

YIELD AND WATER USE EFFICIENCY OF LOW
AND HIGH ABSCISIC ACID WHEAT LINES
UNDER WATER STRESS

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NOMENCLATURE

A	net CO ₂ assimilation rate per unit leaf area
ABA	abscisic acid
A _{max}	CO ₂ saturated A
CE	in vivo carboxylation efficiency
C _i	leaf internal CO ₂ concentration
ELISA	enzyme-linked immunosorbent assay
g _s	leaf stomatal conductance to H ₂ O vapor
Δ	stable carbon isotope discrimination measured in kernels
RWC	leaf relative water content
SP	leaf solute potential
TP	leaf turgor potential
TBS	tris-buffered saline
WP	leaf water potential
WUE	photosynthetic water use efficiency

Chapter I

INTRODUCTION

Chapters II and III of this thesis are separate and complete manuscripts for submission to Crop Science.

Chapter II

LEAF PHOTOSYNTHESIS OF LOW AND HIGH
ABSCISIC ACID WHEAT SELECTIONS
UNDER WATER STRESS

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ABSTRACT

A higher capacity to accumulate abscisic acid (ABA) may promote higher photosynthetic water use efficiency (WUE) in wheat if stomatal closure occurs without a decrease in mesophyll capacity for photosynthesis. Gas exchange characteristics were compared in intact leaves of low-ABA and high-ABA spring wheat selections following a single application of ABA (5×10^{-5} M) or polyethylene glycol (-1.3 MPa). The latter was used to induce water deficits. Bulk-leaf ABA content was significantly higher in high-ABA selections than low-ABA selections under water stress. Photosynthetic capacity, determined by measuring net CO₂ assimilation (A) as a function of leaf internal CO₂ concentration (C_i), was significantly higher in low-ABA than high-ABA selections under well-watered or water-stressed conditions, and following ABA application. Stomatal conductance (g_s) and photosynthetic capacity decreased following exogenous ABA or water stress treatments, and the magnitude of the reduction in A was similar for both ABA selection classes. Exogenous ABA treatment did not significantly increase WUE. In contrast, g_s decreased more than A under water stress so that WUE increased, and high A was an expression of high WUE under water stress. The difference between ABA classes in WUE, however, was not significant. The lower A observed in high-ABA than low-ABA selections under water stress or with exogenously supplied ABA was attributed to lower photosynthetic capacity and a slightly greater (P<0.10) decrease in g_s. These results suggested mesophyll capacity for photosynthesis largely determined WUE in these ABA selections. Aside from the reduction in g_s, there was no indication that higher ABA accumulation further limited A under water stress.

Information on physiological limitations to photosynthesis under water stress is needed to improve photosynthetic water use efficiency (WUE) and drought stress resistance in wheat (Triticum aestivum L.). Stomatal conductance and mesophyll capacity for photosynthesis are two principal components in regulation of net CO₂ assimilation rate (A), WUE (the amount of carbon assimilated compared to the amount of water transpired) and plant resistance to water stress (Farquhar and Sharkey, 1982). Stomatal conductance is determined by stomatal frequency and the degree of stomatal closure, while mesophyll capacity is determined by the amount and activity of enzymes involved in CO₂ assimilation (Sharkey, 1985; Bradford et al., 1983). If stomatal conductance declines and A remains relatively high the leaf internal CO₂ concentration will decrease and a steeper CO₂ gradient from ambient air to inside the leaf will result in increased WUE (Johnson et al., 1987a; Dubbe et al., 1978)

It is generally accepted that stomatal closure under water stress is mediated by the phytohormone, abscisic acid (ABA) (Raschke, 1987). Increased synthesis of ABA occurs in response to leaf water stress (Cornish and Zeevaart, 1985), and increased bulk-leaf ABA content in wheat leaves is usually associated with decreased stomatal conductance under water stress (Nordin, 1976; Quarrie and Jones, 1979). Therefore, a high potential for ABA accumulation might promote higher WUE of wheat, providing stomatal conductance is the main limiting factor to A under water stress. This hypothesis is refuted if the reduction in A associated with leaf water deficits results from decreased mesophyll capacity for photosynthesis rather than a limitation imposed by stomata

alone (Sen Gupta and Berkowitz, 1987).

Results of Dubbe et al. (1978) showed exogenously supplied ABA increased WUE in several crop plants, because reductions in transpiration were greater than reductions in A. In that study, stomata were more sensitive (they closed sooner) to increasing CO₂ concentration in plants supplied with ABA than in untreated plants. This response to exogenous ABA suggests ABA accumulation and subsequent stomatal closure might optimize WUE, especially under severe drought conditions (Dubbe et al., 1978). Similarly, exogenous applications of ABA to leaves of the flacca tomato mutant and its normal parent resulted in decreased stomatal conductance, while A and mesophyll capacity for photosynthesis were only marginally reduced (Bradford et al. 1983). However, recent evidence suggests ABA supplied through the transpiration stream of wheat decreased mesophyll capacity, in addition to causing stomatal closure (Raschke and Hedrich, 1985). The biochemical basis for ABA limitation to mesophyll capacity for photosynthesis is not completely understood, but the mechanism likely involves suppression of carboxylation of ribulose biphosphate (RuBP) by the enzyme ribulose biphosphate carboxylase-oxygenase (Rubisco) (Seeman and Sharkey, 1987; Fischer et al., 1986).

Gas exchange experiments were conducted using spring wheat lines selected divergently for their capacity to accumulate ABA in detached and partially dehydrated leaves (Quarrie, 1981). Our objective was to determine the relationship between ABA accumulation potential and WUE under water stress. Exogenously supplied ABA was also used to verify reported effects of ABA on photosynthesis in intact leaves. The ABA supplied exogenously would be expected to be predominantly in the

apoplast, where ABA is thought to be active in mediating stomatal closure following stress-induced release from the mesophyll (the presumed site of ABA synthesis) (Cornish and Zeevaart, 1985; Cowan et al., 1978) Field studies comparing differences between these wheat selections in yield, water relations and crop water use efficiency under drought stress have been reported elsewhere (Innes et al., 1984; Quarrie and Lister, 1983; Quarrie, 1983). To our knowledge, there are no studies comparing the difference between low and high ABA wheat selections in leaf gas exchange characteristics and limitations to A under water stress.

MATERIALS AND METHODS

Seed of 20 low-ABA and 20 high-ABA selections derived from a single cross between two hexaploid spring wheat lines differing twofold in bulk-leaf ABA accumulation potential, were obtained from the Institute of Plant Science Research, Cambridge, UK. The 40 selections were shown to have heritable differences in ABA accumulation potential based on a detached leaf test (Quarrie, 1981). Plant material for this present study was selected based on a detached leaf test (S.A. Quarrie, personal communication, 1986), and consisted of three low-ABA selections and four high-ABA selections. Average bulk-leaf ABA contents were 364 and 750 ng g⁻¹ fresh wt for the low-ABA and high-ABA selection classes, respectively, (unpublished data). Seeds were pregerminated and individually transplanted into 0.60 L pots containing a washed, coarse sand. Plants were grown in a growth chamber with day/night temperatures of 22/15°C (65/75% RH) and 14 h of light (600 μmol photons m⁻² s⁻¹ PAR at pot level) supplied by fluorescent and incandescent bulbs. Plants were watered every other day and fertilized weekly with 50% Hoagland's solution. Light-saturated (1800 μmol photons m⁻² s⁻¹) rates of steady-state gas exchange were measured on the most recent, fully expanded leaf blade of the main-stem.

Experiment One

To determine the effect of exogenously supplied ABA on net CO₂ assimilation rate (A) of intact leaves, one low-ABA and one high-ABA selection were grown under well-watered conditions for 42 d. A 5x10⁻⁵ M solution was prepared by dissolving 10.58 mg of racemic ABA (Cat. No. A-1012, Sigma Chemicals, St. Louis, MO) in 2 ml methanol and diluting with distilled water to 2 L. The solution was adjusted to pH 6.0 with NaOH

and stored at 4°C in the dark. Treated plants were irrigated once with 150 ml of the ABA solution, while control plants were irrigated with distilled water adjusted to pH 6.0. Gas exchange measurements were made 24 h following treatment with ABA. The response of A to leaf internal CO₂ concentration (C_i) was measured to determine stomatal and nonstomatal limitations to A. Rates of A were determined on flag leaves at ambient CO₂ concentrations of 5, 40, 73, 123, 198, 330, 416, 513 and 648 μL L⁻¹, which gave a similar range of C_i values. To obtain the desired ambient CO₂ concentrations and relative humidity, dry (dew point = -15°C) gases of 770 and 0 μL CO₂ L⁻¹ (210 μL O₂ L⁻¹) were mixed in a stirred, temperature and humidity controlled reaction chamber (cuvette) described by Johnson et al. (1987a). Leaves were measured at 22°C leaf temperature and a dew point of 8°C (60% RH; VPD=1.5 kPa). Steady-state conditions at each of the 9 ambient CO₂ concentrations were usually attained within 30 min. Values for transpiration rate, stomatal conductance to water vapor (g_s), A and C_i were calculated according to von Caemmerer and Farquhar (1981). WUE was calculated as the ratio of A to transpiration rate. Immediately following gas exchange measurements, leaf area (one surface) of the measured leaf was determined using a leaf area meter (LI-3000, Li-Cor, Inc., Lincoln, NE). Leaf relative water content (RWC) was determined from a fully expanded leaf of another tiller on the same plant used for gas exchange. The leaf was excised and fresh, turgid (a minimum of 20 h rehydration in distilled water) and dry (70°C for 3 d) weights were determined for calculation of percent RWC. The stomatal limitation to A and in vivo carboxylation efficiency (CE, the initial slope of the linear portion) was calculated for each A

vs. C_i curve as outlined by Farquhar and Sharkey (1982). The first five points above the CO_2 compensation point (the C_i value where $A=0$) were used in calculating the initial slope. Measured values of CO_2 saturated A (A_{max} , the curve plateau) were also obtained from each A vs. C_i curve. Experimental design was a randomized complete block with four replications. One complete block of 4 plants were measured on each of four days.

Bulk-leaf ABA content was measured on a center section (ca. 0.1 g fresh wt) from each lamina used for gas exchange. The leaf section was cut into square pieces (ca. 4.0 mm²) and transferred to a 10x75 mm disposable centrifuge tube. Tubes were cooled on dry ice, and stored at -70°C. An enzyme-linked immunosorbent assay (ELISA) was used for quantification of physiologically active, unconjugated ABA [2-cis(+)-ABA] in diluted leaf extracts (Idetek Inc., 1986). Standard solutions were prepared by dissolving racemic ABA in methanol and diluting with Tris-buffered saline (TBS: 25 mM Tris, 100 mM NaCl, 1 mM MgCl₂, pH 7.5). Leaf tissue was homogenized over ice using 1 ml 80% aqueous methanol (pH 7.0, containing 100 mg L⁻¹ BHT: butylated hydroxytoluene). Extraction was done in 4 ml 80% aqueous methanol for 24 h in the dark at 4°C. The homogenate was spun for 15 min at 9000xg to purify the extract. The supernatant (0.5 ml) was reduced to dryness under vacuum using a centrifuge concentrator and resuspended with TBS to give an appropriate dilution of leaf extract. Sample concentration was determined by comparison to a standard curve developed from triplicate assays of known ABA concentration. Bulk-leaf ABA content was reported as ng ABA g⁻¹ fresh wt.

Experiment Two

The relationship between bulk-leaf ABA content and leaf gas exchange characteristics under water stress was determined in three low-ABA and three high-ABA selections. The six selections showed earliness in heading date under greenhouse conditions in Stillwater, OK. Plants were grown under well-watered conditions for 56 d. In water-stressed treatments, plants were irrigated with 150 ml of a polyethylene glycol (PEG, avg. MW=8000) solution 48 h prior to sampling. Osmotic potential of the PEG solution was -1.3 MPa based on psychrometric determinations and based on previous results (J.J. Read, unpublished data), g_s decreased by 50% following a 48 h stress period. The amount of PEG needed in water for a -1.3 MPa solution was calculated from a polynomial regression equation (Michel, 1983). The response of A to varying levels of C_i was measured on flag leaves. Dry gases of 0 and 918 $\mu\text{L CO}_2 \text{ L}^{-1}$ were mixed in the cuvette to obtain ambient CO_2 concentrations of 5, 40, 75, 126, 214, 340, 427, 540 and 655 $\mu\text{L L}^{-1}$, which gave a range of C_i values. Measurement conditions were 24°C leaf temperature, and a dew point of 12°C (50% RH, VPD=1.7). Following gas exchange measurements, leaf area and bulk-leaf ABA content of the measured leaf were determined as previously described. For each ABA selection, two determinations of RWC were made; one from the measured leaf, and one from a fully expanded leaf of another tiller. Calculations of transpiration rate, A, g_s , C_i and WUE at each ambient CO_2 concentration were made as previously described. Stomatal limitation to A, CE and A_{max} for each A vs. C_i response curve were also calculated as described. Experimental design was a randomized complete block with four replications. Plants within a well-watered or a water-stressed treatment were measured in a single

day, and the measurement order was randomized with respect to water treatment and ABA selections. Data were analyzed using analysis of variance and variation among ABA selections was partitioned into components representing ABA classes (low and high ABA accumulation) and selections within classes.

Experiments Three and Four

Two independent experiments (Exp. 3 and 4) were conducted to determine if differences in gas exchange characteristics between the ABA classes under water stress resulted from a difference in the degree of water stress or leaf age (plant maturity). Plant material consisted of the same six ABA selections as above. To obtain leaves of equal morphological age in both low-ABA and high-ABA classes it was necessary to establish seedlings of low-ABA selections 10 d earlier than the high-ABA selections. Water stress treatments were applied as previously described when main-stem penultimate leaves were fully expanded (Exp. 3), and when main-stem flag leaves were fully expanded (Exp. 4). Penultimate leaves in Exp. 3 were measured 7 d earlier than the flag leaves in Exp. 4. Steady-state gas exchange measurements were made at an ambient CO₂ concentration of 340 $\mu\text{L L}^{-1}$. Measurement conditions for leaf temperature and dew point were as described in Exp. 2. Following gas exchange measurements, leaf cutter psychrometers (Merrill Specialty, Logan, UT) were used to excise one 0.24 cm² leaf disc from the center of the lamina used for gas exchange and two discs from a fully expanded leaf of another tiller. Psychrometer chambers were equilibrated for 2 h in a 30 °C water bath and wet bulb depression was determined using a microvolt meter (Wescor HP-115, Logan, UT). Microvolt readings from

individually calibrated psychrometers were used for calculation of leaf water potential (WP). Means of the three samples per plant were used in analysis of variance. The tiller leaf used to sample two leaf discs for water potential was used for RWC determination. Each experiment was designed as a randomized complete block with four replications. One complete block of 12 plants were measured on each of four days for each experiment.

RESULTS AND DISCUSSION

Experiment One

As expected, exogenously supplied ABA resulted in significantly higher bulk-leaf ABA content and decreased g_s (Table 1). With the reduction in g_s , there was a significant increase in RWC from 92% in control plants to 95% in ABA treated plants. Higher bulk-leaf ABA content was associated with a significant decrease in A at ambient CO_2 , but the stomatal limitation to A and WUE was not significantly affected. The reduction in A was paralleled by decreased g_s so that the stomatal limitation to A and WUE did not change. Similarly, Raschke and Hedrich (1985) found A and g_s declined in synchrony and to the same degree after feeding ABA (10^{-5} M) through the transpiration stream of detached wheat leaves, resulting in a small decrease in C_i .

The significant drop in C_i , which was associated with decreased g_s , suggests CO_2 supply to the mesophyll was a limitation to A (Sharkey, 1985). However, the reduction in CE (inferred from the initial slope of the response curve) and CO_2 saturated A (A_{max} , measured A at C_i above $340 \mu L L^{-1}$) suggested an additional limitation to A in plants fed ABA resulted from damage to the internal photosynthetic system. Fischer et al. (1986), observed that in addition to stomatal closure, ABA (10^{-4} M) fed to detached leaves of Xanthium strumarium L. limited A by decreasing CE and A_{max} . They found inhibition of A could not be reversed by adjusting C_i to the level that occurred before ABA application, thus leaves of ABA treated plants were unable to use the available CO_2 . Although they were unable to fully explain the mechanism for ABA limitation to mesophyll photosynthesis in whole leaves, the pool size of RuBP did not decrease while 3-phosphoglycerate levels were reduced after

reduced after ABA treatment suggesting inhibition of the carboxylation of RuBP by Rubisco.

In control plants, A at ambient CO₂ was significantly higher in the low-ABA than the high-ABA selection, and this resulted in higher WUE (Table 1). The higher A of the low-ABA selection was associated with a slightly higher CE, while A_{max} was the same in both ABA selections (Fig. 1a). The ABA selections did not differ in WUE when ABA was fed exogenously to plants, but A remained lower in the high-ABA selection. The lower A in the high-ABA than the low-ABA selection after feeding with ABA could occur through decreased g_s, thereby limiting CO₂ supply to the mesophyll. However, because the difference between selections in C_i was not significant, non-stomatal factors (lower mesophyll capacity for photosynthesis) were probably involved in lower A of the high-ABA selection. This was supported by the lower CE and the lower A_{max} in the high-ABA selection when fed ABA (Fig 1b); the difference in A_{max} was significant at P<0.10. Interpretation of these results using the model of Farquhar et al. (1980) suggests lower A in the high-ABA selection after exogenous ABA treatment may have resulted from decreased CE in association with the lower initial slope. The amount or activity of Rubisco has been shown to correlate with CE in bean (Phaseolus vulgaris L.) leaves (von Caemmerer and Farquhar, 1981). Lower A_{max} of the high-ABA selection suggests the capacity for RuBP regeneration was lower after exogenous ABA treatment. Decreased RuBP regeneration may occur at the same time Rubisco activity is decreased and is thought to depend among other things on the capacity for photosynthetic electron transport. Although there is evidence supporting the above

interpretation (Sharkey, 1985), verification of the difference between ABA selections in limitations to mesophyll capacity for photosynthesis when fed ABA would require determination of biochemical factors involved.

Experiment Two

When the response of A to C_i was measured in three low-ABA and three high-ABA selections under well-watered or water-stressed conditions, differences among selections within an ABA class were not significant ($P>0.05$) for any gas exchange parameter. Under well-watered conditions and at ambient CO_2 , A and WUE were significantly higher in the low-ABA than the high-ABA class (Table 2). The higher A was associated with higher CE and A_{max} (Fig. 2a). There was no difference between ABA classes in g_s under well-watered conditions, but C_i was significantly lower in the low-ABA class. For the same g_s , higher mesophyll capacity for photosynthesis would result in a reduction in C_i and the steeper CO_2 gradient from ambient air to inside the leaf would tend to increase A and WUE (Johnson et al., 1987a).

PEG-induced water stress significantly ($P<0.001$) reduced RWC of the secondary stem leaf and the main stem leaf. There was no significant ($P>0.30$) difference between ABA classes (avg. RWC=80%, data not shown) in RWC of the measured, main stem leaf (inside the cuvette), but RWC of the secondary stem leaf was lower in the high-ABA class than the low-ABA class (Table 2). The reduction in plant water status led to significantly ($P<0.001$) lower A at ambient CO_2 . In contrast to exogenously supplied ABA, the reduction in g_s in response to water stress was greater relative to the reduction in mesophyll capacity for photosynthesis, so that stomatal limitation to A and WUE increased

significantly ($P < 0.01$) under water stress. Nevertheless, C_i decreased 11% in the low-ABA class and 15% in the high-ABA class while A decreased by ca. 43% in both ABA classes. Thus, nonstomatal factors (inhibition of mesophyll capacity for photosynthesis) were a dominant limitation to A under water stress. A number of factors involved in both the light and dark reactions of photosynthesis are involved in determining mesophyll capacity for photosynthesis (Sharkey, 1985).

As under well-watered conditions (Fig. 2a), higher A in the low-ABA class under water stress was associated with a significantly higher CE and A_{max} (Fig 2b). Bulk-leaf ABA content was the same in both ABA classes under well-watered conditions, but it was 50% higher in the high-ABA class than the low-ABA class under water stress (Table 2). Higher ABA accumulation in response to water stress was associated with a significantly lower g_s , and the ABA class by water treatment interaction was significant ($P < 0.10$) for g_s . Although this stomatal response to bulk-leaf ABA content was anticipated, there was no evidence that higher ABA accumulation in the high-ABA class under water stress resulted in increased stomatal limitation to A . For stomatal limitation to increase substantially under water stress, g_s must decline to a greater extent than mesophyll capacity for photosynthesis, so that C_i decreases, but the shape and magnitude of the A vs. C_i response curve remains fairly stable (Sharkey, 1985). Our results showed C_i and mesophyll capacity declined to a similar degree in both ABA classes so the difference between ABA classes in stomatal limitation to A did not change in response to water stress. Although C_i and WUE did not differ between ABA classes under water stress, WUE remained higher in the low-

ABA class in association with higher A and g_s (Table 2). There was a negative correlation measured between C_i and WUE ($r=-0.87^*$, sig. at $P=0.05$) suggesting low C_i is an expression of high WUE.

The higher A of the low-ABA class could result from stomatal factors, nonstomatal factors or a combination. We suspect that maintenance of higher A in low-ABA selections under water stress was to a large extent the result of positive coupling between g_s and mesophyll capacity for photosynthesis. Wong et al. (1985), have shown that g_s and A decreased to the same extent when mesophyll capacity for photosynthesis decreases in response to certain environmental stresses, including water deficit, such that C_i remains nearly constant. Their results suggest alterations in stomatal conductance in response to water stress are not completely independent of the mesophyll capacity for photosynthesis (Farquhar and Sharkey, 1982; Cowan et al., 1982). Although the precise mechanism for this physiological coupling is not completely understood, this coordinated response of g_s and mesophyll capacity to water stress appears to explain why C_i remains fairly stable in wheat leaves with the decline in leaf water potential (Johnson et al. 1987a). This positive coupling may also be involved with genotypic differences in A observed among wheat accessions (Johnson et al., 1987b). Although C_i at ambient CO_2 did not remain constant, C_i decreased less than A or g_s in response to water stress (Table 2).

Results suggested g_s is slightly more sensitive in high-ABA than low-ABA selections when ABA is fed exogenously or synthesized in response to water stress. There was also a slightly greater increase in WUE in the high-ABA than the low-ABA class in response to water stress (Table 2). It is possible that lower RWC in the high-ABA class caused

g_s to decrease more than mesophyll capacity for photosynthesis. However, lower g_s cannot fully account for the increased WUE since the magnitude of the difference between ABA classes in stomatal limitation to A was similar under well-watered or water-stressed conditions. The magnitude of the decline in CE was smaller in the high-ABA class than the low-ABA class in response to water stress (interaction sig. at $P < 0.10$), which could account for the slightly greater increase in WUE in response to water stress in the high-ABA class than the low-ABA class (19% vs. 5%, respectively, sig. at $P < 0.15$). Similarly, a significantly ($P < 0.05$) greater increase in WUE under water stress was observed in penultimate leaves of the high-ABA class than the low-ABA class in Exp. 3, but as in Exp. 2 the difference between ABA classes in WUE was not significant (Table 3).

Experiments Three and Four

When gas exchange was measured at ambient CO_2 in flag and penultimate leaves of comparable morphological age in each ABA class, WUE was significantly higher in the low-ABA than the high-ABA class under well-watered conditions (Table 3). Higher WUE was associated with significantly lower C_i and lower g_s . In flag leaves of the low-ABA class, the decreased supply of CO_2 to the mesophyll did not limit A so that A was significantly higher than the high-ABA class. WUE remained higher in the low-ABA than the high-class for the same value of g_s under water stress.

Results were generally consistent with those observed when leaf age differed by 10 d. The only apparent affect of matching morphological age was the lack of a significantly lower A and g_s in the high-ABA than

the low-ABA class under water-stressed conditions (Table 3). In contrast to Exp. 2, there was no indication that the inability of high-ABA selections to use the available CO₂ was due to a greater degree of water stress. The reduction in WP paralleled the decrease in RWC, and WP was higher in the high-ABA than the low-ABA class under well-watered or water-stressed conditions. The decline in RWC was greater in flag leaves of the low-ABA than the high-ABA class, but this did not greatly change the difference between ABA classes in WP. These results support our contention that higher A under water stress in low-ABA selections is a result of the maintenance of a positive coupling between stomatal conductance and mesophyll capacity for photosynthesis.

SUMMARY

A difference between ABA selections in stomatal sensitivity to exogenously supplied or endogenously synthesized ABA was observed. Overall, higher bulk-leaf ABA content in response to a PEG-induced water deficit resulted in greater reductions in g_s than A, so that WUE increased. In penultimate leaves of equal morphological age, the increase in WUE was greater in the high-ABA than the low-ABA class in response to water stress. Further studies with these ABA selections are needed, perhaps with whole plants, to confirm or deny that higher ABA accumulation potential is associated with a moderately greater increase in WUE under drought stress.

Measurements of bulk-leaf ABA content following a 48 h water stress period should represent the amount of ABA in equilibrium with synthesis and degradation (Raschke, 1987; Cornish and Zeevaart, 1985), and does not indicate the location of ABA in the leaf. Therefore, a more precise determination of the relationship between lower g_s and the capacity to accumulate ABA under water stress would require measurements of the relative concentrations of ABA in the apoplast and symplast compartments (Radin and Hendrix, 1988; Cornish and Zeevaart, 1985).

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Table 1. Gas exchange characteristics, initial slope, stomatal limitation, and bulk-leaf ABA measured in main stem flag leaves of a low-ABA and a high-ABA spring wheat selection fed 5×10^{-5} M ABA through the transpiration stream of well-watered plants. Secondary stem flag leaves were used for relative water content (RWC) determination.

Treatment or comparison	ABA selection	A [†]	Amax [§]	g _s	C _i	WUE	Initial slope [§]	Stomatal limitation	RWC	ABA content
		$\mu\text{mol m}^{-2} \text{s}^{-1}$		$\text{mol m}^{-2} \text{s}^{-1}$	$\mu\text{L L}^{-1}$		A/C _i	%	%	ng/g fwt
No ABA	Low	23.6	32.4	0.38	222	4.53	0.125	25.5	93.2	60
	High	19.7	28.0	0.39	238	4.05	0.095	23.1	91.5	46
		†	NS	NS	NS	*	†	NS	NS	NS
+ ABA	Low	18.6	25.3	0.27	210	4.79	0.108	24.9	95.8	335
	High	10.8	15.9	0.16	214	4.44	0.060	29.6	95.2	424
		*	†	*	NS	NS	**	NS	NS	NS
No ABA vs. + ABA		**	**	**	*	NS	**	NS	**	**

†,*,** Difference between ABA selections significant by the F test at $P < 0.10$, $P < 0.05$ and $P < 0.01$, respectively. NS = not significant.

† Measured at an ambient CO₂ concentration of $330 \mu\text{L L}^{-1}$; A, leaf CO₂ assimilation; g_s, stomatal conductance to H₂O vapor; C_i, internal CO₂ concentration; WUE, water use efficiency, $\text{mmol CO}_2 \text{mol}^{-1} \text{H}_2\text{O}$.

§ Amax refers to CO₂ saturated A (at C_i above $330 \mu\text{L L}^{-1}$), while initial slope refers to the linear portion (five points) above the compensation point of the A vs. C_i response curve in Fig. 1.

Table 2. Gas exchange characteristics, initial slope, stomatal limitation and bulk-leaf ABA measured in main stem flag leaves of three low-ABA and three high-ABA spring wheat selections under well-watered and water-stressed conditions. Secondary stem flag leaves were used for relative water content (RWC) determination.

Treatment	ABA class	A [†]	Amax [§]	g _s	C _i	WUE	Initial [§] slope	Stomatal limitation	RWC	ABA content
		μmol m ⁻² s ⁻¹		mol m ⁻² s ⁻¹	μL L ⁻¹		A/C _i	%	%	ng/g fwt
Watered	Low	31.6	45.4	0.57	241	4.23	0.156	21.9 [†]	95.6	52
	High	25.7 **	35.4 **	0.59 NS	259 **	3.36 **	0.119 **	18.3 **	95.8 NS	71 NS
Stressed	Low	18.4	26.1	0.27	215	4.44	0.108	29.5	85.9 [†]	268
	High	14.7 **	20.2 **	0.22 *	221 NS	4.02 NS	0.086 *	26.4 NS	78.5 *	392 **

*,** Difference between ABA classes significant by the F test at P<0.05 and P<0.01, respectively. NS = not significant.

† Within a water treatment, differences among selections within an ABA class are significant at P<0.05.

‡ Measured at an ambient CO₂ concentration of 340 μL L⁻¹; A, leaf CO₂ assimilation; g_s, stomatal conductance to H₂O vapor; C_i, internal CO₂ concentration; WUE, water use efficiency, mmol CO₂ mol⁻¹ H₂O.

§ Amax refers to CO₂ saturated A (at C_i above 340 μL L⁻¹), while initial slope refers to the linear portion (five points) above the compensation point of the A vs. C_i response curve in Fig. 2.

Table 3. Gas exchange characteristics, relative water content (RWC) and water potential measured in penultimate leaves and flag leaves of three low-ABA and three high-ABA spring wheat selections under well-watered and water-stressed conditions.

Treatment	ABA class	A [§]	g _s	C _i	WUE	RWC	Water potential
		μmol m ⁻² s ⁻¹	mol m ⁻² s ⁻¹	μL L ⁻¹		%	MPa
Penultimate leaf							
Watered	Low	29.5	0.41	213 [†]	4.79 [†]	93.1	-1.02
	High	30.1	0.46	226	4.28	93.3	-0.76
		NS	*	**	**	NS	*
Stressed	Low	19.2	0.21	181	5.90	85.3	-1.56
	High	19.2	0.22	185	5.78	84.0	-1.25
		NS	NS	NS	NS	NS	*
Flag leaf							
Watered	Low	31.6 [‡]	0.39 [‡]	200 [‡]	5.32 [‡]	94.1 [†]	-1.67
	High	29.7	0.43	218	4.51	92.6	-1.43
		*	*	**	**	NS	*
Stressed	Low	16.8 [‡]	0.15	149	7.15	78.7	-2.85
	High	16.1	0.17	172	6.24	83.7	-2.41
		NS	NS	**	**	**	**

*,** Difference between ABA classes significant by the F test at P<0.05 and P<0.01, respectively. NS = not significant.

[†] Within an experiment, the water treatment x ABA class interaction is significant at P<0.05.

[‡] Within a water treatment, differences among selections within an ABA class are significant at P<0.05.

[§] Measured at an ambient CO₂ concentration of 340 μL L⁻¹; A, leaf CO₂ assimilation; g_s, stomatal conductance to H₂O vapor; C_i, internal CO₂ concentration; WUE, water use efficiency, mmol CO₂ mol⁻¹ H₂O.

FIGURE LEGENDS

Fig. 1. Assimilation of CO₂ (A) as a function of internal CO₂ concentration (C_i) in flag leaves of a low-ABA and a high-ABA spring wheat selection measured under (a) well-watered conditions and (b) 24 h following an exogenously supplied ABA (5x10⁻⁵ M) treatment. Arrows indicate the A and C_i values at an ambient CO₂ concentration of 330 μL L⁻¹. Leaves were measured at 1800 μmol photons m⁻² s⁻¹, 24°C leaf temperature and 210 mL O₂ L⁻¹ air.

Fig. 2. Average assimilation of CO₂ (A) as a function of average internal CO₂ concentration (C_i) in flag leaves of three low-ABA and three high-ABA spring wheat selections measured under (a) well-watered and (b) water-stressed conditions. Arrows indicate the A and C_i values at an ambient CO₂ concentration of 340 μL L⁻¹. Leaves were measured at 1800 μmol photons m⁻² s⁻¹, 24°C leaf temperature and 210 mL O₂ L⁻¹ air.

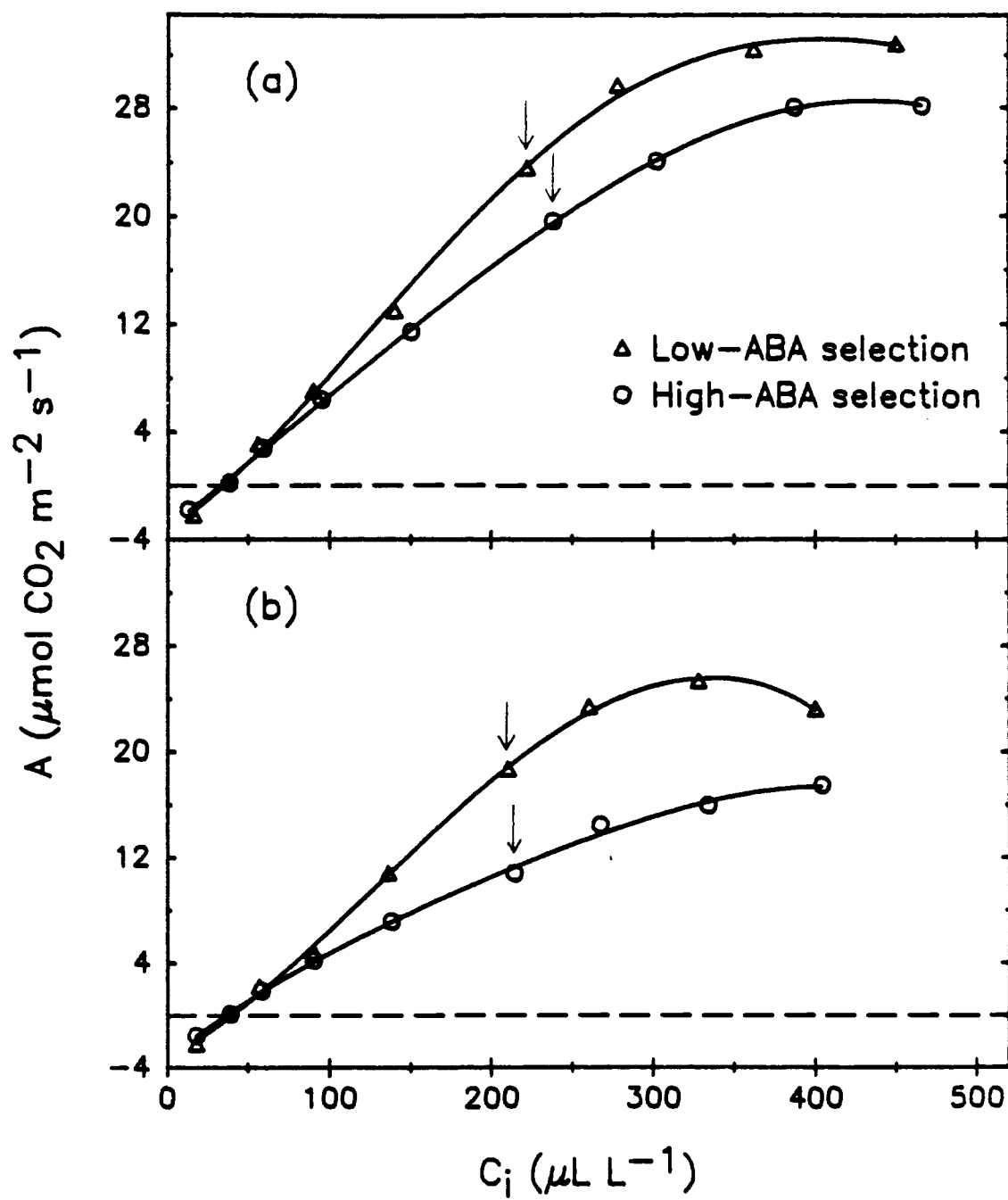


Figure 1.

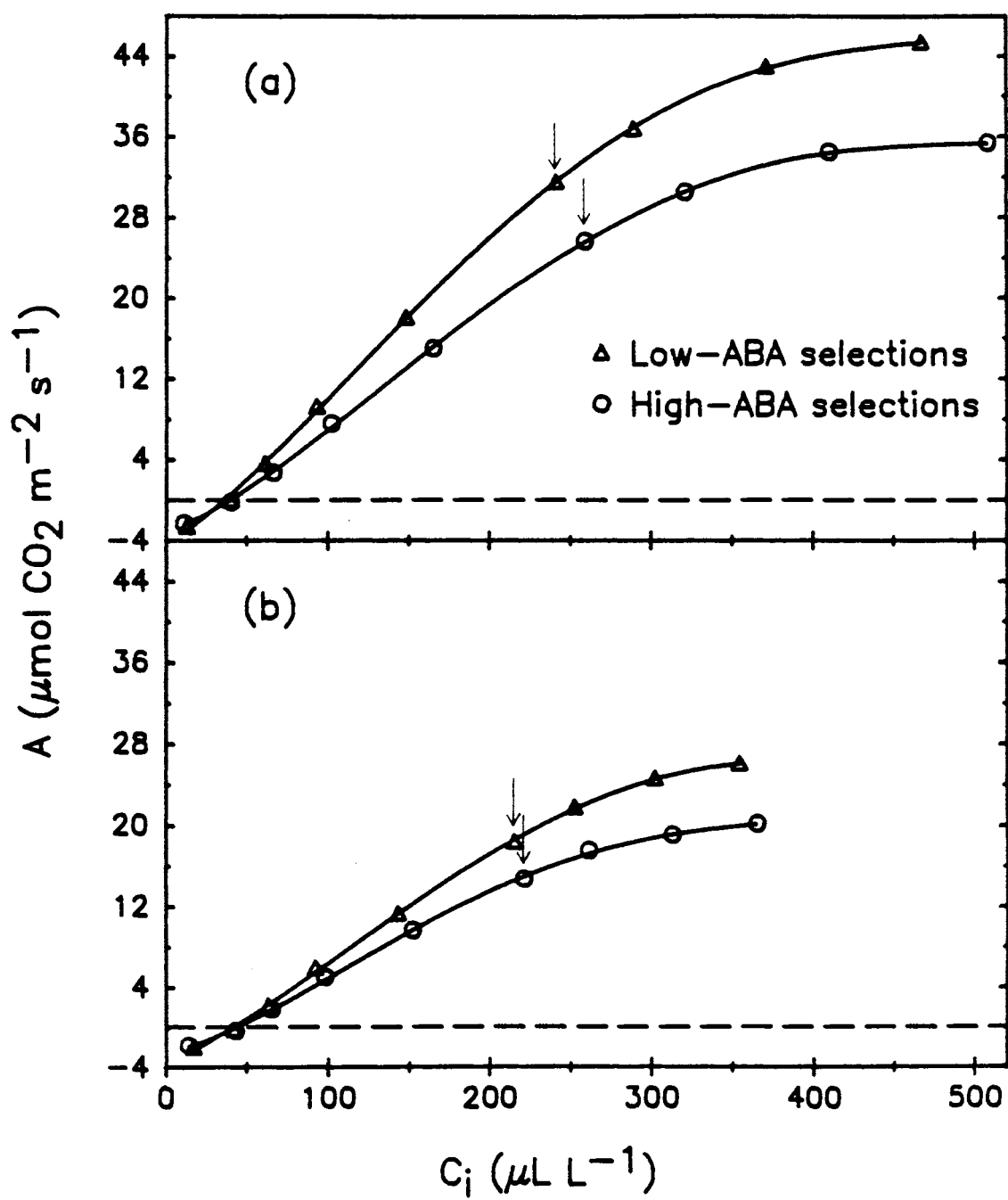


Figure 2.

CHAPTER III

YIELD, CARBON ISOTOPE DISCRIMINATION AND GAS EXCHANGE
OF LOW AND HIGH ABSCISIC ACID SPRING WHEAT SELECTIONS
UNDER DROUGHT STRESS

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ABSTRACT

Based on its role in stomatal closure under drought stress, the phytohormone, abscisic acid (ABA), might be useful as a tool for selecting wheat (Triticum aestivum L.) genotypes with improved drought resistance. Spring wheat lines selected divergently for low and high dehydration-induced ABA accumulation were studied in the field to determine if ABA accumulation potential is related to photosynthetic water use efficiency (WUE), stable carbon isotope discrimination (Δ) and grain yield. Plants were grown in well-watered and drought-stressed regimes under a rain shelter. Measurements of net CO₂ assimilation rate (A), bulk-leaf ABA content, water potential (WP), and relative water content (RWC) were made on fully expanded leaves of 2 low-ABA and 2 high-ABA selections in 1987 and 1988. Aboveground biomass, grain yield, yield components and Δ in kernels were determined at maturity. ABA classes did not differ in A, WP or grain yield, although yield components differed significantly. The low-ABA class tended to have higher WUE than the high-ABA class in association with lower stomatal conductance and higher biomass. In 1988, Δ was lower ($P < 0.06$) in the low-ABA class than the high-ABA class under drought stress. Biomass, grain yield, harvest index and Δ in kernels were also determined in 20 low-ABA and 20 high-ABA selections in 1988. Biomass and grain yield of the low-ABA class were higher, but harvest index was lower compared to the high-ABA class. Biomass decreased more under drought stress in the low-ABA class than the high-ABA class. Drought resulted in lower Δ , but the average difference between ABA classes in was not significant in either the watered or stressed regimes. The importance of stomatal control in determining grain yield was evidenced

by positive correlations of Δ with grain yield, but was not evident in gas exchange measurements. Within each ABA class, variation in grain yield, biomass, harvest index and Δ among selections was significant, and ranking of selections was consistent across water regimes.

Regression analysis indicated low-ABA selections had a twofold higher grain yield per unit increase in Δ than high-ABA selections under drought stress. In conclusion, low-ABA selections were more productive than high-ABA selections under well-watered or drought-stressed conditions.

Identification of physiological factors involved in drought stress resistance is needed to improve the adaptation of wheat (Triticum aestivum L.) to the Southern Great Plains. Selection for lower stomatal conductance under water-limited conditions has been suggested as one method to improve drought resistance (Jones, 1979; Sinclair et al., 1984). In wheat leaves, endogenous levels of the phytohormone abscisic acid (ABA) increase and stomatal conductance decreases with increasing water stress (Wright, 1977; Quarrie and Jones, 1979). This suggests stomatal closure in response to leaf water stress is mediated by ABA. This regulatory function of ABA is well documented (Raschke, 1987). Stomatal closure may limit water and carbon dioxide exchange in the leaf, but yield reduction of wheat might be minimized by reduced tissue dehydration and conservation of soil moisture needed during grain filling.

Reductions in net CO₂ assimilation rate (A) associated with leaf water deficits appear to be associated with decreased mesophyll capacity for photosynthesis rather than a stomatal limitation alone (Kaiser, 1987). Consequently, if mesophyll capacity for photosynthesis is not a major limitation to A under drought stress, higher ABA accumulation and subsequent stomatal closure could increase photosynthetic water use efficiency (WUE, the amount of carbon assimilated compared to the amount of water transpired) (Farquhar and Sharkey, 1982; Krieg, 1983). However, recent evidence suggests exogenously supplied ABA reduces A by decreasing mesophyll capacity for photosynthesis along with its effect on stomatal closure (Raschke and Hedrich, 1985). The biochemical basis of ABA limitation to photosynthesis in the mesophyll is still poorly understood (Fischer et al., 1986; Seeman and Sharkey, 1987).

Determining if ABA actually improves drought resistance or WUE of wheat has been hampered by the lack of genetically related materials varying in ABA accumulation, and by the difficulty of measuring WUE in a large number of field-grown plants.

Differences in dehydration-induced ABA accumulation were reported in spring wheat genotypes from diverse geographical origins (Quarrie and Jones, 1979). Low-ABA lines tended to have higher yields associated with higher leaf water potential under well-watered or drought-stressed conditions, but the relationship of ABA accumulation to stomatal conductance and drought resistance was variable (for a review, see Quarrie, 1983). To estimate this relationship with finer resolution, lines derived from a single cross were selected divergently for their capacity to accumulate ABA (Quarrie, 1981). High-ABA selections had higher WUE (expressed as the amount of grain yield per cumulative amount of water used) than low-ABA selections when water was withheld for four weeks preceeding anthesis (Innes, et al. 1984). Higher water use efficiency was attributed to a combination of slightly lower stomatal conductance and smaller leaves.

Carbon isotope discrimination (Δ), which is determined from measurements of the ratio of ^{13}C to ^{12}C in plant material, has been used to assess genotypic variation in WUE. In the greenhouse, Δ was negatively correlated with WUE, and Δ more clearly distinguished WUE differences among three winter wheat genotypes when water was most limiting growth than under well-watered conditions (Farquhar and Richards, 1984). Grain yield and aboveground biomass of winter wheats were positively correlated with Δ under non-limiting water conditions

at two locations in Australia (Condon et al., 1987). The relationships were similar at the two locations suggesting the expression of Δ may be under genetic control. In C_3 plants, the relationships between WUE, grain yield and Δ depend on the observation that ribulose biphosphate carboxylase-oxygenase (Rubisco) discriminates against the heavier stable carbon isotope, ^{13}C , in favor of ^{12}C during photosynthesis (O'Leary, 1988). There are also minor discriminations accompanying CO_2 diffusion into the leaf, but due primarily to Rubisco discrimination against ^{13}C , plant material becomes enriched in ^{12}C relative to the air. Farquhar et al. (1982), proposed Δ integrates stomatal and photosynthetic behavior over the development of the tissue analyzed because the level of ^{13}C discrimination by Rubisco decreases as the leaf internal CO_2 concentration (C_i) decreases, thereby lowering Δ . Evidence to support this theory has been documented in gas exchange studies (Brugnoli et al., 1988). Since WUE tends to increase with decreasing C_i , measurements of Δ provide an indirect method of assessing WUE. However, differences in mesophyll capacity for photosynthesis and stomatal conductance as well as phenological differences and the timing and duration of drought stress may complicate this interpretation (Farquhar and Richards, 1984; Kirchhoff et al., 1989).

Higher ABA accumulation may result in greater stomatal closure under drought stress, which would lower C_i and increase WUE (and by inference, lower the value of Δ). This would occur if ABA-mediated stomatal closure reduces transpiration rate proportionally more than the decrease in A. However, if ABA decreases mesophyll capacity for photosynthesis and stomatal closure is only a reflection of that inhibition, the result is no increase in WUE (that is, Δ may remain

unchanged in response to drought stress). Estimates of C_i and WUE from leaf gas exchange measurements will accurately describe processes occurring over a short time period. However, processes affected by drought stress as well as stomatal closure and inhibition of vegetative growth may be influenced by high levels of ABA (Quarrie, 1983). For example, ABA applied to well-watered spring wheat plants caused reductions in leaf growth, epidermal cell size, number of stomata per leaf and spikelets per spike (Quarrie and Jones, 1979). Therefore, the integrative capability of Δ may provide a more long-term indication of the effects of ABA accumulation on stomatal and photosynthetic processes than would leaf gas exchange measurements made at several growth stages. This research was conducted to determine if wheat lines selected divergently for dehydration-induced ABA accumulation differed in leaf water relations, WUE, Δ of kernels, aboveground biomass, and grain yield under drought stress.

MATERIALS AND METHODS

Experimental materials were 20 low-ABA and 20 high-ABA lines selected divergently from a cross between two, hexaploid spring wheat lines differing widely in ABA accumulation potential. The 40 selections were shown to have heritable differences in ABA accumulation potential based on a detached leaf test (Quarrie, 1981). Within each ABA selection class, two maturity groups (early and late) and two height groups (short and tall) were identified. We conducted a detached leaf test using six low-ABA and six high-ABA selections to verify the results of Quarrie (1985, personal communication). Methods used were as described by Quarrie (1981). The experiment was completely randomized with two replications. Bulk-leaf ABA content was determined using an enzyme-linked immunosorbant assay (ELISA) described below.

Field experiments were conducted over two years (1987 and 1988) at the Agronomy Research Station in Stillwater, OK. Soil type was Kirkland silt loam (a fine, mixed, thermic Udertic Paleustoll). Nitrogen was applied as diammonium phosphate (50 kg N ha⁻¹) prior to planting. During the growing season malathion (0,0-dimethyl dithiophosphate of diethyl mercaptosuccinate) and bayleton [1-(4-chlorophenoxy) - 3,3dimethyl-1-(1H-1,2,4-triazol-1-yl)-2-butanone] were tank mixed and applied as required to control aphids and powdery mildew, respectively.

Experiment One

Plant materials consisted of four, early maturing selections, two initially selected for low-ABA accumulation potential and two for high ABA accumulation potential. One tall-statured selection and one short-statured selection were included within each ABA class. Seedlings with two to three leaves were transplanted from a greenhouse to the field on

13 March 1987 and on 11 March 1988 (day 72 and 70, respectively of the year). The four ABA selections were arranged in a randomized complete block design with six replications for each of two water regimes. Ten plants per ABA selection were spaced 0.10 m apart within 0.9 m rows; spaced 0.3 m apart. The spring wheat cultivar, Ciano was used in a one-row border between rows within replications and between water regimes. The entire plot area was contained within a rain shelter described by Schonfeld et al., 1988. The well-watered regime was hand irrigated weekly with a sprinkler. The drought-stressed regime was initially irrigated to establish the transplants (usually 2 to 3 d), but water was withheld for the remainder of the growing season.

Pre-harvest data were collected during midday (1100 to 1400 h) on identical sampling dates for both well-watered and drought-stressed regimes. The first set of samples were taken at stem extension and the last set at physiological maturity. Leaves of a single, interior plant in each row were measured at 7-d intervals in 1987 and at 14-d intervals in 1988, totaling 5 sampling dates in 1987 and 4 sampling dates in 1988. Measurements of transpiration, net CO₂ assimilation rate (A), and stomatal conductance to water vapor (g_s) were made at a light intensity above 800 μmol m⁻² s⁻¹ on the youngest, fully expanded leaf blade on the main stem. In 1987 the Li-Cor 6000 photosynthesis system was used while in 1988 the model 6200 system was used (Li-Cor, Inc., Lincoln, NE). Leaves were placed into a 330 mL chamber, which was clamped shut when the microclimate was in equilibrium with ambient conditions. A typical measurement required 20 s during which time vapor pressure was fairly constant. Leaf internal CO₂ concentration (C_i) was calculated using the

starting ambient CO₂ concentration for each observation, typically 340 μmol mol⁻¹. Leaf water use efficiency (WUE) was calculated as the ratio of A to transpiration. Immediately following gas exchange measurements, the section of leaf inside the chamber was transferred to a 10x75 mm plastic test tube on dry ice. Total area (one surface) of the leaf was determined using a leaf area meter (LI-3000, Li-Cor, Inc., Lincoln, NE). A center section of the leaf (ca. 0.1 g fresh wt) was cut into square pieces (ca. 4.0 mm²), transferred to an opaque, plastic test tube and stored at -70°C for quantification of bulk-leaf ABA content. While sampling in the field, leaf cutter psychrometers (Merrill Specialty Inc., Logan, UT) were used to determine water potential (WP), and its components, solute potential (SP) and turgor potential (TP), from a fully expanded leaf of another tiller on the same plant used for gas exchange measurements. Leaf relative water content (RWC) was determined from the leaf sampled for WP. Methods for estimating WP, SP, TP, and RWC were as described by Schonfeld, et al. (1988).

An ELISA technique was used for quantification of physiologically active, unconjugated abscisic acid [2-cis(+)-ABA] in diluted leaf extracts (Idetek, Inc., 1986). Standard solutions were prepared by dissolving the racemic form of ABA (Cat. #A-1012, Sigma Chemicals, St. Louis, MO) in methanol and diluting with Tris-buffered saline (TBS: 25 mM Tris, 100 mM NaCl, 1 mM MgCl₂, pH 7.5). Leaf tissue contained in a plastic test tube was homogenized over ice using 1 ml 80% aqueous methanol (pH 7.0, containing 100 mg L⁻¹ BHT: butylated hydroxytoluene) and extracted with 4 ml 80% aqueous methanol in the dark at 4°C for 24 h. The homogenate was spun for 15 min at 9000xg to purify the extract. The supernatant (0.5 ml) was reduced to dryness under vacuum using a

centrifuge concentrator and resuspended with TBS to give an appropriate dilution of leaf extract. Sample concentration was determined by comparison to a standard curve developed from triplicate assays of known ABA concentration. Bulk-leaf ABA content was reported as ng ABA g⁻¹ fresh weight.

At maturity, four interior plants in each row were cut at the soil surface, bagged separately and dried at 50°C for 5 d. Total aboveground biomass, number of emerged spikes, number of fertile spikes, number of kernels spike⁻¹, dry wt kernel⁻¹ and grain yield plant⁻¹ were measured. Harvest index was expressed as the ratio of grain yield to aboveground biomass. Means of the four plants in each replication were used for analysis of variance. Anthesis dates were estimated as day 121, 1987 and day 117, 1988. Harvest date was day 167 in both 1987 and 1988. For carbon isotope determinations, kernels from the four plants were combined and dried 70°C for 72 h to a constant weight. Samples were ground to a powder using a Cyclone Mill (UDY Corp., Ft. Collins, CO) and placed into individual vials. A 0.05 g subsample was used to measure stable carbon isotopic composition by mass spectrometry under the direction of G.D. Farquhar, Research School of Biological Sciences, Australia National University, Canberra, Australia. Kernel ¹³C discrimination (Δ) was calculated assuming an isotopic composition of the ambient air relative to a Pee Dee Belemnite standard of -8.00 parts per thousand. (Farquhar and Richards, 1984).

Experiment Two

The complete set of 20 low-ABA and 20 high-ABA selections were transplanted on 14 March (day 73) 1988 inside the rain shelter.

Selections were randomized in three replications for each of two water regimes. Experimental design, water regimes and plant and row spacing were the same as in Exp. 1, except each row within a replication contained five plants per ABA selection and there were no alternating border rows of Ciano. Each water regime was fully bordered with three rows of Ciano. Between 1100 and 1400 h on day 124 and 139, water relations of well-watered and drought-stressed plants were determined from the same 12 ABA selections used in the detached leaf test, described above. A fully expanded leaf of a single, interior plant in each row was used for determination of WP, SP, TP and RWC as described above. At maturity, three interior plants per row were cut at the soil surface, bagged and dried. Total aboveground biomass, grain yield and harvest index were measured and expressed as the average of three plants. Kernels from the three plants in each replication were combined for determination of stable carbon isotopic composition and Δ as described above. The means of three replications were used in regression analyses of grain yield vs. Δ under well-watered or drought-stressed regimes. Anthesis dates were estimated as day 125 and 131, and harvest dates were day 166 and 169, for plants in drought-stressed and well-watered regimes, respectively.

RESULTS AND DISCUSSION

Experiment One

Average bulk-leaf ABA content was 347 and 849 ng g⁻¹ fresh wt in detached leaves of the two low-ABA and two high-ABA selections, respectively. This difference was highly significant (P<0.001) (data not presented). Nondehydrated leaves contained 40 ng g⁻¹ fresh wt, which is relatively close to field measurements (Table 1). Our results concerning detached leaves using ELISA were comparable to other measurements of bulk-leaf ABA content using physicochemical techniques (Quarrie and Lister, 1983; Quarrie, 1985, personal communication).

Attached leaves from drought-stressed plants in the field (Table 1) accumulated much less ABA than in the detached leaf test. Differences between selections within an ABA class were not significant (P>0.05) on any sampling day. Leaves of the low-ABA class had ABA contents that were equal to or at times higher than leaves of the high-ABA class. Thus, it was only in detached leaves from well-watered plants that high-ABA selections had higher bulk-leaf ABA contents than low-ABA selections. However, selection for low-ABA accumulation potential based on the detached leaf test resulted in wheat lines which generally yielded more grain, produced more dry matter and had longer development time under well-watered or drought-stressed regimes (Tables 5 and 7). Quarrie and Lister (1983) reported leaves of field-grown plants had a reduced potential to accumulate ABA in a detached leaf test; bulk-leaf ABA content was only 50% higher in high-ABA than low-ABA selections. Because ABA is released from mesophyll cells and redistributed in the leaf under water stress, bulk-leaf ABA content is determined by rates of synthesis and degradation (Cornish and Zeevaart, 1985; Raschke, 1987).

Greater export of ABA from leaves of high-ABA than low-ABA selections was suggested to explain the smaller difference between ABA classes observed in attached than detached leaves (Innes et al., 1984).

The decline in WP and RWC was greater under drought stress than under well-watered conditions, but the magnitude of the decreases were similar in 1987 and 1988 (Table 2). In both ABA classes, there was a greater reduction in WP in response to drought stress on day 130 in 1988 than on other days, and this was associated with a relatively large bulk-leaf ABA content. Cool, cloudy conditions on day 148 in 1987 caused a recovery in midday WP of drought-stressed plants. The low-ABA class maintained a higher RWC than the high-ABA class in 1988 on day 117 and 130 in the watered or stressed regime, but on other days, RWC did not differ significantly between ABA classes.

Reductions in A under drought stress were significant ($P < 0.01$) at grain filling. Because water regimes were not replicated, tests involving water regimes are approximate based on the reps within water regime effect as an error term. No significant differences ($P > 0.05$) between ABA classes in A were observed at any growth stage in either water regime (Table 3). In both years under drought stress, WUE of the low-ABA class was higher than the high-ABA class at heading. In 1988, this higher WUE was associated with lower stomatal conductance and C_i . The low-ABA class tended to have higher WUE than the high-ABA class and lower C_i was associated with lower stomatal conductance. Our results are contrast with Innes et al. (1984), who found low-ABA selections had consistently higher stomatal conductance and lower crop WUE (ca. 8%) than high-ABA selections; these traits were expressed most clearly under

water-limited conditions.

A greater decline in Δ with drought stress was observed in 1988 than in 1987 (Table 4). The gas exchange measurements also found a greater increase in WUE in response to drought stress in 1988 than 1987, which was most evident at grain filling (Table 3). Only in the drought-stressed regime in 1988 was Δ significantly ($P < 0.06$) lower in the low-ABA class than the high-ABA class, suggesting lower C_i (and by inference, higher WUE) of low-ABA selections. Although, differences between ABA classes in C_i and WUE were often significant (Table 3), this was apparently not associated with Δ in kernels. However, the significantly lower values of C_i in the stressed low-ABA selections in 1988 was consistent with the smaller value of Δ in those selections, and a lack of difference in Δ between selections in 1987 was consistent with the lack of variation in C_i in that year. Kirchhoff et al. (1989), reported WUE based on gas exchange measurements was similar for two cowpea (*Vigna unguiculata* L.) genotypes under two contrasting water regimes, but the genotypes differed significantly in Δ measured in leaves. They showed that the inherent difference between genotypes in isotopic discrimination associated with carboxylase enzymes could not explain genotypic differences in Δ . We were also unable to clearly relate gas exchange measurements concerning genotypic differences in WUE to Δ values.

Agronomic data for 1987 and 1988 were pooled over years since only the magnitude of the differences between ABA classes changed between years. Averaged over years, biomass, grain yield and spikes plant⁻¹ decreased while kernel weight and harvest index increased under drought stress. Differences between ABA classes were generally consistent

between water regimes ($P > 0.30$). Grain yield did not differ between ABA classes in either the watered or stressed regime, and yield reductions under stress were attributed to reductions in spikes plant⁻¹ (Table 5). Kernel weight and harvest index were significantly ($P < 0.01$) higher, while kernels spike⁻¹ and biomass were significantly lower in the high-ABA class than the low-ABA class. Thus, kernels spike⁻¹ appeared quite important to grain yield. Except for grain yield, the yield component analyses are comparable to those from the complete set of 40 ABA selections grown under a rain shelter at Cambridge, U.K. (Innes et al., 1984). In that study, surviving tillers of high-ABA selections under drought stress contained fewer but larger kernels than low-ABA selections. In contrast, they reported high-ABA selections had significantly higher (5%) grain yield, and slightly higher (ca. 1%) biomass and harvest index than low-ABA selections under full irrigation or late drought treatments.

Experiment Two

Drought stress resulted in lower WP, but this was not associated with a marked reduction in RWC (Table 6). On day 124, WP and TP were significantly higher in the low-ABA class than the high-ABA class in the drought-stressed regime.

Harvest index was not affected by drought stress, but it was significantly higher in the high-ABA class than the low-ABA class in the well-watered or drought-stressed regime (Table 7). Although biomass decreased more in the low-ABA class than the high-ABA class under drought stress, the low-ABA class maintained a significantly higher biomass and grain yield in the watered or stressed regime. This

suggests that even though A of single leaves was equal for both ABA classes (Table 3), A for whole plants (larger plants with more leaf area) may be greater in low-ABA selections than high-ABA selections. Stomatal conductance was usually lower in low-ABA selections than high-ABA selections, but this may not be a limitation to grain yield under drought stress providing photosynthetic rate or rate of leaf area development is higher. Jones (1977) reported stomatal conductance measured 7 to 14 d preceding anthesis was negatively correlated ($P < 0.05$) with grain yield of spring wheat in irrigated or drought-stressed regimes.

Low-ABA and high-ABA classes did not differ in average Δ under well-watered or drought-stressed regimes (Table 7). However, variation among selections within each ABA class for biomass, grain yield, harvest index and Δ was significant ($P < 0.001$). Within each low-ABA and high-ABA class, the water regime by ABA selection interactions were not significant for any trait ($P > 0.10$). Gas exchange measurements would indicate the low-ABA class should have a lower Δ than the high-ABA class because WUE was usually higher, but this was not the case. Thus, there was no evidence that wheat lines selected for high ABA accumulation had higher WUE under drought stress than those selected for low ABA accumulation, providing Δ and WUE are closely linked in accordance with the theory of Farquhar et al. (1982). In support of this theory, Δ in leaves of pot-grown wheat decreased the most in plants which produced the most dry matter per unit of water transpired (Farquhar and Richards, 1984). They also reported Δ was lower in kernels than in leaves, but Δ values of the two materials were highly correlated.

Positive correlations were measured between harvest index and Δ in both watered ($r=0.80^{**}$) and stressed regimes ($r=0.77^{**}$), but slopes of low-ABA and high-ABA selections were not significantly different within each water regime ($P>0.50$). Positive correlations were also measured among individual selections for the grain yield vs. Δ relationship in both the watered ($r=0.66^{**}$, sig at $P=0.01$) or stressed ($r=0.87^{**}$) regimes (Fig. 1). Large differences in grain yield plant^{-1} were associated with relatively small changes in Δ . A shift in the regression line toward lower Δ values in response to drought stress was associated with decreased grain yields. This suggests C_i (integrated over the grain filling period) decreased under drought stress, with a concomitant increase in WUE, that is, a greater degree of stomatal closure was exhibited by the droughted plants in order to maintain a yield level comparable to well-watered plants. This is supported from gas exchange measurements, which showed WUE was significantly ($P<0.01$) higher at grain filling in 1988 for plants under drought stress than under well-watered conditions (Table 3). Martin and Thorstenson (1988), found Δ and total dry matter of three Lycopersicon species grown outdoors in containers declined with decreasing soil moisture, and Δ in leaves was negatively correlated with season-long WUE (g dry matter produced per kg water applied) at high (100%) and intermediate (50%) soil moisture levels, but not at a low (25%) moisture level. They also reported WUE based on gas exchange measurements increased with decreasing soil moisture, but gas exchange measurements of WUE were not correlated with season-long WUE of the three Lycopersicon species.

Within each ABA class, there was no significant ($P>0.30$) difference

between slopes in watered or stressed regimes for the grain yield vs. Δ relationship. Only in the stressed regime did the slope and intercept of this relationship differ significantly ($P < 0.05$) between low-ABA and high-ABA selections (Fig. 2). Regression equations predicted a twofold greater increase in grain yield among the low-ABA selections than the high-ABA selections for an equivalent increase in Δ under drought stress. In wheat grown under non-limiting water conditions, Condon et al. (1987) reported positive correlations of aboveground biomass and grain yield with Δ , which they suggested indicates the importance of stomatal conductance in determining both biological yield and grain yield. Stomatal conductance and C_i were usually lower in the low-ABA than high-ABA selections, while differences between ABA classes in A were not significant in the watered or stressed regimes (Table 3). This suggests factors in addition to stomatal conductance were involved in the relationship between grain yield and Δ . At a yield level of 2.0 g plant^{-1} or above, low-ABA selections have lower Δ values (and by inference higher WUE and lower C_i) than high-ABA selections, while at grain yields below this the reverse situation is evident. Since grain yields were higher than 2.0 g plant^{-1} in Exp 1. there may be some association between leaf gas exchange measurements, which showed lower C_i among low-ABA selections under drought stress, and the grain yield vs. Δ relationship in Fig 2.

Grain yield of low-ABA selections could also be higher than high-ABA selections if leaf mesophyll capacity for photosynthesis is higher. For the same relative stomatal conductance, higher mesophyll capacity for photosynthesis would result in a lower C_i , and the steeper CO_2 gradient from ambient air to inside leaf would tend to raise A and WUE

(Farquhar and Sharkey, 1982). Condon et al. (1987) explained on a theoretical basis that such a situation would result in negative correlations between A and Δ , and could potentially lead to a negative correlation between biomass and Δ . A weak negative correlation was measured between biomass and Δ in the watered regime ($r=-0.39^*$, sig. at $P=0.05$), but was not significant ($r=-0.21$) in the stressed regime. This suggests selection for low Δ among these ABA selections may not necessarily lead to lower biomass, at least under well-watered conditions.

SUMMARY

In conclusion, based on measurements of leaf gas exchange and Δ in kernels, higher ABA accumulation potential was not associated with higher WUE. Greater yield stability in high-ABA selections than low-ABA selections was evident from a smaller decrease in average biomass and from a smaller decrease in grain yield per unit decrease in Δ under drought stress. Yield stability might be of adaptive value to wheat grown in a drought-prone environment, but low-ABA selections had higher aboveground biomass and grain yields than high-ABA selections, and this was associated with higher WUE. There was considerable variation among the genetically related ABA wheat selections in aboveground biomass, grain yield and Δ , but the ranking of ABA selections for these traits was consistent across water regimes. This suggests that the expression of Δ might be a useful tool in selecting for the optimum combination of high grain yield and high WUE among these low and high ABA accumulating wheat selections.

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Table 1. Bulk-leaf ABA content in attached leaves of two low-ABA and two high-ABA spring wheat selections under two contrasting water regimes in Exp. 1.

Water regime	ABA class	Day of the yr 1987			Day of the yr 1988	
		114	121	135	117	130
----- ng ABA g ⁻¹ fresh wt -----						
Watered	Low	27	52	54	64	64
	High	19	40	60	35	61
		NS	*	NS	*	NS
Stressed	Low	48	64	107	59	133
	High	37	57	85	45	125
		NS	NS	*	NS	NS

* Difference between ABA classes significant by the F test at P<0.05.
NS = not significant.

Table 2. Leaf water potential (WP) and relative water content (RWC) of two low-ABA and two high-ABA spring wheat selections under two contrasting water regimes in 1987 and 1988.

Day of the yr	ABA class	Well-watered		Drought-stressed	
		WP	RWC	WP	RWC
		MPa	%	MPa	%
1987					
114	Low	-0.86a*	89.3a	-0.96a	89.3a
	High	-0.87a	89.5a	-1.02a	91.2a
121	Low	-1.27a	90.0a	-1.58a	84.8a
	High	-1.30a	88.5a	-1.68a	84.6a
128	Low	-1.19a	93.6a	-1.48a	88.2a
	High	-1.29a	94.2a	-1.34a	85.9a
135	Low	-1.73a	85.9a	-2.27a	77.0a
	High	-1.82a	85.8a	-2.02a	77.6a
148	Low	-1.13a	85.0a	-1.70a	72.8a
	High	-1.16a	85.8a	-1.57a	80.6a
1988					
117	Low	-0.52a	92.1a	-0.75a	87.4a [†]
	High	-0.45a	87.3b	-0.77a	84.5b
130	Low	-0.83a	91.8a	-1.69a	79.2a
	High	-0.85a	87.7b	-1.87a	73.8b
145	Low	-1.11a	85.6a	-1.72a [†]	78.8a
	High	-1.05a	84.5a	-1.66a	77.4a

* Within a sampling day, column means followed by the same letter are not significantly different at P=0.05.

[†] Difference between ABA selections within an ABA class are significant at P<0.05.

Table 3. Gas exchange characteristics of two low-ABA and two high-ABA spring wheat selections at three growth stages in 1987 and 1988 under two contrasting water regimes.

Water regime	ABA class	A [§]		g _s		C _i		WUE		
		1987	1988	1987	1988	1987	1988	1987	1988	
		(μmol m ⁻² s ⁻¹)		(mol m ⁻² s ⁻¹)		(μmol mol ⁻¹)		(μmol mmol ⁻¹)		
Heading (Day of the year 114, 1987 and 104, 1988)										
Watered	Low	15.3a [†]	19.2a*	0.31a	0.40a	208a	233a	2.37a	2.69a	
	High	18.0a	18.9a [†]	0.41a	0.42a [†]	220a	246a [†]	2.24a	2.29a [†]	
Stressed	Low	15.9a	20.3a [†]	0.25a	0.33b [†]	190a	213b [†]	2.63a	2.86a [†]	
	High	15.7a	19.0a	0.29a	0.40a	210a	242a	2.32b	2.21b	
Anthesis (Day of the year 121, 1987 and 117, 1988)										
Watered	Low	12.7a	13.6a	0.23b [†]	0.24a	194a	223a [†]	2.27a [†]	2.28a	
	High	14.8a	12.6a	0.32a	0.25a	214a	238a	2.07b	1.85b	
Stressed	Low	14.2a	13.7a	0.24a	0.18a	200a	194b	2.29a	2.58a	
	High	14.5a	13.5a	0.27a	0.22a	194a	222a	2.20a	2.00b	
Grain filling (Day of the year 135, 1987 and 130, 1988)										
Watered	Low	11.3a	15.5a	0.25a	0.35b	219a	226b	1.58a	1.18a	
	High	11.9a	16.7a	0.26a	0.49a	221a	243a	1.55a	1.05b	
Stressed	Low	7.7a	8.9a	0.16a	0.13a	221a	188a	1.30a	1.48a	
	High	8.3a	9.7a	0.16a	0.15a	206a	196a	1.28a	1.39a	

* Within a water regime, column means followed by the same letter are not significantly different at P=0.05.

[†] Except for A at heading in 1987, the water regime x ABA class interactions are not significant at P>0.05.

[‡] Difference between ABA selections within an ABA class is significant at P<0.05.

[§] A, CO₂ assimilation rate; g_s, stomatal conductance to H₂O; C_i, internal CO₂ concentration; WUE, leaf water use efficiency expressed as the ratio of A to transpiration.

Table 4. Kernel carbon isotope discrimination of two low-ABA and two high-ABA spring wheat selections in 1987 and 1988 under two contrasting water regimes.

Water regime	ABA class	Carbon isotope discrimination	
		1987	1988
----- $\Delta \times 10^3$ -----			
Watered	Low	17.77	17.33
	High	17.64	17.19
		NS	NS
Stressed	Low	17.28	15.98
	High	17.18	16.47
		NS	†

† Difference between ABA classes significant by the F test at $P < 0.10$. NS = not significant.

Table 5. Aboveground biomass, grain yield, yield components and harvest index of two low-ABA and two high-ABA spring wheat selections under two contrasting water regimes averaged over two years.

Water regime	ABA class	Biomass	Grain yield	Spikes /plant	Kernels /spike	Kernel weight	Harvest index
		-- g plant ⁻¹ --		----- no. -----		mg	
Watered	Low	13.02	3.58	5.8	31.1	20.2	0.28
	High	9.98 **	3.28 NS	5.2 *	26.3 **	23.6 **	0.33 **
Stressed	Low	7.61	2.58	3.7	32.1	21.1	0.33
	High	6.02 **	2.38 NS	3.5 NS	25.3 **	26.8 **	0.40 **

*,** Difference between ABA classes significant by the F test at P<0.05 and P<0.01, respectively. NS = not significant.

Table 6. Leaf water potential (WP) and relative water content (RWC) of 20 low-ABA and 20 high-ABA spring wheat selections under two contrasting water regimes.

Day of the yr	ABA class	Well-watered		Drought-stressed	
		WP	RWC	WP	RWC
		MPa	%	MPa	%
124	Low	-0.66a*	nd	-0.83a	nd
	High	-0.74a	nd	-1.06b	nd
139	Low	-1.28a	82.9a [†]	-1.76a	82.1a
	High	-1.12a	82.2a	-1.81a	79.6a

* Within a sampling day, column means followed by the same letter are not significantly different at P=0.05. nd= no data.

[†] Differences among ABA selections within an ABA class are significant at P<0.05.

Table 7. Aboveground biomass, grain yield, harvest index, and kernel carbon isotope discrimination of 20 low-ABA and 20 high-ABA spring wheat selections under two contrasting water regimes.

Water regime	ABA class	Biomass	Grain yield	Harvest index	Carbon isotope discrimination
		--- g plant ⁻¹ --			$\Delta \times 10^3$
Watered	Low	13.76 [†]	2.66	0.20	17.21
	High	8.54 **	2.21 **	0.28 **	17.21 NS
Stressed	Low	10.30	2.01	0.20	15.99
	High	7.01 **	1.74 †	0.26 **	16.04 NS

†,** Difference between ABA classes significant by the F test at P<0.10 and P<0.01, respectively. NS = not significant.

‡ Water regime x ABA class interaction significant at P<0.01.

FIGURE LEGENDS

Fig. 1. Relationship between grain yield and kernel carbon isotope discrimination for 20 low-ABA and 20 high-ABA spring wheat selections. Slopes and intercepts for the well-watered regime ($r=0.66^{**}$, $P=0.01$) and drought-stressed regime ($r=0.88^{**}$) are not significantly different at $P>0.20$.

Fig. 2. Relationship between grain yield and kernel carbon isotope discrimination for 20 low-ABA and 20 high-ABA spring wheat selections under a drought-stressed regime. Slopes and intercepts for low-ABA selections ($r=0.89^{**}$, $P=0.01$) and high-ABA selections ($r=0.62^{**}$) are significantly different at $P<0.05$.

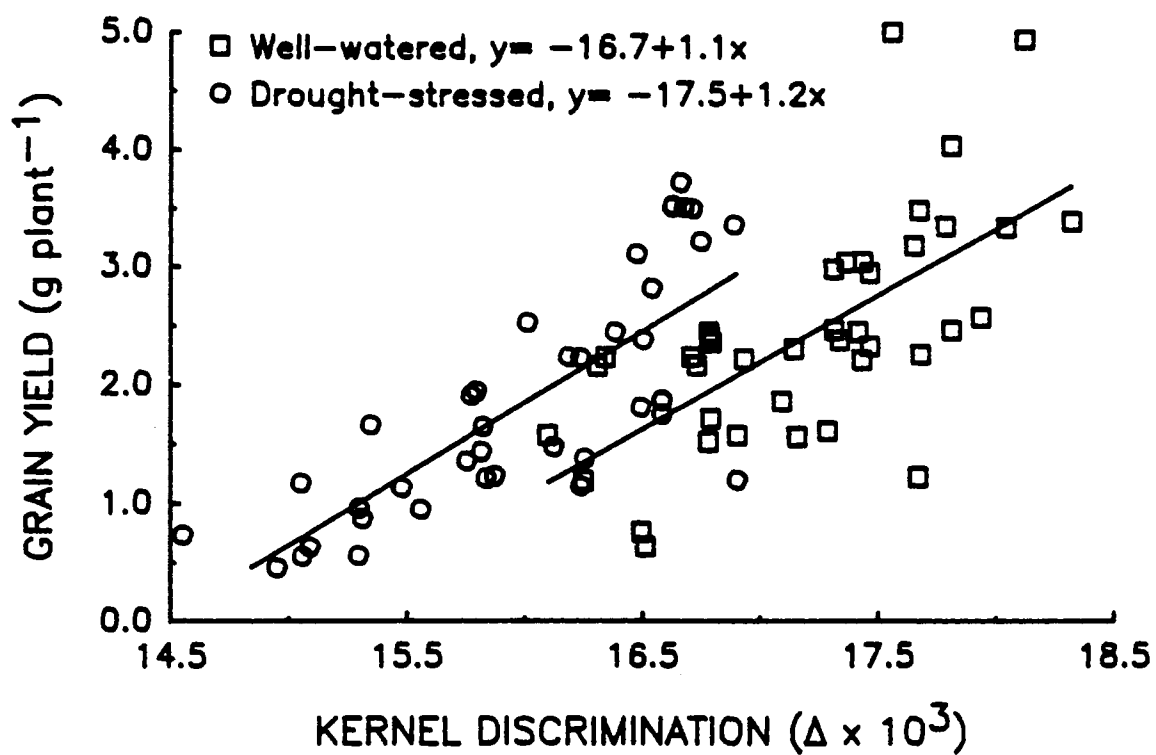


Figure 1.

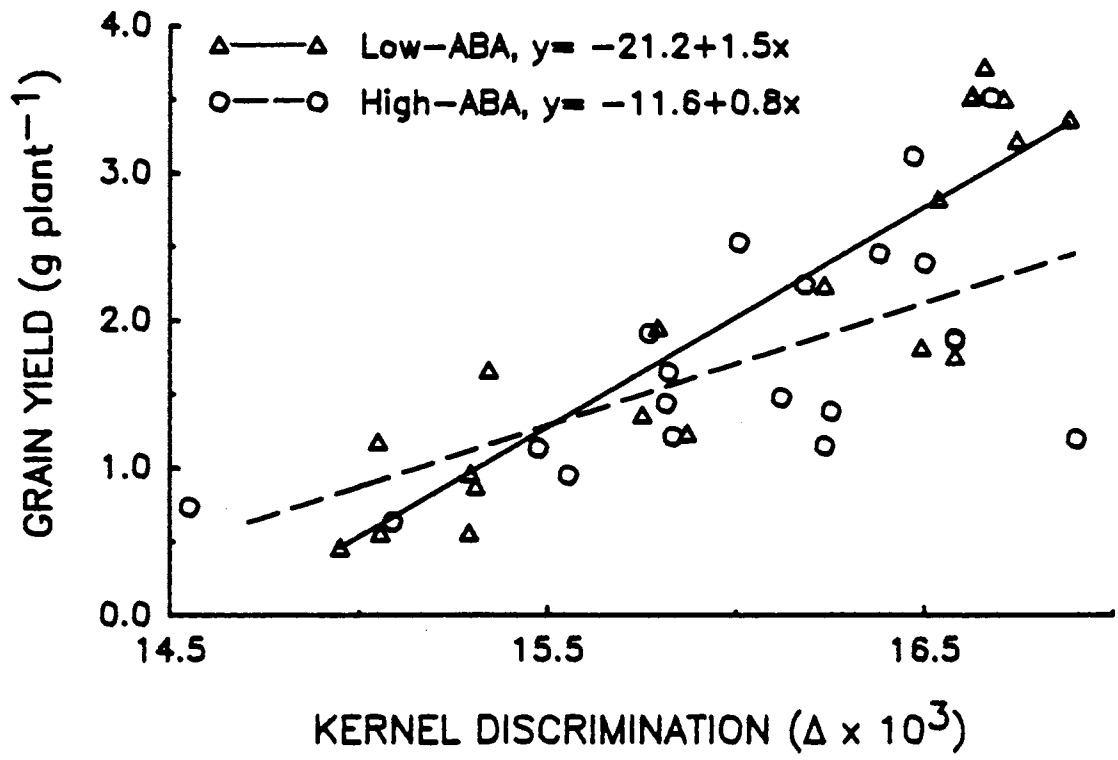


Figure 2.

APPENDIX

Table 1. Bulk-leaf ABA content in detached and attached leaves of six low-ABA and six high-ABA spring wheat selections.

ABA class	I.D. no.	Bulk-leaf ABA content ¹	
		Detached	Attached
-- ng g ⁻¹ fresh wt --			
Low	606	279 [#]	112 ^t
	626	311	101
	635	346	118
	610	348	129
	617	357	118
	629	621	99
High	637	499	123
	622	724	120
	613	815	281
	605	827	166
	625	884	102
	636	871	186
	LSD(0.05)	547	84
	Low-ABA class mean	377	113
	High-ABA class mean	770	163
	LSD(0.05)	224 **	34 **

** Indicates significant difference by the F test at P<0.01.

Differences among selections within an ABA class are not significant at P>0.15.

^t Differences among selections within an ABA class are significant at P<0.05.

¹ Detached leaves, partially dehydrated to 90% initial fresh wt and incubated in the dark at 20°C for 6 h; attached leaves, same leaves as those measured in Appendix Table 2.

Table 2. Gas exchange characteristics, relative water content (RWC), water potential and turgor potential measured in leaves of six low-ABA and six high-ABA spring wheat selections under well-watered and water-stressed conditions.

Treatment	ABA class	A ¹	g _{sc}	C _i	WUE	RWC	Water potential	Turgor potential
		μmol m ⁻² s ⁻¹	mol m ⁻² s ⁻¹	μL L ⁻¹		%	----- MPa -----	
Watered	Low	26.6	0.211	199	4.37	95.1	-0.71	1.15
	High	28.0	0.245	212	4.00	95.1	-0.92	1.04
		NS	**	***	***	NS	*	NS
Stressed	Low	15.6	0.098	162	5.55 ^t	89.2	-1.17	0.74 ^t
	High	20.2	0.135	171	5.28	89.3	-1.37	0.67
		***	***	***	***	NS	**	NS

*,**,*** Difference between ABA classes significant by the F test at P<0.05, P<0.01 and P<0.001, respectively. NS = not significant.

^t Differences among selections within an ABA class are significant at P<0.05.

¹ Measured at an ambient CO₂ concentration of 340 μL L⁻¹; A, leaf CO₂ assimilation; g_{sc}, stomatal conductance to CO₂; C_i, internal CO₂ concentration; WUE, water use efficiency, mmol CO₂ mol H₂O⁻¹.

Table 3. Leaf water potential, water potential components (solute and turgor potential) and relative water content of low-ABA and high-ABA wheat selections in a well-watered regime in 1987 and 1988.

Day of year	ABA class	WP	SP	TP	RWC
		----- MPa -----			%
Exp.1, 1987					
114	Low	-0.86a*	-1.73a ^t	0.86a ^t	89.3a
	High	-0.87a	-1.80a	0.93a	89.5a
121	Low	-1.27a ^t	-2.00a	0.76a ^t	90.0a
	High	-1.30a	-1.90a	0.59a	88.5a
128	Low	-1.19a	-2.29a	1.12a	93.6a
	High	-1.29a	-2.00a	0.72b	94.2a
135	Low	-1.73a ^t	-2.45a	0.73a	85.9a
	High	-1.82a	-2.42a	0.60a	85.8a
148	Low	-1.13a ^t	-2.27a	1.14a	85.0a
	High	-1.16a	-2.23a	1.07a	85.8a
Exp. 1, 1988					
117	Low	-0.52a	-1.76a ^t	1.24a	92.1a
	High	-0.45a	-1.60a	1.12a	87.3b
130	Low	-0.83a	-1.83a	1.00a	91.8a
	High	-0.85a	-1.60a	0.75b	87.7b
145	Low	-1.11a	-2.31a ^t	1.19a	85.6a
	High	-1.05a	-2.10a	1.05a	84.5a
Exp. 2, 1988					
124	Low	-0.66a	-2.04a	1.37a	nd
	High	-0.74a	-2.02a	1.29a	nd
138	Low	-1.28a	-2.12a	0.89a	82.9a [#]
	High	-1.12a	-2.17a	0.99a	82.2a

* Within a sampling day, column means followed by the same letter are not significantly different at P=0.05.

^{#,t} Difference(s) between (among, in Experiment Two) ABA selections within an ABA class are significant at P<0.05 and P<0.10, respectively.

¹ WP, water potential; SP, solute potential; TP, turgor potential; RWC, relative water content.

Table 4. Leaf water potential, water potential components (solute and turgor potential) and relative water content of low-ABA and high-ABA wheat selections in a drought-stressed regime in 1987 and 1988.

Day of year	ABA class	WP	SP	TP	RWC
		----- MPa -----			%
Exp. 1, 1987					
114	Low	-0.96a	-1.86a	0.89a	89.3a
	High	-1.02a	-1.75a	0.74a	91.2a
121	Low	-1.58a	-2.26a	0.84a	84.8a
	High	-1.68a	-2.15a	0.48a	84.6a
128	Low	-1.48a	-2.16a	0.68a	88.2a
	High	-1.34a	-2.02a	0.68a	85.9a
135	Low	-2.27a	-2.49a	0.23a	77.0a
	High	-2.02a	-2.34a	0.34a	77.6a
148	Low	-1.70a	-2.59a	0.89a	72.8a
	High	-1.57a	-2.48a	0.91a	80.6a
Exp. 1, 1988					
117	Low	-0.75a ^t	-1.95a	1.20a	87.4a [#]
	High	-0.77a	-1.92a	1.15a	84.5b
130	Low	-1.69a	-2.18a	0.49a	79.2a
	High	-1.87a	-2.27a	0.40a	73.8b
145	Low	-1.72a [#]	-2.78b	1.07a [#]	78.8a
	High	-1.66a	-2.46a	0.80a	77.4a
Exp. 2, 1988					
124	Low	-0.83a	-2.09a	1.26a [#]	nd
	High	-1.06b	-2.10	1.03b	nd
138	Low	-1.76a	-2.45a	0.68a	82.1a
	High	-1.81a	-2.50a	0.69a	79.6a

- * Within a sampling day, column means followed by the same letter are not significantly different at P=0.05.
- ^{#,t} Difference(s) between (among, in Experiment Two) ABA selections within an ABA class are significant at P<0.05 and P<0.10, respectively.
- ¹ WP, water potential; SP, solute potential; TP, turgor potential; RWC, relative water content.

Table 5. Aboveground biomass, grain yield, yield components, harvest index and carbon isotope discrimination of two low-ABA and two high-ABA spring wheat selections and the spring wheat cultivar, Ciano, under two contrasting water regimes averaged over 1987 and 1988.¹

Water regime	ABA class	Biomass	Grain yield	Total spikes	Fertile spikes	Kernels/spike	Kernel weight	Harvest index	carbon disc.
		--- g plant ⁻¹ ---		-- no plant ⁻¹ --		no.	mg		△ x10 ³
Watered	Low	13.02	3.58	6.3	5.9	31.1	20.2	0.28	17.55
	High	9.98	3.28	5.4	5.2	26.3	23.6	0.33	17.42
	Low vs. High	**	NS	**	*	**	**	**	NS
	Ciano	11.84	3.83	5.0	4.9	37.3	21.4	0.33	nd
Stressed	Low	7.61	2.58	4.1	3.7	32.0	21.1	0.33	16.63
	High	6.02	2.38	3.6	3.5	25.3	26.8	0.40	16.82
	Low vs. High	**	NS	**	NS	**	**	**	NS
	Ciano	7.91	2.98	3.8	3.7	37.0	20.8	0.37	nd
Water regime		**	t	t	t	NS	*	*	**

t,*,** Difference between ABA classes significant by the F test at P<0.10, P<0.05 and P<0.01, respectively. NS = not significant. The check variety (Ciano) is presented for comparison (nd= no data).

¹ The year x ABA class interaction was significant at P<0.01 for harvest index, kernel weight and carbon isotope discrimination under stressed conditions.

Table 6. Aboveground biomass, grain yield, harvest index, and kernel carbon isotope discrimination of 20 low-ABA accumulating wheat selections under two contrasting water regimes.¹

Maturity or ht. class	I.D. number	Well-watered				Drought-stressed			
		DM ²	YLD	HI	KD	DM	YLD	HI	KD
		g plant ⁻¹		Δ x10 ³		g plant ⁻¹		Δ x10 ³	
Short	606	12.84	4.03	0.32	17.81	10.70	3.37	0.31	16.89
"	607	14.41	5.00	0.35	17.56	10.78	3.72	0.34	16.66
"	608	17.77	2.44	0.14	16.78	13.48	1.23	0.09	15.87
"	609	12.18	3.04	0.26	17.44	12.58	3.51	0.28	16.63
"	610	11.10	3.39	0.30	18.32	9.05	3.22	0.35	16.75
Tall	631	13.97	4.94	0.36	18.12	9.76	3.53	0.36	16.63
"	632	13.08	0.76	0.06	16.49	15.09	0.55	0.04	15.06
"	633	18.84	2.36	0.13	16.79	13.34	1.95	0.14	15.79
"	634	14.98	2.24	0.15	16.34	10.75	1.17	0.12	15.05
"	635	12.56	2.44	0.21	17.42	8.21	1.75	0.22	16.58
Early	626	8.81	2.57	0.29	17.94	6.80	1.82	0.26	16.49
"	627	19.40	1.57	0.08	16.10	12.54	1.66	0.13	15.34
"	628	16.11	2.16	0.13	16.31	12.42	0.96	0.08	15.29
"	629	12.39	3.48	0.28	17.68	10.61	3.50	0.32	16.71
"	630	9.93	2.46	0.25	17.31	9.72	2.23	0.21	16.23
Late	616	10.93	0.63	0.06	16.51	7.19	0.45	0.06	14.95
"	617	11.34	3.33	0.30	18.04	8.82	2.82	0.32	16.54
"	618	15.37	1.52	0.10	16.78	10.32	0.87	0.08	15.31
"	619	14.60	1.71	0.12	16.79	8.02	0.55	0.07	15.30
"	620	14.56	3.18	0.22	17.65	5.46	1.35	0.24	15.75
LSD (0.05)		4.28	1.27	0.08	0.61	4.19	1.40	0.08	0.67

¹ Values represent the average of three blocks with three plants sampled per block.

² DM=above-ground dry matter per plant, YLD=grain yield per plant, HI=harvest index, KD=kernel carbon isotope discrimination.

Table 7. Aboveground biomass, grain yield, harvest index, and kernel carbon isotope discrimination of 20 high-ABA accumulating wheat selections under two contrasting water regimes.¹

Maturity or ht. class	I.D. number	Well-watered				Drought-stressed			
		DM ²	YLD	HI	KD	DM	YLD	HI	KD
		g plant ⁻¹		$\Delta \times 10^3$		g plant ⁻¹		$\Delta \times 10^3$	
Short	601	8.24	2.21	0.26	16.93	5.27	1.47	0.28	16.12
"	602	9.69	2.98	0.31	17.31	3.43	1.15	0.33	16.23
"	603	6.87	2.30	0.34	17.14	3.63	0.95	0.26	15.55
"	604	5.87	1.85	0.32	17.09	2.88	1.20	0.42	16.90
"	605	8.33	3.34	0.39	17.79	6.83	2.45	0.36	16.38
Tall	636	4.68	1.60	0.34	17.28	5.75	1.87	0.31	16.58
"	637	6.33	1.57	0.24	16.90	5.51	1.21	0.23	15.83
"	638	8.12	1.55	0.19	17.15	5.97	0.63	0.10	15.09
"	639	9.87	2.24	0.23	16.71	8.71	1.65	0.20	15.82
"	640	9.85	2.40	0.24	16.78	10.23	1.43	0.19	15.81
Early	621	7.25	2.46	0.34	17.81	9.70	3.11	0.31	16.47
"	622	12.56	3.04	0.26	17.36	7.00	2.24	0.31	16.18
"	623	8.60	2.26	0.26	17.68	11.33	3.51	0.31	16.67
"	624	3.79	1.22	0.32	17.67	7.38	2.39	0.32	16.50
"	625	6.82	2.21	0.32	17.43	5.38	1.88	0.34	16.58
Late	611	9.40	2.94	0.31	17.46	8.48	2.53	0.29	16.01
"	612	12.99	1.19	0.09	16.25	11.17	0.73	0.08	14.55
"	613	8.49	2.32	0.27	17.46	6.22	1.91	0.31	15.77
"	614	8.34	2.37	0.29	17.34	5.46	1.38	0.25	16.25
"	615	14.75	2.16	0.15	16.73	9.95	1.13	0.09	15.47
LSD (0.05)		3.66	1.32 ^t	0.09	0.74	5.22	1.28	0.11	0.70

¹ Values represent the average of three blocks with three plants sampled per block.

² DM=above-ground dry matter per plant, YLD=grain yield per plant, HI=harvest index, KD=kernel carbon isotope discrimination.

^t Differences among selections in YLD under well-watered conditions are not significant at P<0.05 by the F test.

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