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On the extent of genetic variation for transpiration efficiency in sorghum

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Abstract. A glasshouse study examined 49 diverse sorghum lines for variation in transpiration efficiency. Three of the 49 lines grown were *Sorghum* spp. native to Australia; one was the major weed Johnson grass (*Sorghum halepense*), and the remaining 45 lines were cultivars of *Sorghum bicolor*. All plants were grown under non-limiting water and nutrient conditions using a semi-automatic pot watering system designed to facilitate accurate measurement of water use. Plants were harvested 56–58 days after sowing and dry weights of plant parts were determined. Transpiration efficiency differed significantly among cultivars. The 3 Australian native sorghums had much lower transpiration efficiency than the other 46 cultivars, which ranged from 7·7 to 6·0 g/kg. For the 46 diverse cultivars, the ratio of range in transpiration efficiency to its l.s.d. was 2·0, which was similar to that found among more adapted cultivars in a previous study. This is a significant finding as it suggests that there is likely to be little pay-off from pursuing screening of unadapted material for increased variation in transpiration efficiency. It is necessary, however, also to examine absolute levels of transpiration efficiency to determine whether increased levels have been found. The cultivar with greatest transpiration efficiency in this study (IS9710) had a value 9% greater ($P < 0 \cdot 05$) than the accepted standard for adapted sorghum cultivars. The potential impact of such an increase in transpiration efficiency warrants continued effort to capture it. Transpiration efficiency has been related theoretically and experimentally to the degree of carbon isotope discrimination in leaf tissue in sorghum, which thus offers a relatively simple selection index. In this study, the variation in transpiration efficiency was not related simply to carbon isotope discrimination. Significant associations of transpiration efficiency with ash content and indices of photosynthetic capacity were found. However, the associations were not strong. These results suggest that a simple screening technique could not be based on any of the measures or indices analysed in this study. A better understanding of the physiological basis of the observed genetic differences in transpiration efficiency may assist in developing reliable selection indices. It was concluded that the potential value of the improvement in transpiration efficiency over the accepted standard and the degree of genetic variation found warrant further study on this subject. It was suggested that screening for genetic variation under water-limiting conditions may provide useful insights and should be pursued.

Additional keywords: growth, biomass, partitioning, water use, carbon isotope discrimination, ash content, selection index.

Introduction

Water limitation is a major constraint to production of sorghum throughout the world. The amount of biomass the sorghum crop produces per unit of water it captures for transpiration, that is transpiration efficiency, has been found to vary among agronomically elite cultivars (Donatelli *et al*. 1992; Henderson *et al*. 1997), but differences reported have been small. However, simulation studies (Muchow *et al*. 1991; Hammer *et al*. 1996) have suggested that even a small increase in transpiration efficiency (i.e. 10%) may have great impact on sorghum yield in some environments. Hence, the potential advantages make pursuing this trait worthwhile. Until a workable degree of genetic variation is revealed, however, detailed crop physiological and breeding effort is premature. As a

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first objective in this study, we examined sorghum lines of diverse genetic background for variation in transpiration efficiency and compared the extent of the variation found with that reported in previous studies on adapted cultivars.

Genetic variation in transpiration efficiency in sorghum is of little value unless some cultivars expressing levels greater than expected are identified. Transpiration efficiency, measured as biomass produced per unit mass of water transpired, is inversely proportional to the vapour pressure deficit of the atmosphere (Tanner and Sinclair 1983). By correcting for ambient vapour pressure deficit, the transpiration efficiency coefficient for any cultivar can be determined. This provides a basis for comparison with expected values, as the transpiration efficiency coefficient for modern sorghum cultivars is accepted as 9 Pa (Tanner and Sinclair 1983) and this value is used in current crop models of sorghum (Hammer and Muchow 1994). This comparison has not been made in previous studies on genetic variation in transpiration efficiency in sorghum (Donatelli *et al.* 1992; Henderson *et al.* 1997). As an adjunct to our first objective, the transpiration efficiency coefficients of the sorghum lines examined were compared with the standard value to determine if any lines showed improved levels.

Theoretical models supported by experimentation in sorghum (Farquhar 1983; Hubick *et al.* 1990; Henderson *et al.* 1997) have shown that transpiration efficiency can be related to the degree of carbon isotope discrimination in leaf tissue and that this discrimination varies among sorghum cultivars. As carbon isotope discrimination can be measured relatively simply using a mass spectrometer, this theory provides the basis for a screening technique should the association between transpiration efficiency and carbon isotope discrimination be as good as that found in other species (e.g. peanuts, Wright *et al.* 1988). Similarly, other recent studies have found that plant mineral or ash content is correlated with transpiration efficiency (Masle *et al.* 1992), although the physiological basis of this association remains unclear. Our second objective was to examine the association of transpiration efficiency in sorghum with either carbon isotope discrimination or ash content.

Methods

Experimental details

A glasshouse experiment was conducted in Toowoomba, Qld, Australia, during the summer growing season of 1993–94. In the season prior to the experiment, sorghum cultivars from collections around the world were gathered and grown through one generation in plant quarantine. Forty-nine cultivars were chosen, representing a diverse range of taxonomic groups and countries of origin. Some Australian native species of sorghum were included for comparison (the full list of cultivars appears in Table 2). A single plant in a pot represented the experimental unit. These were arranged in a randomised block design with 3 replicates.

The experiment required plants to be grown with non-limiting water and nutrients in a way that facilitated accurate measurement of biomass production and plant water use for determination of transpiration efficiency (TE) from their ratio. To maintain non-limiting water supply and measure plant water use without regular weighing of pots, a semi-automatic system was designed (Fig. 1). The system was adapted from the principles of the pot culture system outlined by Hunter (1981). A 9-L bucket was used as the pot. This was connected at the base to a 5-L reservoir by means of a plastic tube with an in-line valve between the two containers. This allowed controlled entry of water to the pot from the bottom. A watertable of approximately 5 cm depth was maintained in the pot by placing a return air tube to the water reservoir from inside the pot at approximately 5 cm above its base. When the water level fell slightly below the end of the air return tube in the pot, air was returned to the water container and water flowed in through the other tube until the watertable was restored and the air return curtailed. The valve in the lower connecting tube was left open, except during refilling of the reservoir when it was closed to prevent water flow into the pot. This watering system ensured stable and non-limiting water availability while maintaining a well-aerated soil volume for root growth and proliferation.

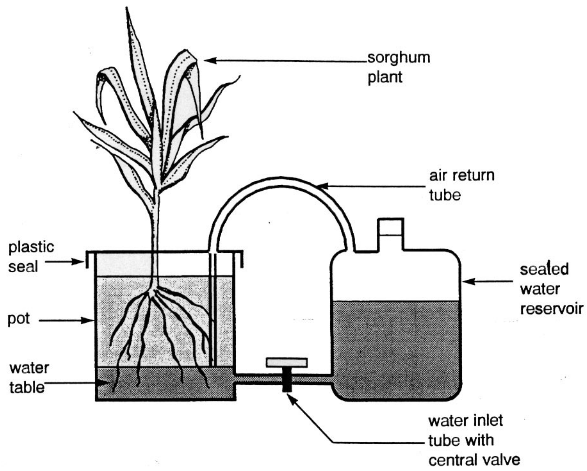

Fig. 1. Schematic of semi-automatic watering system used in the pot study.

Each pot was filled with a 3 : 1 : 1 soil mix of soil, sand, and peat. The soil was a sandy loam with 1–1·5% organic matter. Lime was added to neutralise the acidic effects of the peat. The soil mix was dampened and steam-sterilised at 60°C for 30 min for pathogen and weed control. To maintain non-limiting nutrient supply, 20 g of 5–6-month longevity Osmocote (15 : 4·4 : 10, N : P : K plus 1·2 MgO plus trace elements) was mixed into each pot as it was filled. Eight days after sowing (DAS) the soil was treated with Temik (15% aldicarb) at a rate of 5 mg/kg oven-dry soil to control any likely insect pests.

The experiment was sown on 27 January 1994 after the water reservoirs had been filled, the watertable established, and the pots allowed to equilibrate in water content. The day before sowing, at least 20 seeds of each cultivar were washed with sterilising solution and pre-germinated by treating with 1 mM GA_3 and incubating at 25°C for 24 h. This overcame any dormancy in the Australian native sorghums that were included in the experiment. Six germinated seeds were sown in each pot. At 12–14 DAS the pots were thinned to one plant and the top of the pots around the plants was covered with plastic and sealed to prevent evaporation from the pot. A small cross cut was placed in the plastic to accommodate the plant and allow aeration of the root system. A similarly treated pot with no plant was placed in each replicate to measure the extent of evaporative loss of water.

The temperature in the glasshouse was regulated, with maximum and minimum values of 30 and 20°C, but daily maximum and minimum temperatures were also measured. Total incoming solar radiation was measured and logged hourly inside and outside the glasshouse. Relative humidity and dry bulb temperature were recorded at least once a day (usually 09 00 hours) in the glasshouse in order to calculate vapour pressure deficit (vpd). Daytime average vpd was taken as the average of the 2 vpd values calculated using the dry bulb temperature at 09 00 hours and the maximum temperature for the day. The absolute vapour content determined at the time of humidity measurement was assumed to be constant throughout the day. Some measurements of humidity and temperature were taken throughout a number of days to test this assumption.

The initial weight of each pot plus reservoir was measured at 15 DAS. All water added to the reservoirs during the experiment was measured and the final weight of pot (with plant) plus reservoir was measured immediately prior to harvest, which occurred at 56–58 DAS when most of the cultivars had reached flag leaf stage. The water used by each plant was calculated as the difference between final and initial weights less the plant fresh weight plus the water added. At harvest, plants were cut at ground level and partitioned into component parts by separating leaves and stem, and washing roots from the soil mix. The fresh weights of each component were determined and plant height was recorded by measuring the stem length. The total leaf area of each plant was measured by passing all leaves through an electronic leaf area meter (Delta-T). Dry weights of all plant parts were determined by weighing after drying at 80°C for 4 days. The leaves from each plant were ground and nitrogen concentration, carbon isotope discrimination, and ash content measured on subsamples. Carbon isotope discrimination was determined using mass spectrometry measurements following standard preparation of samples (Henderson *et al.* 1997) and the calculation procedure described by Farquhar and Richards (1984). Ash content was determined by weighing the residue after burning 1 g of pre-dried (80°C for 48 h) ground leaf in a muffle furnace at 750°C for 5 h.

Data analyses

Transpiration efficiency (TE) was determined as the ratio of biomass produced to water transpired. Analyses of variance were conducted to examine treatment effects on biomass, water transpired, TE, and other variables. A standard t-test was used to test for statistical significance of the difference of the highest measured TE from the accepted standard value for sorghum. The associations between TE, carbon isotope discrimination, ash content, and other variables such as specific leaf area and transpiration per unit leaf area were examined using regression analysis.

Results and discussion

Genetic variation in transpiration efficiency

All plants grew extremely well, confirming qualitatively the capacity of the semi-automatic pot watering system to maintain optimal conditions. No major problems with pests or nutrient imbalances occurred. The daily maximum and minimum temperatures were maintained at levels near those proposed on most days. Although the daily maximum ranged from 24 to 33°C and the daily minimum ranged from 14 to 22°C, average values over the experimental period were 29 and 20°C, respectively. Solar radiation outside the glasshouse on clear days declined from values near 30 $MJ/m^2 \cdot day$ at the start of the experiment to values near 25 $MJ/m^2 \cdot day$ at time of harvest. On the few overcast days, values as low as 5 $MJ/m^2 \cdot day$ were recorded. Inside the glasshouse, daily radiation levels were, on average, 50% of those experienced outside. However, throughout the experiment the percentage ranged from 43 to 57%, with no obvious trend over time. Vapour pressure deficit averaged 1·27 kPa during the experiment, with daily values ranging from 0·6 to 2·1 kPa. Measurements of humidity and temperature throughout the day on some days showed that the assumption of constancy of absolute vapour content during the day introduced no significant error into the calculation of daily average vpd in the glasshouse (data not shown).

During the experiment, 4 of the 150 pots developed leaks, so accurate measurement of transpiration could not be obtained from those pots. In addition, in 1 pot of each of 2 of the Australian native sorghums, the selected plant failed to establish satisfactorily after thinning. Hence, analyses were conducted with missing values for these sampling units. The control plot (i.e. without plant) placed in each replicate used very little water, indicating that evaporative loss from the experimental system was negligible and no correction for it was necessary.

The analysis of variance (Table 1) showed significant differences among cultivars for total dry weight produced, water transpired, TE, leaf area, biomass partitioning, carbon isotope discrimination, and ash content. There was a wide range in TE for the 49 cultivars. The ratio of the range to the l.s.d. was 4·1. Previous studies on sorghum (Henderson *et al.* 1997) had found much less variation, with the ratio of range to l.s.d. being 2·0. The significant differences in biomass partitioning (i.e. top/total biomass%) highlighted the need to include root biomass in examining genetic variation in TE.

The ranking of cultivars for TE (Table 2) showed that the Australian native sorghums were much lower in TE than all of the other cultivars. If those 3 species were excluded in calculating the range of variation, then the range for the remaining 46 cultivars diminished to 7·7–6·0 g/kg. Although this range still exceeded that reported by Henderson *et al.* (1997), who studied 30 adapted hybrids, the ratios of range to the l.s.d. became similar at about 2·0, owing to the slightly higher l.s.d. in this study. Hence, the extent of genetic variation in the broad range of genetic material used in this study was no greater than that found among adapted lines.

Table 1. Analysis of variance for glasshouse experiment on 49 sorghum cultivars

TE, transpiration efficiency

Variable	Mean	Range	l.s.d. ($P = 0·05$)	Signif.
Total biomass (g)	91	161–13	29	**
Transpiration (kg)	13·4	23·0–3·1	4·1	**
TE (g/kg)	6·7	7·7–4·4	0·76	**
Leaf area (cm^2)	6278	11 300–1800	1800	**
Top/total biomass (%)	80·6	94–68	6·2	**
Carbon isotope (‰)	3·62	4·15–3·10	0·31	**
Ash content (%)	6·53	8·33–4·83	0·91	**

** $P < 0·01$.

The lack of increase in genetic variation among diverse cultivars is a significant finding. It suggests that the potential range of variation already exists in adapted material and that searching more diverse, wild sources may not be a fruitful avenue to pursue. However, although the range of variation is important, so is the absolute level of TE. If the diverse material includes cultivars operating at an increased level of TE, then it is worth pursuing such sources.

Comparison with expected transpiration efficiency

Although TE varied significantly among cultivars, the question remains of whether any of the cultivars reached TE levels greater than expected. It may have been that all of the variation was associated with cultivars lower in transpiration efficiency coefficient than the accepted value for sorghum of 9 Pa (Tanner and Sinclair 1983; Muchow *et al.* 1991). To examine this question, the TE values measured in the experiment were corrected for the ambient vpd to calculate the associated TE coefficients. The average vpd for the experimental period was 1·27 kPa. Applying this correction, the average TE over all cultivars of 6·7 g/kg converts to an average TE coefficient of 8·5 Pa, which is slightly below the accepted standard of 9 Pa and indicates that a number of the cultivars were functioning at TE levels lower than the accepted standard. The highest TE measured in the experiment was 7·7 g/kg for cultivar IS9710. This converts to a TE coefficient of 9·8 Pa, which is 9% higher than the accepted standard. This degree of difference showed significant ($P < 0·05$) improvement over the accepted standard using the appropriate *t*-test. Hence, at least one line with significantly improved TE coefficient was identified. Further experimentation is warranted to pursue this point as other studies have shown that this level of improvement would likely convert to substantial value in the field (Hammer *et al.* 1996).

Higher levels of TE coefficient and greater differentiation of cultivars may occur under water-limited conditions. Other studies, such as those in peanut (Wright *et al.* 1988) and preliminary studies in sorghum (Donatelli *et al.* 1992), suggest this possibility. As expression of improved TE has greatest consequence in water-limiting environments (Muchow *et al.* 1991; Hammer *et al.* 1996), and as the results of this study under non-limiting conditions show levels of improvement in TE worth pursuing, further study to examine TE and its genetic variation under water limitation is required.

Associations with transpiration efficiency

Isotope discrimination values of leaf samples of cultivars ranged from 4·15 to 3·10‰. This range was greater than that reported by Henderson *et al.* (1997), but the ratios of range to l.s.d. were similar in

Table 2. The ranking of 49 sorghum cultivars in transpiration efficiency (TE) measured in the glasshouse experiment

The l.s.d. ($P = 0·05$) for TE was 0·8 g/kg

TE range (g/kg)	Cultivars
7·5–8·0	IS9710, SC237–14E, IS22253
7·0–7·5	IS22201, M35–1, IS12739, IS20964, IS13446, R9188, IS23419, SC110–14E, IS25132, IS21436
6·5–7·0	Dorado, Tx2817, SC175–14E, IS21479, QL39, IS8564, Malisor84–7, Silk, BTx3197, QL36, SC326–6, IS26966, IS1347, Segeolane, IS121, IS3511, SC33, QL12, SC283–14E, N96, SC173–14E, B35, IS14359
6·0–6·5	IS18463, SC262–14E, AQL41, RTx430, SC272–14E, SC97–14E, SC603–14E, TAM422, Johnson Grass
5·5–6·0	IS18815 (ssp. *arundinaceum*)
5·0–5·5	*S. timorense*, *S. stipoideum*
4·5–5·0	
4·0–4·5	*S. matarenkense*

both studies ($3 \cdot 2$ and $3 \cdot 5$) owing to the slightly higher l.s.d. in this study. When the TE of each genotype was plotted against the carbon isotope discrimination of its leaf tissue, no association was found (Fig. 2). Henderson *et al*. (1997) found a positive correlation between TE and isotope discrimination that matched expectations from theoretical derivation. The major difference between this experiment and that of Henderson *et al*. (1997) was in the diversity of germplasm screened. This experiment used germplasm with a far greater diversity of background. In deriving theoretical expectations of the relationship between TE and carbon isotope discrimination, assumptions are made concerning plant respiration, non-stomatal water loss, and the degree of leakage of carbon between C_3 and C_4 photosynthetic pathways in the bundle sheath and mesophyll cells of sorghum leaves. With the more diverse germplasm, there may be genetic variation for these factors that is confounding the relationship between observation and theory.

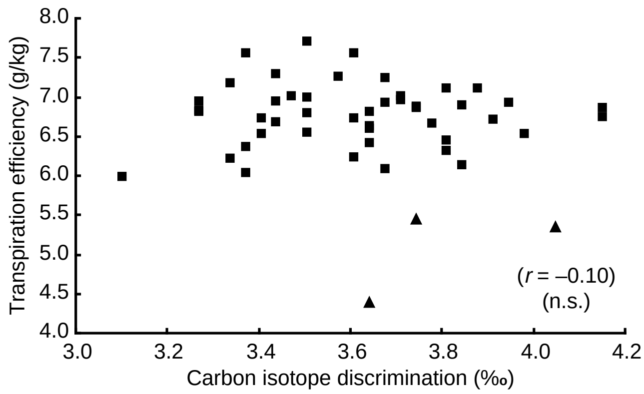

Fig. 2. Transpiration efficiency *v.* carbon isotope discrimination for all 49 *Sorghum* cultivars. The 3 Australian native sorghums are represented by the ▲ symbol.

Biomass production can be examined by breaking it into the components of the identity:

$$\text{Biomass (g)} = \text{T (kg)*TE (g/kg)}$$

where T is transpiration and TE is transpiration efficiency. Most of the genotypic variation in biomass production in this experiment was associated with variation in T (Fig. 3). However, there was a significant contribution from variation in TE (Table 1) and this showed a positive but weak association with biomass production (Fig. 4).

Variation in TE may be associated with variation in conductance and/or photosynthetic capacity. Neither of these aspects was measured directly in this experiment, but indices representing them at the whole plant level can be derived. Transpiration per unit leaf area is a crude measure of conductance, and specific leaf area or specific leaf nitrogen are crude measures of photosynthetic capacity. TE was not associated with transpiration per unit leaf area, which was calculated as the ratio of total transpiration to plant leaf area at harvest (Fig. 5). However, a weak but significant association was found with specific leaf area (SLA), which was calculated as the ratio of leaf area per plant to leaf mass per plant at harvest (Fig. 6). Higher TE was associated with low SLA. This may be related to thicker leaves at lower SLA, but leaf thickness was not measured directly. Cultivars also varied significantly in specific leaf nitrogen (SLN), which ranged from $0 \cdot 8$ to $1 \cdot 8$ g N/m^2 leaf area, and there was a tendency for SLN to increase as SLA decreased (data not shown). Hence, the measured genetic variation in TE showed an association with photosynthetic capacity, but the lack of strength in the association indicated that other factors must also have been involved.

A significant correlation was found between TE and ash content (Fig. 7). Although the strength of the relationship diminished when the 3 Australian native

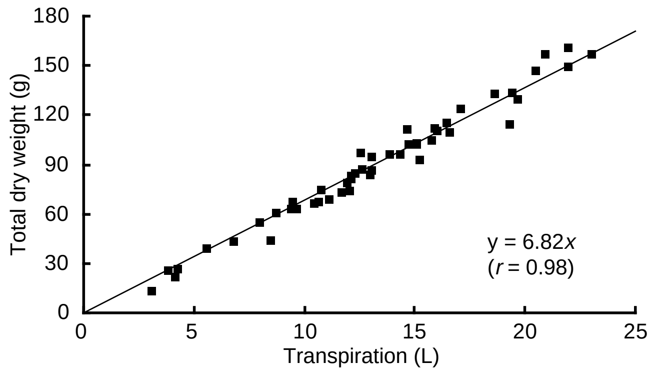

Fig. 3. Total biomass per plant *v.* total transpiration for 46 *Sorghum* cultivars.

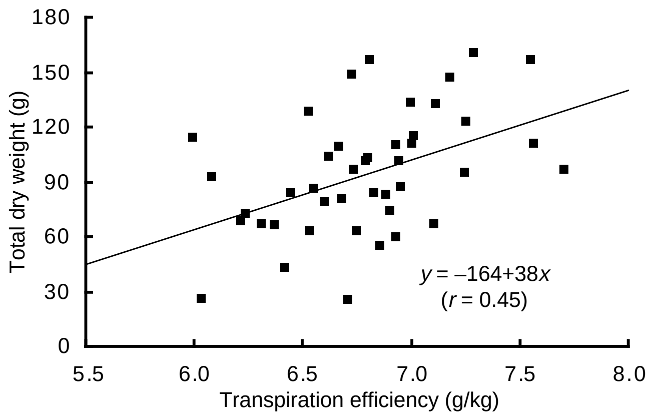

Fig. 4. Total biomass per plant *v.* transpiration efficiency for 46 *Sorghum* cultivars.

sorghums were removed from the analysis ($r = -0 \cdot 40$; data not shown), statistical significance was maintained. This finding is similar to that reported for sorghum by Masle *et al.* (1992). However, in this case, the correlation of TE with ash content was greater than that with carbon isotope discrimination. The physiological basis of the association is unknown at

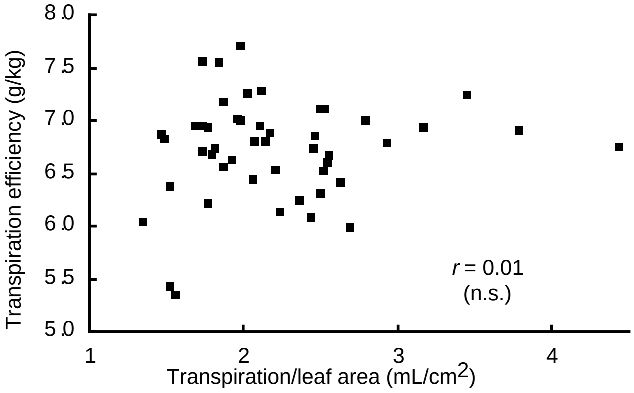

Fig. 5. Transpiration efficiency *v.* transpiration per unit leaf area for 46 *Sorghum* cultivars.

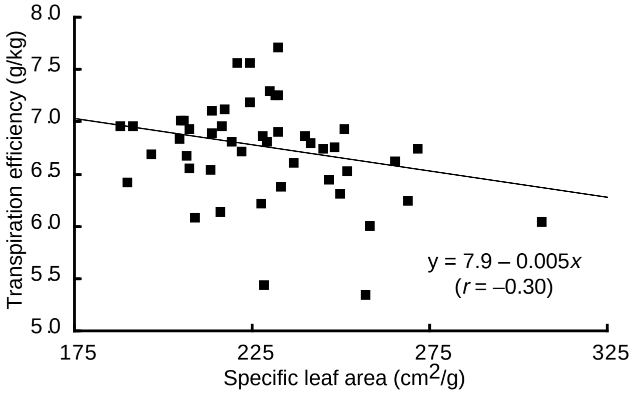

Fig. 6. Transpiration efficiency *v.* specific leaf area for 46 *Sorghum* cultivars.

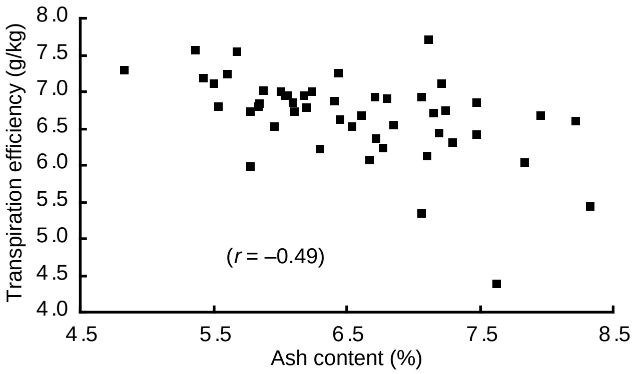

Fig. 7. Transpiration efficiency *v.* ash content for 49 *Sorghum* cultivars.

this stage. Further research in this area may aid interpretation, but the strength of the association would need to increase before ash content, or some derivative measure, could be useful as a selection index.

Conclusions

This study has shown that a significant degree of variation in TE exists among diverse sorghum cultivars. The extent of the variation, however, was not greater than that found among more adapted cultivars in a previous study. The TE measured in this study extended to a level 9% greater than the accepted standard for the species. This degree of increase was a significant ($P < 0 \cdot 05$) improvement on the accepted standard. The variation in TE found among cultivars was not related simply to carbon isotope discrimination. Significant associations of TE with ash content and indices of photosynthetic capacity were found. However, the associations were not strong. These results suggest that the underlying cause of the variation in TE may arise from a multiplicity of physiological mechanisms. The potential value of the improvement over the accepted standard and the degree of genetic variation found warrant further study to clarify some of these issues. It is suggested that screening for genetic variation under water-limiting conditions may provide useful insights and should be pursued.

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