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A comparative assessment of water use efficiency in groundnut (*Arachis hypogaea*) grown in containers and in the field under water-limited conditions

K. B. HEBBAR[1]*, V. R. SASHIDHAR[1]†, M. UDAYAKUMAR[1], R. DEVENDRA[1] AND R. C. NAGESWARA RAO[2]

[1] *Department of Crop Physiology, University of Agricultural Sciences, GKVK Campus, Bangalore 560 065, India*

[2] *International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, PO 502 324, Andhra Pradesh, India*

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SUMMARY

Water use efficiency (WUE) was measured on fourteen genotypes of groundnut (*Arachis hypogaea* L.) grown in containers under adequately irrigated and water-limited conditions. The genotypes used similar amounts of water but produced different quantities of dry matter. WUE accounted for > 92% of the variation in dry matter production under both irrigated and water-limited conditions. There was a significant increase in WUE under water-limited conditions. Four genotypes selected from the container experiment as having either a high or a low WUE under non-limited or limited water input conditions were further tested under prolonged water deficit conditions in a field experiment. WUE varied significantly between genotypes and there was a positive correlation between WUE and the quantity of dry matter produced by the genotypes. The results suggested that, in three out of four genotypes, the WUE measured in the container experiment was positively correlated with the WUE estimated under field conditions.

INTRODUCTION

Groundnut is an important oilseed and cash crop grown mainly under rainfed conditions in the semi-arid regions of the world. About 67% of the world's groundnut production comes from rainfed cultivation (Gibbons 1980). Hence, any trait or practice which can improve groundnut production under rainfed cultivation is of immediate importance to semi-arid farmers.

Dry matter (DM) production is a product of T × WUE (Briggs & Shantz 1914; de Wit 1958) where T is the amount of water transpired and WUE is the water use efficiency, defined as the quantity of DM produced per unit of water transpired. Thus, it is apparent that WUE is one of the most important factors influencing crop productivity, particularly under water-limited conditions (Turner 1986; Uma 1987; Martin & Thorstenson 1988). Significant genotypic variations in WUE between different groundnut genotypes have been reported (Hubick *et al.* 1986; Wright *et al.* 1988; Nageswara Rao *et al.* 1993).

WUE measurements may be made at three levels: (i) in single leaves using gas exchange techniques; (ii) in whole plants grown in containers; and (iii) at the canopy level based on evapotranspiration in the field (Fischer & Turner 1978). Although useful, WUE is difficult to measure in the field because of the lack of suitable techniques for measuring accurately the root mass and water use of plants (Martin & Thorstenson 1988). Recent studies have shown that carbon isotope discrimination occurring during carbon assimilation by leaves is closely related to WUE in various crops (Farquhar & Richards 1984; Hubick *et al.* 1986; Farquhar *et al.* 1989), suggesting that carbon isotope discrimination technology can be used to screen genotypes for WUE. However, measurement of carbon isotope composition requires expensive instrumentation and specific expertise. Thus, the use of carbon isotope methodology to screen genotypes for WUE may be limited in developing countries in the near future.

Experiments involving the use of containers to

* Present address: Water Technology Centre, Indian Agricultural Research Institute, New Delhi 110 012, India.

† To whom correspondence should be addressed.

study whole plant WUE date back to the 19th century (Briggs & Shantz 1913, 1914). Despite the inevitable drawbacks of container studies, this approach has been adopted widely in more recent studies of WUE (Hubick & Farquhar 1987; Wright *et al.* 1988, 1994). The use of containers in WUE studies has been further supported by the observation that the ranking of species (particularly between C_3 and C_4) at the whole plant level showed a close relationship with WUE determined at the single leaf level from gas exchange measurements (Downes 1969; Ravishankar 1988), and that the ranking of species for WUE is remarkably consistent across seasons (Jones 1983).

Limited attempts have been made to compare the relative ranking of WUE in genotypes within a species grown in containers with those grown in the field under both non-limiting and water-limited input conditions (Teare *et al.* 1973; Shashikumar 1983). If WUE has to be considered and used as a trait in crop improvement programmes, such attempts are imperative. In the present study, experiments were therefore conducted to: (i) examine genotypic variability in WUE over a range of groundnut genotypes under non-limited and water-limited conditions; (ii) assess the relationship between the ranking of WUE of genotypes measured under both non-limiting and water-limited input conditions in container studies with that measured under field conditions; and (iii) examine the relevance of WUE as a drought resistance trait under water-limited conditions in the field.

MATERIALS AND METHODS

Experiment 1

A container experiment was conducted during the rainy season (July–October) 1988 in a glasshouse at the University of Agricultural Sciences, Bangalore, in south India. Fourteen groundnut (*Arachis hypogaea* L.) genotypes belonging to the varieties *vulgaris* (spanish) and *fastigiata* (valencia) were used to assess differences in WUE. Plants were grown in containers made of carbonized rubber 28 cm long, 14·4 cm wide and 12·5 cm deep, containing 8 kg of red loamy soil. Basal fertilizer (18 N:40 P:0 K/ha) was mixed into the topsoil at sowing. Each genotype was planted in ten containers and two plants were grown in each container. Plants were watered daily until 30 days after sowing (DAS), when two irrigation regimes were imposed.

At 30 DAS, all containers were saturated with water and any excess was allowed to drain through a drainage hole in the base of the container. When water leakage stopped, the drainage holes were blocked to prevent any further seepage of water from the containers. The exposed soil surface was covered with pieces of polythene to minimize soil evaporation. The containers were arranged in a split-plot design with two irrigation regimes (I_1 and I_2) as the main treatments and the fourteen genotypes as subtreatments. There were five container replicates for each main treatment.

Treatment I_1 received adequate water to maintain the soil at its field capacity of 15·5% moisture (noted from initial soil moisture measurements). The plants in treatment I_2 received 60% of the water given to the plants in I_1. The amount of water loss was determined by weighing the containers daily using a Bench Platform Balance (20 kg capacity with a resolution of 20 g). Two or three containers with soil and plastic mulch, but without plants, were maintained in each treatment to monitor soil evaporation in the absence of plants.

The experiment was terminated at 62 DAS. The shoots were harvested along with the roots, and the dry weight of the whole plant (including roots) was determined after oven-drying at 70 °C for 48 h.

Total dry matter (DM) accumulation including roots during the experimental period was computed as the increase in DM/plant between 30 and 62 DAS.

Transpiration (T) during the experimental period was estimated as $T = I-(Es+Uw)$ where I is the cumulative water added during the treatment period, Es is soil evaporation, and Uw the unused water left in the container at the end of the treatment period. Es was estimated from the water loss from the empty containers in the absence of plants. Water use efficiency (g/kg) was estimated as the ratio of DM produced between 30–62 DAS to transpiration (T) during the same period.

Experiment 2

Four genotypes were selected on the basis of their differing WUE responses under both non-limited (treatment I_1) and water-limited (treatment I_2) input conditions in Expt 1, as follows:

1. Genotype ICGV86843 (Low WUE in I_1, Low WUE in I_2),
2. Genotype ICGV87160 (High WUE in I_1, Low WUE in I_2),
3. Genotype ICGV86315 (Low WUE in I_1, High WUE in I_2),
4. Genotype TMV2 (High WUE in I_1, High WUE in I_2).

The field experiment was conducted on a red loamy soil, during the summer season (February–May) 1989 at the University of Agricultural Sciences experimental farm, Bangalore. The field was disc-ploughed and a basal fertilizer containing 18 N:46 P was incorporated into the soil at land preparation. The experiment was laid out as a split-plot design with two irrigation treatments (I_1 and I_2) as the main plots and the four genotypes as subplots. There were three replications. Seeds of each genotype were hand-sown on 5 February 1989 in ten rows each 4 m in length,

Table 1. *Total dry matter (DM) (g/plant), transpiration (T) (kg/plant) and water use efficiency (WUE) of fourteen groundnut genotypes grown in containers under irrigated (I_1) and water-limited (I_2) conditions between 30 and 62 DAS*

Genotype	Treatment	DM (g)	T (kg)	WUE (g/kg)
ICGV87160	1	13·5	6·0	2·3
	2	8·3	3·4	2·4
ICGV86031	1	15·2	6·0	2·5
	2	10·7	3·4	3·2
TMV2	1	14·8	5·8	2·4
	2	10·2	3·4	2·9
DH3-30	1	14·7	6·0	2·3
	2	10·2	3·4	2·7
ICGS11	1	10·4	5·8	1·5
	2	8·5	3·4	2·5
ICGV86124	1	16·5	5·8	2·7
	2	9·9	3·4	3·0
ICGV86234	1	10·5	5·8	1·7
	2	7·4	3·4	2·2
ICGV86843	1	6·7	5·8	1·2
	2	5·3	3·4	1·6
ICGV86832	1	10·3	5·7	1·7
	2	9·2	3·4	2·6
ICGV86552	1	10·5	5·5	1·9
	2	8·7	3·3	2·8
ICGV86187	1	12·3	5·7	2·2
	2	11·3	3·3	3·5
ICGV86315	1	11·1	5·8	2·0
	2	9·8	3·3	3·2
ICGV86854	1	11·7	5·8	2·1
	2	10·5	3·3	3·3
GNP214	1	10·5	5·7	1·5
	2	9·6	3·3	2·9
S.E. (for genotypes)		0·96	—	0·07
S.E. (for treatments)		0·28	—	0·03
S.E. (G × T interaction)		1·36	—	0·09

with a spacing of 30 cm between rows and 15 cm between plants within rows. The crops were maintained free from pests and weeds by using appropriate plant protection measures as necessary.

All plots received adequate irrigation at 7-day intervals until 44 DAS, after which the two irrigation treatments (I_1 and I_2) were imposed by applying measured quantities of water until 90 DAS. Treatment I_1 was supplied with sufficient water to maintain the soil at field capacity (15·5% soil moisture), while treatment I_2 received 60% of the water applied to I_1. The quantity of water required to maintain the plots at field capacity was estimated using the model of Ritchie (1973). This model was used to estimate evapotranspiration (ET) and transpiration (T) using soil, crop, irrigation and environmental characteristics. At 90 DAS, the plants from a 1 m² area were harvested and the roots were separated. The shoots (vegetative + pods) were oven-dried at 80 °C for 48 h before determining their dry weights.

WUE (g/kg) was calculated from the biomass (shoots + pods) produced during the treatment period (44–90 DAS) and transpiration (T) during the same period.

RESULTS

Experiment 1

The fourteen genotypes used similar quantities of water (5·5–6·0 kg in treatment I_1 and 3·3–3·4 kg in I_2) but were significantly different in DM production, which ranged from 6·7 to 16·5 g/plant in I_1 and 5·3 to 11·3 g/plant in I_2 during the treatment period, resulting in a significant variability in WUE between

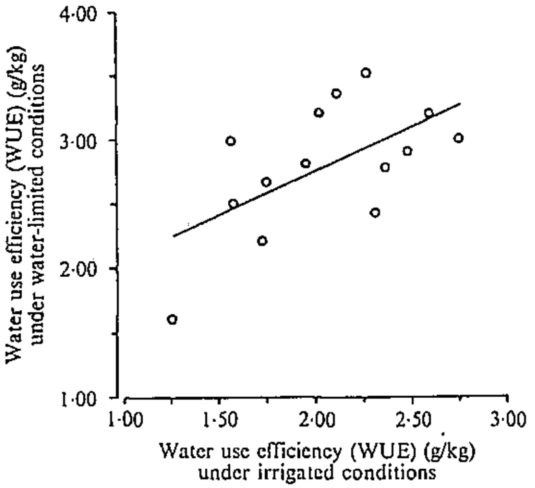

Fig. 1. Relationship between WUE values under irrigated and water-limited conditions in fourteen groundnut genotypes ($r = 0{\cdot}79$, $P < 0{\cdot}05$) in a container experiment.

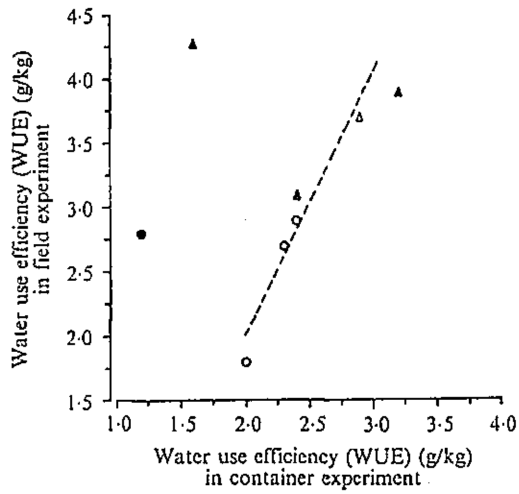

Fig. 2. Relationship between WUE measured in the container experiment and in the field in four groundnut genotypes grown under irrigated (○) and water-limited (△) conditions. ●, ▲ represent genotype ICGV86843 (regression line fitted excluding ICGV86843; $r = 0{\cdot}96$, $P < 0{\cdot}01$).

Table 2. *Dry matter produced (DM) (g/m²), transpiration (T) (kg/m²), and water use efficiency (WUE) of four groundnut genotypes grown under irrigated (I_1) and water-limited (I_2) conditions between 44 and 96 DAS in the field.*

Genotype	Treatment	DM (g)	T (kg)	WUE (g/kg)
ICGV86315				
	1	253	139·5	1·8
	2	243	61·7	3·9
ICGV87160				
	1	434	157·2	2·8
	2	198	63·5	3·1
TMV2				
	1	416	139·4	2·9
	2	254	67·8	3·8
ICGV86843				
	1	422	148·2	2·9
	2	319	73·4	4·3
S.E. (for genotypes)		9·18	—	0·09
S.E. (for treatments)		1·52	—	0·01
S.E. (G × T interaction)		12·98	—	0·14

genotypes (1·2–2·7 g/kg in I_1 and 1·6–3·5 g/kg in I_2) (Table 1). Genotype ICGV86124 had the highest WUE in treatment I_1 (2·7 g/kg), but ICGV86187 had the highest WUE (3·5 g/kg) under water-limited conditions (I_2). Genotype ICGV86843 had the lowest WUE in both irrigation treatments. Regression analysis between WUE and DM showed that *c.* 92% of the variation in DM production was accounted for by the variation in WUE, suggesting the importance of WUE in determining crop productivity. WUE generally increased under water-limited conditions in all genotypes, although there was a positive correlation ($r = 0{\cdot}79$, $P < 0{\cdot}05$) between WUE values recorded for treatments I_1 and I_2 (Fig. 1).

Based on deviation from the mean WUE under non-limited and limited water conditions, the genotypes could be grouped as follows:

1. Low WUE in both I_1 and I_2: ICGV86843, ICGV86234 and ICGS11,
2. High WUE in I_1 and low WUE under I_2: ICGV87160,
3. Low WUE in I_1 and high WUE under I_2: ICGV86315, GNP214, ICGV86832 and ICGV86552,
4. High WUE in both I_1 and I_2: TMV2, ICGV86031, ICGV86187, ICGV86124, ICGV86854 and DH3-30.

Experiment 2

In the field experiment, the water use of the four selected genotypes in I_1 ranged from 139 to 157 kg during the experimental period, while DM production ranged from 253 to 434 g/m². In I_2, water use was 61–73 kg and DM production was 198–319 g/m² (Table 2). WUE for the four genotypes was 1·8–2·9 g/kg in I_1 and 3·1–4·3 g/kg in I_2, representing a significant variation between genotypes. TMV2 and ICGV86843 gave the highest WUE values in treatments I_1 and I_2 respectively.

As in Expt 1, there was an increase in WUE in all genotypes under water-limited conditions, although the extent of this increase varied between genotypes.

There was a significant positive correlation ($r =$

0·96, $P < 0·01$) between the WUE values measured in the container and field experiments for three of the four genotypes (Fig. 2). The exception was ICGV86843, which had the lowest WUE in Expt 1 but a high WUE in Expt 2. Except for this discrepancy, the results suggest that the relative ranking of genotypes for WUE in both experiments and treatments was consistent and that container experiments can be used effectively to assess relative variations in WUE between groundnut genotypes.

DISCUSSION

In Expt 1, WUE in the fourteen genotypes used varied from 1·2 to 2·7 g/kg under irrigated and from 1·6 to 3·5 g/kg under water deficit conditions. These values are in accordance with the WUE range reported for C_3 crops such as groundnut (Hubick *et al.* 1986; Wright *et al.* 1988, 1994). The physiological basis for variations in WUE between genotypes is not clear, although indirect evidence from the present study and earlier work (Hubick *et al.* 1986) suggests that, in groundnut, variation in photosynthetic capacity per unit leaf area might be a factor causing variation in WUE. The increase in WUE observed in all genotypes under deficit conditions (Fig. 1) suggests an intrinsic ability of groundnut plants to adapt to drought conditions. Changes in the WUE of groundnut genotypes across a range of water regimes have been reported previously (Wright *et al.* 1988), but the physiological mechanisms responsible for such an increase in WUE under drought are not clear and this aspect requires further research. Although the positive correlation between the WUE values in treatments I_1 and I_2 seemed to suggest that selection for WUE could be made under either irrigation regime provided that the water status was maintained constant across genotypes, such a positive correlation between the WUE values for treatments I_1 and I_2 was not seen in Expt 2.

The WUE values observed in Expt 2 were generally greater than those in Expt 1. Variations in environmental factors between the glasshouse and the field might have contributed to variation in WUE between the experiments. Several environmental parameters; for example, vapour pressure deficit, temperature and irradiance, have been shown to influence water use efficiency (Tanner & Sinclair 1983). Furthermore, in Expt 2 transpiration was computed using a simple soil water balance model (Ritchie 1973) and the estimates of water use efficiency did not include root biomass. Genotypic variations in root mass, and root:shoot ratios have been reported for groundnut (Ketring 1984). Thus, it is possible that the estimated WUE values in Expt 2 might be confounded by an inability of the model to predict T accurately and/or by genotypic variations in root:shoot ratios. Hence, the WUE data from Expt 2 should be viewed with caution.

Despite these limitations, it is interesting to note that the WUE values for the container experiment correlated well with those measured in the field experiment (Fig. 2), with the exception of genotype ICGV86843, which had the lowest WUE in Expt 1 but not in Expt 2. The WUE values for this genotype were remarkably low in Expt 1 because of poor plant growth in the containers. The reasons for the discrepancy between the performance of this genotype in the container and in the field experiments are not clear. When this genotype was excluded, however, there was a significant positive correlation ($r = 0·95$, $P < 0·01$) between the WUEs as measured in containers and in field experiments.

A close correlation between carbon isotope discrimination measured for groundnut genotypes grown in pots and those grown as part of a field stand has been shown recently by Wright *et al.* (1994). A similar consistency in WUE measurements at the whole plant and canopy level has also been shown in studies of C_3 and C_4 species (Downes 1969).

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