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AGRONOMY & SOILS

Genetic Variation for Waterlogging Tolerance in Cotton

W.C. Conaty, D.K.Y. Tan*, G.A. Constable, B.G. Sutton., D.J. Field, E.A. Mamum

ABSTRACT.

In Australia, periodic waterlogging throughout the cotton growing season can cause production losses of up to 10%. There is limited information on the genetic variation in cotton for waterlogging tolerance. The aim of this study was to identify methods to evaluate physiological responses under waterlogging conditions that may lead to identifying waterlogging tolerant and sensitive cotton cultivars. A field experiment was conducted in Narrabri, north-western New South Wales using thirteen upland cotton (*Gossypium hirsutum* L.) cultivars (Georgia King, McNair 1032, PD93057, LA 887, Codetec 401, DP 16, DP 90, Coker 315, CIM 443, Gohar 87, Sicot 71, Sicot 73 and Sicot 80) and one *Gossypium barbadense* cultivar (Pima A-8) originating from diverse environmental regions. Parameters measured to assess response to waterlogging included: SPAD (leaf colour) readings, leaf nutritional status, leaf photosynthetic rate, plant and root morphology, and final yield. Leaf SPAD readings, nitrogen and potassium concentrations were reduced in waterlogged treatments compared to the respective controls, and varied with cultivar. Leaf phosphorus, calcium, magnesium, manganese and sulphur concentrations were reduced in the waterlogged treatment compared to the respective controls in all cultivars. Waterlogging increased leaf total iron concentration in all cultivars. No aerenchyma on cotton roots were observed in this study. Leaf SPAD readings, nitrogen and potassium concentrations suggested that the most waterlogging tolerant cultivars were Gohar 87, Pima A-8, Sicot 71, Sicot 73 and Sicot 80 which originate from production on heavy clays, and the most susceptible were Georgia King, LA 887, DP 16, DP 90 and CIM 443 which originate from production on lighter texture soils. This study helped to target those measurements that may be of most use to screen for waterlogging tolerance.

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INTRODUCTION

Waterlogging is a world-wide phenomenon that affects crop yield in agricultural regions. It is a major constraint to cotton production in developing countries such as India, Pakistan and China (Pang et al., 2004) and the annual agricultural production losses due to waterlogging in Australia are $A180 million (Price, 1993). Waterlogging can result in yield reductions of up to 10% (Bange et al., 2004) and 40% in severe cases (Hodgson and Chan, 1982). The effect of waterlogging is exacerbated when cotton is grown in heavy clay soil (Vertosol) with low drainage rates in low gradient fields that are almost exclusively furrow irrigated (Bange et al., 2004; Chan and Hodgson, 1981). Furthermore, as cotton in Australia is grown in summer dominant rainfall regions that experience regular high intensity summer storms, there is a strong likelihood of disruption of irrigation schedules and occurrence of waterlogged conditions.

Waterlogging occurs in saturated soils, when the air filled porosity (AFP) falls below 10% (Hodgson, 1982). In a well drained soil, the air filled porosity usually ranges from 10 to 40% of the total soil volume but waterlogging reduces these pores, substantially diminishing root oxygen supply causing hypoxia (Barrett-Lennard, 2003; Boru et al., 2003; Colmer and Islam, 2002). As oxygen diffuses 10,000 times more slowly in water than in air (Armstrong, 1979), plant tissues become hypoxic under anoxic conditions since roots require oxygen for optimal respiration and metabolic activity. The physiological consequences of waterlogged conditions include altered shoot and root hormonal status (Hocking et al., 1985), and nutrient uptake (Arkin and Taylor,

1981; Hocking et al., 1985; Orchard et al., 1986; Rochester, 2001; Wiengweera and Greenway, 2004). Waterlogging also decreases stomatal conductance, leaf water potential and photosynthesis (Meyer et al., 1987; Sojka and Stolzy, 1980; Thongbai et al., 2001). Waterlogging can accelerate cotton leaf and root senescence (Bange et al., 2004; Leonard and Pinckard, 1946; Pendergast and Midmore, 2006), increase the number of aborted flowers, squares and bolls and therefore reduce crop yield (Bange et al., 2004; Hodgson, 1982). Furthermore, waterlogging can alter the availability of nutrients in the soil environment through removal, oxidation or leaching (Orchard and So, 1985). Studies have shown that concentrations of nitrogen, phosphorus, potassium and calcium decreased, while iron, sodium and chloride increased in cotton leaves and stems when plants were exposed to waterlogged conditions (Hocking et al., 1985; Hocking et al., 1987; Hodgson, 1990; Meek et al., 1980; Reicosky et al., 1985). However, there has been no report on the genetic variation in plant nutrient status under waterlogged conditions in cotton.

Many plant species that can tolerate waterlogged conditions contain naturally occurring aerenchyma or develop lysigenous aerenchyma upon waterlogging (Colmer, 2003; Setter and Waters, 2003). Aerenchyma can provide a pathway for the transport and movement of oxygen and other gases within the roots and for removal of toxic compounds such as CO_2, methane and ethylene from the roots. Developed aerenchyma formation in wheat genotypes was associated with improved nutrient uptake and waterlogging tolerance (Huang et al., 1994; Huang et al., 1995; Jackson and Drew, 1984). However, there are no reports on the ability of *Gossypium* sp. to develop aerenchyma as an adaptation to waterlogging. Cotton is reported not to have aerenchyma (Huck, 1970; Leonard and Pinckard, 1946), although there have been suggestions of root adaptation or acclimation under waterlogged conditions (Reicosky et al., 1985; Schaefer et al., 1987).

The aim of this study was to identify methods to evaluate physiological responses under waterlogging that may lead to screening for waterlogging tolerant and sensitive cotton cultivars. Based on known physiological responses to waterlogging, we assessed SPAD (leaf colour) readings, leaf nutritional status, leaf photosynthetic rate, plant and root morphology, and final yield to determine if there was variability amongst diverse cotton cultivars.

MATERIALS AND METHODS

Experimental site. The cotton crop was grown in the 2005–2006 season at the Australian Cotton Research Institute (ACRI) near Narrabri (149°35'E, 30°12'S) on a laser-levelled endocalcareous, self-mulching, grey Vertosol (Isbell, 1996). The soil has a clay fraction of 60-65%, pH of 8.0-8.8, and low organic matter and nitrogen concentration (Bange et al., 2004).

Treatments and experimental design. Thirteen Upland cotton (*Gossypium hirsutum*) cultivars (Georgia King, McNair 1032, PD93057, LA 887, Codetec 401, DP 16, DP 90, Coker 315, CIM 443, Gohar 87, Sicot 71, Sicot 73 and Sicot 80) and one Pimacotton (*Gossypium barbadense*) cultivar (Pima A-8) were selected to represent a diverse range of genotypes, originating from various countries with contrasting climatic regions and soil types (Table 1). These cultivars were planted in two adjacent stands, one each for the waterlogging and control plots. Within each stand, the cultivars were planted in randomized complete blocks with four replicates.

Table 1. Origin and environmental adaptations of cultivars used in this experiment.

Cultivar	Origin	Climate	Soil Texture
Georgia King	USA - Georgia	Humid	Sandy loam
McNair 1032	USA – South Carolina	Humid	Sandy loam
PD93057	USA – South Carolina	Humid	Sandy loam
LA887	USA – Louisiana	Humid	Sandy loam
Codetec 401	Brazil	Wet	Loam
DP 16	USA – Mississippi	Humid	Silt
DP 90	USA - Arizona	Hot	Clay loam
Pima A-8	USA – Arizona	Hot	Clay loam
Coker 315	USA – Texas	Cool	Clay
CIM 443	Pakistan	Dry	Clay
Gohar 87	India	Dry	Clay
Sicot 71	Australia-CSIRO	Mixed	Clay
Sicot 73	Australia-CSIRO	Mixed	Clay
Sicot 80	Australia-CSIRO	Mixed	Clay

The cotton crop was furrow irrigated approximately once a fortnight (two weeks), depending on rainfall. Irrigation was scheduled based on soil water deficit and water holding capacities, with the aim of supplying water when soil water had dropped below 50% plant available water capacity as estimated from crop evapotranspiration. The waterlogged plots were irrigated at the same frequency as the control but the profile was completely saturated to the point of ponding by installing plywood boards in the furrows. Furthermore, the siphons were allowed to run for at least 48 h longer than the control. The field was pre-irrigated on 3rd October and throughout the growing season. The crop was irrigated five times, on 5th January, 17th January, 31st January, 13th February and 8th March. Waterlogging was imposed on the first four crop irrigations only. Rainfall throughout the growing season totalled 486 mm. Soil air filled porosity (AFP) was measured at 5-day intervals to determine when the crop was under waterlogged conditions. The control plots were waterlogged (AFP <10%) for 8 d, compared to 19 d for the waterlogged plots (Fig. 1).

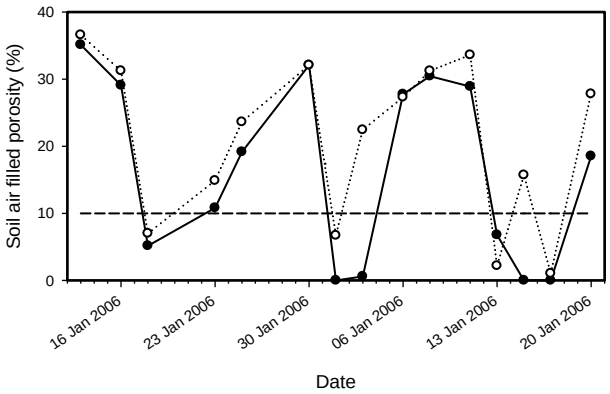

Fig. 1. Mean soil air filled porosity of the waterlogged (—●—) and control (···○···) treatments.

DATA COLLECTION

Soil air filled porosity. Pore space relations of a natural soil core were used to calculate soil AFP throughout the experimental period. Four core samples were collected from four randomly allocated plots in each of the waterlogged and control experiments. Soil cores were collected by driving a 10 cm diameter soil core sampler into the soil to a depth of 20 cm. The cores were dug out, cleaned and placed in a plastic bag to prevent water loss. Cores were weighed with the soil in field condition and then again after oven drying at 110°C. The wetness (g/g) and bulk density (g/cm^3) and subsequently the % volume of air (AFP) of each soil core were calculated.

Leaf colour. Leaf color was measured using a Minolta SPAD 502 (Konica Minolta, U.S.A.) leaf color meter which can be used to compare relative amounts of chlorophyll (SPAD value ranging from 0.0 to 99.9) in leaves (Boquet et al., 1999; Thongbai et al., 2001). Ten SPAD readings were taken on the youngest fully expanded leaf in each plot four times during the experiment on 11th and 30th January and 6th and 17th February 06.

Leaf nutrition. Leaf samples from approximately twenty plants per plot were collected three times during flowering, on 12th January, 6th and 17th February 2006. The youngest fully expanded leaf blade, excluding the petiole, was collected and oven dried at 70°C for one week. Leaf tissue was ground to 1 mm in a Foss Tecator Cyclotec (Foss, Australia) sample mill and analysed using inductively coupled plasma mass spectroscopy (ICP-MS) for calcium (Ca), iron (Fe), magnesium (Mg), manganese (Mn), phosphorus (P), potassium (K), and sulphur (S). Similar numbers of leaves were also collected on 6th and 17th February for Kjeldahl nitrogen (N) analysis.

Photosynthetic rate. Leaf photosynthetic rate was measured using an infra-red gas analyser (IRGA), Portable Photosynthesis System, Li-COR® model 6400-40. Photosynthetic rates were measured between 1000 and 1400 h approximately 24 h before irrigation (11th February), and then 72 h later (14th February). This occurred 24 h after the irrigation event for the control plots, while waterlogged plots were still inundated.

Measurements were taken on the youngest fully expanded leaf of 12 plants for both waterlogged and control plots (three plants per replicate) from two cultivars LA887 and Sicot 71. These cultivars were selected because they had the most contrasting leaf color reaction to early waterlogging events measured by the SPAD. Leaves were tagged during the pre-irrigation measurements to ensure that the same leaves were analysed following irrigation.

Root morphology. Lateral roots 2-4 mm in diameter were sampled from four contrasting cultivars, LA887, Georgia King, Sicot 71 and Sicot 73 at plant maturity. These root samples were collected and washed in water and then fixed in 10% glutaraldehyde (Merck, Crown Scientific, Australia). Samples were then washed in phosphate buffer solution (pH 7) and stored in 70% ethanol. These samples were

then embedded in paraffin wax cassettes. Using a microtome, embedded samples were sectioned at 10 µm and transferred onto SILANE-PREP™ (Sigma-Aldrich, Australia) slides. Slides were deparaffinized in xylene, stained with Harris haematoxylins, Scott's bluing solution, and Eosin and mounted in DPX (Ruzin, 1999). The sections were examined for the presence of aerenchyma and changes in vascular development due to waterlogging with a BX41 Olympus microscope and images were captured using a DP70 digital camera (Olympus Australia Pty Ltd, Melbourne, Australia) at the University of Sydney, Australia.

Yield. Mechanically picked seed cotton weight was recorded at harvest. A 250 g sub-sample was ginned on a 20 saw gin and lint yields calculated from the product of seed cotton weight and lint fraction.

Data analysis. All data were analysed in Genstat v8.0 and assessed at a P=0.05 level of significance. As the variances in both the control and waterlogged experiments were similar, all data were combined, with waterlogging treatment as site/main effect and interactions between cultivar and waterlogging as primary interest and as subplot (Cochran and Cox, 1957). A linear mixed model REML (Residual Maximum Likelihood) analysis was used to test for interactions between the cultivars and waterlogging factors for leaf color and leaf nutrition where repeated measurements were taken. Analysis of variance (ANOVA) was used to test for interactions between the waterlogging and cultivar factors in N (% dry weight content) and photosynthetic rate.

RESULTS AND DISCUSSION

Genetic variability in waterlogging tolerance has been reported in cereal crops such as wheat, barley, oats and maize (Huang et al., 1994; Huang et al., 1995; Setter and Waters, 2003; Srivastava et al., 2007) but not in cotton. To our knowledge, this study is the first report of cotton genetic variability in waterlogging tolerance; Bange *et al*. (2004) found no difference in a limited range of cultivars.

Leaf colour and nutrition. The trends in nutrient concentrations and SPAD readings were similar for the different sampling times and hence, the means across sampling times are presented. There were interactions (P<0.01) between cultivar and irrigation regimes in SPAD readings (relative leaf chlorophyll). Waterlogged conditions decreased SPAD readings in all cultivars studied compared to the respective control (P<0.01) except Sicot 71 (Fig. 2). Cultivars Georgia King and LA 887 had the largest reduction in SPAD readings due to waterlogging conditions while Australian cultivars, Sicot 71, Sicot 73 and Sicot 80 had the smallest relative differences. Waterlogging-induced chlorosis in cotton and other crops is often associated with the decreased availability and uptake of nutrients, particularly N (Drew and Sisworo, 1977; Rochester, 2001; Smethurst and Shabala, 2003) and may result in a reduced photosynthetic rate (Meyer et al., 1987; Thongbai et al., 2001). Given that there was variation in SPAD readings in cultivars from exposure to waterlogging, this methodology may offer the potential to discriminate cultivars in their tolerance to waterlogging.

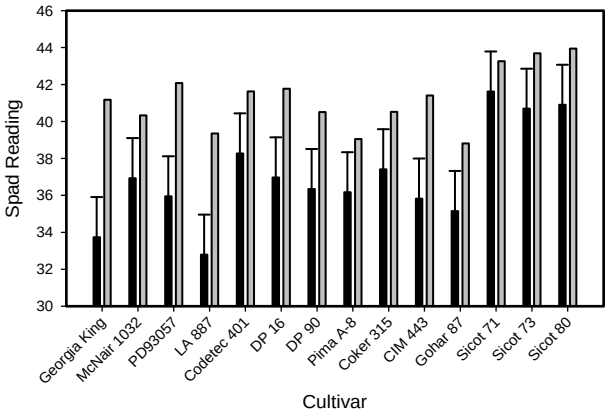

Fig. 2. SPAD reading (relative chlorophyll content, 0.0-99.9) in all cultivars measured at four intervals during the season in two irrigation treatments (waterlogged ■; control □). Vertical bars represent l.s.d. for cultivar by irrigation interaction at P=0.05.

A more definitive measure of a crop's response to waterlogging is leaf nutrition (Hocking et al., 1985; Hocking et al., 1987; Huang et al., 1995). In this study, there were interactions between cultivar and irrigation regimes in leaf blade N, K and Fe concentrations (Table 2, Fig. 3). N (%) and K (mg/kg) concentrations were lower (P<0.05) in the waterlogged treatment for cultivars such as Georgia King, LA 887, DP16 and CIM 443 compared to the control, but not different (P>0.05) for McNair 1032, Codetec 401, Pima A-8, Gohar 87 and Sicot 71, 73 and 80 (Fig. 3). Again, as there were clear differences in the degree of change of leaf N and K after waterlogging among cultivars, this measure also offers opportunity for discrimination of waterlogging tolerance. Similar results have been reported in

wheat and maize showing that N and K concentrations in leaves and/or stems were reduced to a lesser extent in waterlogging tolerant cultivars compared to sensitive ones (Huang et al., 1994; Huang et al., 1995; Srivastava et al., 2007).

Table 2. Probability of cultivar and waterlogging main effects and cultivar by waterlogging interactions for leaf blade nutrient concentration (N, P, K, Fe, Ca, Mg, Mn, S). * - *P*< 0.05, ** - *P*<0.01 and n.s. - not significantly different at *P*=0.05.

Nutrient	Cultivar	Waterlogging	Cultivar* waterlogging
N	**	*	*
P	**	*	n.s.
K	**	n.s.	**
Fe	**	**	*
Ca	**	**	n.s.
Mg	**	*	n.s.
Mn	**	*	n.s.
S	**	*	n.s.

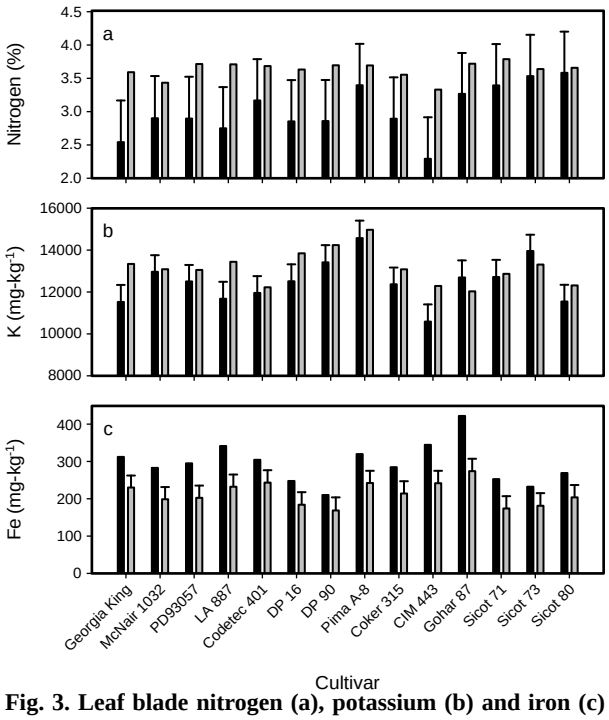

Fig. 3. Leaf blade nitrogen (a), potassium (b) and iron (c) concentrations of all cultivars in two irrigation treatments (waterlogged ■; control □). Vertical bar represents l.s.d. for cultivar by irrigation interaction at *P*=0.05. Averaged across measurement dates.

Total Fe leaf concentrations in the waterlogged treatment were higher ($P<0.05$) than the respective controls in all cultivars. Some cultivars (e.g., Georgia King, LA 887 and Gohar 87) had much higher total Fe leaf concentrations than others (e.g., Codetec 401, Sicot 71, 73 and 80) in the waterlogged treatment compared to their respective controls. This agrees with other studies on cotton and other field crops showing an increase in Fe concentration following waterlogging (Hodgson, 1990; Huang et al., 1995; Khabaz-Saberi et al., 2006). When soil is inundated, ferric iron (Fe^{3+}) is reduced to the more soluble ferrous (Fe^{2+}) ions, increasing soil iron availability. However, total iron concentrations can be misleading as it is the active form of iron, Fe^{2+}, that is critical for plant nutrition and chlorophyll production (Hodgson, 1990; Rochester, 2001). The inherent problem in iron nutrition is that the determination of the Fe^{2+} concentration cannot be achieved by a commercial laboratory, and requires the use of fresh leaves, analysed a few hours after sampling. Therefore the procedure may not offer the best means of cultivar screening because determination of Fe^{2+} concentration is difficult.

P, Ca, Mg, Mn and S leaf concentrations (mg/kg) in the waterlogging treatments for all cultivars were lower ($P<0.05$) than in the control (Fig. 4). There were no interactions with waterlogging for these nutrients. Leaf Mg and Ca concentration were reduced due to waterlogging but remained above the lower limit of adequate nutrition of 4 g/kg for both nutrients in all cultivars (Rochester, 2001). Leaf Mn concentration following saturation was reduced but also remained above the lower limit of adequate nutrition of 50 mg/kg in all cultivars. Like Fe nutrition, waterlogging generally increases the availability of Mn in the soil (Armstrong, 1982). However, total plant concentrations decline as the plant's roots cannot properly function and absorb nutrients under anoxic conditions (Hodgson, 1990; Hook, 1984). Hence, leaf Mg, Ca and Mn may not be as useful for cultivar discrimination as there were no cultivar by irrigation treatment interactions in this study.

Photosynthetic rate and yield. Photosynthetic rates pre-irrigation were lower ($P<0.05$) than post-irrigation presumably due to water stress occurring before irrigation (Fig. 5). Pre-irrigation photosynthetic rates were slightly higher ($P>0.05$) in the waterlogged plots, most probably due to the soil profile having higher levels of soil moisture resulting from the previous waterlogging treatment. During the post-irrigation event, waterlogging reduced ($P<0.05$) the photosynthetic rate by 28% in the susceptible LA 887 and 9% in the more tolerant

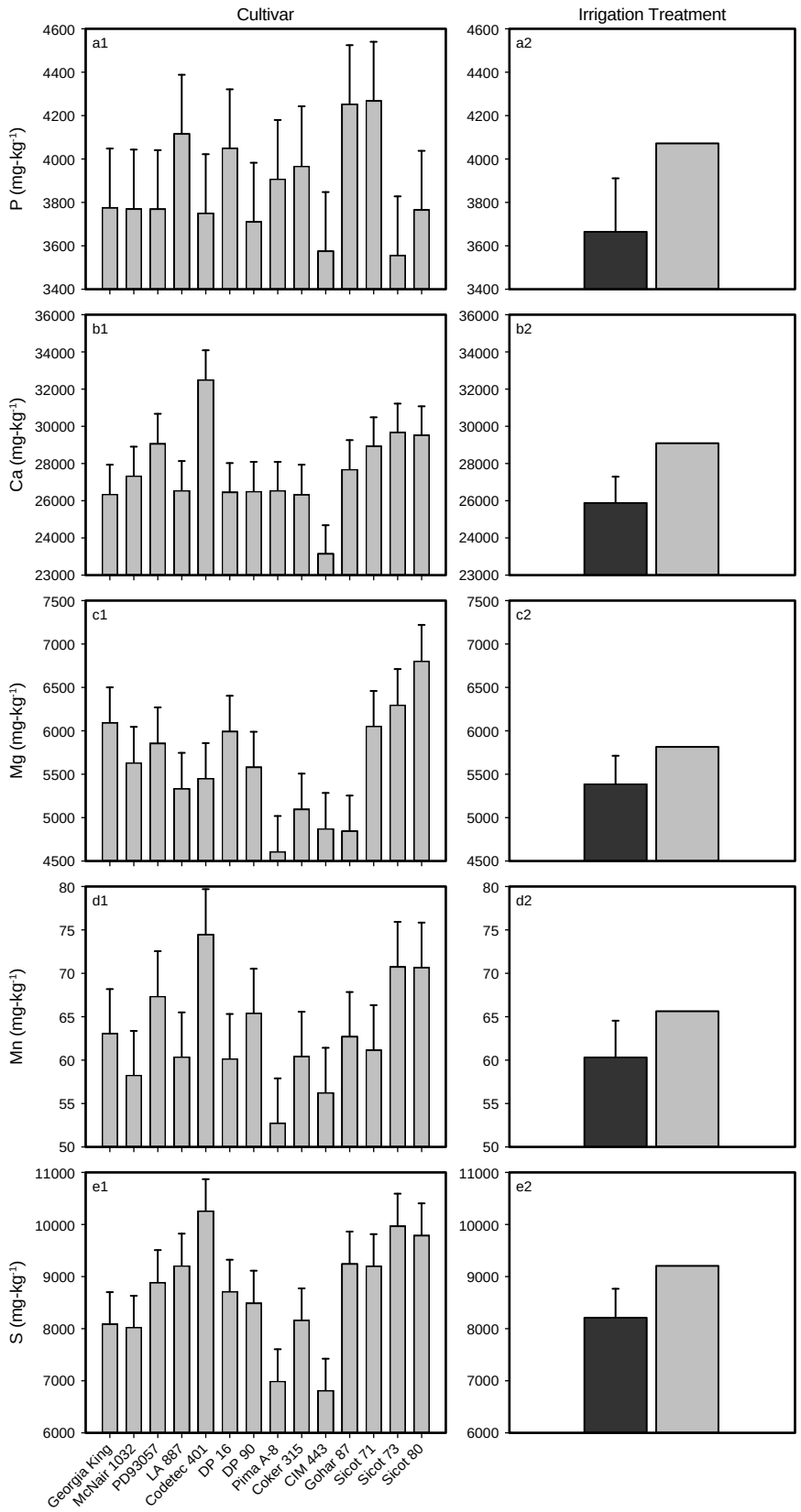

Fig. 4. Leaf blade nutrient concentrations of (a) phosphorus, (b) calcium, (c) magnesium, (d) manganese and (e) sulphur for (1) cultivars; and (2) irrigation treatment (waterlogged ■; control □). Vertical bars represent l.s.d. for cultivar (a1 to e1) and irrigation (a2 to e2) main effect, respectively at *P*=0.05. Averaged across measurement dates.

Sicot 71 compared to their respective controls (Fig. 5). Similar results were observed by other authors with cotton photosynthetic rates decreasing by 16% following seven days of waterlogging (Meyer et al., 1987). It is interesting to note that only the cultivar main effect was significant (P<0.05) (Fig. 7) and there were no significant interaction or irrigation main effects (P>0.05) in our study. Our results are similar to other reports showing that cotton plants exposed to waterlogging-induced nutrient stress later recovered with no detrimental effect on yield (Hocking et al., 1985; Hocking et al., 1987).

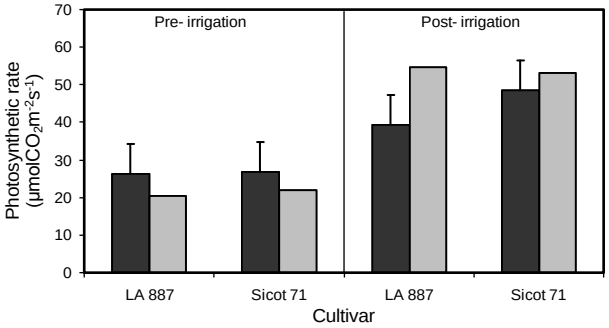

Fig. 5. Pre-and post irrigation photosynthetic rates for the cultivars LA 887 and Sicot 71 under two irrigation treatments (waterlogged ■; control □). Vertical bars represent l.s.d. for cultivar by irrigation interaction at P=0.05.

Root morphology. Root morphology did not change as a result of waterlogged conditions (Fig. 6). Lysigenous aerenchyma, that is the enlarged gas spaces which increase the porosity of the roots, did not form in any of the four representative cultivars observed. Furthermore, the size and proportion of vascular development in the waterlogged and control plants were not different. Prior to this study, there have been no published studies indicating whether cotton roots form lysigenous aerenchyma in response to waterlogged conditions (Huck, 1970; Leonard and Pinckard, 1946), although there have been suggestions of root adaptation (Hocking et al., 1985; Hocking et al., 1987; Reicosky et al., 1985; Schaefer et al., 1987). It is speculated that for significant variations in root morphology to be observed, which was not the case in this study, the cultivars studied would need to come from extremely diverse germplasm. A wider search on the *Gossypium* genus may be beneficial to determine possible differences in vascular development in response to anoxia.

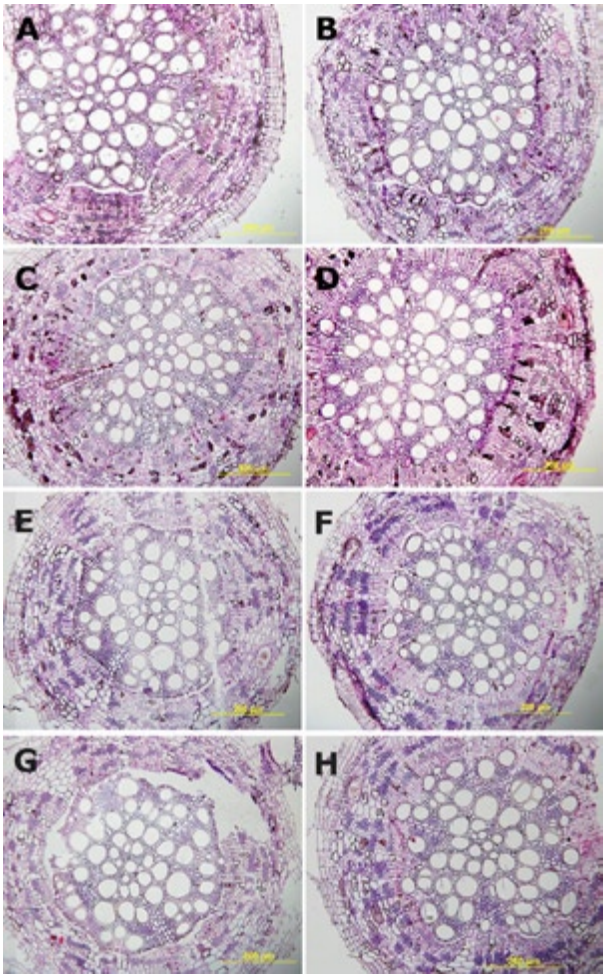

Fig. 6. Root sections of A) Georgia King, C) LA887, E) Sicot 71 and G) Sicot 73 in the control, and B) Georgia King, D) LA887, F) Sicot 71 and H) Sicot 73 in waterlogged treatments.

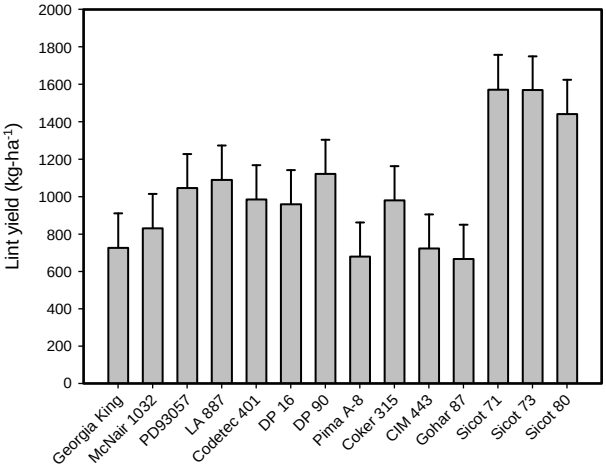

Fig. 7. Mean lint yield (kg/ha) of all cultivars. Vertical bars represent l.s.d. for cultivar main effect at P=0.05.

Based on leaf colour changes and leaf tissue analyses (predominately from N and K), the most sensitive cultivars in this study were Georgia King, LA 887, DP16, DP 90 and CIM 443. These cultivars were bred in the USA for regions with lighter textured soils which are less likely to be exposed to waterlogging. The most waterlogging tolerant cultivars were Pima A-8, Gohar 87, Sicot 71, Sicot 73 and Sicot 80. Sicot 71, Sicot 73 and Sicot 80 are Australian cultivars bred in ACRI, Narrabri by a number of breeding cycles on heavy clay Vertosols which are more likely to be exposed to frequent waterlogging. Pima A-8 is a *G. barbadense* cultivar, bred in Arizona, USA on clay loam soils. The results in this study are further supported given the environments and soils on which these cotton cultivars have been bred and adapted.

CONCLUSIONS

This work found that there was genetic variation in cotton's response to waterlogged conditions. The key variables were SPAD readings, leaf N and K concentrations and leaf photosynthetic rates which were reduced under waterlogged conditions. Comparing those cultivars with their origins and adaptation supported the results in this study. Based on these measurements, the cultivars that showed the potentially best tolerance to waterlogged conditions were Gohar 87, Pima A-8, Sicot 71, Sicot 73 and Sicot 80 which were mainly bred in regions with heavy clays. Other variables such as leaf P, Ca, Mg, Mn and S concentrations showed less discrimination between cultivars.

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