Enhancement of Drought-Induced Senescence by the Reproductive Sink in Fertile Lines of Wheat and Sorghum

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ABSTRACT

The leaf senescence pattern was examined in water-stressed male sterile and fertile lines of wheat (*Triticum aestivum*) and sorghum (*Sorghum vulgare*). The study was conducted at the seedling stage and during grain development. The loss of leaf area and chlorophyll content induced by water stress was similar in the male sterile and fertile lines of wheat at the seedling stage. At the grain filling stage, leaf senescence occurred at a faster rate in the fertile lines as compared to sterile lines of both wheat and sorghum. The study indicates that a reproductive sink accentuates drought-induced leaf senescence.

Key words: Drought resistance, leaf senescence, male sterile, sink.

INTRODUCTION

Breeding for drought resistance in crop plants is a major objective in crop improvement programmes around the world. Therefore, several efforts have been made to develop suitable selection criteria for drought resistance in crop plants (Chang *et al.*, 1982). Most of the criteria are based on responses of seedlings to water stress (IRRI, 1982). However, many studies have shown that the sensitivity of crop plants to drought varies during growth and development, the reproductive phase being the most sensitive in most crops (Eastin *et al.*, 1983). Consequently, the criteria based on seedling responses are not always successful under field conditions (Chang *et al.*, 1982; Reyniers *et al.*, 1982). Varieties assessed as drought resistant on the basis of stability or drought index are usually poor yielders (Fisher and Maurer, 1978; IRRI, 1982; Sinha *et al.*, 1986), suggesting that a strong reproductive sink is not compatible with drought resistance. This suggests the possibility that the strength of the reproductive 'sink' may alter the response of the plant to drought or water stress. In order to investigate this question, the effects of drought on normal and male sterile lines of wheat and sorghum were compared. Leaf senescence, both in terms of area and loss of chlorophyll content, was used as the criterion of drought effects in these studies.

MATERIALS AND METHODS

Normal (FP-83-44, FP-83-33) and genetically male sterile (FP-83-40-2, FP-82-32) lines of wheat (*T. aestivum*) were obtained from the Genetics Division of the Indian Agricultural Research Institute, New Delhi, India. The plants (six per pot) were grown in pots containing 20 kg soil in a glasshouse and given adequate fertilizer to maintain normal growth.

One-month-old wheat plants were water stressed by withholding the water supply and sampled after 0, 5, 7 and 10 d without water. Water potential of the youngest fully expanded leaf was measured at 10·00 h with a pressure chamber (Mode 3005, Soil Moisture Equipment Corp.) according to Scholander *et al.* (1964). Two plants constituted a replicate and there were three replicates per treatment. Green leaf area was recorded using an automatic leaf-area meter (Model AAM-7, Hayashi Denkoh Co. Ltd, Japan). Six plants constituted a replicate and there were three replicates per treatment. Chlorophyll content of leaves was determined according to Arnon (1949).

A separate batch of wheat plants was subjected to four stress treatments by adding 250, 500, 750, 1000 ml water per pot per d from anthesis. Measurements of green leaf area and leaf chlorophyll content were done either on all the leaves of the main shoot (lines FP-83-44 and FP-83-40-2) or

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only on the flag leaf (lines FP-83-33 and FP-83-32) of plants with or without water stress. Leaf water potential was measured using a pressure chamber (as described earlier) on the flag leaf only. For leaf-area measurement, three plants constituted a replicate and there were three replicates in each treatment. For chlorophyll estimation all green leaves from the two main shoots were pooled in each replicate of a treatment. The leaves were chopped into very small pieces and 200 mg leaf samples were randomly drawn for chlorophyll extraction and measurement following Arnon (1949). Three replicates were maintained for each treatment. Flag-leaf water potential was measured at 10·00 h using two flag leaves as replicate and maintaining three replicates for each treatment.

Sorghum (*Sorghum vulgare*) cv. 2077A (male sterile) and 2077B (fertile) were grown in the field in 5 m × 5 m plots in the rainy season in a randomized block design at a population of 18 plants m^{-2} following recommended agronomic practices. The plants were given urea fertilizer at the rate 40 kg N ha^{-1} and irrigated whenever necessary. Half the plots of each genotype were given irrigation (6 cm) at anthesis and 15 d after anthesis while the other half were kept unirrigated. There was no rain after anthesis. Water stress developed slowly in the unirrigated plants.

Leaf ψ_w and leaf area were measured at anthesis, and 15, 30 and 35 d after anthesis. Water potential of the uppermost leaf was measured at 10.00 h with a pressure chamber (as described earlier). Two plants constituted a replicate and three replicates were maintained for each treatment for water potential measurement. For leaf area measurement, only green leaves were selected. Ten plants constituted a replicate and three replicates were maintained for each treatment. Leaf area was measured by automatic leaf area meter.

RESULTS AND DISCUSSION

A range of leaf ψ_w from −1·0 MPa to −3·5 MPa was created as a result of withholding water for different durations from seedlings of normal and male sterile lines of wheat. Both the normal and male sterile lines exhibited a similar reduction of green leaf area, as well as in chlorophyll content per plant, in response to decreasing leaf ψ_w (Fig. 1). However, when a range of leaf ψ_w was created by applying different amounts of water at anthesis, the fertile line showed a sharper decline in green leaf area and chlorophyll content compared to the sterile line with the decline in leaf ψ_w (Figs 2 and 3).

In sorghum, A and B lines which are male sterile and normal, respectively, the leaf ψ_w was −1·8 ± 0·2 MPa and 1·6 ± 0·3 MPa at the time of anthesis. Both lines showed a decline in leaf area per plant after anthesis (Fig. 4). Fifteen days after anthesis the leaf area decreased in the normal time by 34% in irrigated plants and 57% in non-irrigated plants whilst in the 2077A line the decrease in leaf area was 22% (irrigated) and 32% (non-irrigated). By 35 d from anthesis the male-sterile 2077A line had retained higher leaf area

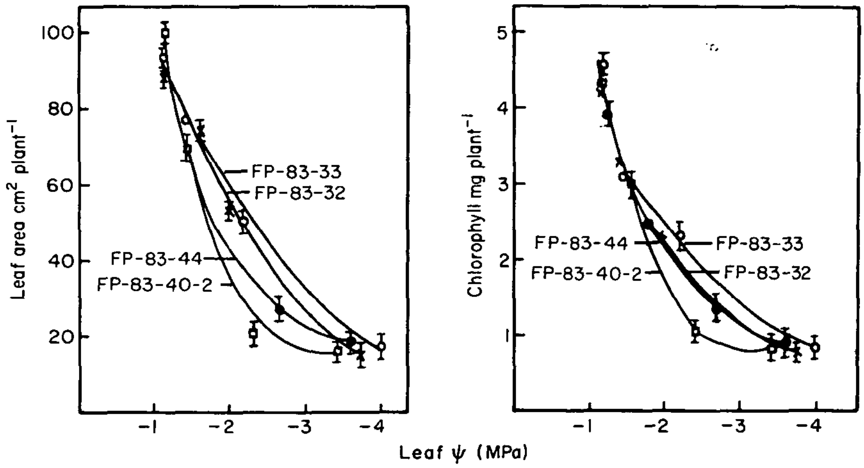

FIG. 1. Effect of water stress on leaf area and chlorophyll content per plant in male fertile lines FP-83-44 (○——○) FP-83-33 (●——●), male sterile lines FP-83-40-2 (×——×) and FP-83-32 (□——□) of wheat at the seedling stage. Values ± s.e. for leaf ψ_w were as follows: FP-83-44: 1·2 ± 0·06, 1·7 ± 0·09, 2·6 ± 0·1 and 3·5 ± 0·2 MPa, respectively. FP-83-40-2: 1·1 ± 0·05, 1·5 ± 0·03, 2·3 ± 0·07 and 3·4 ± 0·05 MPa, respectively. FP-83-33: 1·15 ± 0·05, 1·4 ± 0·1, 2·2 ± 0·1, 4·0 ± 0·2 MPa, respectively. FP-83-32: 1·15 ± 0·05, 1·6 ± 0·3, 2·0 ± 0·2 and 3·7 ± 0·4 MPa, respectively.

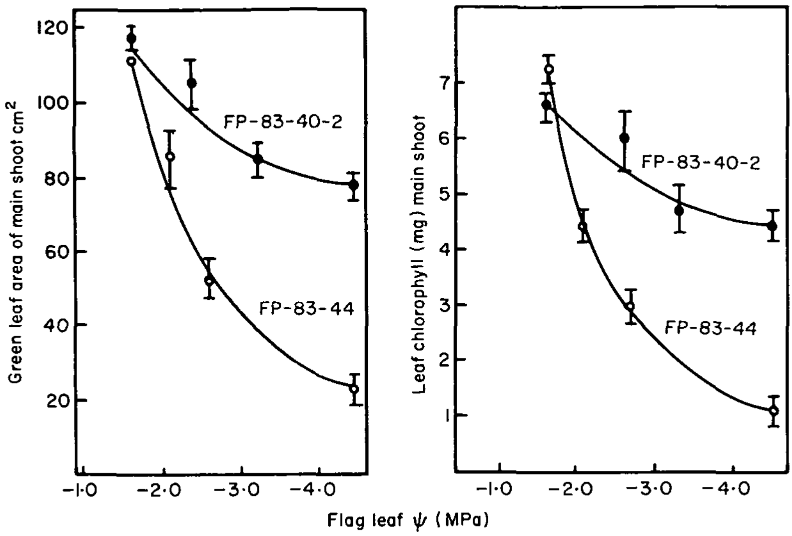

FIG. 2. Effect of water stress on leaf area and chlorophyll content of main shoot in male fertile line FP-83-44 (○——○) and male sterile line FP-83-40-2 (●——●) of wheat during grain development. Values ± s.e. of leaf ψ_w were as follows: FP-83-44: 1·6 ± 0·2, 2·1 ± 0·2, 2·6 ± 0·3, 4·5 ± 0·5 MPa, respectively. FP-83-40-2: 1·6 ± 0·2, 2·35 ± 0·2, 3·2 ± 0·3 and 4·5 ± 0·4 MPa, respectively.

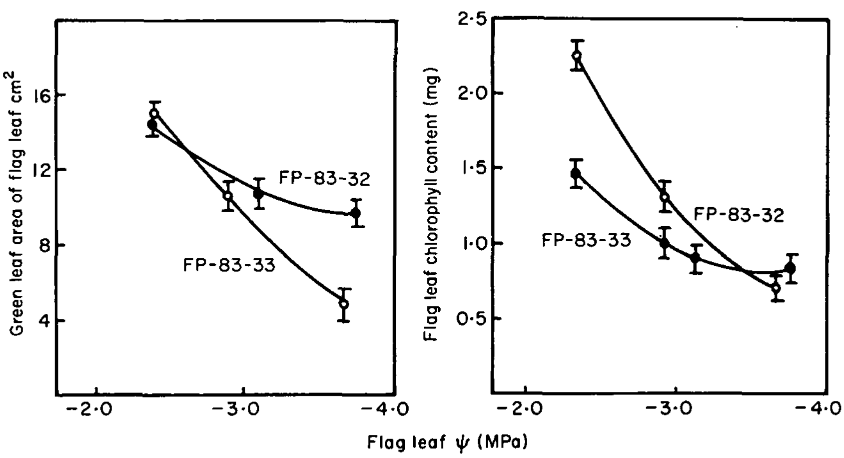

FIG. 3. Effect of water stress on leaf area and chlorophyll content of flag leaf in male fertile line FP-83-33 (○——○) and male sterile line FP-83-32 (●——●) of wheat during grain development. Values ± s.e. of leaf ψ_w were as follows: FP-83-33: 2·3 ± 0·3, 2·9 ± 0·2, 3·6 ± 0·4 MPa, respectively. FP-83-32: 2·3 ± 0·4, 2·9 ± 0·3 and 3·7 ± 0·4 MPa, respectively.

than the normal 2077B line, irrespective of the irrigation treatment.

Fifteen days after anthesis the chlorophyll content in the normal, B line decreased by 38% (irrigated) and 70% (non-irrigated) compared to the anthesis value (Fig. 4). In the male sterile A line, the comparable decrease was 23 and 49%, respectively. By 35 d after anthesis, the A line maintained higher chlorophyll content compared to the B line, irrespective of the irrigation treatment.

The normal and male sterile lines are isogenic, but for the lack of seed set in the latter. They are expected to exhibit similar morphological and physiological characteristics. Indeed, when seedlings of normal and male sterile sorghum and wheat were subjected to water stress, they exhibited a similar response in terms of the loss in chlorophyll

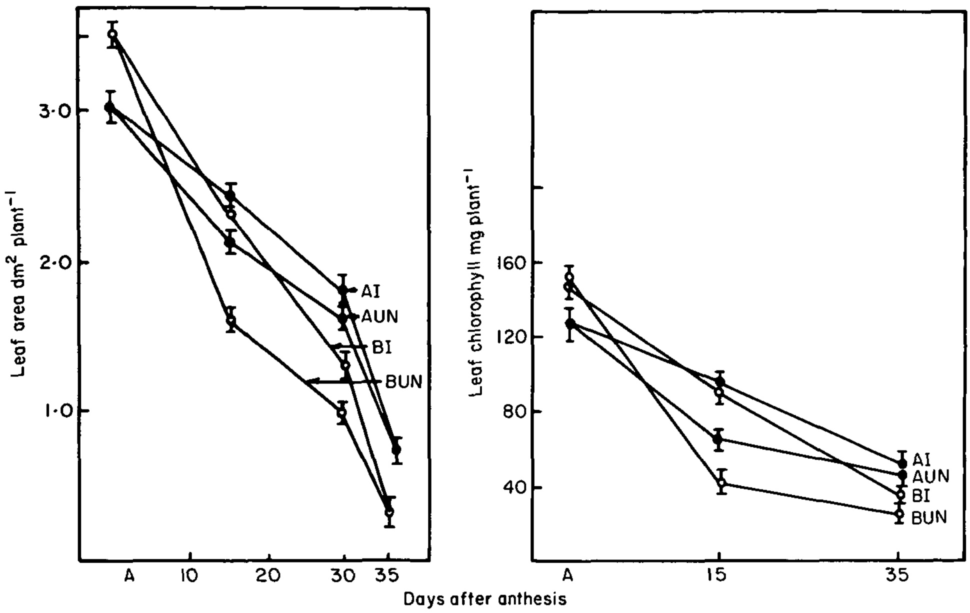

FIG. 4. Leaf area and chlorophyll content per plant during grain development in sorghum under irrigated and non-irrigated conditions in male sterile line 2077A (●——●, A–I, AUN) and male fertile line 2077B (O——O, BI, BUN), respectively.

content and leaf area. However, when normal and male sterile plants were exposed to water stress in the post-anthesis phase, the normal genotype showed a faster rate of senescence. Therefore, on the basis of the senescence pattern of leaf area, the male sterile lines could be described as more drought resistant. This implies that a genotype failing to set seed would appear to be more tolerant to drought than one having reproductive sink. Indeed, most studies have concluded that poor yielding varieties, or wild relatives of many crops, are more drought resistant (Stone, 1974; IRRI, 1982).

A major change during the transition from seedling to reproductive plant is a shift in the site of the 'sink' from roots to the developing grains. In seedlings the roots serve as a major sink where the metabolites mobilized during senescence of leaves in response to drought could be stored (Sharp and Davies, 1979; Aggarwal and Sinha, 1983; Reddy, 1986). However, in the reproductive phase, the leaves subtending the developing grains/fruit translocate nitrogenous compounds to the developing grains (Waters *et al.*, 1980). There is a loss of soluble protein predominantly as RuBP-Case from the leaves and this is coupled with loss of chloroplast integrity (Thomas and Stoddart, 1980). Therefore, a larger reproductive sink possibly hastens the senescence of leaves.

Differences in leaf area between normal and sterile lines were induced in response to water stress during the reproductive phase. However, the chlorophyll content of the remaining leaves did not differ substantially because leaves did not show a parallel loss of chlorophyll. The loss was in acropetal succession leading to a complete senescence of lower leaves. The topmost leaves maintained almost the same amount of chlorophyll, or sometimes even more as compared to the leaves in a similar position in control plants. Therefore, in the whole plant system, the effects of drought are most apparent on the overall chlorophyll content of the plant.

The differences between normal and male sterile lines could be due to difference in leaf turgor. The male sterile lines might preferentially accumulate solutes under water stress in the absence of developing seeds. Leaf osmotic potentials have been shown to be related to the source–sink balance in cotton (Radin *et al.*, 1986). The present study thus shows that the size of the reproductive sink could alter the response of a whole plant to water stress. This could have an important bearing on the degree of drought resistance of a genotype based on grain yield.

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