe onset of stress made it difficult to isolate and evaluate the benefit of subsoil water to yield in the same way as was possible in Expt 1. The difficulty arose because differences in water use in the subsoil layers during the period of stress were accompanied by significant differences

in other soil layers, which presumably also contributed to the yield differences observed. As a result it was only possible to calculate the additional yield associated with differences in total water use, and not with subsoil water alone. Additional water use in the upper soil layers may be associated with the maintenance of green leaf area made possible by the subsoil water, in which case it can be considered to be a legitimate benefit of the subsoil water to yield. Excluding this water use from upper layers in the MWUE calculation generates high MWUE, particularly where water use from the subsoil is only a few millimetres. Adjusting the calculations to include total water use in Expt 2 gave a MWUE of 30–40 kg/ha.mm for the period of stress from early August. The MWUE calculated on post-anthesis water use was 60 kg/ha.mm but these calculations are spurious because much of the benefit to grain yield was associated with increased kernel number/head, an effect likely to have been influenced significantly by water used before anthesis (Fischer 1979). The potential contribution of stored stem WSC to grain yield was much less in Expt 2 (around 40–50 g/m²), presumably because the earlier onset of stress reduced WSC storage before anthesis. Post-anthesis transpiration efficiencies for biomass in Expt 2 were 79, 120, and 107 kg/ha.mm for the 0.85, 1.25, and 1.65 m treatments, respectively (calculated from Fig. 2b and Table 5). Although transpiration efficiency can increase under water stress (Abbate *et al.* 2004; Kemanian *et al.* 2005), the high values in Expt 2 could have resulted partly from effects of the permanent roof on diffuse light and evaporative conditions above the canopies.

Taken together, the experiments indicate that the high value of subsoil water use calculated as MWUE can arise from: (1) a period of higher assimilation during the post-anthesis period when most current assimilate is diverted to grain; (2) remobilisation of pre-anthesis assimilate stored as WSC in the stem contributing to yield, which coincides with the period when subsoil water is used; (3) water available in the subsoil may prolong green leaf area duration and increase water use from upper soil layers, contributing to (1) or (2) indirectly; and (4) the assumption of low evaporative loss.

Seasonal interactions and the value of subsoil water

The value of subsoil water for grain yield will vary according to seasonal rainfall distribution and soil type, although no comprehensive analysis of this has been attempted. General strategies have been proposed to maximise yield in relation to water supply across agro-ecological zones in Australia. For example, it is proposed that crops grown largely on stored water on the deep clay soils of the northern wheatbelt should moderate pre-anthesis water use to preserve sufficient water for grain filling (Passioura 1972), although deeper roots and more roots at depth are also likely to be beneficial in capturing water during grain filling (Ludlow and Muchow 1990). The relatively high mean estimates for post-anthesis WUE of 55 kg/ha.mm in the simulation study by Manschadi *et al.* (2006) for the region presumably involve a considerable contribution from water uptake from deeper subsoil layers. In contrast, on lighter soils in Mediterranean environments, increased early vigour and pre-anthesis water use are thought to reduce unproductive evaporative and drainage loss (Rebetzke and Richards 1999), although deeper roots may capture water and nitrogen leached

from upper layers late in the season, which can dry rapidly during grain fill (Hamblin 1988). On the deep clay loams in the equi-seasonal rainfall regions of southern NSW studied here, high variability in rainfall patterns calls for strategies that balance the water use for dry-matter production and that for grain production (Fischer 1979; Condon *et al.* 2002). The experiments reported here demonstrate that relatively small amounts of water used in deeper soil layers can be highly valuable to crop yield under the conditions of terminal stress imposed, which were not unlike those typical in the northern region. A more detailed simulation analysis of the seasonal variation in the value of subsoil water (1.2–1.8 m) at the site suggested that the MWUE could range from 0 to 84 kg/ha.mm (Lilley and Kirkegaard 2007). Values of 0 for MWUE (36% of seasons) arose from dry seasons in which the subsoil failed to wet up, or when subsoil water failed to increase yield. High values of MWUE (>50 kg/ha.mm) were less frequent (10%) and tended to occur in wetter seasons with high yield potential. In most seasons (57%) the MWUE was in the 30–50 kg/ha.mm range. Kemanian *et al.* (2005) have recently demonstrated that transpiration-use efficiency in cereals can vary from 30 to 80 kg/ha.mm as mean daily VPD declines from 2.0 to 0.5 kPa, and this is likely to explain at least some of the seasonal variation in the MWUE observed.

Simulation studies used in a predictive way are constrained to some extent by the need to make assumptions and use empirical constants to describe water use from dense, highly structured subsoil layers where RLD is low and root distribution heterogeneous (Wang and Smith 2004), which typifies the conditions in the subsoils of most Australian wheat crops. In these cases, significant testing at specific sites over many years, involving root and water uptake measurements, as provided in Lilley and Kirkegaard (2007), is necessary to support the validity of the assumptions made and the parameters used to describe water extraction from deep soil layers.

Root growth and water extraction from the subsoil

The maximum rooting depth measured at maturity in the various treatments in both experiments was generally consistent with previously reported root penetration rates of 11–12 mm/day from sowing to anthesis, and failure of wheat roots to penetrate far into soil layers with <45% PAW (Kirkegaard and Lilley 2007). In Expt 1, roots were measured in all layers in the 1.85-m treatment and significant water uptake was also observed from all depths (Fig. 4a). In the 1.35-m treatment, roots were also found below 1.35 m but at very low densities (<0.08 cm/cm³) and no water was extracted below 1.4 m. The failure to detect significant differences in RLD at individual depths between treatments was presumably due to inadequate sampling to account for the low root densities (0.01–0.1 cm/cm³), the clumping of roots in the highly structured subsoil, and the variation among individual replicates in the precise depth of the wetting front in the 1.35-m treatment (range 1.3–1.5 m). Nevertheless, the difference in the water extracted after anthesis in the 1.35–1.85 m layer in the 2 treatments (4.8 ± 1.6 mm v. 15.3 ± 1.7 mm) suggests that wetter subsoil, higher RLD, and possibly longer duration of green leaf area, combined to increase water uptake. The fact that only 15.3 mm of the estimated 31 mm of available water

was used below 1.35 m in the 1.85-m treatment is consistent with many previous studies on water uptake from structured clay subsoils (Passioura 1991) and presumably reflects the late arrival of the roots, the low RLD and the clumping of roots in structural features, and the rapidly diminishing transpiring surface as green leaf was effectively gone by 35 DAA.

The RLD in the upper soil layers in Expt 2 was generally similar to those in Expt 1; however, in Expt 2, significant differences were detected between treatments in the subsoil layers from 1.0 to 1.2 m. A small amount of available water remained in the 1.25–1.65 m layer in the 1.65-m treatment again possibly reflecting late arrival, the low RLD, clumping, and early maturity. The treatments generally dried the soil to a similar extent at all other depths at maturity, and differences in uptake above 0.85 m were more related to differences in the initial water content at the onset of stress, an artefact of the wetting-up process that was completed before the calculated stress period.

Agronomic implications

The levels of water-use efficiency achieved, up to 3 times that commonly expected for total seasonal water use, justify continued efforts to investigate agronomic and genetic strategies to capture more subsoil water. In areas where deep soils and seasonal rainfall generate such opportunities, these would include traditional agronomic approaches to promote deeper healthy root systems, to prolong the duration of green leaf area on appropriately sized crop canopies, and where possible to ameliorate subsoil constraints that reduce the depth and effectiveness of water extraction by crops. More novel strategies for future consideration include manipulations of canopy development through time using tactical use of nitrogen or fungicides (Gooding *et al.* 2005), or grazing management of dual-purpose wheat (Virgona *et al.* 2006), which can all potentially defer water use from early in the season to later in the season to capitalise on the higher water-use efficiency achieved at that stage. Breeders have developed wheat with high transpiration efficiency at the leaf level, which can conserve subsoil water without sacrificing yield potential; however, few breeding programs are specifically selecting for root traits to increase water use. Recent studies have demonstrated potential benefits and useful genetic variation in root architecture (Manschadi *et al.* 2006), and rooting depth and vigour (Gregory *et al.* 2005). The combination of improved varieties managed appropriately in specific environments may ultimately lead to better use of subsoil water. Further investigations of the seasonal variation in the value of subsoil water using carefully validated simulation models should provide useful direction to identify the most promising strategies to capitalise on improved subsoil water use.

Acknowledgments

We acknowledge financial support from GRDC (CSP00049) and thank landholders Ray and Beverly Norman for provision of land and water for the experiment. Excellent technical support was provided by staff at Ginninderra Research Station and by Ms Sara Hely and Ms Brooke Forsyth. We are also indebted to Dr Tony Condon for advice on plant physiological measurements and comments and discussions on early drafts, and to Dr Colin Jenkins for WSC analyses.

References

- Abbate PE, Dardanelli JL, Cantarero MG, Maturano M, Melchiorri RJM, Suero EE (2004) Climatic and water availability effects on water-use efficiency in wheat. *Crop Science* **44**, 474–483.
- Angus JF, van Herwaarden AF (2001) Increasing water use and water use efficiency in dryland wheat. *Agronomy Journal* **93**, 290–298.
- Asseng S, van Herwaarden AF (2003) Analysis of the benefits to wheat yield from assimilates stored prior to grain filling in a range of environments. *Plant and Soil* **256**, 217–229. doi: 10.1023/A:1026231904221
- Blum A, Shpiler L, Golan G, Mayer J (1989) Yield stability and canopy temperature of wheat genotypes under drought stress. *Field Crops Research* **22**, 289–296. doi: 10.1016/0378-4290(89)90028-2
- Condon AG, Richards RA (1993) Exploiting genetic variation in transpiration efficiency in wheat: an agronomic view. In 'Stable isotopes and plant carbon-water relations'. (Eds JR Ehleringer, AE Hall, GD Farquhar) pp. 435–450. (Academic Press: New York)
- Condon AG, Richards RA, Farquhar GD (1993) Relationships between carbon isotope discrimination, water use efficiency and transpiration efficiency for dryland wheat. *Australian Journal of Agricultural Research* **44**, 1693–1711. doi: 10.1071/AR9931693
- Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2002) Improving intrinsic water-use efficiency and crop yield. *Crop Science* **42**, 122–131.
- Connor DJ, Loomis RS (1991) Strategies and tactics for water-limited agriculture in low-rainfall mediterranean climates. In 'Proceedings International Symposium on Improvement and Management of Winter Cereals under Temperature, Drought and Salinity Stresses'. Cordoba, Spain, 26–29 Oct. 1987. pp. 441–465. (Instituto Nacional de Investigaciones Agrarias: Madrid, Spain)
- Dreccer MF, Rodriguez D, Ogbonnaya F (2002) Tailoring wheat for marginal environments: a crop modelling study. In 'Plant Breeding for the 11th Millennium. Proceedings of the 12th Australasian Plant Breeding Conference'. Perth, W. Aust, 15–20 September 2002. (Ed. JA McComb) pp. 457–462. (CD-ROM, Dept of Agriculture, Perth, WA)
- Dunin FX, Passioura J (2006) Prologue: amending agricultural water use to maintain production while affording environmental protection through control of outflow. *Australian Journal of Agricultural Research* **57**, 251–255. doi: 10.1071/ARv57n3.f0
- Fischer RA (1979) Growth and water limitation to dryland wheat yield in Australia: a physiological framework. *Journal of Australian Institute of Agricultural Science* **45**, 83–94.
- French RJ, Schultz JE (1984) Water use efficiency in wheat in a Mediterranean type environment. II. Some limitations to efficiency. *Australian Journal of Agricultural Research* **35**, 765–775. doi: 10.1071/AR9840765
- Geeves GW, Cresswell HP, Murphy BW, Gessler PE, Chartres CJ, Little IP, Bowman GM (1995) The physical, chemical and morphological properties of soils in the wheat-belt of southern NSW and northern Victoria. NSW Department of Conservation and Land Management/CSIRO Australia Division of Soils Occasional Report.
- Gooding MJ, Gregory PJ, Ford KE, Pepler S (2005) Fungicide and cultivar affect post-anthesis patterns of nitrogen uptake, remobilisation and utilisation efficiency in wheat. *The Journal of Agricultural Science* **143**, 503–518. doi: 10.1017/S002185960500568X
- Gregory PJ (2006) 'Plant roots: growth activity and interaction with soils.' (Blackwell Publishing: Oxford, UK)
- Gregory PJ, Gooding MJ, Ford KE, Hendriks P, Kirkegaard JA, Rebetzke GJ (2005) Genotype and environment influences on the performance of crop root systems. *Aspects of Applied Biology* **73**, 1–10.
- Hamblin AP (1988) Soil physical constraints to root growth: implications for water uptake and management. In 'Constraints to root growth'. FAO/IAEA Technical Bulletin. (Ed. G Bowen) (FAO: Rome)
- Isbell RF (2002) 'The Australian soil classification.' Rev. 1st edn (CSIRO Publishing: Melbourne, Vic.)

- Kemanian AR, Stockle CO, Huggins DR (2005) Transpiration-use efficiency in barley. *Agricultural and Forest Meteorology* **130**, 1–11. doi: 10.1016/j.agrformet.2005.01.003
- King J, Gay A, Sylvester-Bradley R, Bingham I, Foulkes J, Gregory P, Robinson D (2003) Modelling cereal root systems for water and nitrogen capture: towards an economic optimum. *Annals of Botany* **91**, 383–390. doi: 10.1093/aob/mcg033
- Kirkegaard JA, Howe GN, Pitson G (2001) Agronomic interactions between drought and crop sequence. In 'Proceedings of the 10th Australian Agronomy Conference'. Hobart. (www.regional.org.au/au/asa/2001/4/c/kirkegaard1.htm)
- Kirkegaard JA, Lilley JM (2007) Root penetration rate—a benchmark to identify soil and plant limitations to rooting depth in wheat. *Australian Journal of Experimental Agriculture* **47**, 590–602. doi: 10.1071/EA06071
- Lilley JM, Kirkegaard JA (2007) Seasonal variation in the value of subsoil water to wheat: A simulation study in southern NSW. *Australian Journal of Agricultural Research*, (in press).
- Ludlow MM, Muchow RC (1990) A critical evaluation of traits for improving crop yields in water-limited environments. *Advances in Agronomy* **43**, 107–153.
- Manschadi AM, Christopher J, deVoil P, Hammer GL (2006) The role of root architectural traits in adaptation of wheat to water-limited environments. *Functional Plant Biology* **33**, 823–837. doi: 10.1071/FP06055
- Passioura JB (1972) The effect of root geometry on the yield of wheat growing on stored water. *Australian Journal of Agricultural Research* **23**, 745–752. doi: 10.1071/AR9720745
- Passioura JB (1983) Roots and drought resistance. *Agricultural Water Management* **7**, 265–280. doi: 10.1016/0378-3774(83)90089-6
- Passioura JB (1991) Soil structure and plant growth. *Australian Journal of Soil Research* **29**, 717–728. doi: 10.1071/SR9910717
- Passioura JB (2006) Increasing crop productivity when water is scarce—from breeding to field management. *Agricultural Water Management* **80**, 176–196. doi: 10.1016/j.agwat.2005.07.012
- Rebetzke GJ, Read JJ, Barbour MM, Condon AG, Rawson HM (2000) A hand-held porometer for rapid assessment of leaf conductance in wheat. *Crop Science* **40**, 277–280.
- Rebetzke GJ, Richards RA (1999) Genetic improvement of early vigour in wheat. *Australian Journal of Agricultural Research* **50**, 291–302. doi: 10.1071/A98125
- Richards RA, Rebetzke GJ, Condon AG, van Herwaarden AF (2002) Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. *Crop Science* **42**, 111–121.
- Smucker AJM, McBurney SL, Srivastava AK (1982) Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation systems. *Agronomy Journal* **74**, 500–503.
- Tennant D, Hall D (2001) Improving water use of annual crops and pastures—limitations and opportunities in Western Australia. *Australian Journal of Agricultural Research* **52**, 171–182. doi: 10.1071/AR00005
- van Herwaarden AF, Angus JF, Richards RA, Farquar GD (1998) Haying off, the negative grain yield response of dryland wheat to nitrogen fertiliser. II. Carbohydrate and protein dynamics. *Australian Journal of Agricultural Research* **49**, 1083–1093. doi: 10.1071/A97040
- Virgona JM, Gummer FAJ, Angus JF (2006) Effects of grazing on wheat growth, yield, development, water use, and nitrogen use. *Australian Journal of Agricultural Research* **57**, 1307–1319. doi: 10.1071/AR06085
- Wang E, Smith CJ (2004) Modelling the growth and water uptake function of plant root systems: a review. *Australian Journal of Agricultural Research* **55**, 501–523. doi: 10.1071/AR03201

Manuscript received 28 August 2006, accepted 31 January 2007