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Water Deficit Enhanced Cotton Resistance to Spider Mite Herbivory

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We investigated the responses of cotton (*Gossypium hirsutum* L.) to the combined effects of soil water deficit and two-spotted spider mite (*Tetranychus urticae* Koch) infestation. Two mite treatments (−M: uninfested, +M: artificially infested 83 d after sowing), and two water regimes (+W: well watered, −W: water stressed) were combined factorially in four treatments. Mite colonies developed at similar rates in well-watered and water-stressed crops. Despite the similar intensity of infestation, visual symptoms of mite injury were more marked in well-watered host plants (+M+W) than in their water-stressed counterparts (+M−W). Lint yield of unstressed controls (−M+W) was 175 g m^{-2}. In uninfested crops, water deficit reduced yield by 30%, mites reduced the yield of well-watered crops by 92%, and the combination of mite infestatiou and water deficit reduced yield by 72% (water effect: $P < 0{\cdot}01$; mite and interaction effect: $P < 0{\cdot}0001$). Differences in yield responses to mites between well-watered and water-stressed crops were mostly related to differences in reproductive partitioning. The interaction between mites and water deficit was also significant for other crop variables including canopy temperature, leaf water potential, concentration of nitrogen in reproductive structures and seed oil concentration. The magnitude and consistency of the interaction between both stresses indicates that, under our experimental conditions, mechanisms of adjustment to water deficit may have enhanced cotton resistance to mites. This is further supported by (*a*) an increase in specific leaf weight and a parallel increase in leaf penetration resistance due to water deficit; (*b*) a negative association between macroscopic symptoms of mite injury and leaf penetration resistance; and (*c*) a choice test showing that adult female mites preferred to feed and oviposit on leaves from well-watered plants.

Key words: *Gossypium hirsutum*L., *Tetranychus urticae* Koch, leaf water potential, leaf penetration resistance, canopy temperature, multiple stresses, specific leaf weight, radiation use efficiency, nitrogen concentration, reproductive allocation.

INTRODUCTION

The two-spotted spider mite (*Tetranychus urticae* Koch) is a mesophyll feeder whose effects on cotton (*Gossypium hirsutum* L) have been investigated at the cytological, leaf and crop levels. Research at the leaf level demonstrated that *T. urticae* can reduce stomatal conductance, photosynthesis and transpiration rate (Bondada *et al*., 1995), responses that are consistent with increased foliage temperature and reduced radiation-use efficiency measured in mite-infested crops (Sadras and Wilson, 1997*a*).

However, plants in the field are frequently exposed to multiple stresses (Chapin *et al*., 1987; Mooney, Winner and Pell, 1991). Water deficit and arthropod herbivory can substantially reduce plant productivity and the interactions between these stresses have received considerable attention (Jones and Coleman, 1991; Waring and Cobb, 1992). Interactions between arthropod pests and water deficit in cotton have been investigated in studies dealing with *Bemisia* spp. (Flint *et al*., 1994), *Pectinophora gossypiella* (Saunders) (Kittock *et al*., 1983), *Lygus hesperus* Kingh, *Empoasca* spp., *Geacoris oallens* Stal and *Orius tristicolor* White (Leigh *et al*., 1970; Leigh *et al*., 1974; Flint *et al*., 1994). Only one of these studies considered the interactions between mites, *T. pacificus* McGregor, and crop water regime (Leigh *et al*., 1970). No attempt has been made, however, to measure the physiological responses of cotton to the combined effects of mites and water stress.

Importantly, maintenance of leaf and canopy temperature within a range from about 23 to 32 °C through stomatal regulation of transpiration seems to be critical for the growth and yield of *Gossypium* spp. (Burke, Mahan and Hatfield, 1988; Radin *et al*., 1994). Because mites disrupt the functionality of the stomatal apparatus (Bondada *et al*., 1995) the interactions between mites and water stress in cotton are likely to be important.

This study investigated the responses of field-grown cotton to the combined effects of soil water deficit and *T. urticae* infestation. Our approach involved measurements at the leaf and crop levels in contrast with studies of interactions between mites and water stress in other species that concentrated on leaf-level responses (Youngman and Barnes, 1986; Hare *et al*., 1989).

MATERIALS AND METHODS

A field experiment was carried out at Narrabri (30° S, 150° E) on a deep uniform grey clay soil (Northcote, 1979). Crops of cultivar NuCotn 37 were sown on 9 Oct. 1996. This cultivar produces *Bacillus thuringiensis* subsp. kurstaki insecticidal proteins (Cry IAc) that reduce the need of chemical control of *Helicoverpa* spp (Lepidoptera: Noctuidae), the main pests of cotton in Australia. Additionally,

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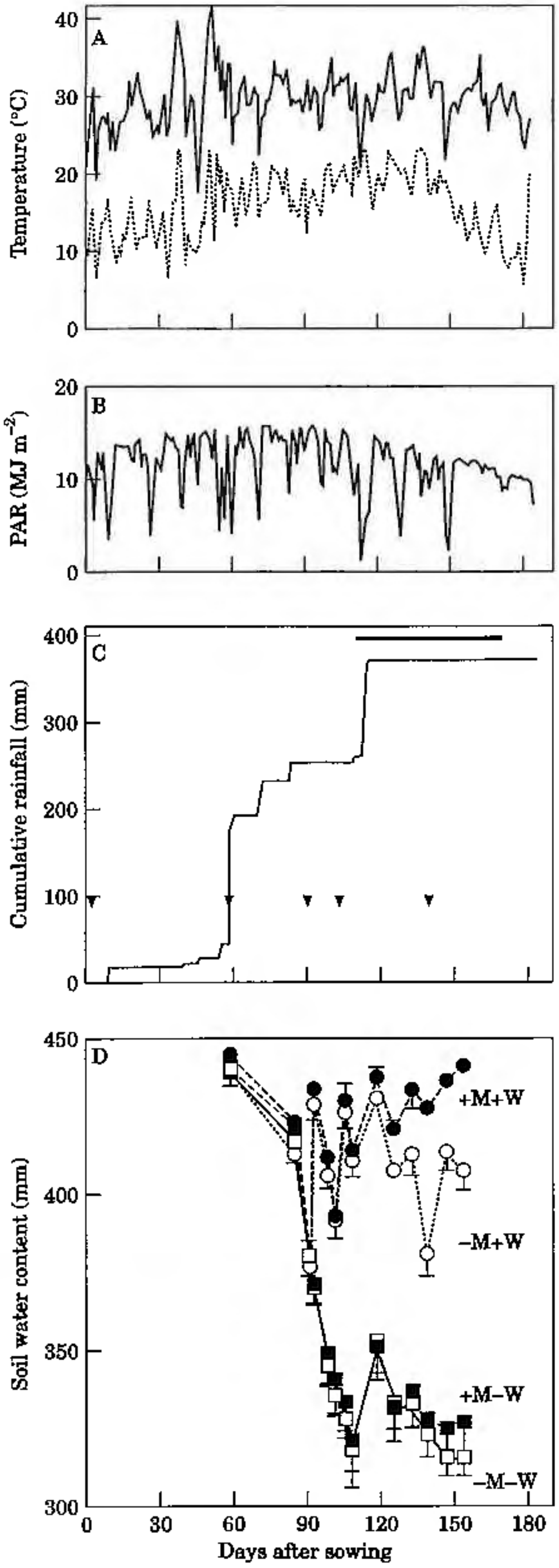

FIG. 1. Meteorological variables and soil water content during the experiment. A, Maximum (——) and minimum (· · · ·) temperature; B, incident PAR; C, cumulative rainfall (continuous line); arrows show dates of irrigation and the horizontal bar the period when soil in −W plots was covered; D, soil water content; bars are one s.e.m. and were not plotted when smaller than symbols.

insect pests were monitored twice weekly and controlled with insecticide when necessary. Plant density was 13 plants m^{-2} and rows were 1 m apart. Crops were fertilized with 100 kg N ha^{-1} before sowing. Figure 1 shows temperature, incident photosynthetically active radiation (PAR, 0·4–0·7 μm) and rainfall during the experiment.

Treatments and experimental design

Two mite treatments (−M, +M) and two water regimes (−W, +W) were combined factorially in four treatments that were replicated four times in a split-plot design; water treatments were applied to main plots and mite treatments to subplots. Each subplot was eight rows 18 m long and was separated from others by a 4-m alley to reduce cross-infestation of mites among treatments.

Mite treatments included uninfested control (−M) and plots artificially infested with *T. urticae* 83 d after sowing (DAS) (+M). Shortly before infestation (76 DAS), the whole experimental area was treated with a mixture of broad spectrum insecticides (thiodicarb, 375 g ha^{-1} and dimethoate, 140 g ha^{-1}) to reduce populations of natu[illegible] enemies hence facilitating mite establishment in +M pl[illegible]. These insecticides are non-acaricidal at the rates used in this experiment (Tomlin, 1994; Herron *et al.*, 1997). The +M plots were infested using mite-infested cotton seedlings raised in a glasshouse while mites in −M plots were suppressed with acaricides (propargite, 1500 g ha^{-1} applied 133 and 153 DAS). Further details on mite rearing and methods of infestation are given in Wilson (1993).

All crops were furrow irrigated before sowing. Thereafter well-watered crops (+W) were irrigated each time a soil water deficit of 50–60 mm was reached (Hearn and Constable, 1984) while water-stressed crops (−W) received no further irrigation. To reduce rainfall infiltration, the soil between rows in −W plots was covered with transparent polyethylene film 111 DAS. To assess the effect of polyethylene cover on light reflection, measurements were taken with a ceptometer (Decagon Devices, Inc. Pullman, WA, USA) positioned about 0·20 m above the canopy. Owing to high canopy light interception, differences in light reflection from covered (−W) and uncovered (+W) ground were negligible at 111 DAS when +W crops were intercepti[illegible] 80–90% of PAR, i.e. noon PAR reflection from the −W crops in which soil was covered with polyethylene was 4·1% of incident PAR compared with a 3·5% reflection in uncovered plots. As leaf senescence progressed, differences in reflectance increased; the largest difference in the amount of PAR reflected was, nonetheless, small in relation to the total amount of PAR intercepted by the canopy, i.e. 7·6% of incident PAR in −W *vs.* 4·0% in +W. The polyethylene cover was removed 168 DAS.

Measurements

Mites and their predators. Mite populations were assessed by counting the adult females on the third or fourth mainstem leaf below the apex, the leaves where mites tend to concentrate and the recommended sampling units for mites in commercial crops in Australia (Wilson and Morton, 1993). Between ten and 20 leaves per subplot were sampled at weekly intervals and these leaves were also kept for damage scoring (see below). Full details and justification of sampling procedures are given in Wilson (1993) and Wilson and Morton (1993).

A preference test was carried out to assess whether adult female mites would, given the choice, discriminate between leaves from well-watered ($+W$) and water-stressed ($-W$) plants. We used adult females from a glasshouse culture and third (from the apex) mainstem leaves taken from $-W-M$ and $+W-M$ plots 122 DAS. Leaf discs (2·5 cm in diameter) consisted of two semicircles, one from each treatment, placed in contact with the abaxial side uppermost. These were placed in petri dishes lined with moist cotton wool to maintain turgor, and five adult females were placed on each half-disc. After 24 h in a growth chamber (temperature: $28 \pm 0{\cdot}5$ °C, light/dark period: 14/10 h) the number of adult females and eggs on each half disc was counted.

Predator abundance in each treatment was assessed on two dates (97 and 120 DAS) using suction samplers as described by De Barro (1991). On each sample date a complete row was sampled in the centre of each subplot. A zigzag sampling technique, where the suction device was passed along the lower, middle and top strata of the canopy, was adopted to ensure adequate coverage of the canopy. Insects collected were killed using chloroform and the abundance of spider mite predators, as described in Pyke and Brown (1996), was scored.

Crop and soil. Soil water content was measured with a neutron probe at about weekly intervals and, when possible, shortly after irrigation. One access tube was located in the central row of each subplot and measurements were taken at 0·05, 0·15, 0·25, 0·35, 0·45, 0·60, 0·80, 1·0 and 1·2 m depths.

Shoots and tap roots were sampled at fortnightly intervals from 85 DAS (sample size = 0·5 m^2). Plant components were separated and over-dried to constant weight. Green leaf area of at least two whole plants was measured with a leaf area meter (LI-3100, LICOR, Lincoln, NE, USA) to estimate specific leaf weight, and this variable used to estimate leaf area index (LAI) of the crop from green laminae biomass values. Leaves and other abscissed plant parts were collected fortnightly in 1 m^2 trays placed between the rows. Mature fruit ('open bolls') were counted weekly in 2 m^{-2} crop sections. Lint yield was measured in large crop samples (30 m^2) by harvesting the two centre rows of each subplot with a spindle picker 189 DAS. Sub-samples were ginned with small saw gins to estimate lint fraction, i.e. lint/(lint+seed). Oil concentration of delinted seed was measured by the NMR technique using a cotton-oil standard.

Plant organs taken in the fortnightly harvests were milled after drying and nitrogen content was determined using a near-infrared protein analyser (Inframatic 8100, Perten Instruments, Sweden) as described in Rochester, Constable and MacLeod (1993). Small amounts of plant material allowed nitrogen analysis in reproductive structures for some dates only (97 DAS for flowerbuds, 132 and 146 DAS for capsule walls).

At approximately weekly intervals, the fraction of PAR intercepted by the canopy at noon (Qn) was calculated from measurements made with a ceptometer. Noon canopy temperature was measured with an infrared thermometer (Everest Interscience, Tustin, CA, USA) on clear days following the procedure described in Idso, Reginato and Farah (1982). Temperature was measured at weekly intervals from 92 to 132 DAS; four readings per subplot were taken and averaged.

Leaf. All leaf variables were measured on the third or fourth mainstem leaf below the apex. Leaf damage was scored immediately after mite counts on ten to 20 leaves per subplot. Leaf damage was scored by visually recording the percentage of the leaf area damaged by mites, irrespective of damage intensity as described in Wilson (1993). Starting at 116 DAS we also recorded the percentage of leaf area severely damaged by mites, i.e. where the effects of cumulative mite feeding caused the abaxial side of the leaf to become brown and desiccated. For samples taken after 104 DAS, leaf area and dry weights were measured and specific leaf weight calculated.

Leaf water potential was measured using the pressure chamber technique following the procedures described by Hsiao (1990). Measurements were taken at around solar noon (±1 h) on clear days; two leaves per replicate were sampled at 107, 124 and 133 DAS. Percent water content, i.e. 100 × (fresh weight − dry weight)/dry weight, was measured on samples (20 leaves per subplot) taken at 133 DAS. Note that this definition of leaf water content, often used in studies of plant/herbivore relationships (Sagers, 1992) is different from the definition of relative water content used in studies of plant water relations (Wright, Morgan and Jessop, 1996).

Penetration resistance was measured on attached leaves with a dial tension gauge (probe diameter 0·73 mm; Chatillon AG50, John Chatillon & Sons, New York, NY, USA) as in Sands and Bracantini (1991). Three leaves per subplot and three positions per leaf near the insertion of the petiole, where mites prefer to feed (Wilson, 1994), were measured and averaged at approximately weekly intervals between 99 and 132 DAS. Mechanical properties of leaves depend on a number of factors, including their turgor pressure (Sands and Bracantini, 1991). Thus, measurements were taken early in the morning (before 0800 h) to minimize the importance of turgor pressure as a source of variation in leaf penetration resistance. This procedure implies that differences caused by treatments were more likely to be structural than turgor-related. This assumption is further supported by visual inspection of $-W$ crops indicating no wilting early in the morning, in contrast to marked wilting often observed in the afternoon.

Calculations and statistical analyses

Mite, soil, crop and leaf variables were analysed by ANOVA with mite treatment, water regime and their interaction as experimental sources of variation. Mite numbers were $\log_e$ transformed and proportions arcsin transformed prior to analysis, but untransformed values are shown in figures for easier interpretation of data. Relationships between some variables that require measurements at the same time of the day, e.g. (noon) canopy temperature and leaf water potential, were established with variables measured usually on the same day, but on some occasions measurements were taken on two successive days under similar weather conditions.

The daily fraction of PAR intercepted by the crop (Q) was calculated as a function of measured noon interception (Qn) using the equation of Charles-Edwards and Lawn (1984): $Q = 2Qn/(1+Qn)$. Cubic polynomials were used to describe the progression of Q with time for each individual subplot (Trápani *et al.*, 1992; Sadler and Karlen, 1994). The daily amount of PAR intercepted by the canopy was estimated as the product of: (*a*) daily values of solar radiation measured in a meteorological station 0·5 km from the experimental site; (*b*) Q values obtained from the fitted functions; and (*c*) 0·5, a conversion factor between solar radiation and PAR.

Radiation-use efficiency (RUE) was calculated as the slope of the linear regression between cumulative intercepted PAR and shoot dry matter. Because fruits and stems contribute substantially to crop PAR interception when LAI is low at the end of the season (Sadras, 1996), calculation of RUE was limited to the period from 85 to 132 DAS.

The mass of organic-N compounds in seed was calculated by multiplying nitrogen concentration by 6·25 (Poorter and Bergkotte, 1992).

Allometric analysis (Pearsall, 1927) was used to investigate the effects of treatments on reproductive partitioning. Using values of reproductive dry matter (y) and total shoot dry matter (x) for the period 85-146 DAS, allometric coefficients (i.e. slopes) and their standard errors were calculated with least-squares linear regressions of $\log_e$-transformed variables (Coleman, McConnaughay and Ackerly, 1994).

RESULTS

Soil water content

Differential irrigation and rainfall exclusion generated substantial soil water deficits in $-$W plots in contrast to +W crops where soil water deficit was maintained within the limits recommended for optimal cotton growth (Hearn and Constable, 1984) (Fig. 1D). Although some water infiltrated the soil of $-$W plots after heavy rainfall between 114 and 116 DAS (Fig. 1C and D), large differences persisted between +W and $-$W plots. Mite-infested and uninfested crops used similar amounts of water until 138 DAS, as indicated by non-significant effects of mite treatment on soil water. Thereafter, severely defoliated +M+W crops (see below) used less water than their uninfested counterparts ($-$M+W) and this was reflected in a significant ($P < 0{\cdot}01$) effect of mites on soil water content (Fig. 1D).

Abundance of mites and their predators, leaf damage and mite preference

In +M plots, the number mites increased exponentially shortly after infestation, reached a maximum of about 35 adult females per leaf at 124 DAS, and declined sharply afterwards (Fig. 2A). This pattern was unaffected by water regime ($P > 0{\cdot}05$). The lack of effect of water regime on the number of mites per leaf was also found when mite density was expressed as the number of adult females per unit leaf area ($P > 0{\cdot}16$). In contrast with +M treatments, the number of mites in $-$M crops was negligible (Fig. 2A). Predator abundance was low ($< 0{\cdot}6\ \mathrm{m}^{-2}$) as expected from the application of broad spectrum insecticides and it was unaffected by either water or mites (both $P > 0{\cdot}7$) or their interaction ($P > 0{\cdot}9$).

Despite the similarity in number of mites (Fig. 2A), the proportion of leaf area with visual symptoms of damage (Fig. 2B) and of severe damage (Fig. 2C) was greater in leaves of well-watered plants than in leaves of water-stressed ones (cf. also Fig. 3). The rate of increase in the percentage of leaf damaged by mites was 2·5 % per mite in the +M+W treatment compared with 1·6 % per mite in the +M$-$W treatment (Fig. 2B inset).

In a choice test, adult female mites preferred to feed ($P < 0{\cdot}05$) and oviposit ($P < 0{\cdot}001$) on +W leaves rather than on $-$W leaves (Table 1).

Leaf water potential and canopy temperature

Leaves from water-stressed crops had lower water potential than those from watered crops on all three dates of measurement ($P < 0{\cdot}001$, Table 2). Mite effects were not observed at 107 DAS (Table 2), when +M plants had about 20 adult female mites per leaf (Fig. 2A). At 124 DAS, when mite numbers peaked (Fig. 2A), leaves with mites (+M) had higher water potential than those from $-$M crops ($P < 0{\cdot}01$, Table 2). At this stage, leaf water potential was unaffected by the interaction between mites and water stress ($P > 0{\cdot}50$). A significant interaction was found at 133 DAS ($P < 0{\cdot}001$, Table 2) that was further explored following Grace (1995): (*a*) mites caused an increase in leaf water potential of 0·2 MPa in well-watered crops (i.e. the difference between +M+W and $-$M+W); (*b*) water deficit caused a reduction in water potential of 1·25 MPa in uninfested leaves (i.e. the difference between $-$M$-$W and $-$M+W); and thus (*c*) the expected effect of mites and water stress in the absence of interaction was a 1·05 MPa reduction which compares with the observed 0·31 MPa reduction due the combined effects of mites and water stress (i.e. the difference between +M$-$W and $-$M+W). Hence leaves from crops that were both mite-infested and water-stressed had a water potential 70 % higher (i.e. less negative) than expected from the additive effects of both stresses. Also at 133 DAS (Table 2), leaf water content and leaf water potential were correlated in $-$M crops ($r^2 = 0{\cdot}83$, $n = 8$, $P < 0{\cdot}01$) but not in +M crops ($P > 0{\cdot}40$).

Consistent with previous studies in cotton (Hatfield *et al.*, 1987) canopies of uninfested, well-watered crops ($-$M+W) were 1·8 to 5·0 °C cooler than the air except at 117 DAS, when air temperature was only 25·4 °C (Fig. 4). Irrespective of mite treatment, $-$W canopies were hotter than their well watered counterparts by 92 DAS. As mite populations increased (Fig. 2A), +M canopies were hotter than those of uninfested controls ($-$M) with the first significant effect of mite treatment detected at 98 DAS. The effects of mites and water deficit on canopy temperature were additive initially,

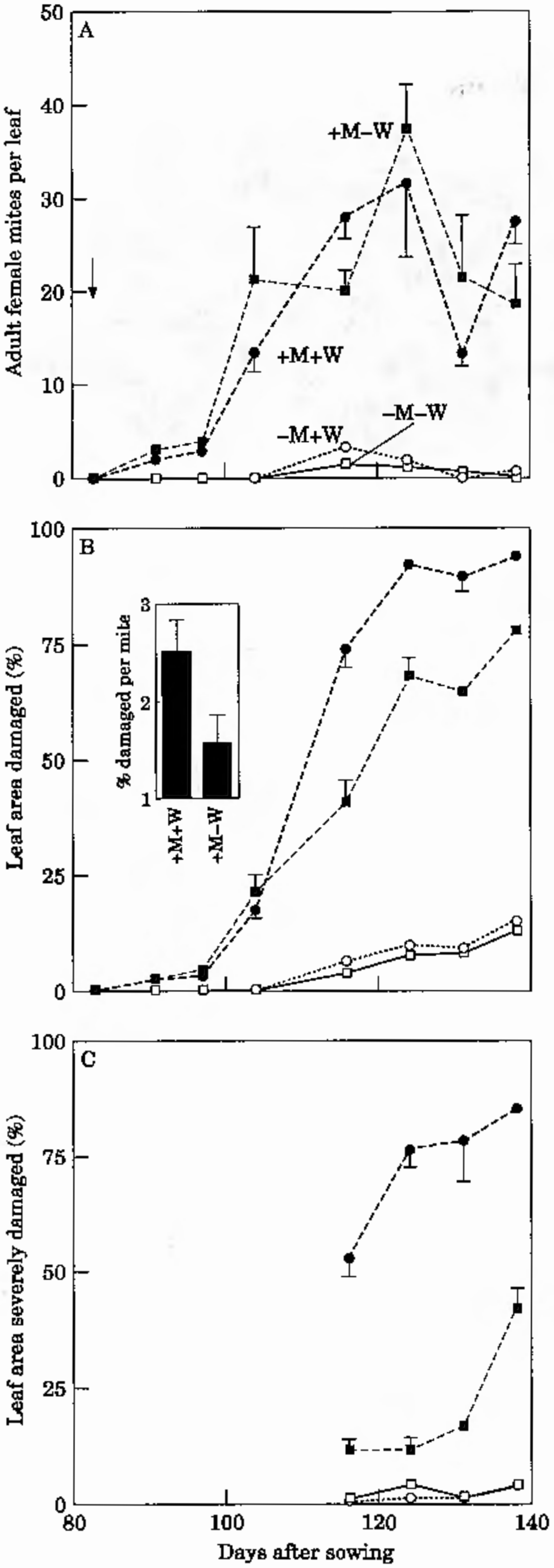

FIG. 2. A, Number of adult female mites as a function of time and treatments; the arrow indicates the time of artificial infestation; B, percentage of leaf area with visual symptoms of mite damage (irrespective of intensity of damage). Inset shows the slope of the regression between mite number and % leaf damage; C, percentage of leaf area with severe symptoms of mite damage. Error bars in A, B and C are one s.e.m. and were not plotted when smaller than symbols; error bars in the inset are s.e. of the regression coefficients.

but significant interactions developed as the intensity of both stresses increased (Fig. 4). Calculations to estimate the effect of each individual stress as described above indicate that +M−W canopies were 7% (98 DAS) to 44% (132 DAS) cooler than expected from the additive effects of mites and water stress.

At 107 DAS, canopy temperature was closely associated with leaf water potential irrespective of mite treatment (slope $= -3{\cdot}6$ °C MPa^{-1}; $r^2 = 0{\cdot}80$, $P < 0{\cdot}0001$, $n = 16$, Table 2). For uninfested crops, the relationship was consistent through time with an average rate of change in canopy temperature of $-3{\cdot}4$ °C MPa^{-1} (Table 2). Canopy temperature in crops with more than 20 mites per leaf was unrelated to leaf water potential (+M crops at 124 and 133 DAS, Table 2).

Leaf penetration resistance

Penetration resistance was greater in leaves from water-stressed crops than in leaves from well-watered treatments (Fig. 5A). We did not find any consistent effect of mites or mite × water treatment interaction on leaf penetration resistance. Specific leaf weight was also greater in the water-stressed treatment ($P < 0{\cdot}001$) and there was a close association between specific leaf weight and leaf penetration resistance (Fig. 5B). Significant negative associations were found between leaf penetration resistance (Fig. 5A) and leaf injury caused by mites (Fig. 2B and C) with leaf penetration resistance accounting for 59 to 74% of the variance in total leaf damage ($P < 0{\cdot}05$) and for 66 to 93% of the variance in severe leaf damage ($P < 0{\cdot}01$).

LAI, PAR interception, RUE and crop growth

Figure 6 shows the dynamics of LAI, PAR interception and shoot dry matter between 85 and 146 DAS. Average LAI at the beginning of the measurement period was 1·7. In control crops (−M+W), LAI reached a maximum of 2·7 at about 135 DAS. Irrespective of mite treatments, LAI of water-stressed crops (−M−W, +M−W) did not increase during the measurement period. It remained stable until 100 DAS (+M−W) or 132 DAS (−M−W) and declined rapidly thereafter. Well-watered, mite infested crops (+M−W) maintained rates of LAI increase similar to controls (−M+W) until 102 DAS and declined sharply afterwards. Changes in PAR interception reflected, with some delay, changes in LAI (Fig. 6B).

Control crops (−M+W) maintained a stable rate of shoot dry matter accumulation during the 85-146 DAS period (Fig. 6C). There was a clear sequence of the effect of stresses on shoot growth whereby stressed crops maintained growth rates similar to controls until (*a*) 97 DAS in mite-infested, water-stressed crops (+M−W); (*b*) 119 DAS in mite-infested, well-watered (+M+W) crops; and (*c*) 132 DAS in uninfested, water-stressed crops (−M+W). The

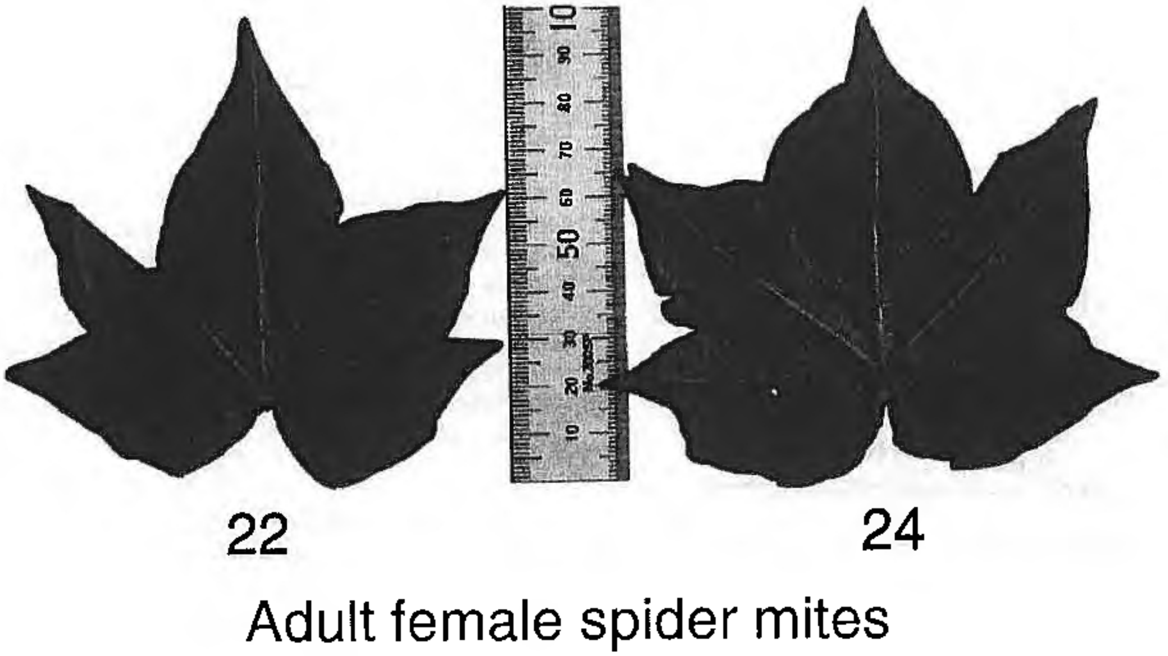

FIG. 3. Leaves from well watered plants (left) have more marked symptoms of mite damage than leaves form water-stressed plants (right) despite similar levels of mite infestation (22–24 adult females per leaf). Samples taken at 133 DAS.

TABLE 1. *Preference test to assess the ability of adult female mites to discriminate between leaves from watered (+W) and water-stressed (−W) plants*

	Response variable	
Treatment	Number of adult females	Number of eggs
+W	5·9 (0·57)	48 (4·3)
−W	3·9 (0·59)	28 (3·6)

Values are means (s.e.).

sharp drop in shoot dry matter between 119 and 132 DAS for +M+W crops (Fig. 6C, arrow) was partially due to abscission of fruits and leaves (Fig. 6D).

Crops with both stresses (+M−W) had an early fall in RUE from 1·34 to 0·44 g MJ^{-1} while crops with only one stress maintained RUE similar to controls until 119 DAS (+M+W) or until 132 DAS (−M−W) (Fig. 7).

Reproductive growth and yield

Crops reached peak fruit number between 132 and 146 DAS. Irrespective of water regime ($P > 0{\cdot}5$ for both water

TABLE 2. *Leaf water potential and canopy temperature as affected by mite and water treatments at 107, 124 and 133 d after sowing (DAS)*

		Treatment			
DAS	Variable	−M+W	−M−W	+M+W	+M−W
107	Leaf water potential (MPa)	−1·31 (0·024)	−3·16 (0·097)	−1·28 (0·040)	−3·09 (0·077)
	Canopy temperature (°C)	25·6 (0·49)	33·2 (0·79)	27·6 (0·90)	33·4 (1·17)
124	Leaf water potential (MPa)	−1·32 (0·089)	−2·63 (0·086)	−1·08 (0·058)	−2·26 (0·114)
	Canopy temperature (°C)	32·5 (0·39)	37·4 (0·72)	38·6 (0·83)	38·6 (1·25)
133	Leaf water potential (MPa)	−1·26 (0·058)	−2·51 (0·122)	−1·06 (0·070)	−1·57 (0·081)
	Leaf water content (%)	79 (0·3)	71 (1·1)	69 (0·8)	68 (0·5)
	Canopy temperature (°C)	29·3 (0·21)	33·4 (0·83)	37·1 (0·50)	36·1 (0·70)

Leaf water content at 133 DAS is also shown. Values are means (s.e.).

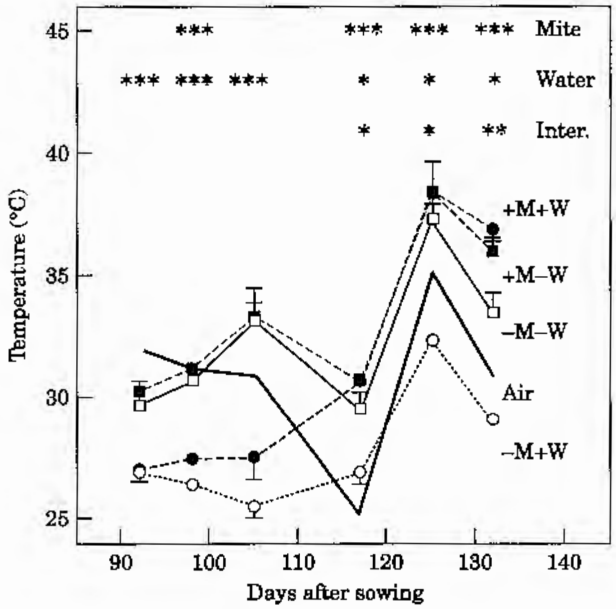

FIG. 4. Canopy temperature as affected by mite infestation and water deficit. Air temperature, measured at a meteorological station 0·5 km from the experimental plot, is shown as a reference. Error bars are one s.e.m. and were not plotted when smaller than symbols. Levels of significance are: $P < 0{\cdot}05$ (*), $P < 0{\cdot}01$ (**) and $P < 0{\cdot}001$ (***).

treatment and water × mite interaction), peak fruit number was reduced from 115 m^{-2} in uninfested crops to 63 m^{-2} in mite infested crops ($P < 0{\cdot}01$) (Fig. 8, horizontal lines). Fruit matured faster in water-stressed crops than in well-watered ones; for instance, at 145 DAS, −W crops had 31 mature fruit m^{-2} in comparison to +W crops that only had 5. At the end of the season, the proportion of fruit that reached maturity was $0{\cdot}79 \pm 0{\cdot}09$ in uninfested crops irrespective of water regime; mites reduced this fraction to $0{\cdot}68 \pm 0{\cdot}05$ in −W crops and to $0{\cdot}28 \pm 0{\cdot}03$ in +W crops (mite effect significant at $P < 0{\cdot}01$, interaction significant at $P < 0{\cdot}05$) (Fig. 8).

Lint yield is a function of dry matter production and partitioning. Relevant partitioning variables in cotton include: fruit/shoot (Fig. 9A), seed cotton per fruit (Fig. 9B) and lint fraction (Fig. 9C). Fruit/shoot partitioning of crops affected by both stresses (+M−W) was 53% greater than that of control crops (−M+W), while it was unaffected by either mites or water stress acting separately (Fig. 9A). Seed cotton per fruit was reduced by mites ($P < 0{\cdot}0001$) and unaffected by water deficit ($P > 0{\cdot}93$) or the interaction between stresses ($P > 0{\cdot}05$). Irrespective of water regime, lint fraction was 0·41 in uninfested crops; mites reduced lint fraction to 0·37 in −W crops and to 0·33 in +W crops (water effect: $P < 0{\cdot}001$; mite and interaction effect: $P < 0{\cdot}0001$). Lint yield of unstressed controls was 175 g m^{-2} (Fig. 9D). In uninfested crops, water deficit reduced yield by 30%, mites reduced the yield of well-watered crops by 92%, and the combination of mite infestation and water deficit reduced yield by 72% (water effect: $P < 0{\cdot}01$; mite and interaction effect: $P < 0{\cdot}0001$).

Nitrogen and oil concentration

Figure 10 shows the dynamics of nitrogen concentration in vegetative organs. Leaf nitrogen concentration declined with time in all treatments. The rate of decline was accelerated by mites and unaffected by water deficit or the interaction between them. Stem nitrogen concentration in uninfested, well watered plants (−M+W) declined steadily from 1·2% at 85 DAS to 0·32% at 146 DAS. In the same

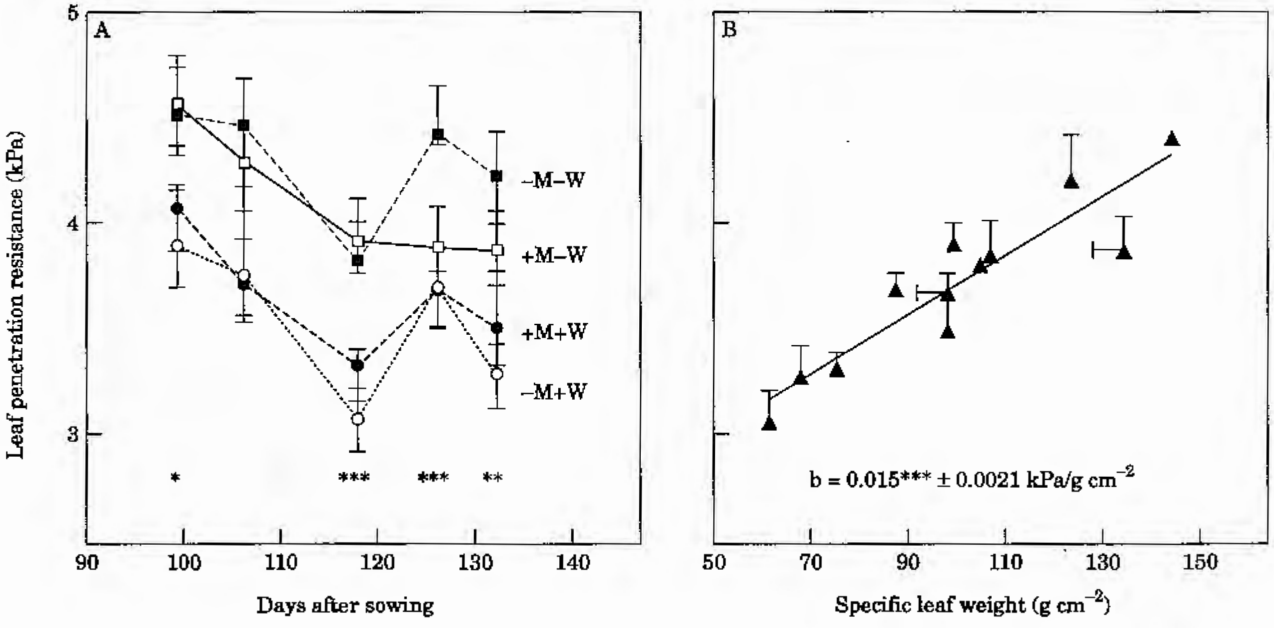

FIG. 5. A, Leaf penetration resistance as affected by mite infestation and water deficit; B, relationship between leaf penetration resistance and specific leaf weight. Error bars are one s.e.m. and were not plotted when smaller than symbols. In A, asterisks indicate effects of water treatment; in A and B, levels of significance are: $P < 0{\cdot}05$ (*), $P < 0{\cdot}01$ (**) and $P < 0{\cdot}001$ (***).

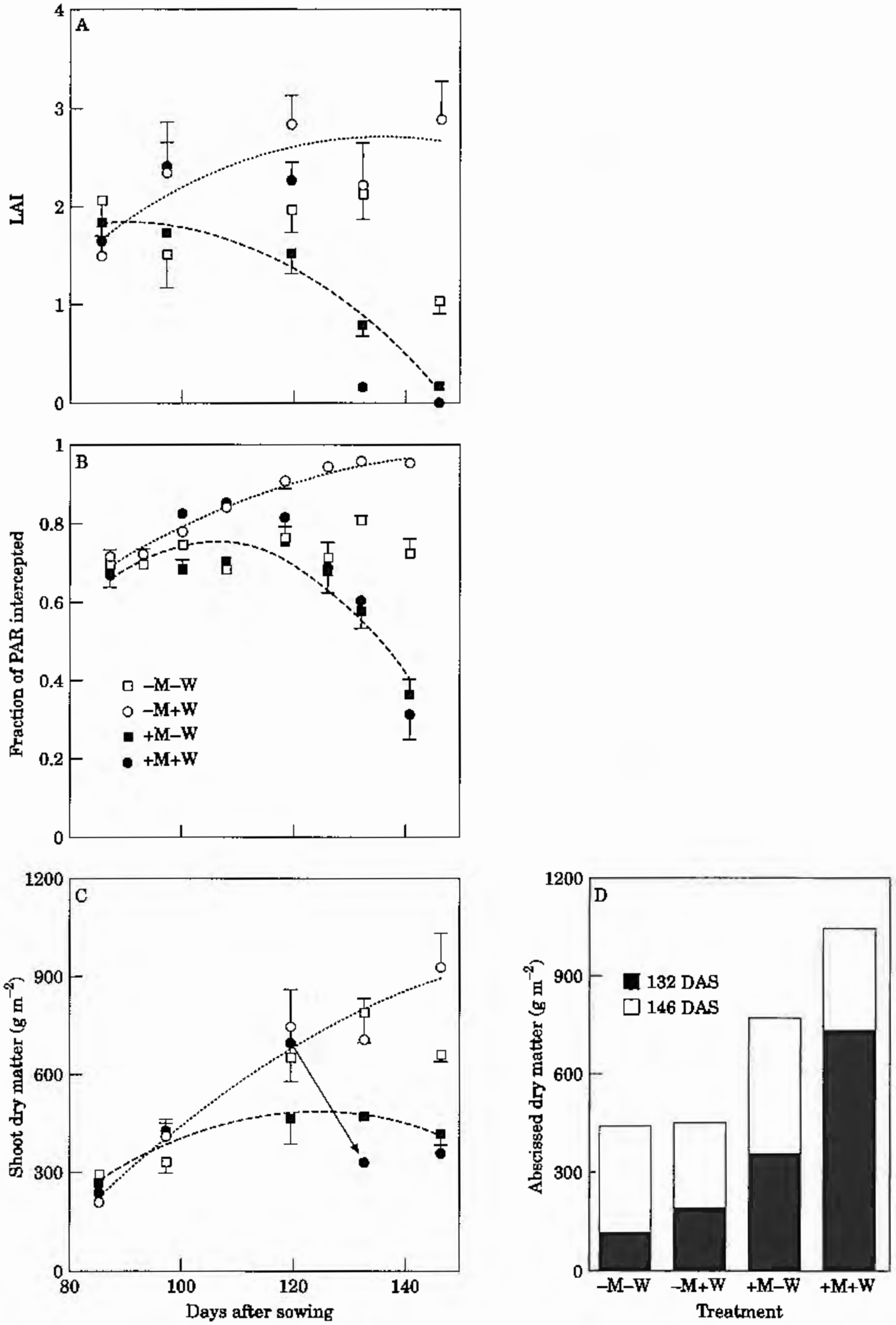

FIG. 6. Effect of mite infestation and water deficit on: leaf area index (A), PAR interception (B), shoot dry matter (C) and abscissed dry matter (D). The arrow in C highlights the drop in shoot dry matter of +M+W crops between 119 and 132 DAS. Error bars are one s.e.m. and were not plotted when smaller than symbols. For clarity, curves (quadratic polynomials) are shown only for the treatments −M+W and +M−W.

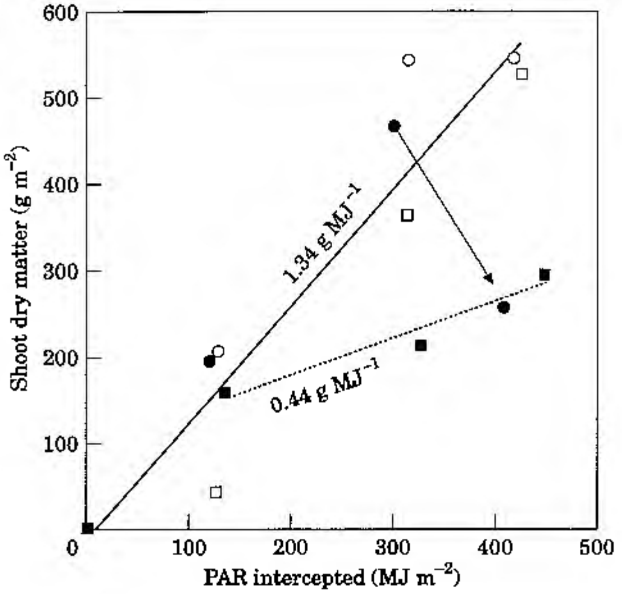

FIG. 7. Relationship between shoot dry matter and cumulative PAR interception as affected by mite infestation and water deficit. The solid line (slope = 1·34 g MJ^{-1}) was fitted to data from uninfested crops (−M−W, −M+W) and the dotted line (slope = 0·44 g MJ^{-1}) was fitted to +M−W data; the arrow indicates the drop in shoot dry matter of +M+W crops between 119 and 132 DAS (cf. Fig. 6C). □, −M−W; ○, −M+W; ■, +M−W; ●, +M+W.

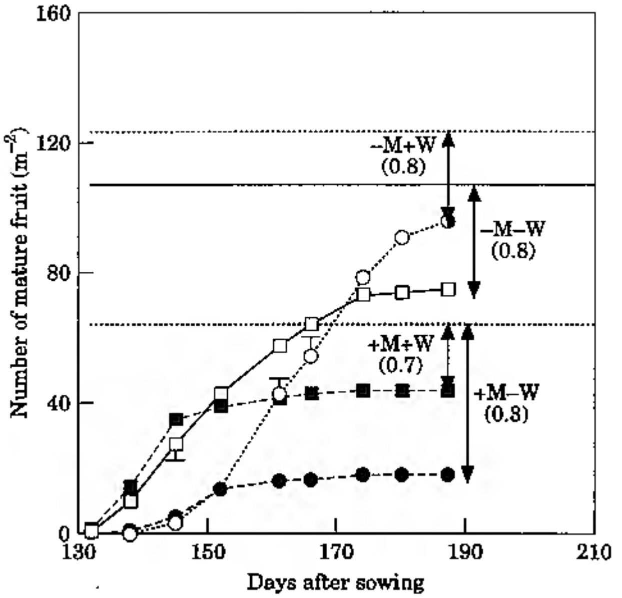

FIG. 8. Dynamics of mature fruit production as affected by mite infestation and water deficit. Horizontal lines show peak number of immature fruit, reached between 132 and 146 DAS. Numbers in parentheses are the ratio between total number of mature fruit at 187 DAS and peak fruit number. Error bars are one s.e.m. and were not plotted when smaller than symbols.

period, well watered, mite-infested plants (+M+W) had a much smaller fall in stem nitrogen concentration (from 1·3 to 0·98%). Irrespective of mite treatments, stem nitrogen concentration of water-stressed plants (−W) declined sharply between 85 and 97 DAS ($P < 0{\cdot}0001$). Thereafter, stem nitrogen concentration remained stable in −M−W plants while it increased in +M−W plants. Changes in nitrogen concentration in tap-roots were comparable to those in stems except for a less clear pattern in −M+W plants. At the end of the measurement period, and irrespective of water treatment, mite-infested plants had significantly ($P < 0{\cdot}001$) greater nitrogen concentration in both stems and roots than uninfested plants.

Water deficit significantly reduced the nitrogen concentration of flowerbuds at 97 DAS ($P < 0{\cdot}0001$) when the effect of mites was non-significant (Fig. 11A). At 132 DAS, nitrogen concentration of capsule walls was significantly increased by mites ($P < 0{\cdot}0001$) and was reduced by water deficit in mite-infested but not uninfested plants (water effect: $P < 0{\cdot}05$, interaction: $P < 0{\cdot}01$). At 146 DAS, the trend was similar and the magnitude of these effects was more marked (all three factors significant at $P < 0{\cdot}0001$) (Fig. 11A).

Seed nitrogen concentration increased from 3·4% in −M+W controls to 4·2% in all stressed treatments (Fig. 11B). In comparison to unstressed controls, seed oil concentration was moderately reduced by water deficit. Mites reduced seed oil concentration substantially and their effect was greater in water stressed crops than in well-watered ones. As a result of these changes in seed composition (Fig. 11B), the ratio between oil and N-compounds declined from 1·17 in controls (−M+W) to 0·96 in −M−W, 0·87 in +M−W and 0·76 in +M+W.

DISCUSSION

The aim of this study was to investigate the responses of cotton to the combined effects of mites and water deficit in the field. The methods used in this experiment allowed us to generate contrasting soil water contents in −W and +W plots 90 DAS (Fig. 1D), and substantial mite infestations in +M crops while maintaining negligible mite numbers in −M crops (Fig. 2A).

Effects of water-stressed cotton on mites

In comparison with unstressed host plants, the abundance of spider mites in water-stressed hosts can increase, decrease or remain unchanged (English-Loeb, 1989). Actual mite responses seem to depend on the intensity of water deficit experienced by the host plant (English-Loeb, 1989; 1990). Under our experimental conditions, cotton water status did not affect the abundance of adult female mites.

Further analysis of the effects of water-stressed cotton on mites requires details of life history, population dynamics and behaviour of mites (e.g. Smitley and Kennedy, 1985) that were beyond the scope of this study. Nonetheless, we will discuss three findings related to the growth and activity of mite colonies in water-stressed cotton namely: (*a*) the lack of effect of host-plant water status on the number of adult females (Fig. 2A); (*b*) the greater extent and intensity of injury per mite in well-watered plants (Figs 2B, C and 3); and (*c*) the preference of adult female mites for leaves from

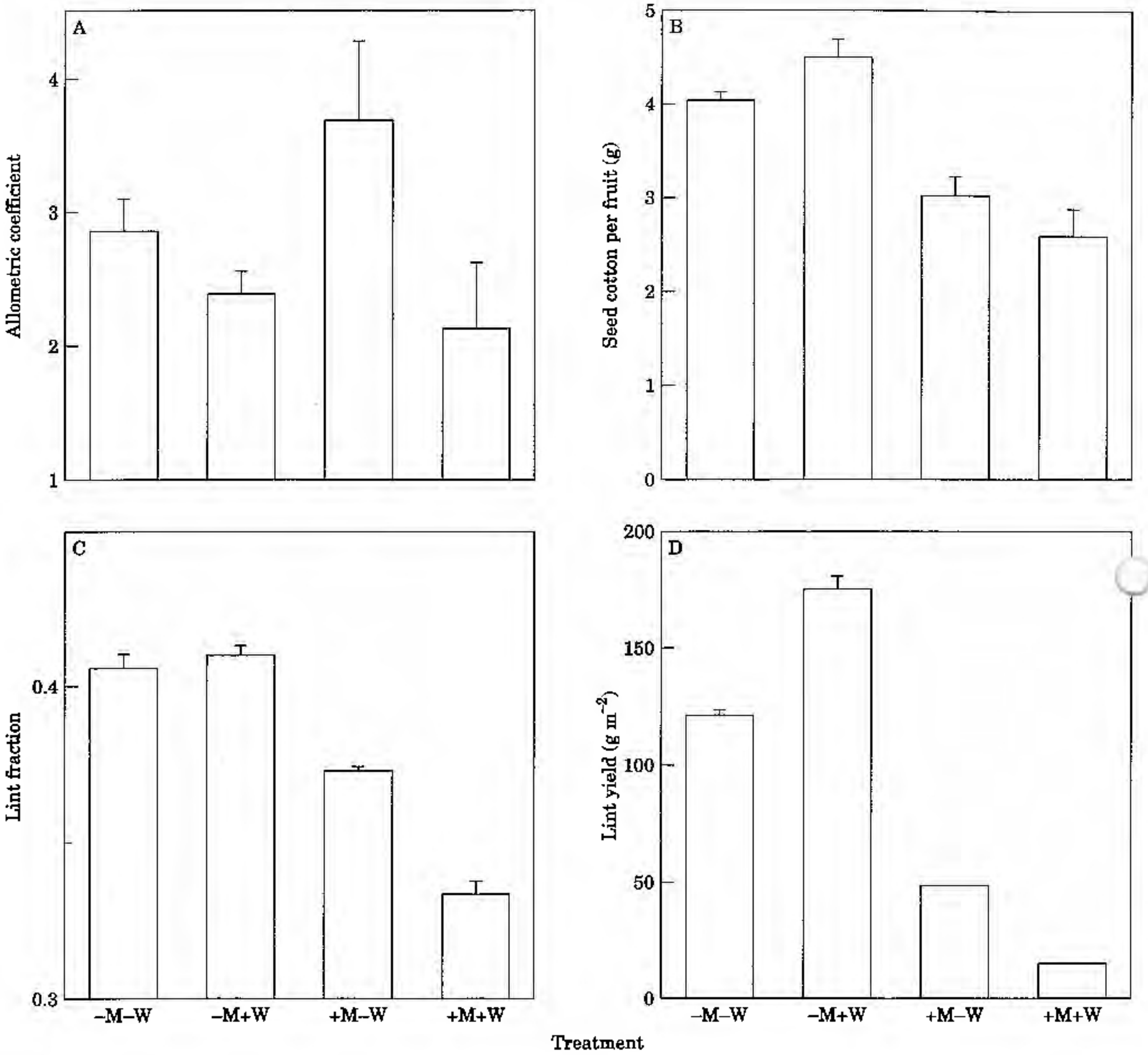

FIG. 9. Effects of mite infestation and water deficit on reproductive allocation (A), as quantified by allometric coefficients (dimensionless); seed cotton per fruit (seed cotton = seed + lint) (B); lint fraction, i.e. lint/(lint + seed) (dimensionless) (C); and lint yield (D). Errors bars are one s. of the regression coefficient (A) or one s.e.m. (B, C and D).

well-watered plants (Table 1). In the following discussion, we will assume that the effects of plant water status on herbivore mites were not mediated by changes in the third trophic level (Kytö, Nimelä and Larsson, 1996); this assumption is justified by the low numbers of mite predators and the lack of treatment effects on their abundance.

In a number of studies covering a wide range of intensity of water stress, it has been shown that: (*a*) mite fecundity was unaffected by plant water status; (*b*) sex ratios were female biased in offspring of mites raised on water-stressed hosts; and (*c*) mites developed faster on water stressed hosts due to increased foliar temperature (Youngman, Sanderson and Barnes, 1988; English-Loeb, 1989; Oi *et al.*, 1989). If these responses applied to our experimental system then we could have expected more adult mites in water stressed crops than in well watered crops. The lack of a difference in mite numbers in our study (Fig. 2A) may be due to other changes in the host plant which counteracted the possible effects of (*b*) and (*c*) above.

Leaf damage per mite was less on water stressed than on well-watered plants and, importantly, the area of leaf severely damaged was far less on water stressed plants. The low ratio of intense damage to overall leaf damage on the water-stressed plants (0·18 to 0·55) contrasts with that observed on well-watered cotton (0·72 to 0·91) (Fig. 2B and C) where mites tend to feed preferentially in protected sites on the leaf surface, spreading only as the area damaged becomes unsuitable (Wilson, 1994). The fact that mites spread on water-stressed leaves before causing severe damage, together with the preference of adult females for

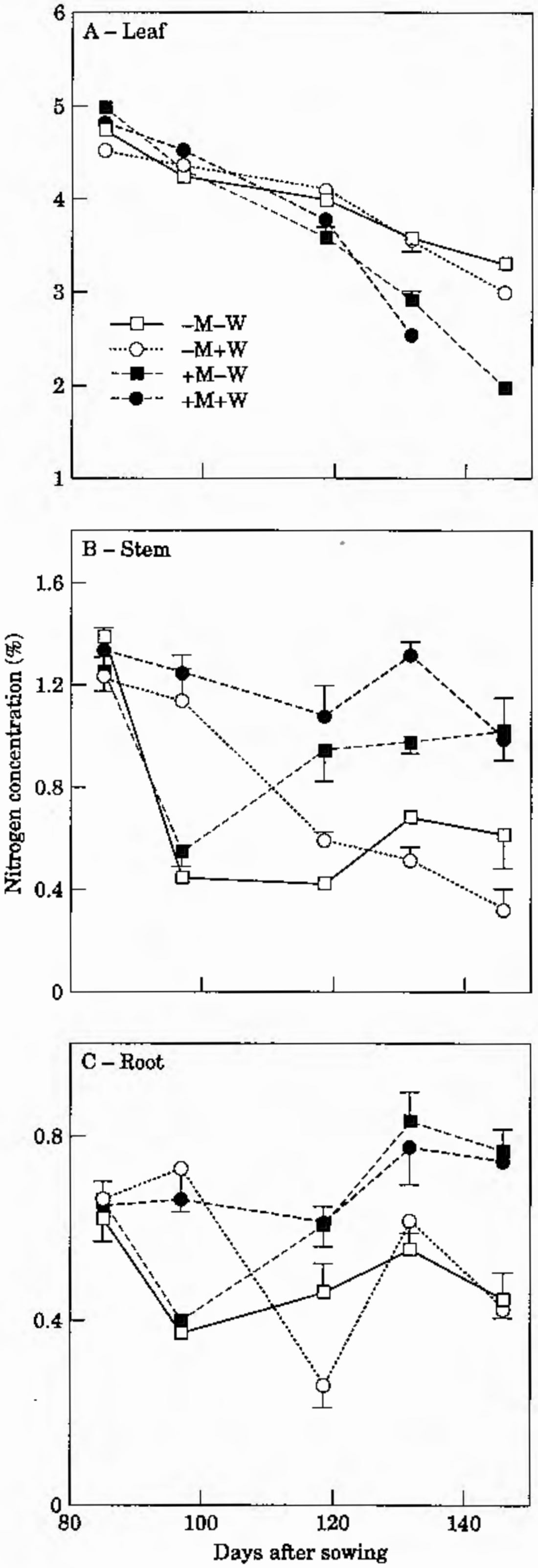

FIG. 10. Dynamics of nitrogen concentration in vegetative organs of cotton plants as affected by mite infestation and water deficit. Error bars are one s.e.m. and were not plotted when smaller than symbols.

leaves from well-watered plants (Table 1) reinforces the hypothesis that chemical and/or physical changes in cotton leaves due to water-stress made them less suitable for mites. Water-stressed leaves had greater penetration resistance than leaves from well-watered plants (Fig. 4), a factor that probably contributed to the greater damage on (Figs 2B, C and 3) and preference of mites for leaves from well-watered plants (Table 1). Jiang and Ridsdill-Smith (1996) also found a negative association between redlegged earth mite (*Halotydeus destructor* Tucker) feeding damage and penetration resistance of subterranean clover (*Trifolium subterraneum* L.) cotyledons. Causes of increased leaf penetration resistance in water-stressed plants and its consequences on herbivory are discussed further in the next section. Other changes induced by water deficit that may have reduced leaf suitability for mites include: (*a*) more, and qualitatively different, epicuticular waxes (Bondada *et al.*, 1996) that are known to influence herbivory (Eigenbrode and Espelie, 1995); and (*b*) changes in concentration of nutrients and of secondary metabolites in plant tissues, often invoked to explain differences in herbivore responses to host plant water status (Jones and Coleman, 1991).

Effects of mites and water deficit on cotton

Well-watered, uninfested crops maintained canopy temperature within the optimal 'window' of 23 to 32 °C (Fig. 4) (see Introduction). Transpirational cooling was restricted by water deficit and, as mite colonies grew, by mite infestation. As the intensity of both stresses increased through the season, interactions were increasingly significant. Likewise, leaf water potential was sequentially affected by water stress, mite infestation and by the interaction of both stresses (Table 2). For uninfested crops, or for infested crops with less than about 20 adult female mites per leaf, there was (*a*) a negative association between canopy temperature and leaf water potential (Table 2), similar to that found by Reddy, Hodges and McKinion (1997) and (*b*) a positive association between leaf water potential and leaf water content (Table 2) comparable to those reported previously (Jordan and Ritchie, 1971; Ackerson *et al.*, 1977). Mites decoupled these variables (Table 2) when their density was over 20 adult females per leaf, a threshold that coincides with that for RUE responses to mites in well-watered cotton (Sadras and Wilson, 1997*a*). Histological studies and details of leaf water relations are needed to elucidate the mechanisms of mite injury in water-stressed cotton, including physical damage, stomatal conductance as affected by both hydraulic and chemical root signals, and changes in leaf osmotic potential and turgor. Irrespective of the mechanisms, it is worth emphasizing that crops with both stresses were cooler and their leaf water potential was higher than expected from the additive effects of mites and water deficit.

Specific leaf weight usually increases with water stress (Wright *et al.*, 1996) in part because leaf expansion is more sensitive than photosynthesis to water deficit (Sadras and Milroy, 1996). Greater specific leaf weight is related, in some cases, to differences in the amount of cell wall material (Dijkstra, 1989). In our study, leaves from water stressed

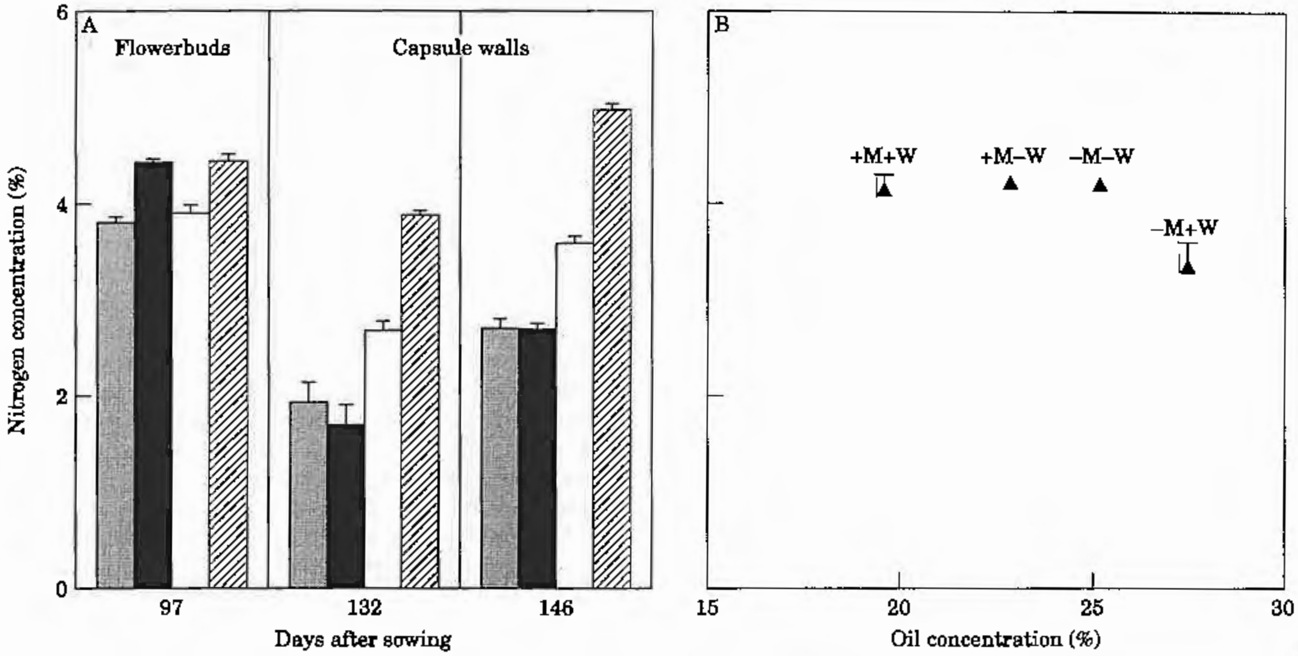

FIG. 11. Nitrogen concentration of flowerbuds and capsule walls (A) and nitrogen and oil concentration of seeds (189 DAS) (B) as affected by mite infestation and water deficit. Symbols in A: ⊡, −M−W; ■, −M+W; □, +M−W; ▨, +M+W. Error bars are one s.e.m.

plants had greater specific leaf weight, and variation in specific leaf weight accounted for 83% of the variance in leaf penetration resistance (Fig. 5B). Thus, it is possible that responses in the cell wall associated with water deficit, and reflected in variations in specific leaf weight, may have changed leaf penetration resistance and hence the suitability of leaves for the development of mite colonies, as discussed previously. Tissue 'toughness' and its association with cell wall properties are major factors influencing herbivory (Hochuli, 1996). Further work on the responses of mites to changes in leaf penetration resistance associated with water deficit should take into account that structural changes in leaves (e.g. changes in cell wall material) may interact with changes in resistance related to turgor pressure. Consideration of structural and turgor-related components of leaf penetration resistance is important for two reasons. Firstly, it may be that the relative importance of these two components changes with the intensity of water stress. Secondly, changes in turgor-related resistance may follow diurnal patterns that need to be considered in relation to the diurnal patterns of herbivore feeding.

Growth responses occurred earlier and were more gradual in crops that were subjected to both stresses than in crops subjected to one stress only (Fig. 6). The arrow in Fig. 6C highlights the sharp drop in dry matter of well-watered, mite-infested crops between 119 and 132 DAS. The loss of dry matter (365 g m^{-2}) was much greater than the mass of abscised plant parts in the same period (155 g m^{-2}, Fig. 6D) indicating that a negative carbon balance contributed to the decline in shoot dry matter, as found previously in well-watered cotton infested with mites (Sadras and Wilson, 1997*a*).

Although the growth trajectories were different, mite infested crops produced, irrespective of water treatment, similar amounts of shoot dry matter at the end of the growing cycle (Fig. 6C). In contrast, the yield reduction caused by mites was much greater in well-watered than in water-stressed crops (Fig. 9D), highlighting the non-additive effect of mites and water deficit on fruit retention and reproductive partitioning (Figs 8 and 9). These results are consistent with other studies of reproductive partitioning in cotton showing no responses to spider mite infestation in well-watered crops (Sadras and Wilson, 1997*b*), the stability of reproductive partitioning of plants grown under a range of single abiotic stresses, and the trend to increase reproductive allocation when two stresses were combined (Sadras, Bange and Milroy, 1997).

In the period from 85 to 97 DAS, nitrogen concentration in both stems and tap-roots of water-stressed plants declined sharply (Fig. 10B and C) in parallel to the rapid decline in soil water content (Fig. 1D). Water deficit also reduced nitrogen concentration in flowerbuds (Fig. 11A). In contrast, water deficit did not affect leaf nitrogen concentration in this period (Fig. 10A). These responses, together with the lack of measurable effect of water deficit on RUE during this period (Fig. 7) indicates that water deficit diminished nitrogen assimilation before affecting carbon assimilation. Less nitrogen uptake (Doss and Scarsbrook, 1969), lower nitrate reductase activity following a decline in nitrate uptake (Giyasov *et al.*, 1992) and probably less export of reduced nitrogen from leaves, where the bulk of inorganic nitrogen is reduced in cotton (Radin, 1977), may all have contributed to the early drop in flowerbud, stem and root nitrogen concentration in response to water deficit (Figs 10 B, C and 11A).

Mites accelerated leaf senescence (Fig. 6A) and thus triggered rapid loss of foliar nitrogen (Fig. 10A) (Sadras and Wilson, 1997*a*). Small plant size (Fig. 6C) and nitrogen relocated from senescing leaves accounted for the increase in nitrogen concentration of stems, roots and reproductive organs of mite-infested plants (Figs 10 and 11) (Sadras and Wilson, 1997*c*). Despite changes in trajectory, final concentration of nitrogen in stems and roots was unaffected by water stress or the interaction between water and mite treatments. In contrast, significant effects of both water deficit and water × mite interaction were still evident 146 DAS for capsule walls (Fig. 11). The accelerated loss of leaf nitrogen and the nitrogen 'enrichment' in stems, roots and reproductive structures of mite-infested cotton can further affect mites and other herbivores (Sadras and Wilson, 1997*c*).

Mites can reduce cotton oil yield by reducing both seed mass and seed oil concentration (Sadras and Wilson, 1996). Reduction in seed oil concentration due to mite feeding was more severe in well-watered crops than in water-stressed ones (Fig. 11B) indicating again that mite damage was greater in well-watered plants.

CONCLUSIONS

oth *Tetranychus urticae* infestation and water deficit had detrimental effects on several aspects of the water, carbon and nitrogen economies of cotton plants and crops. Under our experimental conditions, mites caused more damage to well-watered plants than to their water-stressed counterparts, i.e. mite-infested, well-watered plants had more extended and more intense symptoms of leaf injury, lower reproductive partitioning and lower lint yield than their water-stressed counterparts. The magnitude and consistency of the interaction between both stresses indicates that mechanisms of adjustment to water deficit may have enhanced cotton resistance to mites.

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LITERATURE CITED

Ackerson RC, Krieg DR, Miller TD, Zartman RE. 1977. Water relations of field grown cotton and sorghum: temporal diurnal changes in leaf water, osmotic and turgor potentials. *Crop Science* **17**: 76–84.

Bondada BR, Oosterhuis DM, Murphy JB, Kim KS. 1996. Effect of water stress on the epicuticular wax composition and ultrastructure of cotton (*Gossypium hirsutum* L.) leaf, bract, and boll. *Environmental and Experimental Botany* **36**: 61–69.

Bondada BR, Oosterhuis DM, Tugwell NP, Kim KS. 1995. Physiological and cytological studies of two spotted spider mites, *Tetranychus urticae* K., injury in cotton. *Southwestern Entomologist* **20**: 171–180.

Burke JJ, Mahan JR, Hatfield JL. 1988. Crop specific thermal kinetic windows in relation to wheat and cotton biomass production. *Agronomy Journal* **80**: 553–556.

Chapin FS, Bloom AJ, Field CB, Waring RH. 1987. Plant responses to multiple environmental factors. *BioScience* **37**: 49–57.

Charles-Edwards DA, Lawn RJ. 1984. Light interception by grain legume row crops. *Plant, Cell and Environment* **7**: 247–251.

Coleman JS, McConnaughay KDM, Ackerly DD. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution* **9**: 187–191.

De Barro PJ. 1991. A cheap lightweight efficient vacuum sampler. *Journal of the Australian Entomological Society* **30**: 207–208.

Dijkstra P. 1989. Cause and effect of differences in specific leaf area. In: Lambers H, Cambridge ML, Konings H, Pons LT, eds. *Causes and consequences of variation in growth rate and productivity of higher plants.* The Hague: SPB Academic, 125–140.

Doss BD, Scarsbrook CE. 1969. Effect of irrigation on recovery of applied nitrogen by cotton. *Agronomy Journal* **61**: 37–40.

Eigenbrode SD, Espelie EK. 1995. Effect of plant epicuticular lipids on insect herbivores. *Annual Review of Entomology* **40**: 171–194.

English-Loeb GM. 1989. Nonlinear responses of spider mites to drought-stressed host plants. *Ecological Entomology* **14**: 45–55.

English-Loeb GM. 1990. Plant drought stress and outbreaks of spider mites: a field test. *Ecology* **71**: 1401–1411.

Flint HM, Wilson FD, Hendrix D, Leggett J, Naranjo S, Henneberry TJ, Radin JW. 1994. The effect of plant water stress on beneficial and pest insects including the pink bollworm and the sweetpotato whitefly in two short-season cultivars of cotton. *Southwestern Entomologist* **19**: 11–21.

Giyasov TD, Kluyuikova AI, Yakubova MM, Alekhina ND. 1992. Functioning of nitrate reductase in germinating cotton seedlings: effect of light and substrate availability. *Soviet Plant Physiology* **39**: 532–536.

Grace J. 1995. On the measurement of plant competition intensity. *Ecology* **76**: 305–308.

Hare JD, Pehrson JE, Clemens T, Youngman RR. 1989. Combined effects of differential irrigation and feeding injury by the citrus red mite (Acari: Tetranychidae) on gas exchange of orange leaves. *Journal of Economic Entomology* **82**: 204–208.

Hatfield JL, Burke JJ, Mahan JR, Wanjura DF. 1987. Foliage temperature measurements: a link between the biological and physical environment. *International Conference on Measurement of Soil and Plant Water Status. Centenial of Utah State University, July 6–10, 1987.* **2**: 99–102.

Hearn AB, Constable GA. 1984. Irrigation of crops in a sub-humid environment. VII. Evaluation of irrigation strategies for cotton. *Irrigation Science* **5**: 75–94.

Herron GA, Edge V, Wilson LJ, Rophail J. 1997. Organophosphate resistance in spider mites (Tetranychidae) from cotton in Australia. *Experimental and Applied Acarology* (in press).

Hochuli DF. 1996. The ecology of plant/insect interactions: implications of digestive strategy for feeding by phytophagous insects. *Oikos* **75**: 133–141.

Hsiao TC. 1990. Measurements of plant water status. In: Stewart BA, Nielsen DR, eds. *Irrigation of agricultural crops.* Madison: ASA, CSSA, SSSA, 244–279.

Idso SB, Reginato RJ, Farah SM. 1982. Soil- and atmopshere-induced plant water stress in cotton as inferred from foliage temperatures. *Water Resources Research* **18**: 1143–1148.

Jiang Y, Ridsdill-Smith TJ. 1996. Examination of the involvement of mechanical strength in antixenotic resistance of subterranean clover cotyledons to the redlegged earth mite (*Halotydeus destructor*) (Acarina: Penthaleidae). *Bulletin of Entomological Research* **86**: 263–270.

Jones CG, Coleman JS. 1991. Plant stress and insect herbivory: Toward an integrated perspective. In: Mooney HA, Winner WE, Pell EJ, eds. *Response of plants to multiple stresses.* New York: Academic Press, 249–280.

Jordan WR, Ritchie JT. 1971. Influence of soil water stress on evaporation, root absorption, and internal water status of cotton. *Plant Physiology* **48**: 783–788.

Kittock DL, Henneberry TJ, Bariola LA, Taylor BB, Hoffman WC. 1983. Cotton boll period response to water stress and pink bollworm. *Agronomy Journal* **75**: 17–20.

Kytö M, Niemelä P, Larsson S. 1996. Insects on trees: population and individual response to fertilisation. *Oikos* **75**: 148–159.

pattern, plant population, irrigation and insect interactions in cotton. *Environmental Entomology* 3: 492–496.

Leigh TF, Grimes DW, Yamada H, Bassett D, Stockton JR. 1970. Insects in cotton as affected by irrigation and fertilisation practices. *California Agriculture* 24: 12–14.

Mooney HA, Winner WE, Pell EJ. 1991. *Response of plants to multiple stresses.* New York: Academic Press.

Northcote KH. 1979. *A factual key for the recognition of Australian soils.* Rellim, Glenside.

Oi DH, Sanderson JP, Youngman RR, Barnes MM. 1989. Developmental times of the Pacific spider mite (Acari: Tetranychidae) on water-stressed almond trees. *Environmental Entomology* **18**: 208–212.

Pearsall WH. 1927. Growth studies. VI. On the relative sizes of growing plant organs. *Annals of Botany* **41**: 549–556.

Poorter H, Bergkotte M. 1992. Chemical composition of 24 wild species differing in relative growth rate. *Plant, Cell and Environment* **15**: 221–229.

Pyke BA, Brown EH. 1996. *The cotton pest and beneficial guide.* Woolloongaba: Cotton Res. Dev. Corp. and Coop. Res. Centre Trop. Pest Manag.

Radin JW. 1997. Contribution of the root system to nitrate assimilation in whole cotton plants. *Australian Journal of Plant Physiology* **4**: 811–819.

Radin JW, Lu Z, Percy RG, Zeiger E. 1994. Genetic variability for stomatal conductance in Pima cotton and its relation to improvements of heat adaptation. *Proceedings of the National Academy of Science, USA.* **91**: 7217–7221.

Reddy RK, Hodges HF, McKinion JM. 1997. Crop modelling and applications: a cotton example. *Advances in Agronomy* **59**: 225–290.

Rochester IJ, Constable GA, MacLeod DA. 1993. Cycling of fertilizer and cotton crop residue nitrogen. *Australian Journal of Soil Research* **31**: 597–609.

Sadler EJ, Karlen DL. 1994. Higher-order analysis of nutrient accumulation data. *Agronomy Journal* **86**: 26–31.

Sadras VO. 1996. Cotton responses to simulated insect damage: radiation-use efficiency, canopy architecture and leaf nitrogen content as affected by loss of reproductive organs. *Field Crops Research* **48**: 199–208.

Sadras VO, Bange MP, Milroy SP. 1997. Reproductive allocation of cotton in response to plant and environmental factors. *Annals of Botany* **80**: 75–81.

Sadras VO, Milroy SP. 1996. Soil-water thresholds for the responses of leaf expansion and gas exchange. *Field Crops Research* **47**: 253–266.

Sadras VO, Wilson LJ. 1996. Effect of timing and intensity of spider mite infestation on the oil yield of cotton crops. *Australian Journal of Experimental Agriculture* **36**: 577–580.

infested with spider-mites. I. Light interception and radiation-use efficiency. *Crop Science* **37**: 481–491.

Sadras VO, Wilson LJ. 1997*b*. Growth analysis of cotton crops infested with spider-mites. II. Partitioning of dry matter and nitrogen. *Crop Science* **37**: 492–497.

Sadras VO, Wilson LJ. 1997*c*. Nitrogen accumulation and partitioning in shoots of cotton plants infested with two-spotted spider mites. *Australian Journal of Agricultural Research* **48**: 525–533.

Sagers CL. 1992. Manipulation of host plant quality: Herbivores keep leaves in the dark. *Functional Ecology* **6**: 741–743.

Sands DPA, Bracantini VA. 1991. A portable penetrometer for measuring leaf toughness in insect herbivory studies. *Proceedings of the Entomological Society of Washington* **93**: 786–788.

Smitley DR, Kennedy GG. 1985. Photo-oriented aerial-dispersal behaviour of *Tetranychus urticae* (Acari: Tetranychidae) enhances escape from the leaf surface. *Annals of the Entomological Society of America* **78**: 609–614.

Tomlin C. 1994. *British Crop Protection Council and the Royal Chemical Society.* Bath, U.K.: The Bath Press.

Trápani N, Hall AJ, Sadras VO, Vilella F. 1992. Ontogenic changes in radiation-use efficiency of sunflower (*Helianthus annuus* L.) crops. *Field Crops Research* **29**: 303–316.

Waring GL, Cobb NS. 1992. The impact of plant stress on herbivore population dynamics. In: Bernays EA, eds. *Insect-plant interactions.* Boca Raton: CRC Press, 167–226.

Wilson LJ. 1993. Spider mites (Acari: Tetranychidae) affect yield ar fiber quality of cotton. *Journal of Economic Entomology* 8 566–585.

Wilson LJ. 1994. Resistance of okra-leaf cotton genotypes to twospotted spider mites (Acari: Tetranychidae). *Journal of Economic Entomology* **87**: 1726–1735.

Wilson LJ, Morton R. 1993. Seasonal abundance and distribution of *Tetranychus urticae* (Acari: Tetranychidae), the two spotted spider mite, on cotton in Australia and implications for management. *Bulletin of Entomological Research* **83**: 291–303.

Wright PR, Morgan JM, Jessop RS. 1996. Comparative adaptation of canola (*Brassica napus*) and Indian mustard (*B. juncea*) to soil water deficits: Plant water relations and growth. *Field Crops Research* **49**: 51–64.

Youngman RR, Barnes MM. 1986. Interaction of spider mites (Acari: Tetranyschidae) and water stress on gas-exchange rates and water potential of almond leaves. *Environmental Entomology* **15**: 594–600.

Youngman RR, Sanderson JP, Barnes MM. 1988. Life history parameters of *Tetranychus pacificus* McGregor (Acari: Tetranychidae) on almonds under differential water stress. *Environmental Entomology* **17**: 488–495.

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