

315 AGRO

315

THE BRITISH LIBRARY

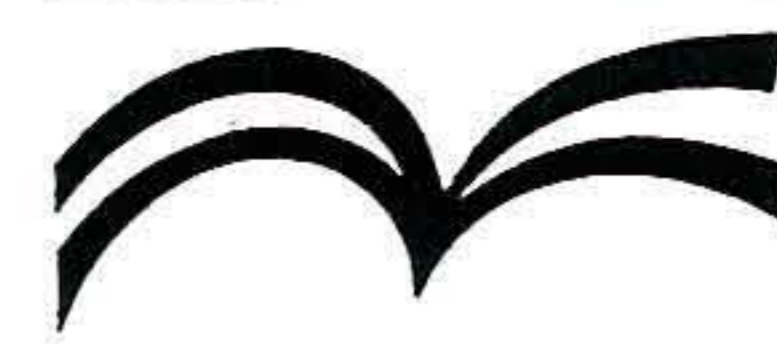


Document Supply Centre

This document has been supplied by, or on behalf of,  
The British Library Document Supply Centre  
Boston Spa, Wetherby, West Yorkshire LS23 7BQ  
UNITED KINGDOM

**WARNING:** Further copying of this document  
(including storage in any medium by electronic  
means), other than that allowed under the copyright  
law, is not permitted without the permission of the  
copyright owner or an authorised licensing body.

- Pitcher LH, Brennan E, Hurley A, Dunsmuir P, Tepperman JM, Zilinskas BA. 1991. Overproduction of petunia chloroplastic copper/zinc superoxide dismutase does not confer tolerance in transgenic tobacco. *Plant Physiology* **97**, 452-5.
- Polle A, Rennenberg H. 1991. Superoxide dismutase activity in needles of Scots pine and Norway spruce under field and chamber conditions: lack of ozone effects. *New Phytologist* **117**, 335-43.
- Scandalios JG. 1993. Oxygen stress and superoxide dismutases. *Plant Physiology* **101**, 7-12.
- Sen Gupta AS, Webb RP, Holaday AS, Allen RD. 1993. Overexpression of superoxide dismutase protects plants from oxidative stress. *Plant Physiology* **103**, 1067-73.
- Van Camp W, Willekens H, Bowler C, Van Montagu M, Inzé D, Reupold-Popp P, Sanderman Jr H, Langebartels C. 1994. Elevated levels of superoxide dismutase protect transgenic plants against ozone damage. *Bio/Technology* **12**, 165-8.
- Vaughan D, DeKock PC, Ord BG. 1982. The nature and localization of superoxide dismutase in fronds of *Lemma gibba* L. and the effect of copper and zinc deficiency on its activity. *Physiologia Plantarum* **54**, 253-7.
- Wenzel AA, Schlautmann H, Jones CA, Küppers K, Mehlhorn H. 1995. Aminoethoxyvinylglycine, cobalt and ascorbic acid all reduce ozone toxicity in mung beans by inhibition of different steps during ethylene biosynthesis. *Physiologia Plantarum* **93**, 286-90.



# Water uptake resumption following soil drought: a comparison among four barley genotypes

Jon M. Wraith<sup>1,3</sup>, John M. Baker<sup>2</sup> and Thomas K. Blake<sup>1</sup>

<sup>1</sup> Plant, Soil and Environmental Sciences Department, Montana State University, Bozeman, MT 59717-0312, USA

<sup>2</sup> USDA-ARS Soil and Water Management Unit, 1991 Upper Buford Circle, St Paul, MN 55108, USA

Received 6 January 1995; Accepted 29 March 1995

## Abstract

Soil water resulting from episodic growing season rainfall evaporates rapidly in semi-arid regions. Plants may not benefit from such water additions if near-surface roots are unable to resume water uptake rapidly following periods of soil water deficit. Our objectives were to develop a means of quantifying root uptake responses in the upper soil layer following rewetting after soil water deficit, and to evaluate the existence of genotypic differences among four diverse barley (*Hordeum vulgare* L.) genotypes in this regard. Plants were grown in replicate soil columns having hydraulically isolated surface and subsoil layers, and instrumented with time-domain reflectometry (TDR) waveguides. The upper 0.05 m soil layer was allowed to dry to  $-1.8$  to  $-3.0$  MPa for 10–14 d, during which time subsoil wetness was maintained at about  $-0.6$  to  $-0.7$  MPa. The time-course of soil water uptake was monitored at 0.5 h intervals following rewetting of the surface layer. Substantial water uptake began 1 d after rewetting following 10 d, and 2–3 d after rewetting following 14 d of water deficit. Rate of water uptake was more rapid in response to a second rewetting 5–7 d later. Consistent genotypic responses in terms of cumulative water uptake on a whole plant and leaf area-specific basis were observed during each trial. These results have application to evaluating drought hardiness and interspecific competitive ability under semi-arid conditions, and to investigations of root physiological and morphological changes that contribute to recovery from water deficit.

Key words: *Hordeum vulgare*, root water uptake, soil water deficit, time-domain reflectometry.

## Introduction

Plant water status in many arid and semi-arid areas is dependent on rainfall for replenishment of near-surface soil water. These upper soil layers generally contain the greatest concentrations of both roots and nutrients, but are subject to severe dehydration from the combined effects of root uptake and direct evaporative loss to the atmosphere. Potential loss of water from roots to dry soil may be minimized by suberization and by secondary thickening of endodermal cell walls (Sanderson, 1983; North and Nobel, 1991; Cruz *et al.*, 1992), but this may also inhibit absorption of soil water that might subsequently become available following rainfall or irrigation. In such situations, the transpiring plant and the evaporating soil surface are competitors for the water that has been added to the system. This is particularly so in the case of light or moderate rains which may rewet only the upper few centimetres of the profile. Any lag in recovery of root absorptive function favours soil evaporation at the expense of transpiration. In water-limited environments, reductions in transpiration result in concomitant reductions in dry matter production (Tanner and Sinclair, 1983). Typical precipitation patterns in the small grain production region of north-central Montana emphasize the importance of relatively small and infrequent rainfall during the growing season. Mean annual precipitation in this area ranges from about 250–450 mm, and is representative of conditions in many semi-arid regions of the Western United States (Sala *et al.*, 1992) and elsewhere. Typical growing season rainfall events are separated by 7–20 d, and usually supply between 2 mm and 20 mm of water.

The majority of investigations concerning plant response during and following drought have focused on

<sup>3</sup> To whom correspondence should be addressed. Fax: +1 406 994 3933.

leaf or canopy water relationships. These have generally indicated that the extent of the drought effects are related to the magnitude and duration of the stress period, and that leaf water potential ( $\Psi_1$ ) recovers more rapidly than does stomatal function. For example, recovery of transpiration rate following water stress imposed by cooling roots of 8-d-old wheat plants to 1 °C for 1–3 h was linearly related to length of the stress period (Bengsten *et al.*, 1977). Sala *et al.* (1982) found that pre-dawn and midday  $\Psi_1$  of *Bouteloua gracilis* (H.B.K.) Griffiths recovered rapidly following prolonged drought, while leaf conductance ( $g_s$ ) response was much slower in comparison. BassiriRad and Caldwell (1992) noted that  $\Psi_1$  required 3 d and  $g_s$  12 d to return to pre-stressed levels following rewetting in two perennial tussock grasses. Although the magnitude of  $\Psi_1$  and  $g_s$  were affected by drought severity, BassiriRad and Caldwell (1992) reported no differential response in recovery of these indices following rewetting between their moderate and severe drought treatments. Sala *et al.* (1982) suggested that the primary significance of prolonged drought and its after-effects rests in their impact on carbon assimilation.

Although of considerable interest from a photosynthetic standpoint, above-ground measures of plant response during and following soil drought provide only indirect indications of associated root system responses or actual soil water uptake, particularly under normal conditions of spatially variable soil wetness and root system density. Improved understanding of root function during and immediately following soil drought is of considerable practical and fundamental importance (Passioura, 1983, 1988; Lauenroth *et al.*, 1987; Baker *et al.*, 1992). Methods for quantifying and comparing the ability of desiccated root systems to resume water uptake following rewetting are needed to assess the competitive ability of plant species or cultivars in this regard. Existence of genotypic variation in the ability of crop species to respond rapidly to ephemeral near-surface water reserves may provide opportunities for incorporation of such traits into breeding programmes. This ability may be expected to confer superior productivity under transient drought conditions typical in semi-arid regions (Sala *et al.*, 1992), and in the presence of competing ruderal species (Jordan, 1993). Similar differences among species and genotypes may also be ecologically significant, particularly with respect to plant succession, invasion by non-native species, and plant community responses to short- or long-term climatic fluctuation.

Current knowledge of root hydraulic properties and water uptake following water stress is based largely on work with desert succulents. Nobel and coworkers (e.g. Lopez and Nobel, 1991; North and Nobel, 1991, 1992;

Huang and Nobel, 1992, 1993) have characterized changes in root hydraulic conductance for several CAM species during and following imposition of water stress. However, the degree of correspondence between their results and those for temperate plant species is presently unknown. The relatively high degree of dissimilarity among sympatric plant species in temperate wildland ecosystems, combined with temporal and spatial heterogeneity of limiting soil resources (e.g. see chapters in Caldwell and Pearcy, 1994), suggests substantial relevance of these topics.

Wraith and Baker (1991) found that a water-stressed sorghum (*Sorghum bicolor* [L.] Moench) plant was unable to extract significant quantities of water from the soil surface layer for at least 2 d following rewetting. The latter investigation demonstrated the potential to use automated and multiplexed time-domain reflectometry (TDR) to evaluate plants' abilities to resume soil water uptake following drought. A primary advantage of this approach is the ability to measure responses of plants having intact and undisturbed root systems in natural rooting media. We report here on comparisons among four diverse barley genotypes for the ability to resume water uptake rapidly from the surface soil layer following 10–14 d of soil water deficit. We selected these plant materials for two reasons: (i) to evaluate and index potential variance in water uptake resumption within the genome of an important semi-arid crop species; and (ii) to serve as a rigorous test of our ability to differentiate water uptake responses among plants having similar morphology and physiology.

## Materials and methods

### *Plant material and growth conditions*

Four barley genotypes were selected based on their genetic dissimilarity and their prior use as parents in molecular mapping experiments (Kleinhofs *et al.*, 1993; Blake, 1993). Dicktoo, a winter barley, requires vernalization to initiate flowering and did not flower in our experiments. Harrington (a 2-rowed variety), Steptoe (a 6-rowed derivative of the Coast germplasm group), and Morex (a 6-rowed derivative of the Manchuria germplasm group) are all spring barleys and do not require vernalization. Three seeds were planted in each column, and thinned to a single plant after 21 d. Soils were watered liberally during plant establishment, followed by imposition of drought treatments about 30 d after planting.

Two trials were conducted in greenhouse facilities at the Montana State University Plant Growth Center. Environmental conditions were monitored continuously using an electronic datalogger (21X, Campbell Scientific, Inc., Logan, UT, USA<sup>1</sup>). *PPFD* levels (top of soil columns) ranged from 600–900  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (LI190, LiCOR, Lincoln, NE, USA) during sunny days to about 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  under primary

<sup>1</sup> Mention of company names or commercial products is for the convenience of the reader and does not imply endorsement by Montana State University or USDA-ARS.

illumination by 1000 W metal halide lamps. Daylength was 14 h with 1 h ramp periods at morning and evening. Air temperature fluctuated between about 12 °C (night) and 20–25 °C (day), with uncontrolled RH of 0.2 to 0.4 (HMP35C, Vaisala, Inc., Woburn, MA, USA) over the 5-month experimental period.

#### Soil columns, water content measurement, and drought treatments

Twenty four 0.15 m diameter by 0.5 m deep PVC columns were packed with Brocko silt loam soil (coarse-silty, mixed Borollic Calciorthids) to about 1.2 Mg m<sup>-3</sup> bulk density. Mineral nutrients (N, P, K, micronutrients) were added to each column in accordance with soil test results and soil fertility recommendations for small grains. A length of tubing routed to the base of each column enabled sub-irrigation.

Surface and subsoil layers were hydraulically isolated using barriers at 0.05 m depth. This depth was chosen to define an approximate zone of expected rewetting from small rainfall events in semi-arid regions (Sala and Lauenroth, 1982; Sala *et al.*, 1992), and where competitive water loss to evaporation would be maximal. The initial investigation utilized a cheesecloth layer impregnated with beeswax. These were impermeable to water while offering minimal resistance to root penetration. Barriers in the second trial consisted of two layers of no. 10 mesh stainless wire cloth separated by about 5 mm of 3 mm diameter styrofoam beads (loose rhombohedral packing). Layers of cheesecloth outside each wire screen prevented intrusion of soil particles, and large pore size within the barriers resulted in an effective impediment to upward flow of liquid water, while precluding development of saturated conditions above.

One 0.4 m length 3-rod TDR waveguide was installed vertically through the subsoil layer of each soil column, and a second 0.10 m waveguide was horizontally inserted midway between the hydraulic barrier and the soil surface (Fig. 1). These were monitored using an automated TDR control and acquisition system consisting of a metallic TDR cable tester (1502C, Tektronix, Redmond, OR, USA), coaxial TDR multiplexers (Vadose Zone Equip. Co., Amarillo, TX, USA), and notebook microcomputer. Volume water content ( $\theta_v$ ) was measured in each soil stratum of all columns at 1 or 2 h intervals during plant establishment and drought imposition, then at 0.5 h intervals following rewetting. Each cable tester output represented an internal average of eight sampled waveforms, and two of these were acquired and analysed for each (mean) water content determination. The TDR control and acquisition program, modified from Baker and Allmaras (1990), required about 3.5 min to complete a set of measurements for the 24 surface soil layers. A soil water retention relationship ( $\Psi/\theta$ ) for the Brocko soil was determined using a combination of pressure plate and psychrometric techniques. Resulting data were fitted to van Genuchten's (1980) parametric equation to facilitate interpolation of soil matric potential based on measured volume water contents.

Minimum soil water potential levels of -1.8 to -3.0 MPa ( $\theta_v=0.1-0.09$ ) were maintained for 10 d (first trial) to 14 d (second trial) in surface soils, during which time subsoil reserves were drawn down and maintained at -0.6 to -0.7 MPa ( $\theta_v=0.14-0.16$ ) for about 1 week prior to rewetting. These soil conditions are representative of what may occur in the field under semi-arid climatic regimes (Wraith *et al.*, 1987; Richards and Caldwell, 1987). Time from planting to rewetting was 64 d during the first trial and 48 d during the second trial.

Immediately prior to rewetting, plants in two columns were severed about 20 mm above-ground to provide controls for

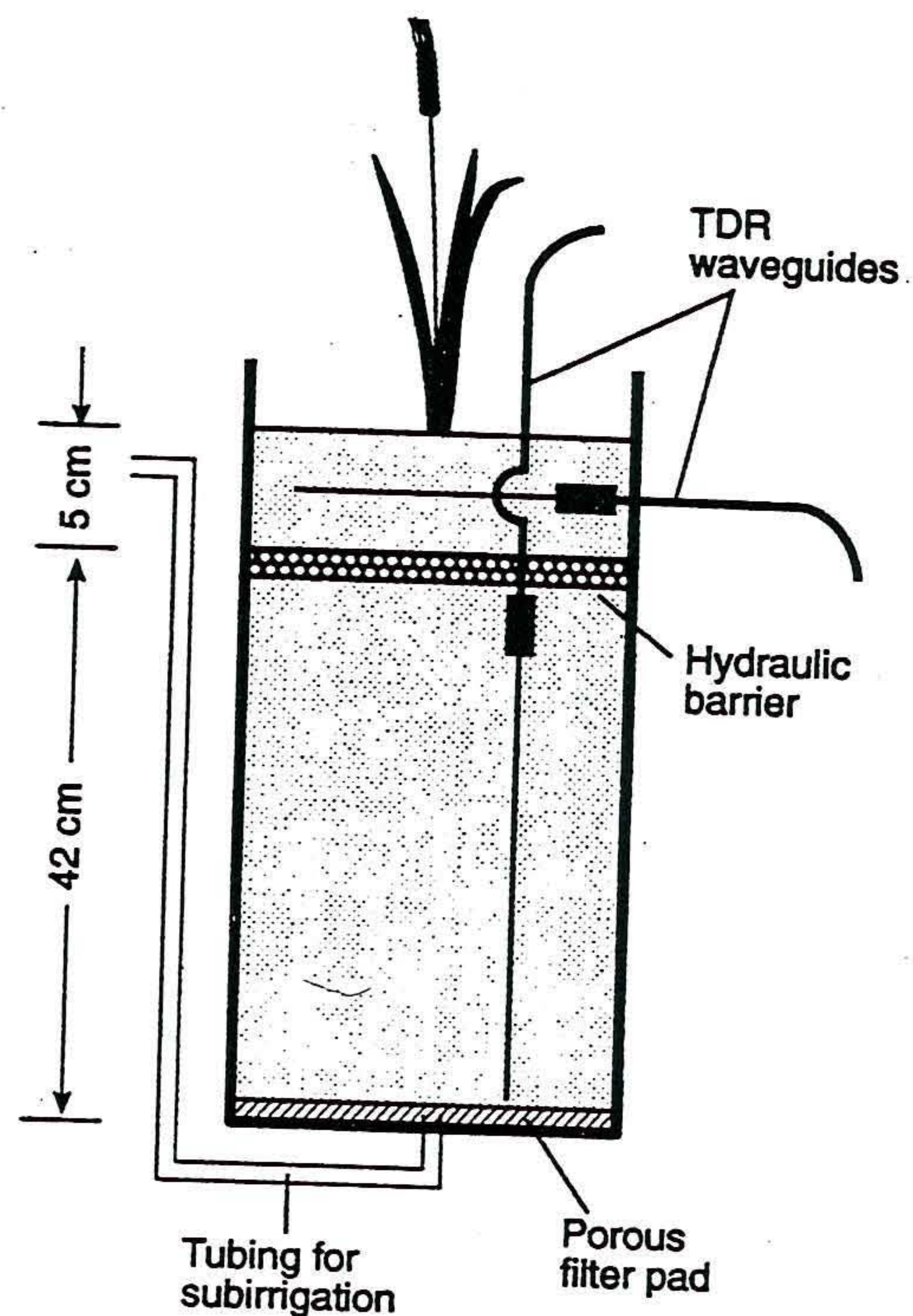


Fig. 1. Diagrammatic representation of soil columns for estimation of near-surface soil water uptake resumption (not to scale).

estimating direct soil evaporation. Near-surface soil layers were then rewet to column capacity, and the time-course for water uptake resumption monitored for each column. After 5–7 d, surface layers were rewet a second time and changes in soil water content followed for an additional 4 d. Subsurface soil layers were maintained at about -0.6 MPa ( $\theta_v=0.15$ ) during this time. The second rewatering of the surface layer allowed us to evaluate any effects of 'preconditioning' following the first water application on subsequent plant uptake responses. A 20 mm-thick foam disc was fitted against the soil surface inside each column to minimize evaporative water loss during the resumptive phase. A slit accommodated the barley plant and coaxial TDR cable. Identical discs were fashioned for control columns, and were fitted around severed culms to duplicate more closely the treatment column surface conditions. Plant water uptake for each column was estimated as the difference between total water loss and mean evaporative water loss from control (severed plant) columns. Volume of soil water change (mm<sup>3</sup>) was divided by column surface area (mm<sup>2</sup>) to obtain length units. Results of our initial trial indicated appreciable loss of water from control columns. Aluminium foil was therefore fitted over open column ends in addition to the above precautions during the second trial.

At the conclusion of each experiment, plants were rehydrated for 1 d by wetting columns to container capacity, and projected leaf area of severed plants was determined using a flatbed area meter (Li-3100, LiCOR, Lincoln, NE, USA). Cumulative soil water uptake following each surface rewetting was calculated on a whole plant basis, and in terms of specific (projected) leaf area in order to adjust for different plant sizes. Soil water uptake data were smoothed and first derivatives calculated using a least-squares convolution procedure (Savitzky and Golay, 1964) to estimate instantaneous rates of water uptake (Wraith and Baker, 1991).

## Results

Soil water content data confirmed that hydraulic/capillary barriers separating near-surface and subsoil layers resulted in individually manipulable and discrete soil volumes, while inspection of root systems following harvest revealed no discernible impediment to root growth and proliferation. Visual examination indicated abundant roots in the upper 50 mm soil layer, as well as in the subsoil; the proportion of total root length in the near-surface layer was estimated to be about 0.15 to 0.2. This is in reasonable agreement with field measurements of root depth distribution for barley (Dwyer *et al.*, 1988; Soon, 1988).

Leaf areas at termination of the initial trial, i.e. 73 d after planting, increased in the order Steptoe < Morex < Harrington < Dicktoo (Fig. 2a). All Steptoe and a few Morex plants had fully-exserted grain heads by this time, while two Harrington plants had awns projecting above the leaf sheath. Substantial uptake of soil water from the surface layer was evident beginning on the first day following rewetting for most genotypes (Figs 3, 4). Although we observed considerable variation among replicate columns, significant differences in water uptake response among genotypes were apparent. Specific cumulative water use by Harrington was somewhat greater than for the other genotypes by the third and fourth days after water addition, although significantly so only for a portion of this time (Fig. 3). Following a second addition of surface water, Harrington exhibited significantly greater leaf-specific cumulative uptake for about 3 d, beginning 1 d post-addition. Steptoe tended to lag behind the other genotypes in terms of its specific soil water uptake, although differences were seldom significant (Fig. 3). Because Steptoe had the smallest leaf areas

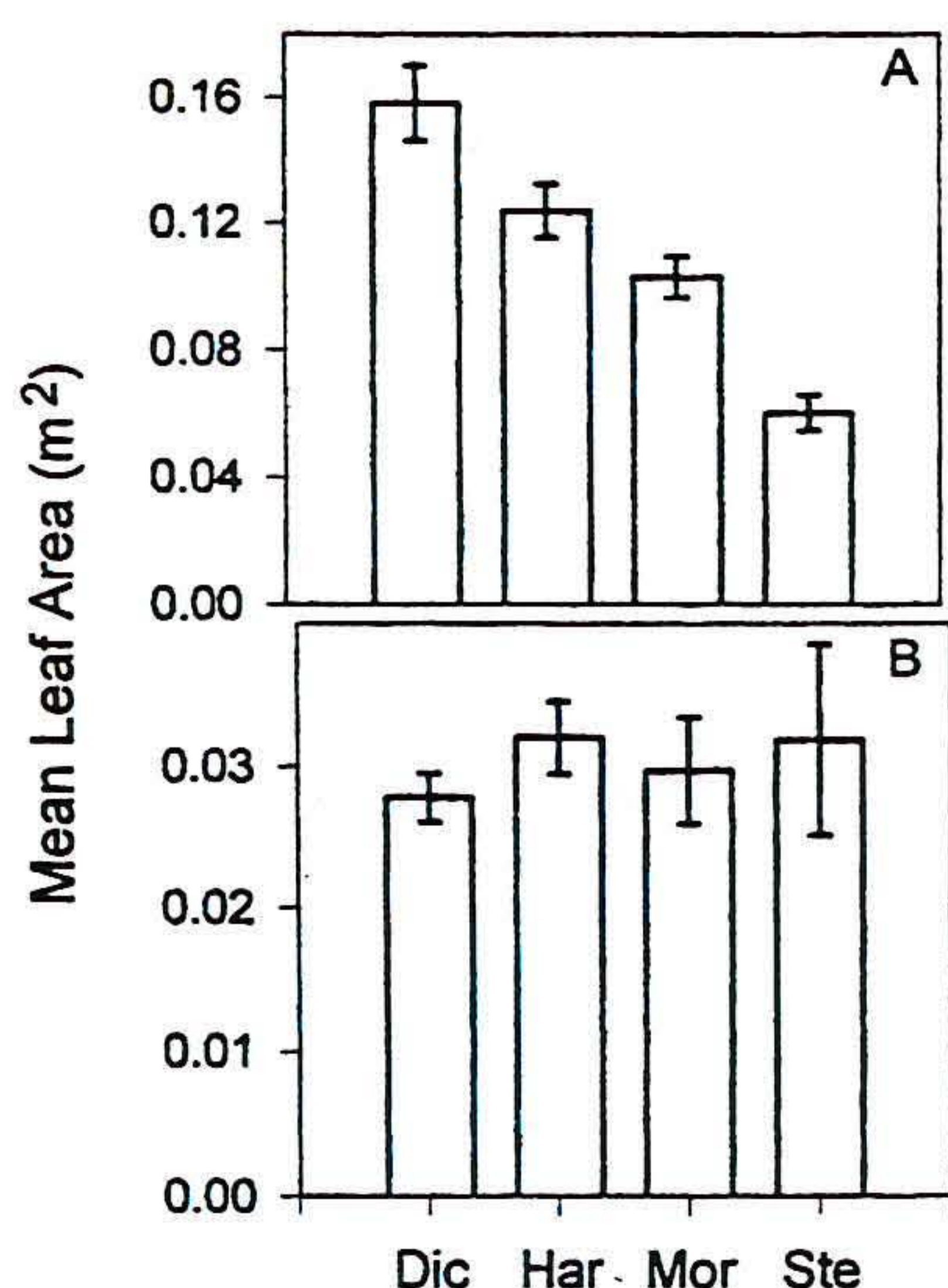


Fig. 2. Mean leaf area per plant  $\pm$ SEM ( $m^2$ ;  $n=4$  or  $5$ ) one day after termination of first (A) and second (B) experiments.

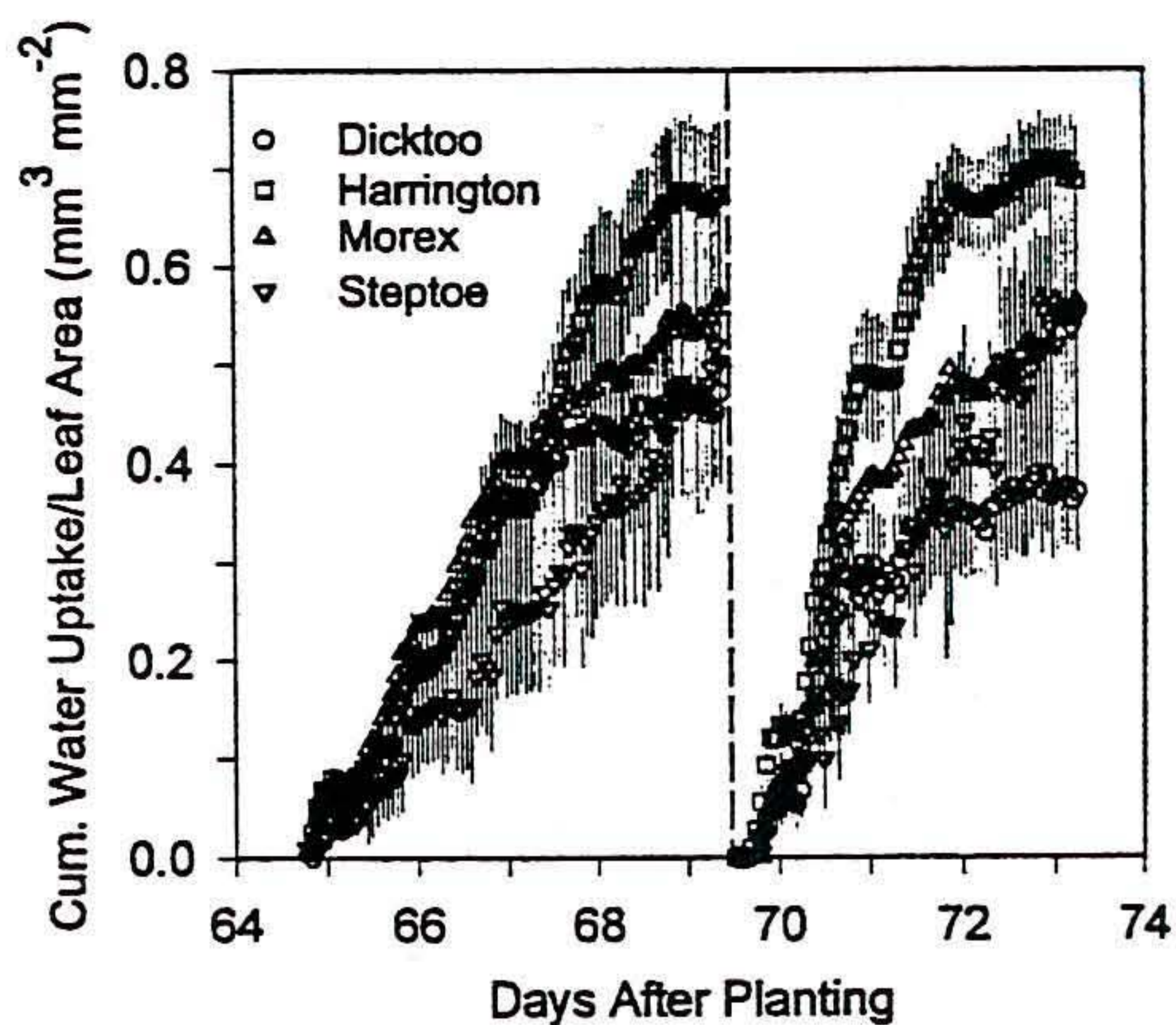


Fig. 3. Cumulative water uptake from upper 50 mm soil (mean  $\pm$ SEM;  $n=4$  or  $5$ ) on leaf area-specific basis ( $mm^3 mm^{-2}$ ) following first and second column rewetting during first uptake resumption trial. Columns were rewetted on Days 64.7 and 69.4. For clarity, every third data point illustrated, Morex error bars not shown (NSD all other genotypes).

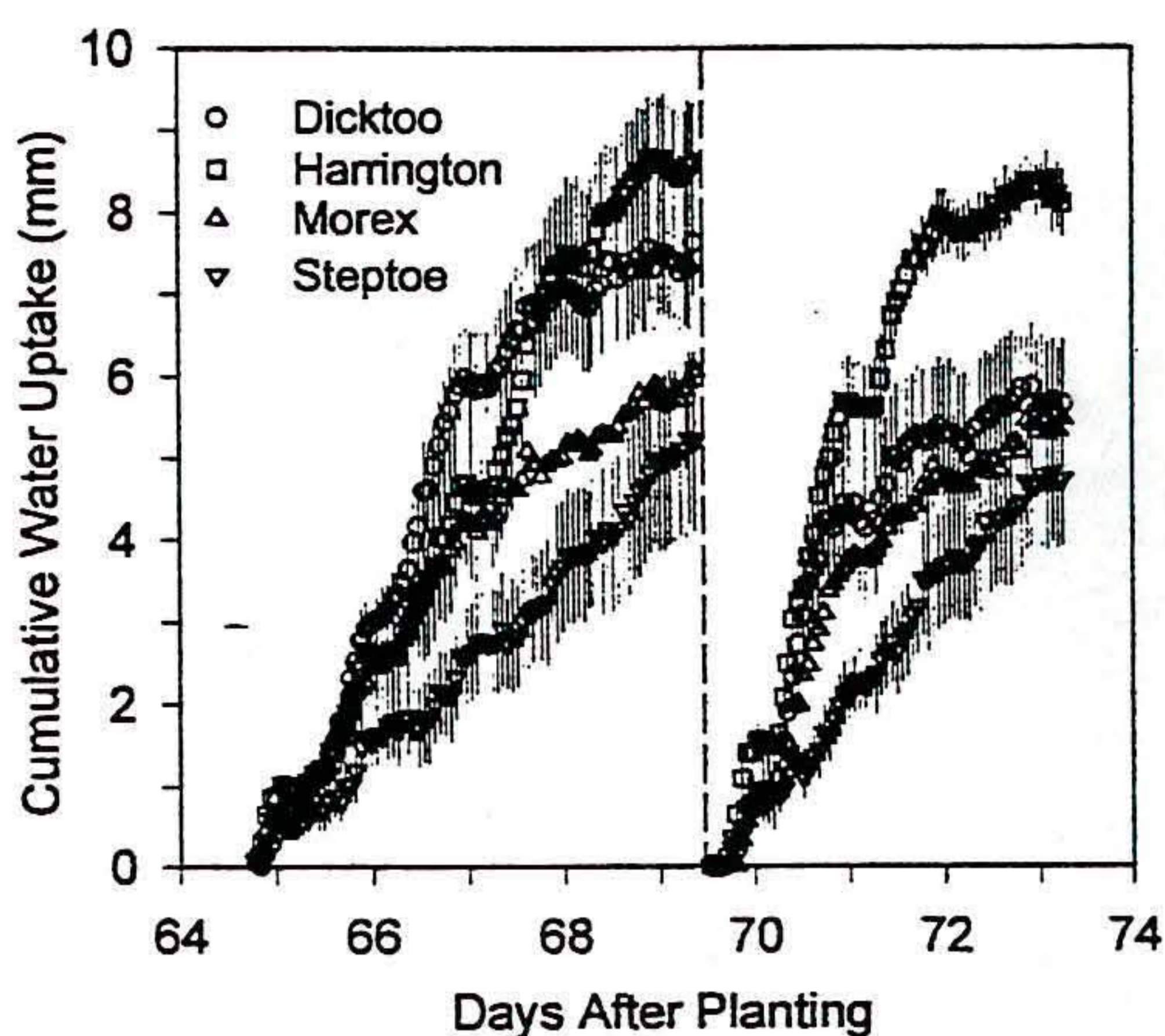


Fig. 4. Cumulative water uptake from upper 50 mm soil (mean  $\pm$ SEM;  $n=4$  or  $5$ ) on whole-plant basis (mm) following first and second column rewetting during first uptake resumption trial. Columns were rewetted on Days 64.7 and 69.4. For clarity, every third data point illustrated. Morex error bars not shown; significantly different than Harrington during Days 68 to second rewetting, 71 to completion, otherwise NSD.

(Fig. 2a), cumulative water use on a per-plant basis was much lower than for two of the three remaining genotypes (Fig. 4). Cumulative water uptake (whole plant basis) by Harrington was greater than for Morex beginning 3 d following the initial rewetting, and was greater than for all other genotypes beginning 2 d after the second water application (Fig. 4).

Time from planting to rewetting was 16 d less (i.e. 48 versus 64 d) during the second trial than for our initial investigation. Plants were thus less phenologically advanced, and mean leaf area at harvest was similar for all genotypes (Fig. 2b). Total leaf areas were considerably smaller than following the initial trial, ranging from about one-half for Steptoe (the fastest maturing) to one-fifth

for Dicktoo (a winter annual). A few Steptoe plants had awns protruding from the leaf sheath.

Significant water use was not evident until the second (Dicktoo, Harrington, Morex) or third (Steptoe) day following surface rewetting (Fig. 5). Cumulative water uptake on a leaf-specific basis was lower for Steptoe by late in the second day, and remained so for the duration of the initial resumption phase as well as for much of the second resumption period. Only when water use levelled off in response to diminished available water supply did cumulative depletion become similar among genotypes following the second watering (Fig. 5). Cumulative leaf-specific water uptake was greater for Harrington from the third through fifth days following initial water application, but uptake declined as available water reserves were depleted. Soil matric potential in surface layers of Harrington columns was about  $-1.2$  to  $-1.7$  MPa prior to the second water application and at termination of the experiment, and was somewhat less negative for the remaining genotypes. Harrington, Morex, and Dicktoo all exhibited high rates of leaf-specific uptake on the day following the second addition of water to the surface soil layer (as inferred from slopes of measured water uptake), while Steptoe achieved similar rates 1 d later (Fig. 5).

Because mean leaf area was similar between genotypes (Fig. 2b), patterns of cumulative water uptake on a whole-plant basis (Fig. 6) were similar to those expressed relative to projected leaf area (Fig. 5). Cumulative soil water usage by Harrington was greater by the end of the second day following initial water application, and remained so nearly until the second rewetting (Fig. 6). Steptoe had lower cumulative water uptake during the third and fourth days post-initial rewetting. Response time and rate of water uptake following the second surface water application were more rapid than following the first, with high extraction evident on the day following

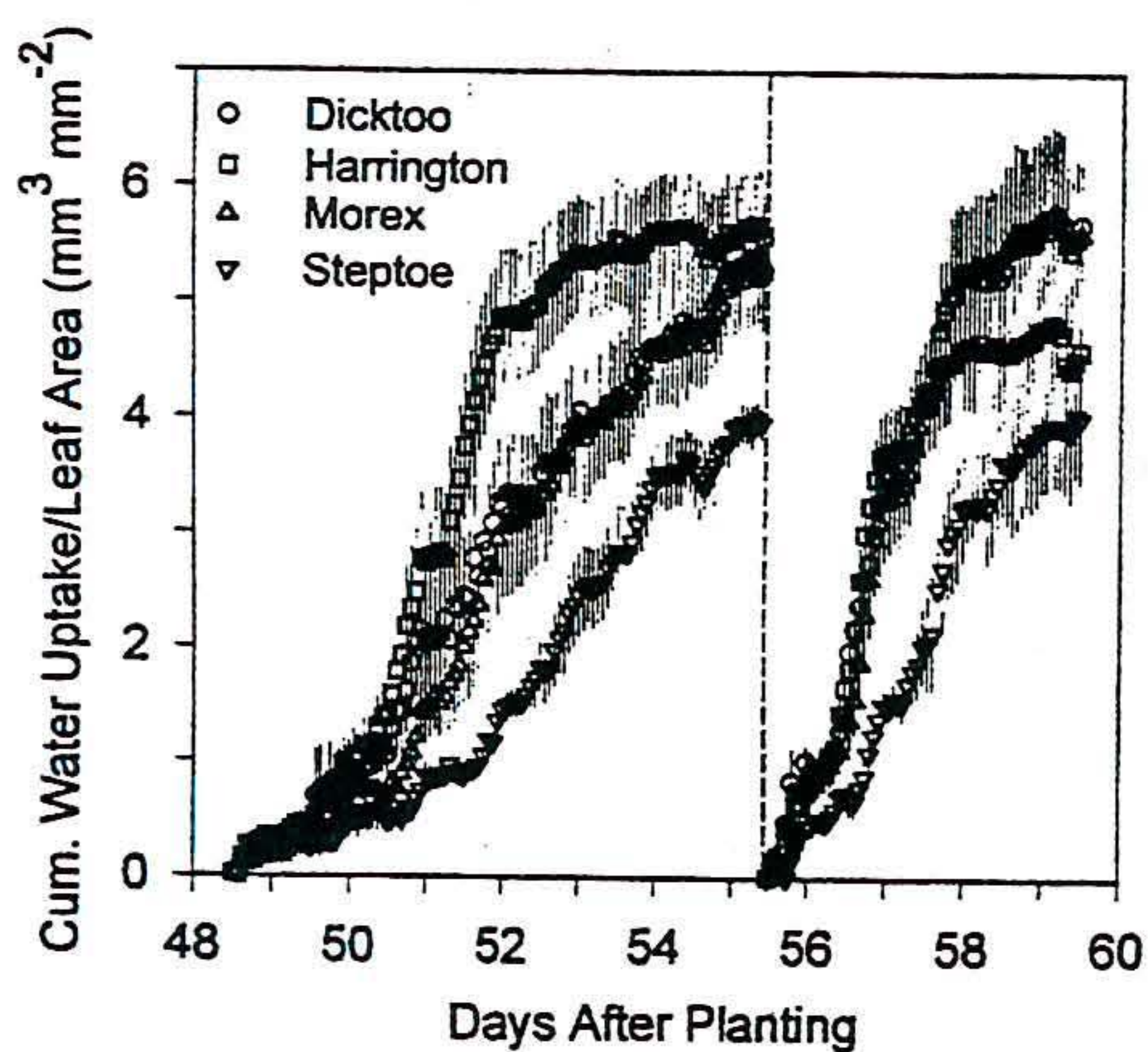


Fig. 5. Cumulative water uptake from upper 50 mm soil (mean  $\pm$  SEM;  $n=4$  or 5) on leaf area-specific basis ( $\text{mm}^3 \text{mm}^{-2}$ ) following first and second column rewetting during second uptake resumption trial. Columns were rewatered on Days 48.5 and 55.4. For clarity, every third data point illustrated.

water addition (Figs 6, 7). Figure 7 confirms relative daily magnitudes and patterns of water uptake rate among the four genotypes as may be inferred from Figs 3–6, as well as depicting diurnal patterns of soil water uptake. Rates corresponding to the beginning and end of the measurement period in Fig. 6 (partial Days 48, 59), and during the second rewetting (Day 55) are not shown in Fig. 7 because these points were external to the smoothing and differentiation algorithm (Savitzky and Golay, 1964).

Cumulative water usage on a whole plant basis was of a similar magnitude during the first and second trials (Figs 4, 6), while that on a leaf-specific basis differed by about an order of magnitude (Figs 3, 5).

One puzzling aspect of our data is a small but noticeable thermal influence on the TDR measurement, which we have not yet resolved. Control (evaporation only) columns were affected to a somewhat greater degree, probably because they received more direct solar radiation through having no plant canopy. Because water uptake was

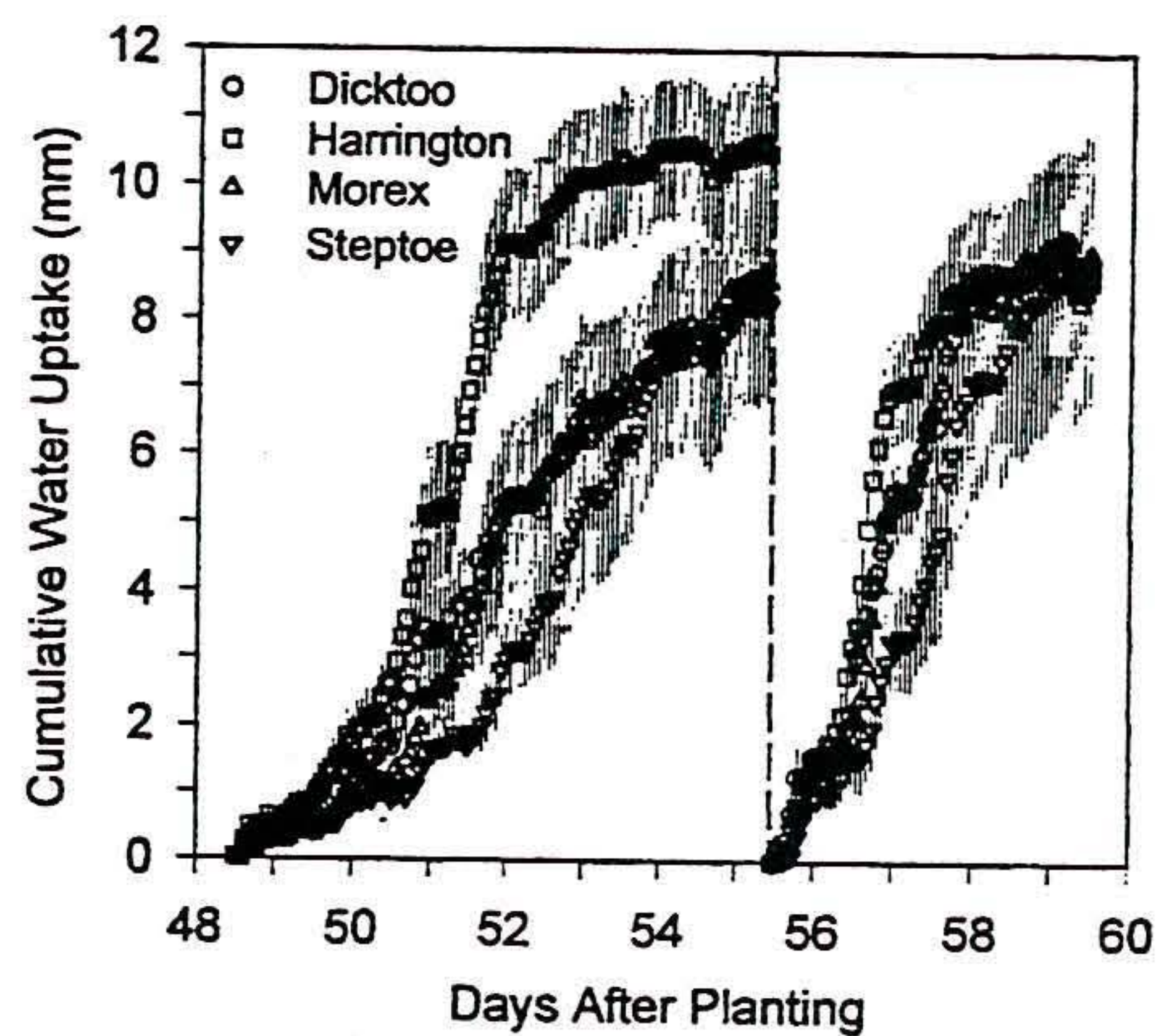


Fig. 6. Cumulative water uptake from upper 50 mm soil (mean  $\pm$  SEM;  $n=4$  or 5) on whole-plant basis (mm) following first and second column rewetting during second uptake resumption trial. Columns were rewatered on Days 48.5 and 55.4. For clarity, every third data point illustrated.

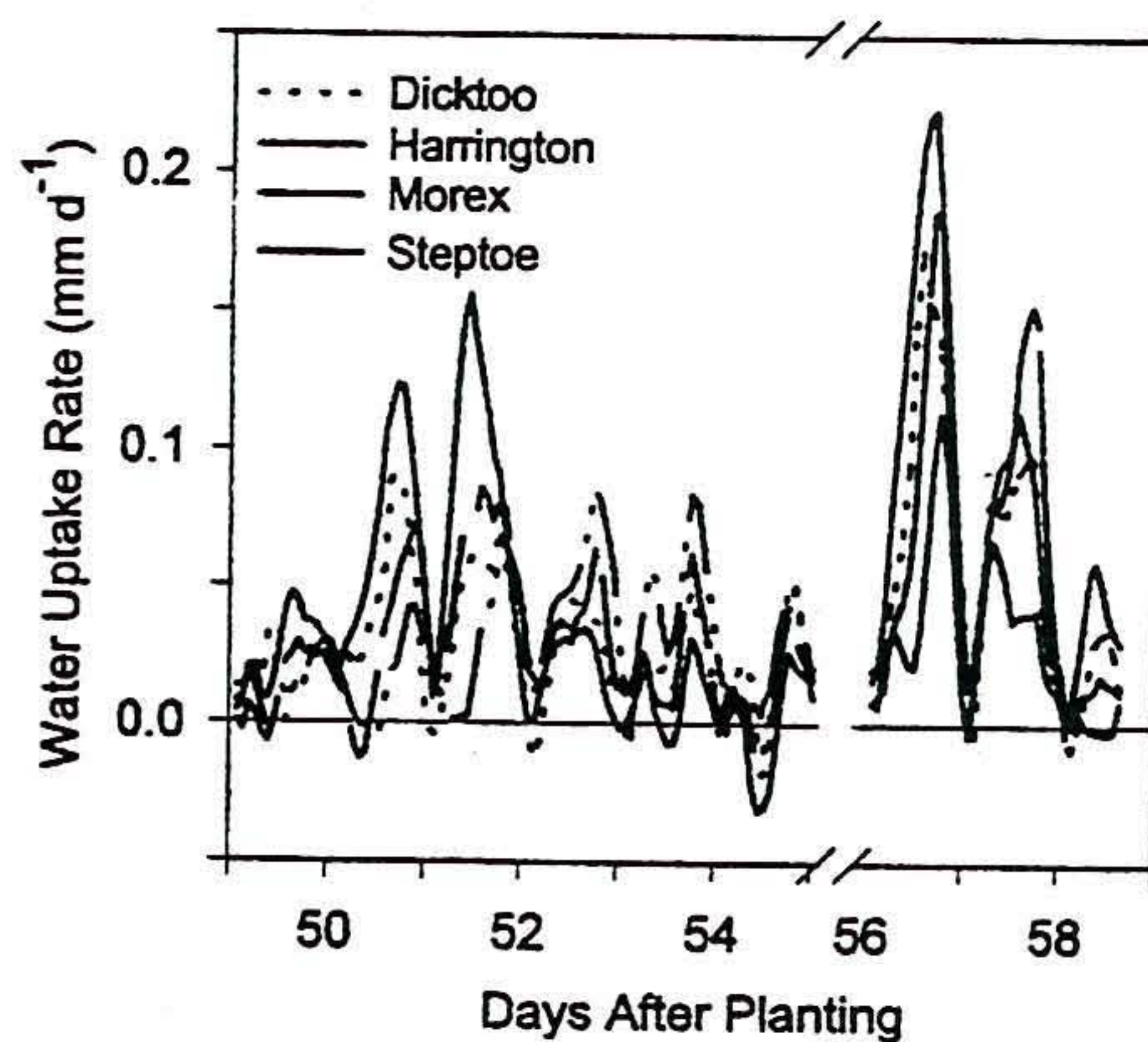


Fig. 7. Mean water uptake rates from upper 50 mm soil on whole-plant basis ( $\text{mm d}^{-1}$ ) following column rewetting during second uptake resumption trial. Water uptake rates were calculated as the first derivative of data shown in Fig. 6.

calculated as the difference in water content between consecutive measurements minus the mean corresponding change in control columns, slight apparent decreases in cumulative uptake were occasionally evident at night. These effects may be observed in Figs 3–6, and the inflections from positive to negative cumulative uptake are translated (and enhanced somewhat through numerical smoothing and differentiation) to negative uptake rates in Fig. 7. The measurement artefact is apparently not related to the liquid water dielectric, as this attribute has only a slight temperature dependence, and would produce results opposite to those observed. We suspect some phenomenon involving vapour phase transport may be involved. Resolution of the source, and subsequent compensation for its effects, should increase the potential accuracy of measurements.

## Discussion

The first trial was conducted during mid-October to late December, while the second extended from mid-January to mid-March. It is therefore possible that seasonal light quality and/or duration influenced rate of leaf development, resulting in the observed differences in leaf area between the second as compared to the initial investigation. Once a plant or canopy reaches a given leaf area index, further increases in leaf area have a negligible effect on the amount of absorbed radiation, and hence transpiration. This is probably responsible for the observed similarity in whole-plant water uptake during both trials, in contrast to that on a leaf-specific basis. An alternative hypothesis is that similarity in whole-plant uptake under these conditions indicates some below-ground (i.e. root-mediated) limitation to water uptake. This might result from time required to eliminate air embolism (Tyree and Sperry, 1989), or if limited root uptake resulting from decreased absorptive function in the upper soil layer caused partial stomatal closure through hydraulic and/or chemical signals (Tardieu and Davies, 1993).

The greater delay in uptake resumption for the second versus the first trial presumably follows the greater duration of soil drought (14 d versus 10 d), as magnitude of the imposed drought was similar during each trial. This is in agreement with previous observations by ourselves and others. Wraith and Baker (1991) found that water uptake by a sorghum plant did not return to previous levels within 3 d after rewetting the surface soil layer following 3 weeks of drought. Sala *et al.* (1982) suggested that the extent of after-effects of drought on *B. gracilis* depends on both the duration and magnitude of drought. Their conclusions were based on field observations of  $g_s$  following short (Sala and Lauenroth, 1982) or prolonged (Sala *et al.*, 1982) drought. Although BassiriRad and Caldwell (1992) found that rates of recovery of  $\Psi_1$  and  $g_s$  were not different between their drought severity treatments, others (e.g. Bengston *et al.*, 1977; Ludlow *et al.*,

1980; Sala *et al.*, 1982) have reported differential recovery responses based on drought severity. Each of these studies indicated significantly faster recovery of leaf water status than of stomatal function.

Variation in air temperature or the radiation environment may affect the magnitudes of daily water uptake in the greenhouse. However, we do not believe observed water uptake patterns would have been substantially altered by the relatively minor measured differences in the physical environment between the first and second trials. Greenhouse air temperature was rather consistent, leaving daily and seasonal irradiance and *PPFD* as the primary climatic variables. It is particularly unlikely that the observed contrast in time lag before substantial water uptake commenced (1 versus 2–3 d for first and second trials) could be explained by modest daily or seasonal variation in the radiation regime.

Capacity for renewal of permeability in desiccated roots (Nobel and Sanderson, 1984) has been shown to decrease with increasing root age (North and Nobel, 1992). However, age differences in near-surface root system components would have been quite small during our experiments in comparison with age classes examined by North and Nobel (1992), who compared changes in hydraulic conductivity of 1-, 3-, and 12-month-old root segments of two desert succulents in response to rewetting following 30 d of drying. Growth of new roots probably did not contribute significantly to measured uptake responses until several days after rewetting (Nobel and Sanderson, 1984; Lauenroth *et al.*, 1987). Thus the greater delay in substantial water uptake during the second trial (Figs 3–6) probably indicates duration of water deficit rather than age of affected roots as a principal determining factor. Plant age and developmental status in relation to soil conditions should nevertheless be considered in comparative studies of water uptake following soil water deficit, as dissimilar responses may be anticipated based on these factors.

Surface soils typically dry more rapidly and to a greater extent than do deeper layers as a result of direct soil evaporation combined with high root density (Sala *et al.*, 1992; Dwyer *et al.*, 1988; Soon, 1988). Thus variable initial wetness and degree of water uptake from deeper layers before and during a drying cycle may modify response time of desiccated near-surface roots. Subsoil water status may impact recovery of near-surface root function through its moderation of whole-root-system vascular tissue water status (Slavikova, 1967). In a preliminary investigation (Wraith *et al.*, unpublished data) we found little lag in near-surface root uptake by the four barley genotypes following 14 d drought when the subsoil was maintained well-watered. Xu and Bland (1993) grew sorghum plants with vertically-split root systems, with or without access to subsurface water. After withholding surface water for 39 d, all containers were watered to container-capacity, and roots growing into subsurface



reservoirs were excised. During the first day of rewetting, transpiration on a leaf area basis was 2.6-fold greater in plants having access to a free water reservoir during the drying period. After 3 d, transpiration was equivalent in both treatments. In an earlier study, Dirksen and Raats (1985) found that sub-irrigated alfalfa (*Medicago sativa* L.) resumed water uptake at a high rate immediately after rewetting of surface roots in soil that had dried for 50 d. The magnitude of a 'distal hydration' effect will likely depend on both extent and severity of desiccation, and on the degree of coupling between hydration in the cortex and steel. Formation of cortical lacunae resulting from cellular dehydration and collapse in response to water deficit has been reported for *Agave deserti*, *Zea mays*, and sorghum (North and Nobel, 1991; Stasovski and Peterson, 1991; Cruz *et al.*, 1992). In the latter study (Cruz *et al.*, 1992), structural changes with concomitant substantial decreases in root conductance were observed for shallow roots exposed to severe water deficit while lower rooting zones were maintained moist.

In many cases knowledge concerning the magnitude, timing, and location of water uptake following drought may be of primary interest. However, this information does not in itself improve our understanding of mechanisms underlying these responses. Resumption of water uptake capacity following soil drought may be a result of renewed permeability or function of existing roots as well as new root growth (Nobel and Sanderson, 1984; Franco and Nobel, 1990; BassiriRad and Caldwell, 1992; Huang and Nobel, 1993). More rapid uptake resumption following the second as compared to first rewetting during each of our trials (Figs 3–6) is likely a combined result of these processes. While the methods presented here do not provide direct information concerning uptake partitioning between new and existing roots, combining similar non-invasive measurements on intact root systems in representative soil media with concurrent analyses of root growth and structural/hydraulic changes should greatly aid in clarifying these issues.

The relevance of measured differences in water uptake response among barley genotypes is intimately related to location-specific soil and climatic conditions. Sensitivity analyses concerning seasonal evaporative versus transpirational water use as affected by genotypically- or species-variable uptake responses may be facilitated through the use of multiple years of weather data in combination with deterministic computer simulation techniques. Field experimentation will also be required to document the importance of differential uptake resumptive capacity in cultivated crops and within a variety of ecological frameworks.

## Summary

Soil water uptake resumption among four barley genotypes was quantified and contrasted following rewetting

of the upper 0.05 m rooting zone, using a non-invasive soil-based methodology. This approach potentially provides information concerning spatial as well as temporal aspects of root water uptake, and is amenable for use under field and controlled environment conditions. Resumption of water uptake was more rapid following 10 d than 14 d of soil drought, and was more rapid following a second rewetting 5–7 d after initial water application. Uptake response varied among the genotypes, indicating a potential for varietal selection or genetic modification to enhance efficiency of water usage in regions characterized by relatively light and/or infrequent growing season rainfall. The influences of drought duration and of soil water status in distal portions of intact root systems on uptake responses by desiccated near-surface roots merit additional inquiry, as do investigations concerning mechanisms of root system function during recovery from water deficit. These studies may be substantially enhanced through incorporation of measurements similar to those reported here.

## Acknowledgments

Research support from NRI Competitive Grants Program/USDA (Agreement No. 92-37106-8087), Montana Agricultural Experiment Station, MONTA, and USDA-ARS is gratefully acknowledged. Contribution of the Montana Agric. Exp. Stn. (No. J-3029) and USDA-ARS. We thank Dr Paul B. Hook for a particularly valuable review of the draft manuscript.

## References

- Baker JM, Allmaras RR. 1990. System for automating and multiplexing soil moisture measurement by time-domain reflectometry. *Soil Science Society of America Journal* **54**, 1–6.
- Baker JM, Wraith JM, Dalton FN. 1992. Root function in water transport. *Advances in Soil Science* **19**, 53–72.
- BassiriRad H, Caldwell MM. 1992. Temporal changes in root growth and <sup>15</sup>N uptake and water relations of two tussock grass species recovering from water stress. *Physiologia Plantarum* **86**, 525–31.
- Bengsten C, Falk SO, Larsson S. 1977. The after-effect of water stress on transpiration rate and changes in abscisic acid content of young wheat plants. *Physiologia Plantarum* **41**, 149–54.
- Blake TK. 1993. Completing and using the barley genome map. *Probe* **2**, 14–17.
- Caldwell MM, Percy RW (eds). 1994. *Exploitation of environmental heterogeneity by plants*. New York: Academic Press.
- Cruz RT, Jordan WR, Drew MC. 1992. Structural changes and associated reduction of hydraulic conductance in roots of *Sorghum bicolor* L. following exposure to water deficit. *Plant Physiology* **99**, 203–12.
- Dirksen C, Raats PAC. 1985. Water uptake and release by alfalfa roots. *Agronomy Journal* **77**, 621–6.
- Dwyer LM, Stewart DW, Balchin D. 1988. Rooting characteristics of corn, soybeans and barley as a function of available water and soil physical characteristics. *Canadian Journal of Soil Science* **68**, 121–32.

- Franco AC, Nobel PS. 1990. Influences of root distribution and growth on predicted water uptake and interspecific competition. *Oecologia* 82, 151-7.
- Huang B, Nobel PS. 1992. Hydraulic conductivity and anatomy for lateral roots of *Agave deserti* during root growth and drought-induced abscission. *Journal of Experimental Botany* 43, 1441-9.
- Huang B, Nobel PS. 1993. Hydraulic conductivity and anatomy along lateral roots of cacti: changes with soil water status. *New Phytologist* 123, 499-507.
- Jordan N. 1993. Prospects for weed control through crop interference. *Ecological Applications* 3, 84-91.
- Kleinhofs A, Kilian A, Saghai Maroof MA, Biyashev RM, Hayes P, Chen FQ, Lapitan N, Fenwick A, Blake TK, Kanazin V, Ananiev E, Dahleen L, Kudrna D, Bollinger J, Knapp SJ, Liu B, Sorrells M, Heun M, Franckowiak JD, Hoffman D, Skadsen R, Steffenson BJ. 1993. A saturated medium-density map of the barley genome. *Theoretical and Applied Genetics* 86, 705-12.
- Lauenroth WK, Sala OE, Milchunas DG, Lathrop RW. 1987. Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. *Functional Ecology* 1, 117-24.
- Lopez FB, Nobel PS. 1991. Root hydraulic conductivity of two cactus species in relation to root age, temperature, and soil water status. *Journal of Experimental Botany* 42, 143-9.
- Ludlow MM, Ng TT, Ford CW. 1980. Recovery after water stress of leaf gas exchange in *Panicum maximum* var. *trichoglume*. *Australian Journal of Plant Physiology* 7, 299-313.
- Nobel PS, Sanderson J. 1984. Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany* 35, 727-37.
- North GB, Nobel PS. 1991. Changes in hydraulic conductivity and anatomy caused by drying and rewetting roots of *Agave deserti* (Agavaceae). *American Journal of Botany* 78, 906-15.
- North GB, Nobel PS. 1992. Drought-induced changes in hydraulic conductivity and structure in roots of *Ferocactus acanthodes* and *Opuntia ficus-indica*. *New Phytologist* 120, 9-19.
- Passioura JB. 1983. Roots and drought resistance. *Agricultural Water Management* 7, 265-80.
- Passioura JB. 1988. Water transport in and to roots. *Annual Review of Plant Physiology and Plant Molecular Biology* 39, 245-65.
- Richards JH, Caldwell MM. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73, 486-9.
- Sala OW, Lauenroth WK. 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53, 301-4.
- Sala OW, Lauenroth WK, Parton WJ. 1982. Plant recovery following prolonged drought in a shortgrass steppe. *Agricultural Meteorology* 27, 49-58.
- Sala OW, Lauenroth WK, Parton WJ. 1992. Long-term soil water dynamics in the shortgrass steppe. *Ecology* 73, 1175-81.
- Sanderson J. 1983. Water uptake by different regions of the barley root. Pathways of radial flow in relation to development of the endodermis. *Journal of Experimental Botany* 34, 240-53.
- Savitzky A, Golay MJE. 1964. Smoothing and differentiation of data by simplified least squares procedures. *Analytical Chemistry* 36, 1627-39.
- Slavikova J. 1967. Compensation of root suction force within a single root system. *Biologia Plantarum* 9, 20-7.
- Soon YK. 1988. Root distribution of and water uptake by field-grown barley in a black solod. *Canadian Journal of Soil Science* 68, 425-32.
- Stasovski E, Peterson CA. 1991. The effects of drought and subsequent rehydration on the structure and vitality of *Zea mays* seedling roots. *Canadian Journal of Botany* 69, 1170-8.
- Tanner CB, Sinclair TR. 1983. Efficient water use in crop production: research or re-research? In: Taylor HM, Jordan WR, Sinclair TR, eds. *Limitations to efficient water use in crop production*. Madison: American Society of Agronomy, 1-28.
- Tardieu F, Davies WJ. 1993. Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. *Plant Cell and Environment* 16, 341-9.
- Tyree MT, Sperry JS. 1989. The vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology* 40, 19-38.
- van Genuchten MTh. 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America Journal* 44, 892-8.
- Wraith JM, Baker JM. 1991. High resolution measurement of root water uptake using automated time-domain reflectometry. *Soil Science Society of America Journal* 55, 928-32.
- Wraith JM, Johnson DA, Hanks RJ, Sisson DV. 1987. Soil and plant water relations in a crested wheatgrass pasture: response to spring grazing by cattle. *Oecologia* 73, 573-8.
- Xu X, Bland WL. 1993. Resumption of water uptake by sorghum after water stress. *Agronomy Journal* 85, 696-702.