UTILIZATION OF PHYSIOLOGICAL TRAITS AS SELECTION CRITERIA FOR DROUGHT RESISTANCE OF WINTER WHEAT

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RESISTANCE OF WINTER WHEAT

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NOMENCLATURE

ABA	Abscisic acid
CV	Coefficient of variation
EIA	Enzyme immunoassay
F3, F4	Third and fourth filial generations
MeOH	Methanol
RWC	Relative water content
TBS	Tris-buffered saline

CHAPTER I

INTRODUCTION

Chapters II and III of this thesis are separate and complete manuscripts to be submitted to _Crop Science_ and _Plant Physiology_, respectively.

CHAPTER II

Relationship of Relative Water Content at Successive Reproductive Growth Stages to Yield Potential of Winter Wheat

ABSTRACT

Water is one of the most limiting factors to winter wheat (Triticum aestivum L.) production in the southern Great Plains. The lack of reliable screening criteria has precluded direct selection for drought tolerance of wheat. Leaf relative water content (RWC) has been shown to have high heritability when measured under field drought conditions. Its adoption as a screening tool for yield improvement under drought stress, however, requires further genetic investigation of the relationship between grain yield and RWC. Plants representing high and low yield potential under drought stress and a random group of plants were selected from an F2 population derived from the cross, TAM W-101/ Sturdy. Two sets of entries, each set comprised of two parents and 24 F2-derived lines, were evaluated in the field under a rainshelter to determine differences in yield potential and leaf RWC during reproductive development in 1986 and 1987. One set of entries did not receive any water after the jointing stage, whereas the other set was grown under well-watered conditions. A positive relationship was observed between grain yield and RWC measured during anthesis or mid grain-fill, as the high-yield selections maintained a significantly higher RWC than low-yield selections. The same association between grain yield and RWC was observed among random selections segregating for both traits. Path-coefficient analysis of grain yield, yield components and RWC indicated that high RWC under drought reduced the loss of spike-bearing tillers at early reproductive stages and led to greater grain filling potential during late reproductive stages. Based on these results, RWC may serve as a reliable physiological indicator of wheat genotypes possessing high yield potential under drought stress.

Additional index words: *Triticum aestivum L.*, Relative water content, grain yield, yield components, path coefficient analysis.

Wheat production in the southern Great Plains is frequently subject to drought stress, often leading to substantial grain yield reductions. Genetic variation in productivity under drought stress exists among wheat cultivars (Blum, 1985). The development of cultivars with increased drought resistance is the most effective way to improve and stabilize wheat production in semi-arid areas (Jones and Qualset, 1984). However, genetic improvement has had the least impact on recent wheat yield increases in areas where soil moisture was limiting (Feyerherm et al., 1984). Many physiological and morphological traits are interactively involved with drought resistance mechanisms, and, therefore, drought resistance per se has been difficult to quantify in a wheat breeding program (Simpson, 1981). The lack of reliable selection criteria has limited drought resistance breeding to selection for grain yield under natural field conditions and selection for early maturity. Future genetic improvement of drought resistance in wheat will require an evaluation of morpho-physiological attributes which may serve as a basis for developing a screening procedure (Hanson and Nelsen, 1980).

Recently, leaf relative water content (RWC) was suggested as a reliable parameter of plant water status (Sinclair and Ludlow, 1985). Schonfeld et al. (1988) showed significant genetic variation and high heritability for this trait in winter wheat populations grown under drought conditions. Further genetic investigation is needed to determine the relationship between RWC and grain yield before recommending RWC as a possible selection criterion for drought resistance. The objective of the present study was to examine the genetic association between RWC and grain yield under nonstress and drought stress conditions during reproductive stages in a winter wheat population derived from a cross between cultivars differing in drought resistance.

MATERIALS AND METHODS

Development of Experimental Materials

Experimental materials were derived from an F2 population of hard red winter wheat (TAM W-101/Sturdy) utilized in a previous study (Schonfeld et al., 1988). TAM W-101 was considered more drought resistant than Sturdy under field conditions (O. Merkle, K. Porter, 1983, personal communication). In 1985, 96 F2 plants were assigned to four field blocks, each containing 24 plants. Grain yield was measured on 16 plants from each block which received drought stress during reproductive development. The two highest yielding and two lowest yielding plants were selected, along with two random plants with no yield record. No further selection was made on F3 plants. An equal number of seed was composited from each F3 plant from a given line to form F4 lines.

Field Design

The experiment was conducted in 1986 (F3) and 1987 (F4) under a rainshelter at the Agronomy Research Station in Stillwater, OK. Soil type under the shelter was a Kirkland silt loam (fine, mixed, thermic Udertic Paleustolls). Details of shelter construction and environmental conditions inside the shelter were presented in a previous publication (Schonfeld et al., 1988).

Two sets each of the 24 lines (eight high, eight low, and eight random selections per generation) and the two parent cultivars were planted in single-row plots with a common border (TAM 107) between plots. Four plants were spaced 0.15m apart within 0.45m rows and rows were spaced 0.23m apart. One set of entries did not receive any rain after jointing when the shelter was covered with polyethylene film on 3 Mar. 1986 and on 5 Mar. 1987. The other set was grown inside the shelter with supplemental water applied regularly to prevent any stress. The experimental design was a randomized complete block with three replications for each of the two water stress levels, stressed and nonstressed.

Experimental and Statistical Procedures

Data were collected in both years for the same traits on an individual plant basis. RWC was measured on the youngest fully expanded leaf during three reproductive stages (pre-anthesis, anthesis, and mid-grain fill). Sampling days corresponding to these stages were 31 Mar. to 2 Apr., 14 to 16 Apr., and 28 to 30 Apr. in 1986, and 7 to 9 Apr., 27 to 29 Apr., and 11 to 13 May in 1987. Leaves were sampled at mid-day, and immediately wrapped in aluminum foil sealed in air-tight bags. Fresh weights were measured within three hours after harvest in the same order in which leaf samples were collected. The leaves were then soaked in distilled water for 16 to 18 h and turgid weights were measured from blotted-dry leaves. After oven-drying for ca. 72 h at 70°C, dry weights were measured. From these three weight measurements, RWC was determined using equation:

$$\text{RWC (\%)} = \frac{\text{Fresh weight - Dry weight}}{\text{Turgid weight - Dry weight}} \times 100$$

Head emergence dates were also recorded for each plant. Total kernel weight (grain yield), spike number, kernel number, and biomass (total plant weight above ground level) were measured at harvest. From these data, kernel number per spike, kernel weight and harvest index were calculated as total kernel number divided by spike number, total kernel weight divided by kernel number, and total kernel weight divided by biomass, respectively.

All data were averaged over four plants within a plot prior to analysis. Combined analyses of variance were performed over stress levels and years (generations) for RWC, grain yield, yield components, biomass, and harvest index. The entry source was partitioned into sources due to parents, selections, and their contrast. Variation among selections were further partitioned into sources due to among and within selection groups. Because stress levels were not replicated in each year, statistical tests involving this variance source were approximate based on the reps(stress levels) source as an error term.

Phenotypic and genetic correlations were estimated between grain yield and RWC at anthesis or mid grain-fill among random lines grown under drought stress conditions. Because random lines X year interactions were significant for grain yield, correlation analyses were performed for each year. Phenotypic correlations were calculated as the sample linear correlation (Steel and Torrie, 1980) using entry means over replications, whereas genetic correlations were calculated from components of genetic variances and covariances obtained from multivariate analysis of variance (MANOVA statement of ANOVA procedure in SAS (SAS Institute Inc., 1985)).

Phenotypic path correlation analysis (Li, 1972) was employed using data from random lines grown under drought stress to determine the cause-effect relationships between yield components and yield, between

RWC at three reproductive stages and grain yield, and between RWC and each yield component (Fig. 1). Entry means were used for all analyses but data were logarithmically transformed for total yield and yield components to relate grain yield to an additive set of yield component variables. Path coefficients for direct effects were estimated as partial regression coefficients after standardizing both causal and resultant variables. Because of standardization, path coefficients may not represent actual influences if causal variables have different magnitudes of variability. Thus, fixed components of variance for random lines were estimated for comparison among causal variables.

RESULTS

Leaf relative water content (RWC) decreased as plants matured. The degree of reduction was greater in drought-stressed plots than in well-watered plots (Fig. 2). Visual signs of drought stress were observed only in the stress plots and included mid-day leaf rolling beginning at anthesis and early senescence of lower leaves during the mid grain-fill stage. Plots in 1987 appeared to show more vegetative growth and developed slower than those in 1986. Average spike emergence dates differed by 11 days between years. However, drought development in 1987 was more intense and rapid than the previous year, especially as the plants approached maturity.

At the pre-anthesis stage (approximately 10 days prior to spike emergence), RWC of plants in drought-stressed plots equaled that of well-watered plants in both years, even though water was withheld from stress plots for 28 to 35 days (Fig. 2). All variance sources except among low-yield selections were nonsignificant indicating that development of drought conditions was not sufficient to cause detectable variation in plant water deficits (Tables 1 and 2). Prolonged stress during reproductive development resulted in significant differences in RWC among stress levels and among entries within stress levels at anthesis and mid grain-fill. Significant variability was observed among the eight random lines for RWC at the anthesis and mid grain-fill sampling (Table 2). Although patterns of plant growth and drought development differed markedly between years, no interactions at the anthesis sampling were significant. Entry means were thus computed over years and stress levels for this sampling. At the mid grain-fill stage, both the entry X year and entry X stress level interactions were declared significant. Partitioning these variances resulted in significant interactions between years and selection groups, but nonsignificant interactions between stress levels and selection groups or parents (Table 2). Therefore, entry means at mid grain-fill were computed over stress levels (as were means for other growth stages), but for each year. Coefficients of variation (CV) were much smaller (<6.5%) for all RWC measurements than the CV for grain yield (Table 1).

Grain yield responses differed significantly between stress levels, years, and among entries (Table 1). Average yield over two years under drought stress was 72% of that under well-watered conditions. In addition to RWC variability noted before, significant yield variability was also observed among the eight random lines in both years (Table 2). Entry X year interactions were significant, but partitioning of this interaction did not reveal significant interactions of years with selection groups or with parents. Thus, grain yield responses were averaged over years for comparison among selection groups and parents. Somewhat surprisingly, entry X stress level and entry X year X stress level interactions were not significant. Similar results were obtained from analyses of variance for yield components, biomass, and harvest index (Table 3). Significant differences occurred between stress levels (with exception of kernels per spike), between years, and among entries, but among all interactions, only entry X year interactions were significant for spike number per plant, kernel number per spike, and biomass. Partitioning of these interactions showed that the magnitude of selection group differences varied between years for these two yield components, but not for biomass. Coefficients of variation for these traits were larger than those for RWC (Table 1 and 3).

TAM W-101 had a significantly higher RWC than Sturdy at anthesis and mid grain-fill in 1986 but not in 1987 (Table 4). The high-yield selection group also had significantly higher RWC than the low-yield selection group for the same growth stages and years. TAM W-101 also had a significantly higher biomass, spike number per plant, and kernel weight than Sturdy, but the higher grain yield of TAM W-101 was not statistically significant. (Fig. 3a). Biomass, harvest index, grain yield, and all yield components differed significantly among selection groups. Compared to the low-yield selection group, a high-yield selection group produced more biomass, including a higher grain yield ($p<0.10$), but its harvest index score was lower (Fig. 3b). In 1986, high-yield selections produced more spikes per plant but fewer kernels per spike than low-yield selections. Combining these yield components, the high-yield selection group produced more kernels per plant in 1986. In 1987, no differences were observed between selection groups for these yield components. Kernel weights, however, differed consistently over years and stress levels, and contributed to the yield advantage of high-yield selections.

Positive phenotypic and genetic correlations between grain yield and RWC measured at either anthesis or mid grain-fill were estimated for F3 random lines (Fig. 4a). As drought stress intensified, RWC differences among random lines became greater, and estimates of both correlations were larger. Among F4 random lines, similar results were observed only at the mid grain-fill stage (Fig. 4b). At anthesis, variability in RWC was not sufficiently large to determine any significant relationship with grain yield.

Phenotypic path coefficient analysis showed that spike number per plant had the largest direct effect on grain yield for both F3 and F4 random lines (Table 5). The direct effect was intermediate for kernel weight and lowest for kernel number per spike. Spike number per plant showed the greatest variability among yield components:the fixed components of variance for spike number, kernel number, and kernel weight were 11.6, 0, and 0.732 in 1986, and 11.4, 2.58 and 6.36 in 1987, respectively. Indirect effects were generally smaller in magnitude than the corresponding direct effect of each causal variable. Since grain yield was equal to the product of yield components, variation in grain yield was almost entirely explained by the yield components, except for small residuals derived from rounding error.

When path analysis was used to explain RWC and grain yield relationships, the results differed between F3 and F4 random lines (Table 6). Among F4 lines grown under drought stress conditions, 97% of the variability in grain yield was accounted for by RWC measured at three reproductive stages, and all of the direct path coefficients were nonzero. RWC measurements at anthesis and at mid grain-fill had positive coefficients for direct effects on grain yield among F4 lines, but the direct effect of RWC at pre-anthesis resulted in a negative coefficient with a large absolute value. However, the fixed component of variance value for this RWC measurement was zero while those at anthesis and at mid grain-fill were 1.27 and 5.53, respectively. In contrast, yield variability among F3 lines was less explained (45%) by RWC, and none of the direct path coefficients were significantly different from zero. The cause-effect relationships between yield potential and RWC were further examined based on yield components of F4 random lines grown under drought stress. Spike number per plant and kernel weight were linearly related to the three RWC variables (Table 7). RWC at pre-anthesis and at anthesis had nonzero direct effects on spike number per plant, and RWC at mid grain-fill had a positive direct effect on kernel weight. Only 32% of variability for kernel number per spike was explained by RWC.

DISCUSSION

Intense drought development caused rapid leaf senescence during late reproductive growth stages in 1987, resulting in relatively small differences in RWC among all lines in drought-stressed plots at mid grain-fill. With this exception, high-yield F2 selections maintained a significantly higher RWC than low-yield selections following anthesis in the F3 and F4 generations. Despite the very low estimate of heritability for grain yield in this population reported previously (Schonfeld et al., 1988), the high-yield selections showed higher productivity in biomass and grain yield than the low-yield selections under drought stress conditions. The greater yield potential of the high-yield selection group largely resulted from a greater number of grain-producing tillers and higher kernel weight. TAM W-101, the more drought resistance parent, also maintained a higher RWC than Sturdy. The same associations were observed in the parents between RWC and biomass or grain yield production, and between grain yield and yield components. Therefore, the association of high RWC with high productivity under drought appeared to be characteristics inherited from TAM W-101.

The grain yield-RWC association was also exemplified in the set of random lines showing segregation both in grain yield and RWC with increasing drought stress. The positive genetic correlation between RWC and grain yield among random lines indicated that genes controlling RWC were likely involved in grain yield determination under drought stress conditions.

Considering the magnitude of path coefficients and variability of each yield component, the ability to retain more grain-producing tillers was the most important factor influencing to yield of both F3 and F4 random lines under drought stress. In contrast, kernel number per spike had the least influence on grain yield. These results are agreement with those from different winter wheat populations examined at the same location previously (Sidwell et al., 1976) and under field drought conditions (Keim and Kronstad, 1981). Spike number per plant and kernel weight were also major grain yield-contributing factors between high- and low-yield selections and between parents.

Small variability in RWC at pre-anthesis may nullify its nonzero direct path coefficient, and thus, reduce its actual influence (direct or indirect) on yield potential. In contrast, RWC at anthesis and at mid grain-fill had substantial direct influences on grain yield. Higher RWC values at anthesis were related to higher yield values via increased number of grain-producing tillers. In general, winter wheat plants form more tillers than those which ultimately produce grain (Simmons, 1987). Drought stress treatments applied to wheat plants at maximum tiller accumulation showed higher tiller death rates and reduced grain-producing tiller number than well-watered treatments (Begg and Turner, 1976). In a previous experiment under similar drought stress conditions (Schonfeld et al., 1988), tiller number of both TAM W-101 and Sturdy started to decrease in mid-March, but the rate of decrease differed markedly between stress levels and genotypes. Based on these results, the observed higher RWC during anthesis apparently reduced tiller abortion.

Higher RWC values at mid grain-fill contributed to higher yield mostly through increased kernel weight. Water stress during grain-fill reduced yield of barley by decreasing photosynthesis rate per unit leaf area and leaf area through early senescence (Legg et al., 1979). When the photosynthetic source is limited, grain filling of wheat plants largely depends upon translocation of assimilates stored in leaves and stems; but, water stress also reduces the translocation rate by decreasing vein loading of assimilates in leaves (Wardlaw, 1966). Higher RWC and thus greater relative turgity should reduce these adverse effects of drought stress by maintaining larger leaf area and higher rates of photosynthesis and translocation. No distinct cause-effect relationships were determined between RWC and kernel number per spike, due in part to the small influence of this yield component to grain yield.

In a previous study (Schonfeld et al., 1988), heritability of RWC in an F2 population of TAM W-101 and Sturdy was as high as 0.64 and much higher than those for grain yield or any of yield components. In the present experiment, a consistent genetic association between high RWC and high yield potential under drought stress was clearly shown among the F3 and F4 progenies of the F2 population examined in the previous study. Methodology for estimating leaf RWC is quite simple and applicable for screening large populations. In a single day, over 200 plants were sampled for RWC estimation. In addition, RWC was measured more precisely than grain production traits; CV values for RWC were by far smaller than those for grain yield and yield components. With high heritability and close association with improved yield under drought, RWC should serve as a practical and reliable indicator to identify wheat genotypes possessing high yield potential under drought stress.

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Table 1. Mean squares for leaf relative water content (RWC) at three reproductive growth stages and for grain yield.

Source	df	RWC			Grain
		Pre-anthesis	Anthesis	Mid grain-fill	yield
Stress levels	1	35.3	929.1**	6392.1**	1741.5**
Years	1	250.7	321.8*	2068.7**	6957.4**
Entries	25	5.6*	15.5**	33.2**	44.2**
Entries X years	25	3.4	8.1	27.4*	28.6**
Entries X stress levels	25	2.8	7.6	28.9*	14.2
Entries X years X stress levels	25	2.5	6.1	25.9	12.7
Error	200	3.3	5.4	16.7	12.5
CV (%)		2.0	2.7	6.4	22.3

*,** Significant at p=0.05, 0.01, respectively.

Table 2. Mean squares partitioned among entries and entry interactions with stress levels or years for relative water content (RWC) at three reproductive stages and for grain yield.

Source	df	RWC Pre-anthesis	RWC Anthesis	RWC Mid grain-fill	Grain yield
		mean square			
Parents	1	14.68	40.90**	38.8	15.0
Selections	23	5.386*	13.80**	32.4**	45.8**
Among selection groups	2	0.85	65.63**	71.5*	62.3**
High vs low‡	1	1.03	110.14**	132.9**	38.3†
Within selection group	21	5.82*	8.87*	28.7*	44.3**
High yielding group	7	4.43	5.54	14.4	22.8†
Low yielding group	7	10.80*	8.29	42.0*	33.5**
Random group	7	2.22	12.77*	29.5†	76.5**
Parents vs selections	1	0.17	29.45*	45.1	35.2†
High vs low X stress levels	1	0.48	0.04	6.7	25.5
High vs low X years	1	0.06	4.93	94.7**	7.0
Parents X stress levels	1	0.27	0.02	25.9	2.1
Parents X years	1	3.36	11.03	122.2**	2.0

†,*,** Significant at p=0.10, 0.05, and 0.01, respectively.
‡ Contrast between high and low yielding groups.

Table 3. Mean squares for yield components, biomass, and harvest index.

Source	df	Yield components: Spikes/ plant	Yield components: Kernels/ spike	Yield components: Kernel weight	Biomass	Harvest index
Stress levels	1	753.7**	1.4	668.16**	8694.9**	327.5*
Years	1	4268.9**	5586.8**	233.80*	57294.6**	419.6**
Entries	25	69.6**	65.4**	66.24**	425.6**	52.0**
Entries X years	25	34.2**	20.7**	8.95	218.9**	19.3
Entries X stress levels	25	14.4	10.3	6.62	81.6	10.5
Entries X years X stress levels	25	11.2	10.2	7.06	86.9	7.3
Error	200	9.9	10.1	7.99	75.9	12.5
CV (%)		17.3	11.7	9.89	21.8	9.47

*,** Significant at p=0.05 and 0.01, respectively.

Table 4. Average relative water content of TAM W-101, Sturdy, and their progeny groups computed over two stress levels in 1986 and 1987.

Entry or contrast	Pre-anthesis†	Anthesis†	Mid grain-fill 1986	Mid grain-fill 1987
	%			
Entry				
TAM W-101	92.0	87.9	85.3	76.6
Sturdy	90.5	85.3	78.2	78.6
High-yielding selections	91.2	86.1	82.0	75.9
Low-yielding selections	91.0	84.5	79.0	75.6
Random line selections	91.2	85.9	81.6	75.4
Contrast				
TAM W-101 vs Sturdy	NS	**	**	NS
High vs low selections	NS	**	**	NS

** Significant at p=0.01;NS=not significant (p>0.05).
† Average over years (1986 and 1987).

Table 5. Phenotypic path analysis of direct and indirect effects by yield components on grain yield under drought stress conditions.

Entry	Causal variable	Direct effects	Indirect effects via Spikes /plant	Kernels /spike	Kernel weight
F3 random lines	Spikes/plant	0.897	-	-0.040	0.106
	Kernels/spike	0.163	-0.219	-	-0.109
	Kernel weight	0.288	0.329	-0.062	-
	Residuals	0.064	-	-	-
F4 random lines	Spikes/plant	0.951	-	-0.324	0.194
	Kernels/spike	0.342	-0.117	-	-0.246
	Kernel weight	0.499	0.102	-0.359	-
	Residuals	0.063	-	-	-

Table 6. Phenotypic path analysis of direct and indirect effects by relative water content (RWC) at three reproductive stages on grain yield under drought stress conditions.

Entry	Causal variable	Direct effects	Indirect effects via RWC at Pre-anthesis	Anthesis	Mid grain-fill
F3 random lines	RWC at				
	Pre-anthesis	0.242NS	-	-0.242	0.415
	Anthesis	-0.593NS	0.099	-	0.801
	Mid grain-fill	0.906NS	0.111	-0.524	-
	Residuals	0.797	-	-	-
F4 random lines	RWC at				
	Pre-anthesis	-1.263**	-	0.524	0.686
	Anthesis	0.754**	-0.878	-	0.135
	Mid grain-fill	0.477**	-0.429	0.213	-
	Residuals	0.166	-	-	-

** Significant at p=0.01;NS=not significant (p>0.10).

Table 7. Phenotypic path analysis of direct and indirect effects by relative water content (RWC) at three reproductive stages on yield components among F4 random lines grown under drought stress conditions.

Resultant variable	Causal variable	Direct effects	Indirect effects via RWC at		
			Pre-anthesis	Anthesis	Mid grain fill
	RWC at				
Spikes /plant	Pre-anthesis	-1.273**	-	-0.885	-0.433
	Anthesis	0.745**	0.518	-	0.211
	Mid grain-fill	0.280NS	0.095	0.079	-
	Residuals	0.351	-	-	-
Kernels /spike	Pre-anthesis	0.169NS	-	0.117	0.057
	Anthesis	-0.512NS	-0.356	-	-0.145
	Mid grain-fill	-0.407NS	-0.138	-0.115	-
	Residuals	0.826	-	-	-
Kernel weight	Pre-anthesis	-0.363NS	-	-0.252	-0.123
	Anthesis	0.557NS	0.387	-	0.158
	Mid grain-fill	0.679†	0.231	0.192	-
	Residuals	0.511	-	-	-

†,*,** Significant at p=0.10, 0.05, and 0.01, respectively.

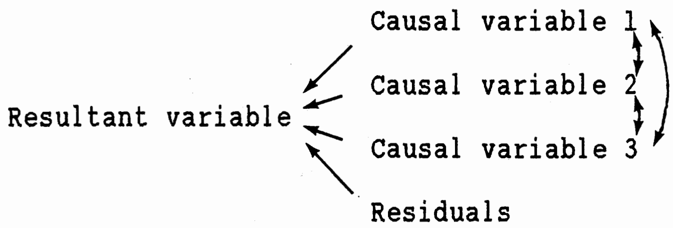


Fig. 1. Path diagram for determining cause-effect relationships in Tables 5, 6, and 7. Resultant variables are grain yield (Tables 5 and 6) or each yield component (Table 7), and the three causal variables are yield components (Table 5) or relative water content at three reproductive stages (Tables 6 and 7). Single-headed arrows and double-headed arrows indicate direct effects measured as path coefficients and associations between a pair of causal variables measured as correlation coefficients, respectively.

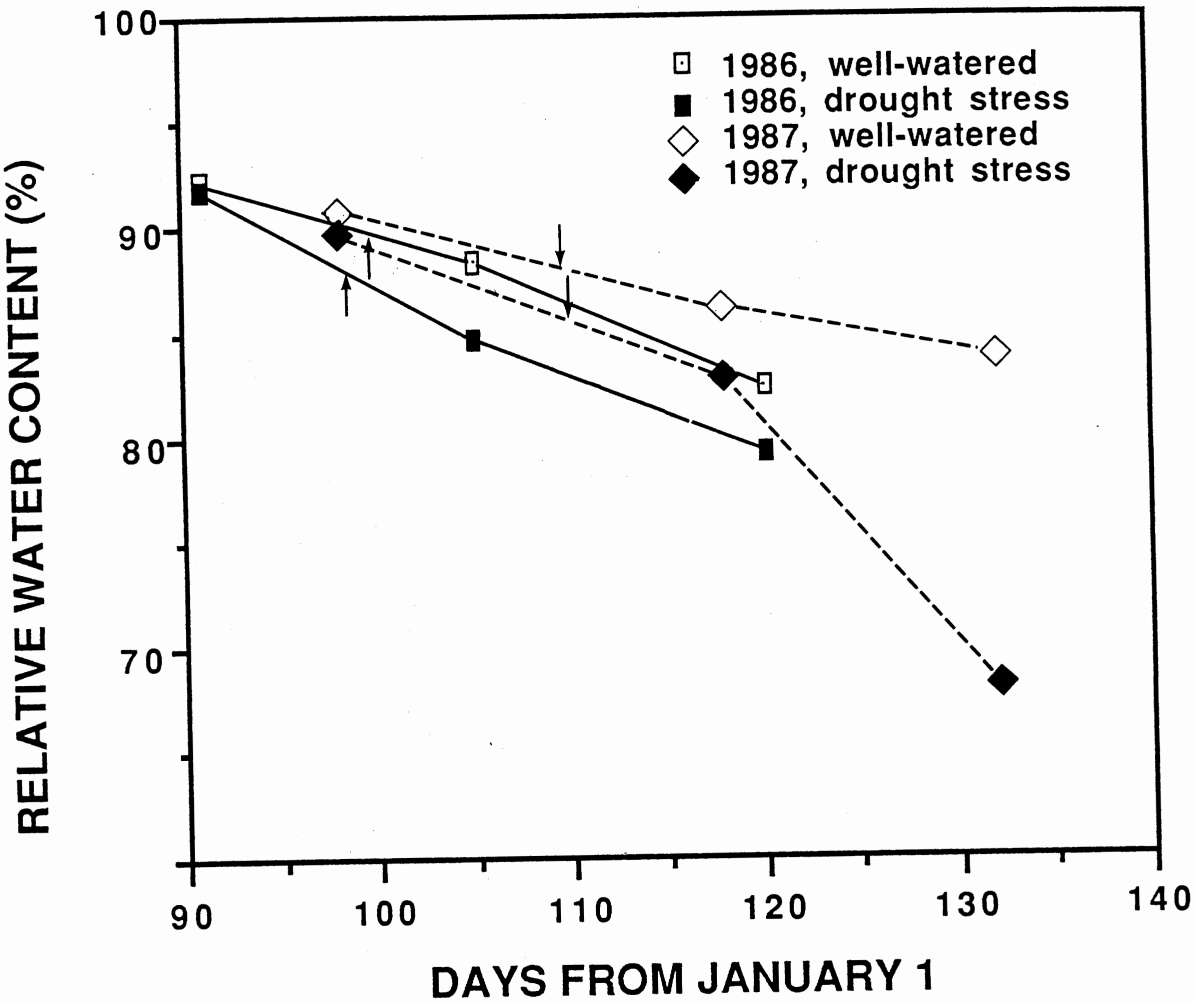


Fig. 2. Leaf relative water content (RWC) under drought stress and well-watered conditions averaged over all entries. Arrows indicate average spike emergence date for each stress level in 1986 (↑) and 1987 (↓), respectively.

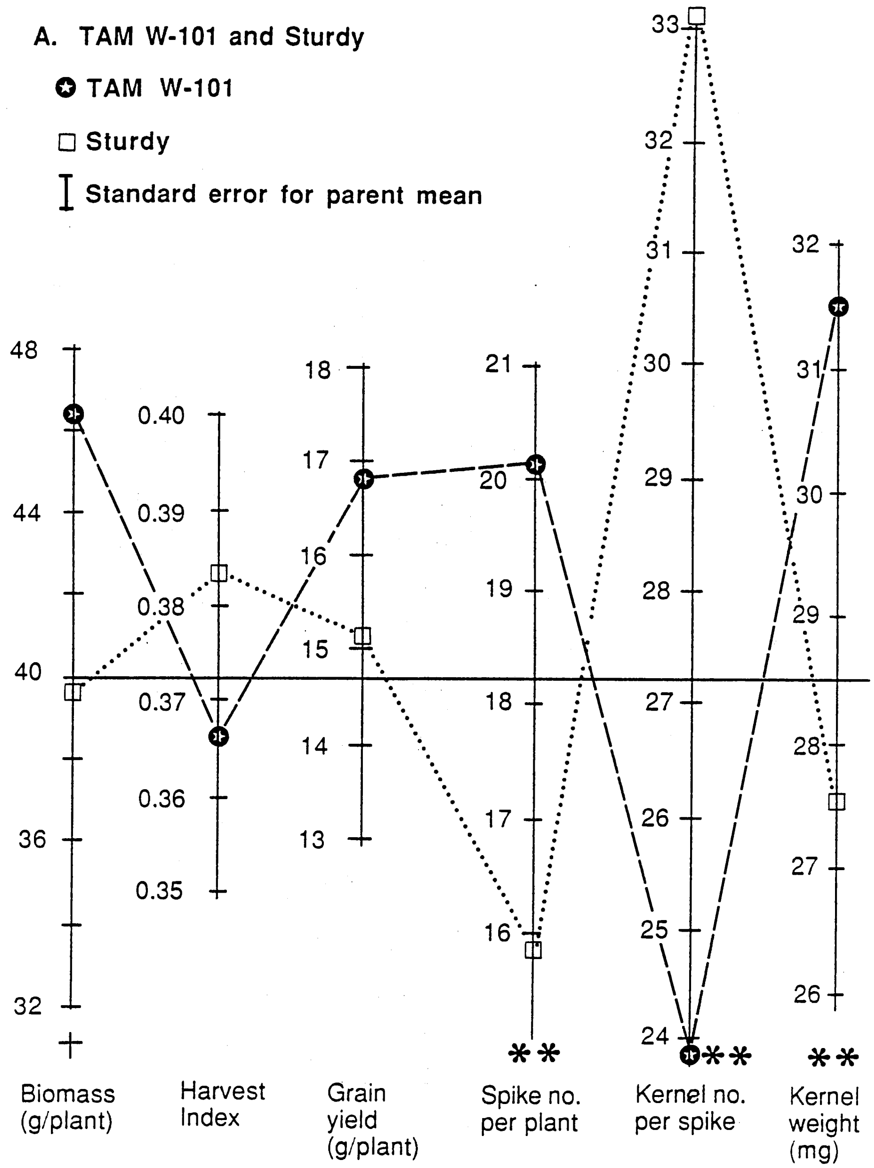


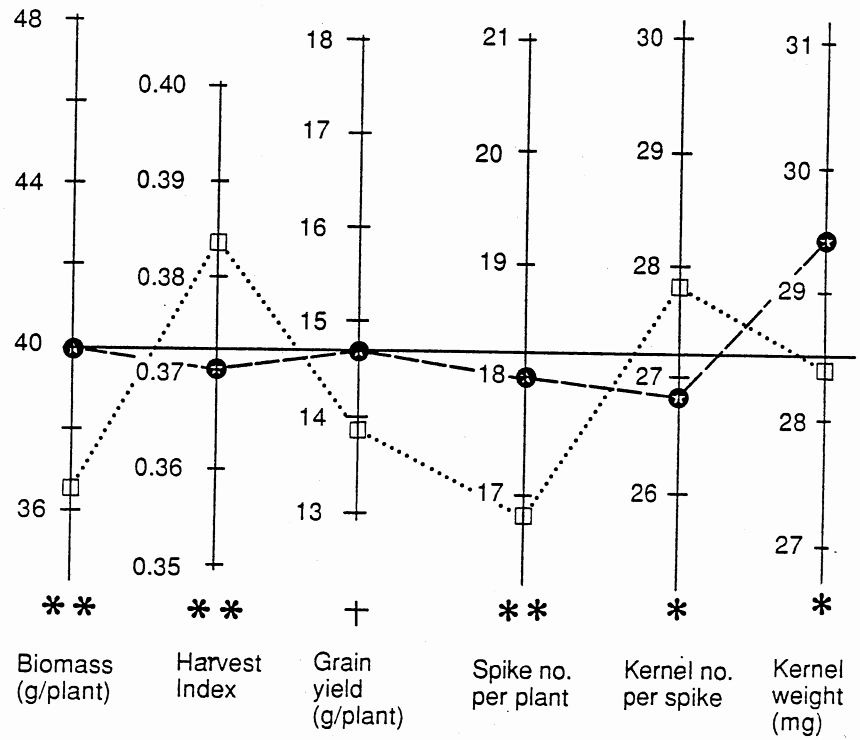
Fig. 3. Distribution of biomass, harvest index, and yield component means for TAM W-101 and Sturdy (A) and for high- and low-yield selection groups (B) averaged over two years (1986, 1987). The horizontal line indicates grand mean of all entries for each trait. Vertical scales are adjusted against standard errors such that one unit of the standard error has uniform vertical length for all traits within each figure. †, *, ** indicate significant differences between two parents, or between selection groups at the 0.10, 0.05, and 0.01 probability level, respectively.

B. High- and low-yield selection groups

High-yield selection group

Low-yield selection group

Standard error for selection group mean



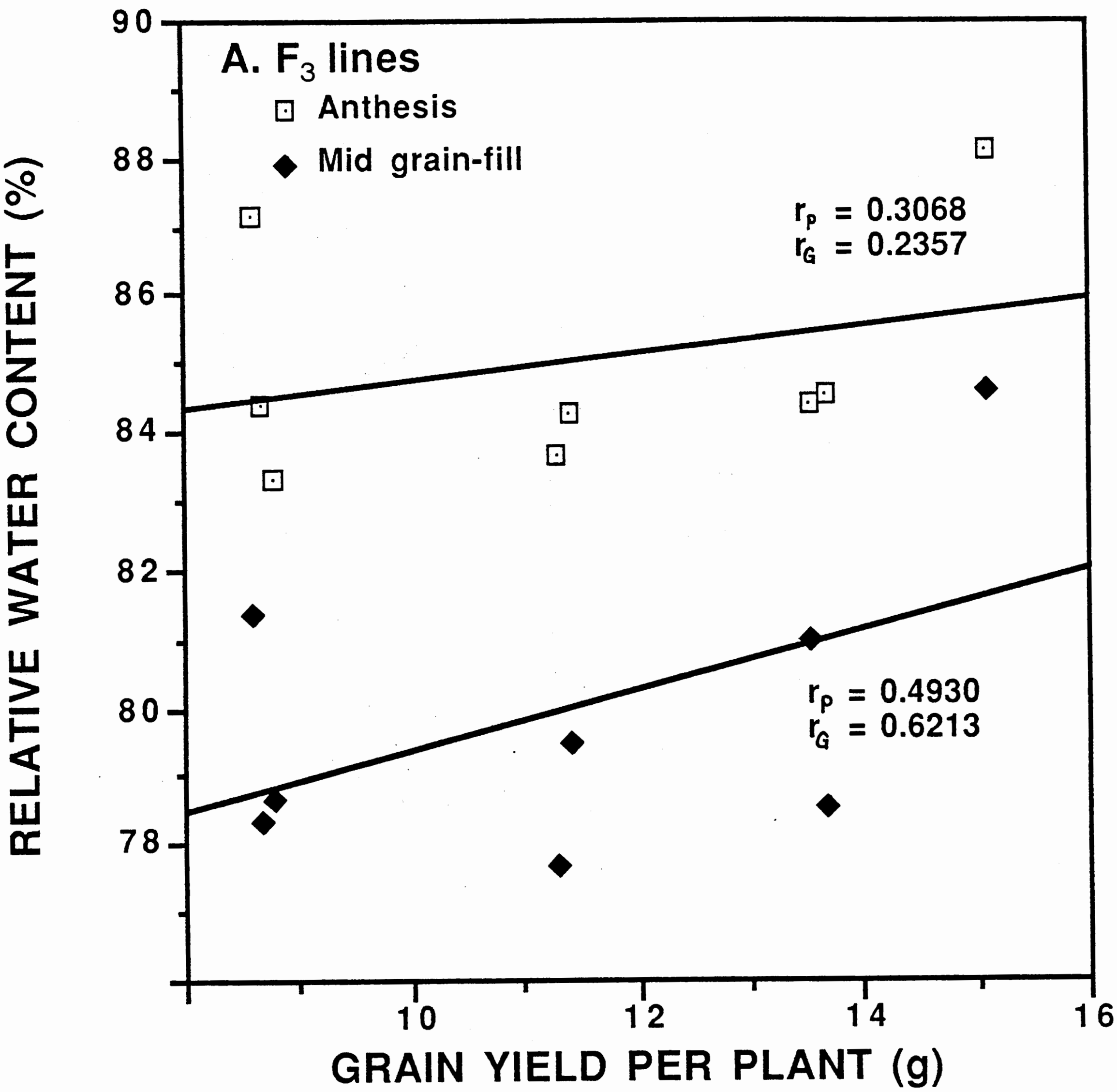
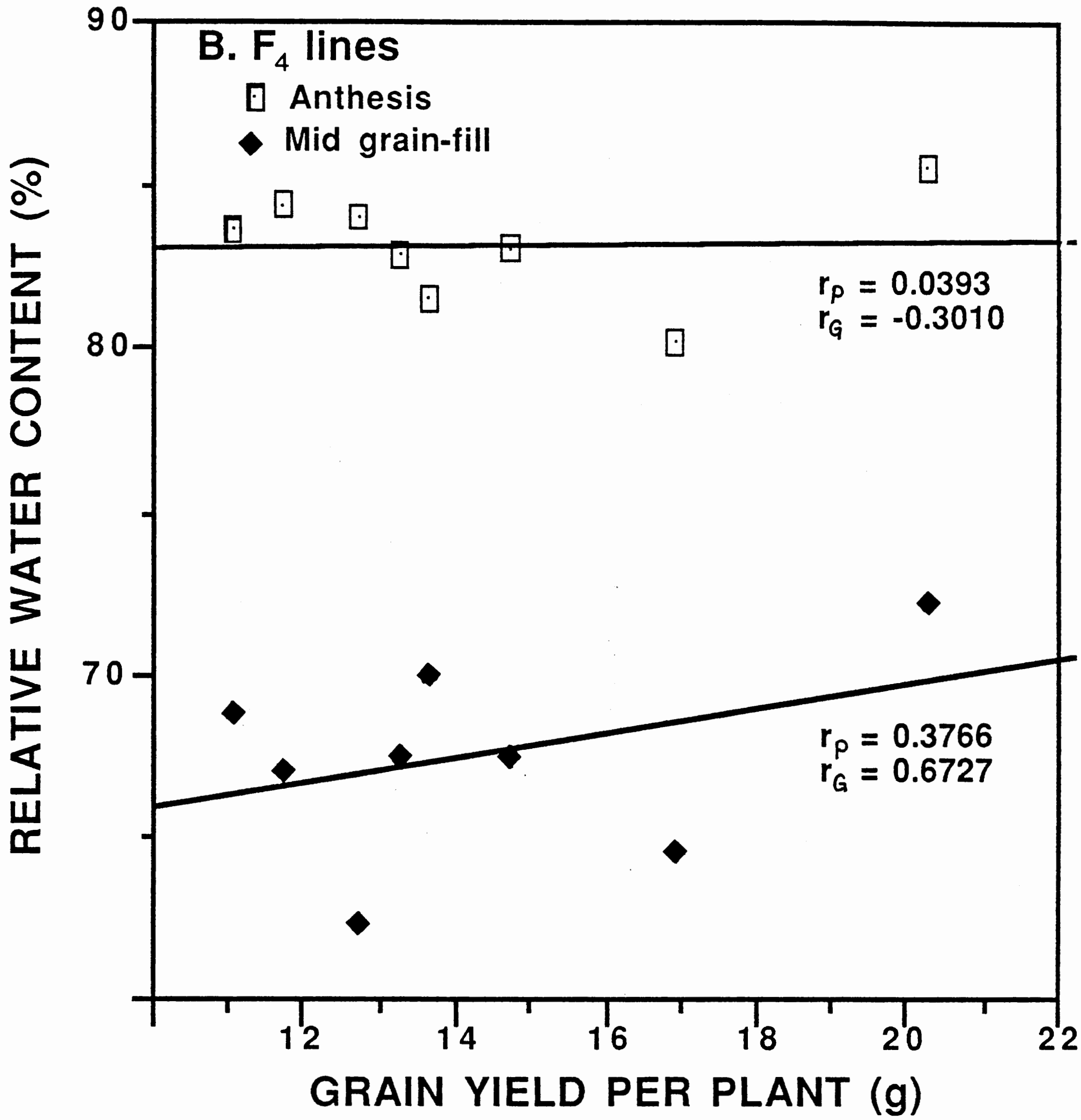


Fig. 4. Phenotypic and genetic correlations between grain yield and relative water content at anthesis or at mid-grain fill among eight F3 (A) and F4 (B) random lines under drought stress.


B. F4 lines
Anthesis
Mid grain-fill
rP = 0.0393
rG = -0.3010
rP = 0.3766
rG = 0.6727
90
80
70
12
14
16
18
20
22
RELATIVE WATER CONTENT (%)
GRAIN YIELD PER PLANT (g)

CHAPTER III

Quantification of Abscisic Acid in Wheat Leaf Tissue by Enzyme Immunoassay[1]

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Footnotes

1. Journal manuscript J-________ of the Oklahoma Agric. Exp. Stn.

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3. Abbreviations: EIA, enzyme immunoassay; MeOH, methanol; TBS, Tris-buffered saline.

ABSTRACT

Sample preparation methods were compared for their abscisic acid (ABA) yield in wheat leaf tissue based on enzyme immunoassay (EIA). Results showed that volatilization of extraction solvent did not affect ABA determination. Interference due to methanol (MeOH) in the solvent was minimized when diluted to 8% or less while 24 to 36 h extraction in 80% aqueous MeOH maximized ABA yield in the homogenate. No apparent inhibitors to EIA were detected by a parallelism test of dilution curves or by partial purification of leaf extract using C18 reverse-phase chromatography. Highly effective procedures are proposed which facilitate the analysis of a large number of samples at minimal expense and labor without sacrificing accuracy of ABA estimation.

Abscisic acid plays an important role in the control of plant response to water stress. Genetic capacity to increase endogenous ABA content under water stress might be amenable to selection for improved drought resistance (2). Genetic investigations supporting this hypothesis have been limited primarily due to technical difficulties in ABA quantification. Recently, an EIA[3] technique was developed for rapid ABA analysis of plant tissue (1, 3, 5). Since this technique has not been widely used for ABA analysis of wheat leaf tissue, methodological research is needed to establish efficient leaf sample preparation procedures. The general procedure currently used to prepare plant tissue for EIA can be summarized as follows (4) :1) homogenization of plant tissue in extraction solvent (80% MeOH), 2) ABA extraction for 12 to 48 h from the homogenized tissue, 3) centrifugation and extract collection, 4) extract purification by C18 reverse-phase chromatography, 5) partial or complete solvent volatilization from extract (MeOH removal), and 6) extract dilution with buffer. Further refinement of this procedure was attempted in a series of experiments dealing with the effects of extraction solvent volatilization on ABA determination, the optimum extraction time, the efficiency of C18 reverse-phase chromatography purification, and the bias to ABA estimation by interfering compounds extracted from leaf tissue.

MATERIALS AND METHODS

EIA. PHYTODETEK EIA (Idetek, Inc., San Bruno, CA) utilizes a monoclonal antibody specific for 2-cis-(+)-ABA coupled to a reaction well. Alkaline phosphatase-conjugated ABA and free ABA compete for a limited number of binding sites in the reaction well. The enzyme reacts with a colorless substrate, p-nitrophenyl phosphate, to produce the yellow product, p-nitrophenol. The relative concentrations of conjugated and free ABA in an assay aliquot are determined from the activity of resulting antibody-bound enzyme. Several standards (0.1 ml) of known ABA concentration (0.2 to 50 nM) were used to establish a quantitative relationship between ABA concentration and antibody-bound enzyme activity. The percent binding of enzyme-conjugated ABA for each standard was calculated by the following:

$$\%\ \text{binding} = B/B0 = \frac{\text{Sample OD} - \text{NSB OD}}{\text{B0 OD} - \text{NSB OD}} \times 100 \qquad [1]$$

where sample OD is light absorbance (OD) at 405 nm, and B0 OD and NSB OD are the OD values for exclusive bindings of enzyme-conjugated and free ABA, respectively. The relationship between % binding and ABA concentration is converted to a linear system by using a Log-LOGIT transformation:

$$\text{LOGIT}\ B/B0 = \log \frac{B/B0}{100 - B/B0} \qquad [2]$$

The ABA concentration in the test sample is extrapolated from its OD value using a linear standard curve (equation [2]).

Expected values of linear standard curve parameters. The sample OD value is directly proportional to the amount of enzyme-conjugated ABA bound to antibodies in the reaction well. This amount is determined by multiplying the ratio of conjugated ABA to total ABA by the total amount of ABA actually bound to the antibody. The amount of bound ABA depends upon the kinetic coefficient of the antigen-antibody reaction and the concentrations of ABA and antibody present in the reaction well. Assuming the amount of bound ABA does not vary despite the wide range of free ABA addition (0 to 5.0 pmoles in 0.1 ml), and equal amounts (0.1 ml) of conjugated ABA and sample solutions are placed for binding, equation [1] can be expressed as:

$$\% \text{ binding} = (\text{TTLBD} \times \frac{t}{s+t}) / \text{TTLBD} \times 100 \qquad [3]$$

where TTLBD is the total amount of bound ABA, and s and t are free and conjugated ABA concentrations, respectively. Combining this equation with equation [2],

$$\text{LOGIT } B/B0 = \log t - \log s. \qquad [4]$$

Thus, the expected slope of the linear standard curve [4] is -1, and the y intercept is a logarithmic conversion of enzyme-conjugated ABA concentration.

Leaf material and extract. Fully-expanded flag leaves of wheat (<u>Triticum aestivum</u> <u>L.</u>) plants at anthesis were collected from the field, wrapped in aluminum foil, immediately frozen in dry ice, and stored at -20 ^{o}C. Prior to extraction, several frozen leaves were cut into ca. 2 mm-square pieces and mixed thoroughly to minimize sample variability. A 0.2 g sample was homogenized in a 10 x 75 mm polypropylene centrifuge tube containing 1 ml of cold extraction solvent (80% (V/V) aqueous MeOH, pH 7.0, containing 10 mg/L 2,6-di-tert-butyl-4-methylphenol) for 15 seconds at 18,000 rpm. The homogenizer was rinsed three times with 1 ml of extraction solvent in a separate tube and all rinses were added to the homogenate. Except for extraction time experiments, the homogenate was agitated on a reciprocating shaker for 24 to 36 h at $4^{o}C$ in the dark. Samples were then centrifuged for 15 minutes at 9000 x g, and the entire supernatant was collected as leaf extract.

Volatilization of extraction solvent from ABA sample. The influence of partial and complete volatilization of solvent on ABA quantification in standards and leaf extracts was investigated using vacuum-centrifugation. One set of eight ABA standards in 25 mM TBS (0.25 ml, including two samples corresponding to B0 and NSB) was mixed with 0.75 ml of extraction solvent. The samples were completely dried in a Speed-Vac Concentrator (Savant Instrument Inc., Hicksville, NY), redissolved with 0.25 ml of TBS, and assayed. Assay results (LOGIT B/B0) were compared to another set of eight standards which were assayed directly.

Three sets of leaf extracts were prepared as previously described after 24 h extraction of the leaf homogenate. One set of extracts (1 ml) was completely dried and another set was partially dried to a final volume of ca. 0.1 ml to remove MeOH. Volumes of all samples were readjusted to 1 ml with 25 mM TBS, and further diluted 1:9 (V/V) with TBS prior to EIA. The third set of leaf extracts were simply diluted 1:9 (V/V) with TBS and assayed without removing MeOH.

Extraction time. Five sets of leaf homogenates were prepared as described above. One set was centrifuged immediately after homogenization (0 h extraction), and the other four sets were capped and placed on a reciprocating shaker for 12, 24, 36, or 48 hours. All samples were then centrifuged as before to collect the supernatant. Pellets from 0 and 48 h samples were homogenized again in the same manner as the leaf sample. Homogenates were centrifuged immediately and the second supernatant was collected. This procedure was repeated, and the third supernatant was also saved. The supernatants, fresh pellets, and a final oven-dried pellet were weighed to estimate the amount of extracted ABA carried through consecutive supernatants.

Partial purification of extract. Reverse phase chromatography was utilized to remove nonpolar compounds from leaf extracts according to procedures adapted from Dr. B. Woods (USDA-ARS, Byron, GA, personal communication). Leaf extracts (3 ml) were applied to a Sep-Pak C18 cartridge (Waters Associates, Milford, MA) pre-equilibrated with extraction solvent. The extract was forced through the cartridge with a syringe, and the eluent was collected for ABA analysis. Retention of ABA on the C18 cartridge was determined by independently applying 4 ml of extraction solvent containing 15, 150, and 1500 pmole ABA to separate cartridges and quantifying ABA recovered in the eluents.

Leaf extract interference. Three sets of leaf homogenates were diluted with 0 (no dilution), 1:1, or 1:3 (V/V) fresh extraction solvent. Each treatment was then split into two aliquotes, one of which was spiked with additional ABA (12 nM). The ABA was added so that interferences to assay performance by compounds extracted along with ABA from leaf tissue could be determined. Controls consisted of extraction solvents with or without added ABA.

RESULTS AND DISCUSSIONS

Volatilization of extraction solvent from ABA sample. Volatilization of extraction solvent from ABA standards did not significantly affect ABA estimation, measured as mean LOGIT B/B0 (Table 1). Linear regression of LOGIT B/B0 on ABA concentration combined over volatilization treatments explained 99.7% of the variation due to the differences in ABA concentrations of standard samples. Treatment by concentration interactions were nonsignificant. Regression coefficients (-1.03 and -1.10 for nonvolatilized and volatilized treatments, respectively) were not significantly different from each other, nor from the expected value of -1. The results indicated that ABA estimation was accurate in the concentration range of 0.2 to 50 nM, and that chemical breakdown of ABA by complete drying was negligible. Therefore, drying of standards is not required to establish an appropriate standard curve, even when ABA extracts are dried and concentrated rather than directly diluted with TBS due to low expected ABA concentrations in test samples.

Concentrations of ABA in diluted leaf extracts containing 8% MeOH (19.7 nM ABA) were not different from those of completely or partially dried samples both containing no MeOH (19.0 and 19.2 nM ABA, respectively). Interference of MeOH to EIA was negligible at concentrations of 8% or less. Complete drying of extracts caused no significant ABA loss even though ABA was dried in the presence of various compounds extracted from leaf tissue.

Extraction time. Significant differences in amounts of ABA were observed among the first supernatants collected after varying hours of extraction. Partitioning this variance into orthogonal polynomial components resulted in significant linear and quadratic effects (Table 2); thus, a second-degree curve was calculated to fit the data (Fig. 1). ABA yield increased as extraction time increased until an estimated peak at 32 h was reached. Comparatively little change in ABA yield occurred when extraction time increased from 24 to 36 h. The second and third supernatants collected after repeated homogenizations generally contained smaller amounts of ABA compared to the first supernatant (Table 3). The second supernatant collected from the 0 h extraction treatment, however, had a relatively high ABA concentration. After collecting the supernatant, a small amount of extraction solvent was usually present in the tightly-packed pellet. The amount of extracted ABA from the liquid phase of the pellet was estimated by the ABA concentration in the supernatant (pmol/g of supernatant) multiplied by the liquid weight of the pellet (the difference between fresh and oven-dry weights of the pellet). Carry-over ABA concentrations were predicted for the second and third supernatants and compared with observed concentrations. No significant difference was found between observed and expected values for the second and third supernatants collected after 48 h extraction. Thus, extraction from plant tissue was virtually complete in the first supernatant at 48 hours after homogenization. In contrast, the observed ABA content in the second supernatant after 0 h extraction was significantly greater than that expected, suggesting additional ABA was extracted from plant tissue through repeated homogenization. The total amount of extracted ABA combined over three supernatants of the 0 h extraction treatment was equivalent to those amounts in the first supernatant of the 24, 36, and 48 h extraction treatments. Repeated homogenization of plant tissue, each time with fresh solvent, may reduce extraction time without sacrificing ABA yield. One-time homogenization with an extraction time of 24 or more hours was equally effective in obtaining optimum ABA yield. The latter method is preferable in practice due to reduced labor and potential loss of ABA during sample preparation.

Partial purification of ABA. Partial purification of leaf extracts and ABA standards by C18 reverse phase chromatography resulted in no significant differences in ABA estimates (Table 4). With this method, in which much of the ABA remained in a deprotonated form due to neutral pH, no significant retention of ABA on the C18 cartridge was detected regardless of sample type or ABA concentration. Nonpolar compounds were removed from the leaf extract as evidenced by adsorption of pigments to the chromatography. However, these compounds appeared to have no adverse effects on EIA performance.

Leaf extract interference. When observed ABA concentrations of a diluted leaf extract were compared to expected values, reduction in ABA estimates were proportional to dilution factors as expected (Fig. 2). Slopes were not significantly different from 1, and intercepts were not significantly different from 0 and 12 nM. These data, in addition to the results from partial purification of leaf extracts, indicate no apparent interference to EIA due to other compounds extracted from the leaf tissue.

In summary, wheat leaf sample preparation procedures were refined as summarized in Fig. 3. Results of this study verified that EIA could be used to assay crude samples for ABA quantification (6). In the refined procedures, accidental loss of ABA during sample preparation was minimal. The minimum requirement of 40 pmoles ABA/g fwt is sufficiently low to allow direct assay of the diluted supernatant for most wheat tissue. These refinements should simplify broadscale testing of genetic materials in which endogenous ABA content is of interest.

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Table 1. Analysis of variance for the effect of extraction solvent volatilization on ABA estimation (LOGIT B/B0)

Source	df	M.S.
Volatilization treatments (Trt)	1	0.10
ABA Concentrations in standards (ABA conc)	5	32.26 **
Linear	1	160.74 **
Residual	4	0.14
Trt x ABA conc	5	0.10
Trt x ABA conc (Linear)	1	0.18
Residual	4	0.09
Error	22	0.12

**:significant at p<0.01.

Table 2. Partitioned variance for ABA concentrations among extraction time

Source	df	M.S.
Extraction time	4	8.99 *
Linear	1	19.82 **
Quadratic	1	14.94 *
Residual	2	1.07
Error	16	1.98

* :significant at $p<0.05$
**:significant at $p<0.01$

Table 3. Observed and expected ABA concentrations in supernatants collected after repeated homogenization using fresh solvent

Extraction time	ABA estimation	After 2nd homogenization	After 3rd homogenization
Hours		------------nM------------	
0	Observed	3.25	0.855
	Expected	1.04	0.0943
48	Observed	1.32	0.438
	Expected	1.38	0.137

Table 4. Influence of partial purification by C18 reverse phase chromatography on ABA quantification

Method[a]	Leaf extract (3 ml)	Amount of ABA in 4 ml of standard solutions(pmol) 15	150	1500
	--Amount of ABA detected (pmol)--			
No purification	76	13.1	145	1570
C18 chromatography purification	77	13.8	129	1590

[a] Difference between methods was not significant ($p>0.05$) for all measurements

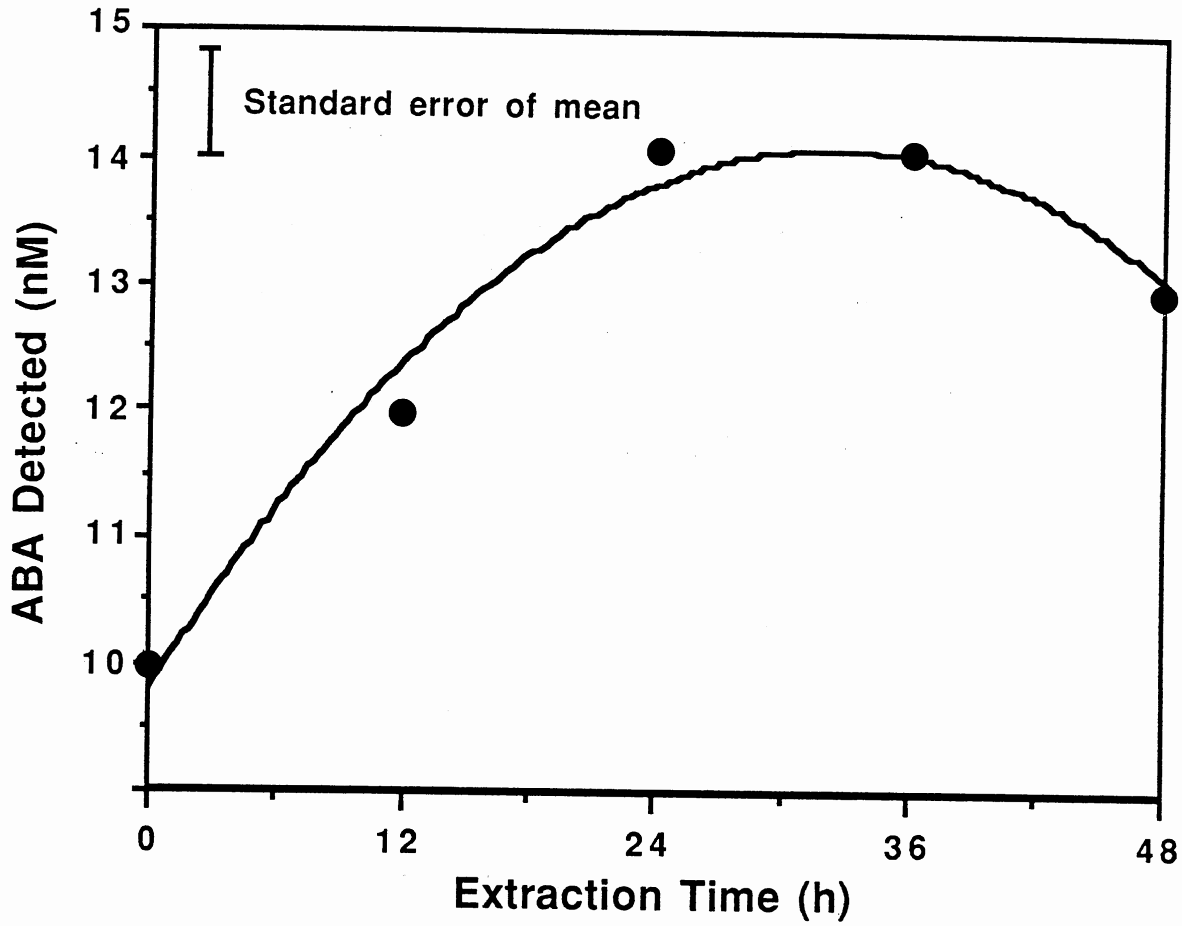

FIG. 1. Extraction of ABA from wheat leaf tissue.

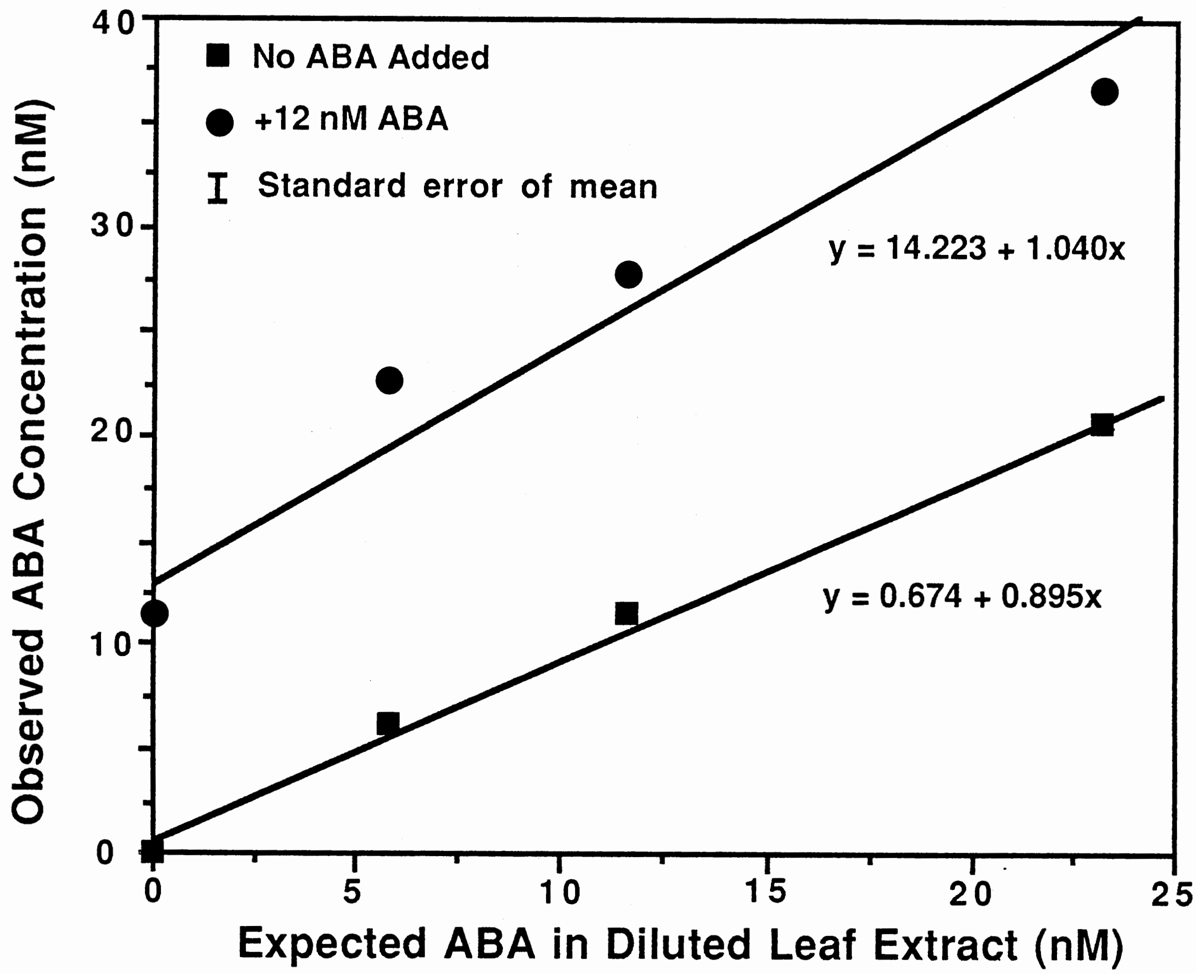

FIG. 2. Expected vs. observed ABA concentrations in diluted leaf extract.

Homogenization

Homogenize leaf tissue with 1 ml 80% (V/V) aqueous MeOH per 0.2 g fwt
Rinse off homogenizer with 1 ml of fresh solvent three times
Combine homogenate and rinses

↓

Extraction

Extract in dark for 24 h at 4 ^{o}C on reciprocating shaker

↓

Centrifugation

Centrifuge homogenate at 9,000 x g for 15 minutes
Collect supernatant

↓*

Dilution

Dilute supernatant 1:9 (V/V) or more with 25 mM TBS

↓

EIA

Quantify ABA using EIA

* If the expected ABA concentration is less than 40 pmoles/g fwt., then concentrate supernatant using vacuum centrifugation

FIG. 3. Flowchart of refined sample preparation procedures for EIA of ABA.

APPENDIX

TABLE 1

AVERAGE LEAF RELATIVE WATER CONTENT AT THREE REPRODUCTIVE GROWTH STAGES OF TAM W-101, STURDY AND THEIR F3 (1986) PROGENY

Entry	Pre-anthesis			Anthesis			Mid grain-fill		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	%								
HI 4-1	92.0	92.2	92.1	85.9	87.6	86.7	80.3	81.5	80.9
HI 17-4	90.5	91.6	91.1	84.4	88.3	86.4	78.6	82.3	80.4
HI 41-4	91.5	92.1	91.8	82.9	89.7	86.3	76.9	84.6	80.7
HI 8-4	91.1	91.5	91.3	85.0	89.0	87.0	80.2	86.4	83.3
HI 30-2	92.0	92.9	92.5	86.7	89.2	87.9	81.9	85.6	83.7
HI 14-4	92.3	91.6	91.9	86.4	89.9	88.2	82.3	85.4	83.8
HI 30-3	92.0	92.3	92.2	85.7	87.4	86.5	81.4	82.7	82.1
HI 44-3	93.3	92.2	92.7	85.8	90.3	88.1	79.4	82.9	81.2
LO 3-4	92.7	92.8	92.7	82.8	86.4	84.6	75.9	79.5	77.7
LO 16-3	91.2	91.2	91.2	84.4	86.2	85.3	78.4	80.6	79.5
LO 13-3	92.1	92.2	92.1	85.7	87.5	86.6	74.9	81.0	78.0
LO 43-2	92.1	91.8	91.9	83.9	87.7	85.8	80.3	79.5	79.9
LO 44-2	92.3	92.4	92.3	85.8	87.6	86.7	82.3	80.8	81.5
LO 27-4	90.5	91.4	91.0	81.3	84.8	83.1	76.3	76.5	76.4
LO 8-3	91.9	91.9	91.9	83.1	87.1	85.1	77.2	80.8	79.0
LO 16-1	90.4	92.5	91.4	82.2	88.6	85.4	77.1	82.1	79.6
RA 8-0	91.1	91.8	91.5	84.4	88.1	86.3	78.3	79.5	78.9
RA 13-0	92.3	93.8	93.0	88.1	92.4	90.3	84.6	87.1	85.9
RA 1-0	92.7	93.5	93.1	84.3	89.1	86.7	79.5	81.7	80.6
RA 1-5	92.2	91.7	92.0	83.7	89.7	86.7	77.7	82.7	80.2
RA 4-0	92.5	92.6	92.5	87.2	89.0	88.1	81.4	84.8	83.1
RA 16-5	92.3	92.2	92.2	84.4	89.9	87.2	80.9	86.0	83.5
RA 3-0	91.4	92.8	92.1	83.3	87.8	85.6	78.7	82.8	80.8
RA 3-5	91.9	91.2	91.5	84.6	86.6	85.6	78.5	81.3	79.9
TAM W-101	93.6	92.3	93.0	88.7	90.5	89.6	85.5	85.1	85.3
STURDY	92.0	92.3	92.1	84.5	86.8	85.6	76.4	80.0	78.2

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 2

AVERAGE LEAF RELATIVE WATER CONTENT AT THREE REPRODUCTIVE GROWTH STAGES OF TAM W-101, STURDY AND THEIR F4 (1987) PROGENY

Entry	Pre-anthesis			Anthesis			Mid grain-fill		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	%								
HI 4-1	87.2	89.8	88.5	85.4	83.2	84.3	75.2	80.3	77.7
HI 17-4	90.5	91.9	91.2	85.2	85.7	85.5	72.0	79.7	75.9
HI 41-4	86.8	91.0	88.9	80.4	87.7	84.1	68.7	80.3	74.5
HI 8-4	91.6	90.7	91.2	82.7	90.1	86.4	71.6	83.2	77.4
HI 30-2	91.0	90.6	90.8	85.1	87.9	86.5	70.9	83.8	77.4
HI 14-4	89.9	90.7	90.3	81.0	87.0	84.0	65.8	83.5	74.6
HI 30-3	91.7	91.1	91.4	81.5	87.3	84.4	61.7	85.6	73.7
HI 44-3	90.7	91.7	91.2	84.9	84.0	84.5	67.0	84.8	75.9
LO 3-4	92.6	91.1	91.8	83.5	86.9	85.2	61.3	82.6	71.9
LO 16-3	87.4	91.3	89.4	77.9	85.8	81.8	67.8	85.2	76.5
LO 13-3	90.2	90.9	90.6	84.8	86.1	85.5	58.3	85.2	71.8
LO 43-2	89.9	90.7	90.3	81.6	84.6	83.1	77.0	84.2	80.6
LO 44-2	93.1	92.1	92.6	79.9	85.4	82.6	70.1	82.4	76.3
LO 27-4	88.1	89.4	88.8	83.6	86.7	85.1	68.6	86.0	77.3
LO 8-3	89.7	88.3	89.0	81.6	82.1	81.9	69.4	84.0	76.7
LO 16-1	89.1	89.8	89.5	82.0	87.4	84.7	64.9	82.6	73.8
RA 8-0	89.9	91.9	90.9	83.0	85.9	84.5	67.4	84.5	76.0
RA 13-0	89.3	90.6	89.9	83.0	86.2	84.6	67.4	79.9	73.7
RA 1-0	89.4	91.2	90.3	84.0	85.2	84.6	62.4	83.3	72.8
RA 1-5	90.9	90.1	90.5	83.8	86.4	85.1	68.8	79.8	74.3
RA 4-0	91.0	91.1	91.1	84.4	84.8	84.6	67.0	88.5	77.7
RA 16-5	89.4	89.2	89.3	85.5	88.1	86.8	72.3	83.8	78.1
RA 3-0	87.0	91.3	89.1	80.3	86.7	83.5	64.6	84.5	74.5
RA 3-5	89.1	91.5	90.3	81.6	86.0	83.8	69.9	82.6	76.3
TAM W-101	89.5	92.6	91.1	84.4	88.2	86.3	67.9	85.3	76.6
STURDY	87.6	89.9	88.8	83.5	86.6	85.0	76.0	81.2	78.6

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 3

AVERAGE LEAF RELATIVE WATER CONTENT AT THREE REPRODUCTIVE GROWTH STAGES OF TAM W-101, STURDY AND THEIR PROGENY COMPUTED OVER YEARS (1986, 1987)

Entry	Pre-anthesis			Anthesis			Mid grain-fill		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	%								
HI 4-1	89.6	91.0	90.3	85.6	85.4	85.5	77.7	80.9	79.3
HI 17-4	90.5	91.8	91.1	84.8	87.0	85.9	75.3	81.0	78.2
HI 41-4	89.2	91.5	90.3	81.6	88.7	85.2	72.8	82.4	77.6
HI 8-4	91.4	91.1	91.2	83.8	89.6	86.7	75.9	84.8	80.3
HI 30-2	91.5	91.7	91.6	85.9	88.6	87.2	76.4	84.7	80.5
HI 14-4	91.1	91.2	91.1	83.7	88.5	86.1	74.0	84.4	79.2
HI 30-3	91.9	91.7	91.8	83.6	87.3	85.5	71.6	84.2	77.9
HI 44-3	92.0	91.9	91.9	85.4	87.2	86.3	73.2	83.8	78.5
LO 3-4	92.6	92.0	92.3	83.1	86.6	84.9	68.6	81.0	74.8
LO 16-3	89.3	91.3	90.3	81.2	86.0	83.6	73.1	82.9	78.0
LO 13-3	91.1	91.6	91.4	85.3	86.8	86.0	66.6	83.1	74.9
LO 43-2	91.0	91.3	91.1	82.7	86.1	84.4	78.7	81.8	80.2
LO 44-2	92.7	92.2	92.5	82.8	86.5	84.7	76.2	81.6	78.9
LO 27-4	89.3	90.4	89.9	82.5	85.7	84.1	72.5	81.3	76.9
LO 8-3	90.8	90.1	90.5	82.4	84.6	83.5	73.3	82.4	77.9
LO 16-1	89.8	91.2	90.5	82.1	88.0	85.1	71.0	82.4	76.7
RA 8-0	90.5	91.9	91.2	83.7	87.0	85.4	72.9	82.0	77.4
RA 13-0	90.8	92.2	91.5	85.6	89.3	87.4	76.0	83.5	79.8
RA 1-0	91.0	92.3	91.7	84.2	87.1	85.7	70.9	82.5	76.7
RA 1-5	91.6	90.9	91.2	83.7	88.0	85.9	73.3	81.3	77.3
RA 4-0	91.8	91.9	91.8	85.8	86.9	86.3	74.2	86.7	80.4
RA 16-5	90.9	90.7	90.8	85.0	89.0	87.0	76.6	84.9	80.8
RA 3-0	89.2	92.0	90.6	81.8	87.2	84.5	71.6	83.7	77.6
RA 3-5	90.5	91.3	90.9	83.1	86.3	84.7	74.2	81.9	78.1
TAM W-101	91.6	92.4	92.0	86.5	89.4	87.9	76.7	85.2	80.9
STURDY	89.8	91.1	90.5	84.0	86.7	85.3	76.2	80.6	78.4

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 4

AVERAGE BIOMASS, HARVEST INDEX, AND GRAIN YIELD OF TAM W-101, STURDY AND THEIR F3 (1986) PROGENY

Entry	Biomass			Harvest index			Grain yield		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	-----g/plant-----			--------%-------			-----g/plant----		
HI 4-1	26.8	23.2	25.0	38.7	39.3	39.0	10.3	9.1	9.7
HI 17-4	23.5	26.3	24.9	41.6	41.6	41.6	9.7	11.1	10.4
HI 41-4	17.0	25.2	21.1	34.8	34.8	34.8	6.0	9.0	7.5
HI 8-4	21.5	24.0	22.7	36.1	39.4	37.7	8.0	9.4	8.7
HI 30-2	30.9	27.0	28.9	38.5	37.3	37.9	11.9	10.0	10.9
HI 14-4	31.1	29.0	30.0	36.0	34.2	35.1	10.8	10.0	10.4
HI 30-3	33.0	25.7	29.3	43.4	51.0	47.2	14.2	10.9	12.5
HI 44-3	33.6	29.0	31.3	37.9	36.4	37.1	12.9	10.6	11.7
LO 3-4	24.7	22.6	23.7	36.5	39.4	38.0	9.0	8.9	9.0
LO 16-3	32.6	25.4	29.0	39.0	39.8	39.4	12.5	10.1	11.3
LO 13-3	14.1	19.5	16.8	40.9	41.5	41.2	5.9	8.2	7.1
LO 43-2	15.2	15.6	15.4	43.6	40.1	41.8	6.6	6.3	6.5
LO 44-2	27.7	27.8	27.7	37.8	38.1	37.9	10.6	10.9	10.7
LO 27-4	21.4	22.1	21.7	37.9	33.5	35.7	8.3	7.4	7.8
LO 8-3	28.2	24.4	26.3	37.7	37.2	37.5	10.7	9.1	9.9
LO 16-1	22.9	23.5	23.2	40.5	40.2	40.4	9.4	9.5	9.4
RA 8-0	25.1	24.2	24.6	34.4	35.5	34.9	8.7	8.7	8.7
RA 13-0	42.4	32.5	37.4	35.2	36.4	35.8	15.1	11.9	13.5
RA 1-0	30.3	35.4	32.9	37.8	39.0	38.4	11.4	14.0	12.7
RA 1-5	29.6	21.5	25.6	38.2	40.6	39.4	11.3	8.6	9.9
RA 4-0	21.7	29.9	25.8	40.1	41.4	40.8	8.6	12.3	10.5
RA 16-5	36.7	34.7	35.7	37.3	41.2	39.2	13.5	14.1	13.8
RA 3-0	22.0	29.7	25.8	40.4	39.1	39.8	8.8	11.6	10.2
RA 3-5	39.9	33.2	36.5	34.3	36.3	35.3	13.7	12.2	12.9
TAM W-101	25.9	19.3	22.6	37.8	37.5	37.7	9.8	7.4	8.6
STURDY	16.7	23.6	20.2	39.3	37.0	38.2	6.4	8.8	7.6

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 5

AVERAGE BIOMASS, HARVEST INDEX, AND GRAIN YIELD OF TAM W-101, STURDY AND THEIR F4 (1987) PROGENY

Entry	Biomass			Harvest index			Grain yield		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	-----g/plant-----			---------%-------			-----g/plant----		
HI 4-1	47.3	70.1	58.7	32.5	38.5	35.5	16.0	27.6	21.8
HI 17-4	45.9	68.1	57.0	31.4	36.3	33.8	14.6	25.1	19.8
HI 41-4	40.7	57.4	49.1	33.3	33.8	33.6	13.8	19.5	16.6
HI 8-4	40.0	78.3	59.2	34.0	35.4	34.7	13.3	28.1	20.7
HI 30-2	29.6	57.6	43.6	35.3	37.4	36.3	10.3	21.2	15.8
HI 14-4	46.4	67.6	57.0	32.8	38.5	35.6	15.1	26.2	20.6
HI 30-3	41.9	57.6	49.8	34.7	40.6	37.7	15.1	23.2	19.2
HI 44-3	42.4	64.6	53.5	34.1	39.9	37.0	14.3	25.3	19.8
LO 3-4	45.6	66.6	56.1	36.9	42.4	39.7	17.0	28.2	22.6
LO 16-3	36.0	56.9	46.4	33.8	40.3	37.0	13.5	23.0	18.2
LO 13-3	39.0	46.6	42.8	40.5	42.0	41.3	15.8	19.5	17.7
LO 43-2	40.6	44.0	42.3	39.2	40.1	39.7	15.8	17.2	16.5
LO 44-2	45.6	79.5	62.5	36.2	34.5	35.4	16.5	26.5	21.5
LO 27-4	38.7	53.2	45.9	35.0	36.6	35.8	13.8	20.1	16.9
LO 8-3	45.8	53.1	49.4	36.1	36.8	36.4	16.6	19.4	18.0
LO 16-1	38.0	64.0	51.0	32.9	39.1	36.0	12.7	24.7	18.7
RA 8-0	39.1	67.4	53.3	33.5	33.5	33.5	13.2	22.7	17.9
RA 13-0	46.2	70.3	58.3	30.8	36.5	33.6	14.7	25.6	20.2
RA 1-0	41.7	80.8	61.3	30.1	36.7	33.4	12.7	30.2	21.4
RA 1-5	30.9	43.9	37.4	35.3	39.5	37.4	11.0	17.1	14.1
RA 4-0	33.4	46.5	40.0	34.6	40.1	37.4	11.7	18.8	15.3
RA 16-5	62.5	83.9	73.2	32.2	35.4	33.8	20.2	30.0	25.1
RA 3-0	47.5	70.5	59.0	36.5	40.6	38.5	16.9	28.6	22.7
RA 3-5	40.6	66.3	53.5	33.6	36.0	34.8	13.6	23.8	18.7
TAM W-101	51.8	88.1	70.0	33.7	37.0	35.3	17.7	32.1	24.9
STURDY	46.9	70.6	58.8	35.4	41.1	38.2	16.7	28.8	22.7

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 6

AVERAGE BIOMASS, HARVEST INDEX, AND GRAIN YIELD OF TAM W-101, STURDY AND THEIR PROGENY COMPUTED OVER YEARS (1986, 1987)

Entry	Biomass			Harvest index			Grain yield		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	-----g/plant-----			---------%-------			-----g/plant----		
HI 4-1	37.1	46.6	41.9	35.6	38.9	37.2	13.1	18.3	15.7
HI 17-4	34.7	47.2	40.9	36.5	38.9	37.7	12.2	18.1	15.1
HI 41-4	28.8	41.3	35.1	34.0	34.3	34.2	9.9	14.2	12.0
HI 8-4	30.8	51.1	41.0	35.0	37.4	36.2	10.7	18.8	14.7
HI 30-2	30.2	42.3	36.3	36.9	37.4	37.1	11.1	15.6	13.3
HI 14-4	38.7	48.3	43.5	34.4	36.4	35.4	13.0	18.1	15.5
HI 30-3	37.5	41.6	39.5	39.1	45.8	42.4	14.7	17.0	15.9
HI 44-3	38.0	46.8	42.4	36.0	38.2	37.1	13.6	17.9	15.7
LO 3-4	35.2	44.6	39.9	36.7	40.9	38.8	13.0	18.6	15.8
LO 16-3	34.3	41.1	37.7	36.4	40.0	38.2	13.0	16.5	14.8
LO 13-3	26.6	33.0	29.8	40.7	41.8	41.2	10.9	13.9	12.4
LO 43-2	27.9	29.8	28.8	41.4	40.1	40.8	11.2	11.8	11.5
LO 44-2	36.7	53.6	45.1	37.0	36.3	36.7	13.5	18.7	16.1
LO 27-4	30.0	37.6	33.8	36.5	35.1	35.8	11.1	13.7	12.4
LO 8-3	37.0	38.8	37.9	36.9	37.0	37.0	13.6	14.3	14.0
LO 16-1	30.4	43.7	37.1	36.7	39.7	38.2	11.0	17.1	14.1
RA 8-0	32.1	45.8	38.9	33.9	34.5	34.2	10.9	15.7	13.3
RA 13-0	44.3	51.4	47.8	33.0	36.4	34.7	14.9	18.8	16.8
RA 1-0	36.0	58.1	47.1	33.9	37.8	35.9	12.0	22.1	17.1
RA 1-5	30.3	32.7	31.5	36.7	40.0	38.4	11.2	12.9	12.0
RA 4-0	27.6	38.2	32.9	37.4	40.7	39.1	10.1	15.6	12.9
RA 16-5	49.6	59.3	54.4	34.7	38.3	36.5	16.9	22.0	19.4
RA 3-0	34.7	50.1	42.4	38.4	39.9	39.2	12.8	20.1	16.5
RA 3-5	40.3	49.7	45.0	33.9	36.1	35.0	13.7	18.0	15.8
TAM W-101	38.9	53.7	46.3	35.7	37.3	36.5	13.7	19.8	16.8
STURDY	31.8	47.1	39.5	37.3	39.1	38.2	11.6	18.8	15.2

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 7

AVERAGE YIELD COMPONENTS OF TAM W-101, STURDY, AND THEIR F3 (1986) PROGENY

Entry	Spike no. per plant			Kernel no. per spike			Kernel weight		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
							-------mg-------		
HI 4-1	13.4	14.8	14.1	27.9	21.7	24.8	26.8	27.9	27.3
HI 17-4	13.8	14.3	14.0	24.0	22.5	23.3	29.3	30.5	29.9
HI 41-4	9.5	13.6	11.6	19.8	20.4	20.1	30.2	31.0	30.6
HI 8-4	14.8	15.0	14.9	16.8	20.9	18.9	29.2	30.6	29.9
HI 30-2	16.1	15.8	16.0	21.8	19.3	20.6	32.8	31.3	32.0
HI 14-4	16.3	15.9	16.1	23.0	20.6	21.8	28.3	30.1	29.2
HI 30-3	18.4	16.9	17.7	24.3	21.2	22.8	32.2	29.8	31.0
HI 44-3	15.6	14.6	15.1	25.2	19.9	22.5	32.6	33.8	33.2
LO 3-4	12.9	11.1	12.0	28.1	27.4	27.7	25.9	31.0	28.5
LO 16-3	16.1	14.1	15.1	24.7	20.2	22.4	29.9	31.0	30.5
LO 13-3	10.2	11.7	10.9	21.8	25.6	23.7	24.1	26.3	25.2
LO 43-2	9.7	9.4	9.5	21.9	23.1	22.5	30.6	29.5	30.0
LO 44-2	14.8	14.0	14.4	23.1	23.0	23.0	29.3	31.6	30.4
LO 27-4	11.4	12.8	12.1	27.2	22.9	25.1	28.2	25.8	27.0
LO 8-3	14.8	12.4	13.6	22.3	20.2	21.2	31.8	34.4	33.1
LO 16-1	12.7	13.9	13.3	23.2	24.7	24.0	28.4	26.5	27.4
RA 8-0	12.8	12.3	12.5	22.4	19.9	21.2	29.0	31.2	30.1
RA 13-0	23.1	17.5	20.3	23.0	23.1	23.0	28.4	28.9	28.6
RA 1-0	17.0	17.7	17.3	25.6	24.8	25.2	26.7	29.7	28.2
RA 1-5	15.7	12.2	13.9	25.9	22.2	24.0	27.9	30.4	29.2
RA 4-0	13.9	20.3	17.1	24.6	24.0	24.3	24.0	25.6	24.8
RA 16-5	17.8	16.2	17.0	24.4	24.7	24.5	30.6	34.4	32.5
RA 3-0	12.6	18.3	15.5	25.5	21.1	23.3	26.6	28.2	27.4
RA 3-5	19.9	17.3	18.6	23.8	22.2	23.0	28.0	30.4	29.2
TAM W-101	13.2	13.1	13.1	21.8	15.2	18.5	32.7	31.3	32.0
STURDY	9.8	11.2	10.5	25.3	26.5	25.9	27.0	30.1	28.5

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 8

AVERAGE YIELD COMPONENTS OF TAM W-101, STURDY, AND THEIR F4 (1987) PROGENY

Entry	Spike no. per plant			Kernel no. per spike			Kernel weight		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
							mg		
HI 4-1	18.5	24.8	21.6	36.2	38.2	37.2	22.7	27.2	25.0
HI 17-4	20.7	23.4	22.0	28.9	35.4	32.2	24.2	29.7	26.9
HI 41-4	16.3	18.5	17.4	30.5	29.5	30.0	27.4	34.8	31.1
HI 8-4	18.5	33.2	25.8	29.8	31.7	30.7	24.0	26.1	25.0
HI 30-2	13.4	21.9	17.7	25.9	30.2	28.0	27.7	31.9	29.8
HI 14-4	17.8	23.5	20.7	33.5	34.0	33.8	25.1	32.6	28.8
HI 30-3	19.7	24.6	22.1	30.5	30.5	30.5	24.5	31.1	27.8
HI 44-3	17.8	22.5	20.2	30.1	31.5	30.8	26.4	35.2	30.8
LO 3-4	20.4	26.1	23.3	34.3	38.4	36.4	24.0	28.8	26.4
LO 16-3	17.6	21.9	19.8	27.4	30.8	29.1	24.7	32.8	28.8
LO 13-3	19.8	23.6	21.7	34.2	32.3	33.2	23.4	26.0	24.7
LO 43-2	18.7	19.3	19.0	28.9	28.7	28.8	28.2	30.4	29.3
LO 44-2	19.2	27.3	23.3	31.3	32.2	31.8	27.6	29.7	28.6
LO 27-4	16.0	20.8	18.4	30.2	28.9	29.5	28.2	31.7	30.0
LO 8-3	17.7	18.0	17.8	30.3	29.5	29.9	31.0	35.4	33.2
LO 16-1	18.3	28.3	23.3	33.7	35.2	34.5	20.4	24.1	22.3
RA 8-0	17.6	24.0	20.8	27.5	27.5	27.5	26.7	33.5	30.1
RA 13-0	21.1	30.0	25.5	26.1	33.2	29.6	26.1	26.0	26.0
RA 1-0	18.3	27.2	22.7	30.8	37.1	34.0	22.3	29.7	26.0
RA 1-5	13.8	20.0	16.9	30.7	31.3	31.0	26.0	27.4	26.7
RA 4-0	18.0	25.2	21.6	28.5	28.6	28.5	22.6	25.9	24.3
RA 16-5	25.5	30.0	27.8	26.4	28.8	27.6	30.0	34.2	32.1
RA 3-0	23.6	35.0	29.3	31.9	32.8	32.3	22.3	25.7	24.0
RA 3-5	18.4	25.6	22.0	30.0	31.8	30.9	23.7	28.6	26.2
TAM W-101	23.2	30.9	27.0	27.9	30.0	29.0	26.8	34.7	30.8
STURDY	17.9	23.9	20.9	38.3	42.9	40.6	24.3	28.3	26.3

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 9

AVERAGE YIELD COMPONENTS OF TAM W-101, STURDY, AND THEIR PROGENY COMPUTED OVER YEARS (1986, 1987)

Entry	Spike no. per plant			Kernel no. per spike			Kernel weight		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
							-------mg-------		
HI 4-1	16.0	19.8	17.9	32.0	30.0	31.0	24.7	27.6	26.2
HI 17-4	17.3	18.8	18.0	26.5	28.9	27.7	26.7	30.1	28.4
HI 41-4	12.9	16.1	14.5	25.1	25.0	25.0	28.8	32.9	30.8
HI 8-4	16.7	24.1	20.4	23.3	26.3	24.8	26.6	28.4	27.5
HI 30-2	14.8	18.9	16.8	23.9	24.8	24.3	30.2	31.6	30.9
HI 14-4	17.1	19.7	18.4	28.3	27.3	27.8	26.7	31.3	29.0
HI 30-3	19.0	20.8	19.9	27.4	25.9	26.6	28.4	30.5	29.4
HI 44-3	16.7	18.5	17.6	27.6	25.7	26.7	29.5	34.5	32.0
LO 3-4	16.7	18.6	17.6	31.2	32.9	32.0	25.0	29.9	27.4
LO 16-3	16.8	18.0	17.4	26.0	25.5	25.8	27.3	31.9	29.6
LO 13-3	15.0	17.6	16.3	28.0	28.9	28.5	23.7	26.1	24.9
LO 43-2	14.2	14.4	14.3	25.4	25.9	25.7	29.4	29.9	29.7
LO 44-2	17.0	20.7	18.8	27.2	27.6	27.4	28.5	30.6	29.5
LO 27-4	13.7	16.8	15.2	28.7	25.9	27.3	28.2	28.8	28.5
LO 8-3	16.2	15.2	15.7	26.3	24.8	25.5	31.4	34.9	33.2
LO 16-1	15.5	21.1	18.3	28.5	30.0	29.2	24.4	25.3	24.8
RA 8-0	15.2	18.1	16.7	25.0	23.7	24.3	27.8	32.3	30.1
RA 13-0	22.1	23.8	22.9	24.5	28.1	26.3	27.2	27.4	27.3
RA 1-0	17.6	22.4	20.0	28.2	30.9	29.6	24.5	29.7	27.1
RA 1-5	14.8	16.1	15.4	28.3	26.8	27.5	26.9	28.9	27.9
RA 4-0	16.0	22.7	19.3	26.5	26.3	26.4	23.3	25.8	24.5
RA 16-5	21.7	23.1	22.4	25.4	26.8	26.1	30.3	34.3	32.3
RA 3-0	18.1	26.7	22.4	28.7	26.9	27.8	24.5	26.9	25.7
RA 3-5	19.2	21.4	20.3	26.9	27.0	27.0	25.8	29.5	27.7
TAM W-101	18.2	22.0	20.1	24.9	22.6	23.7	29.8	33.0	31.4
STURDY	13.9	17.5	15.7	31.8	34.7	33.3	25.7	29.2	27.4

HI, LO, and RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 10

AVERAGE HEADING DATE OF TAM W-101, STURDY AND THEIR F3 (1986) AND F4 (1987) PROGENY

	1986			1987			Two year average		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	days from January 1								
Grand mean	98.8	100.4	99.6	110.3	110.2	110.3	104.6	105.3	104.9
Selection groups									
High	99.8	101.5	100.7	111.5	110.8	111.1	105.7	106.2	105.9
Low	96.5	97.0	96.7	108.3	108.3	108.3	102.4	102.6	102.5
Random	99.6	101.8	100.7	111.0	111.7	111.3	105.3	106.7	106.0
Parents	100.9	104.2	102.5	111.2	109.6	110.4	106.0	106.9	106.5
Individual lines									
HI 4-1	101.0	101.1	101.0	112.8	110.3	111.5	106.9	105.7	106.3
HI 17-4	98.9	102.7	100.8	112.2	111.3	111.8	105.5	107.0	106.3
HI 41-4	101.2	102.1	101.6	110.3	112.5	111.4	105.7	107.3	106.5
HI 8-4	106.0	102.1	104.0	111.9	111.6	111.8	109.0	106.8	107.9
HI 30-2	99.5	99.8	99.6	112.3	110.0	111.2	105.9	104.9	105.4
HI 14-4	100.9	103.5	102.2	111.2	111.6	111.4	106.0	107.5	106.8
HI 30-3	95.1	99.5	97.3	109.3	110.3	109.8	102.2	104.9	103.5
HI 44-3	96.2	101.6	98.9	112.0	108.8	110.4	104.1	105.2	104.6
LO 3-4	96.3	95.8	96.1	109.2	106.3	107.7	102.8	101.0	101.9
LO 16-3	95.0	97.4	96.2	109.2	108.5	108.8	102.1	103.0	102.5
LO 13-3	95.5	94.4	95.0	106.0	106.3	106.1	100.8	100.3	100.5
LO 43-2	94.9	93.6	94.2	106.3	105.3	105.8	100.6	99.5	100.0
LO 44-2	101.7	100.6	101.1	110.5	112.9	111.7	106.1	106.8	106.4
LO 27-4	94.0	95.5	94.7	106.8	105.5	106.2	100.4	100.5	100.5
LO 8-3	96.9	98.5	97.7	108.4	110.3	109.3	102.7	104.4	103.5
LO 16-1	97.4	100.1	98.8	110.4	111.3	110.8	103.9	105.7	104.8
RA 8-0	101.9	102.9	102.4	111.9	112.6	112.3	106.9	107.8	107.3
RA 13-0	102.2	107.9	105.0	111.4	115.2	113.3	106.8	111.5	109.2
RA 1-0	100.5	98.0	99.3	109.8	110.8	110.3	105.2	104.4	104.8
RA 1-5	94.6	96.9	95.7	109.0	108.8	108.9	101.8	102.9	102.3
RA 4-0	100.1	102.4	101.3	113.1	111.3	112.2	106.6	106.8	106.7
RA 16-5	96.9	101.3	99.1	109.7	110.2	109.9	103.3	105.7	104.5
RA 3-0	98.3	104.8	101.5	109.3	109.8	109.6	103.8	107.3	105.6
RA 3-5	102.1	100.0	101.0	113.4	114.8	114.1	107.8	107.4	107.6
TAM W-101	103.3	110.6	107.0	112.4	111.1	111.8	107.9	110.8	109.4
Sturdy	98.4	97.7	98.1	110.0	108.1	109.0	104.2	102.9	103.6

Heading date:the date when the first spikelet of a plant became visible.
High or HI, Low or LO, and Random or RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 11

AVERAGE FLAG LEAF SENESCENCE DATE OF TAM W-101, STURDY AND THEIR F3 (1986) AND F4 (1987) PROGENY

	1986			1987			Two year average		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	days from January 1								
Grand mean	124.5	128.5	126.5	134.9	141.6	138.2	129.7	135.0	132.3
Selection groups									
High	125.6	129.4	127.5	135.2	141.6	138.4	130.4	135.5	132.9
Low	123.2	125.9	124.6	134.3	140.5	137.4	128.8	133.2	131.0
Random	124.7	129.6	127.1	134.8	142.4	138.6	129.7	136.0	132.8
Parents	124.0	130.8	127.4	136.2	142.8	139.5	130.1	136.8	133.5
Individual lines									
HI 4-1	125.5	128.9	127.2	136.3	141.7	139.0	130.9	135.3	133.1
HI 17-4	124.4	130.4	127.4	135.9	141.4	138.7	130.2	135.9	133.0
HI 41-4	123.7	127.6	125.7	133.0	139.7	136.4	128.4	133.7	131.0
HI 8-4	129.2	129.5	129.3	136.7	143.9	140.3	132.9	136.7	134.8
HI 30-2	127.0	128.4	127.7	135.6	141.6	138.6	131.3	135.0	133.1
HI 14-4	126.7	129.9	128.3	134.7	141.5	138.1	130.7	135.7	133.2
HI 30-3	125.0	128.8	126.9	135.2	142.1	138.7	130.1	135.5	132.8
HI 44-3	123.3	131.3	127.3	134.3	140.4	137.4	128.8	135.9	132.4
LO 3-4	122.4	125.7	124.0	136.6	140.9	138.7	129.5	133.3	131.4
LO 16-3	123.2	127.2	125.2	134.3	139.5	136.9	128.8	133.4	131.1
LO 13-3	123.2	123.9	123.5	133.6	140.1	136.8	128.4	132.0	130.2
LO 43-2	125.2	126.4	125.8	134.0	139.9	137.0	129.6	133.2	131.4
LO 44-2	126.2	128.4	127.3	135.6	142.7	139.1	130.9	135.5	133.2
LO 27-4	118.2	122.2	120.2	132.9	139.2	136.1	125.5	130.7	128.1
LO 8-3	122.8	126.2	124.5	132.5	139.4	136.0	127.7	132.8	130.2
LO 16-1	124.7	127.4	126.0	134.9	142.1	138.5	129.8	134.7	132.3
RA 8-0	123.3	128.6	126.0	133.7	141.3	137.5	128.5	135.0	131.7
RA 13-0	126.7	133.3	130.0	135.3	145.1	140.2	131.0	139.2	135.1
RA 1-0	124.5	126.0	125.2	132.7	141.7	137.2	128.6	133.9	131.2
RA 1-5	122.7	129.6	126.1	134.5	140.7	137.6	128.6	135.2	131.9
RA 4-0	127.3	130.8	129.1	137.7	143.9	140.8	132.5	137.4	134.9
RA 16-5	123.5	130.0	126.7	133.7	140.2	137.0	128.6	135.1	131.9
RA 3-0	124.4	131.4	127.9	135.7	142.7	139.2	130.0	137.0	133.5
RA 3-5	124.8	126.9	125.9	135.0	143.2	139.1	129.9	135.1	132.5
TAM W-101	126.0	135.3	130.7	136.7	144.9	140.8	131.3	140.1	135.7
Sturdy	121.9	126.2	124.1	135.8	140.7	138.3	128.9	133.5	131.2

Flag leaf senescence date:the date when 50% of flag leaves of a plant senesced.
High or HI, Low or LO, and Random or RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 12

AVERAGE FLAG LEAF DURATION OF TAM W-101, STURDY AND THEIR F3 (1986) AND F4 (1987) PROGENY

	1986			1987			Two year average		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	days								
Grand mean	25.7	28.1	26.9	24.5	31.4	28.0	25.1	29.7	27.4
Selection groups									
High	25.8	27.8	26.8	23.7	30.8	27.2	24.8	29.3	27.0
Low	26.8	28.9	27.9	26.0	32.2	29.1	26.4	30.6	28.5
Random	25.1	27.8	26.4	23.8	30.7	27.3	24.5	29.3	26.9
Parents	23.1	26.6	24.9	25.0	33.2	29.1	24.1	29.9	27.0
Individual lines									
HI 4-1	24.5	27.8	26.2	23.6	31.5	27.5	24.0	29.7	26.9
HI 17-4	25.5	27.8	26.6	23.8	30.1	26.9	24.6	28.9	26.8
HI 41-4	22.6	25.6	24.1	22.8	27.3	25.0	22.7	26.4	24.5
HI 8-4	23.2	27.4	25.3	24.8	32.3	28.5	24.0	29.9	26.9
HI 30-2	27.5	28.7	28.1	23.3	31.6	27.4	25.4	30.1	27.8
HI 14-4	25.8	26.4	26.1	23.5	29.9	26.7	24.6	28.2	26.4
HI 30-3	29.9	29.3	29.6	26.0	31.8	28.9	28.0	30.5	29.3
HI 44-3	27.2	29.8	28.5	22.3	31.6	27.0	24.8	30.7	27.7
LO 3-4	26.1	29.8	28.0	27.4	34.7	31.0	26.8	32.2	29.5
LO 16-3	28.3	29.8	29.0	25.2	31.0	28.1	26.7	30.4	28.6
LO 13-3	27.7	29.5	28.6	27.6	33.8	30.7	27.6	31.7	29.6
LO 43-2	30.3	32.8	31.6	27.8	34.6	31.2	29.0	33.7	31.4
LO 44-2	24.6	27.8	26.2	25.1	29.8	27.4	24.8	28.8	26.8
LO 27-4	24.2	26.7	25.4	26.1	33.7	29.9	25.1	30.2	27.7
LO 8-3	25.9	27.7	26.8	24.1	29.2	26.6	25.0	28.4	26.7
LO 16-1	27.3	27.3	27.3	24.5	30.8	27.7	25.9	29.1	27.5
RA 8-0	21.4	25.7	23.5	21.8	28.8	25.3	21.6	27.2	24.4
RA 13-0	24.5	25.4	25.0	23.9	29.9	26.9	24.2	27.7	25.9
RA 1-0	24.0	28.0	26.0	22.8	31.0	26.9	23.4	29.5	26.5
RA 1-5	28.1	32.7	30.4	25.5	31.9	28.7	26.8	32.3	29.5
RA 4-0	27.3	28.4	27.8	24.6	32.7	28.6	25.9	30.5	28.2
RA 16-5	26.6	28.8	27.7	24.0	30.1	27.0	25.3	29.4	27.4
RA 3-0	26.2	26.6	26.4	26.3	32.8	29.6	26.3	29.7	28.0
RA 3-5	22.8	26.9	24.8	21.6	28.5	25.0	22.2	27.7	24.9
TAM W-101	22.7	24.8	23.7	24.3	33.8	29.0	23.5	29.3	26.4
Sturdy	23.5	28.5	26.0	25.8	32.7	29.3	24.7	30.6	27.6

Flag leaf duration:the number of days between heading and flag leaf senescence.
High or HI, Low or LO, and Random or RA:high-yield, low-yield selections, and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 13

AVERAGE PLANT HEIGHT AT HARVEST OF TAM W-101, STURDY AND THEIR F3 (1986) AND F4 (1987) PROGENY

	1986			1987			Two year average		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	cm								
Grand mean	56.0	59.1	57.5	72.5	79.5	76.0	64.2	69.3	66.8
Selection groups									
High	57.2	60.5	58.8	74.6	82.8	78.7	65.9	71.7	68.8
Low	54.6	57.6	56.1	71.4	76.9	74.2	63.0	67.3	65.1
Random	55.5	59.1	57.3	71.3	78.2	74.7	63.4	68.7	66.0
Parents	58.3	59.7	59.0	73.5	81.8	77.7	65.9	70.8	68.3
Individual lines									
HI 4-1	60.4	60.3	60.4	75.2	84.0	79.6	67.8	72.2	70.0
HI 17-4	55.3	59.9	57.6	72.9	94.8	83.9	64.1	77.4	70.7
HI 41-4	64.0	66.5	65.2	87.2	101.7	94.5	75.6	84.1	79.9
HI 8-4	53.7	59.6	56.6	68.0	77.7	72.9	60.8	68.7	64.7
HI 30-2	55.4	55.6	55.5	73.2	72.7	73.0	64.3	64.1	64.2
HI 14-4	56.4	64.5	60.5	86.2	84.2	85.2	71.3	74.4	72.9
HI 30-3	48.2	50.7	49.5	57.7	61.9	59.8	53.0	56.3	54.6
HI 44-3	63.9	66.9	65.4	76.7	85.2	81.0	70.3	76.1	73.2
LO 3-4	51.7	55.2	53.5	61.9	64.6	63.2	56.8	59.9	58.4
LO 16-3	58.4	60.7	59.5	69.0	91.7	80.4	63.7	76.2	70.0
LO 13-3	43.7	47.8	45.7	57.5	61.2	59.4	50.6	54.5	52.6
LO 43-2	49.9	56.7	53.3	70.2	71.5	70.8	60.0	64.1	62.1
LO 44-2	60.3	61.7	61.0	74.8	81.3	78.1	67.6	71.5	69.5
LO 27-4	52.2	58.7	55.4	76.1	81.7	78.9	64.1	70.2	67.2
LO 8-3	68.6	72.3	70.5	96.1	97.2	96.7	82.3	84.8	83.6
LO 16-1	51.8	48.0	49.9	65.9	65.7	65.8	58.9	56.9	57.9
RA 8-0	63.9	71.0	67.5	86.6	101.5	94.0	75.2	86.2	80.7
RA 13-0	54.1	55.0	54.5	66.8	64.8	65.8	60.5	59.9	60.2
RA 1-0	54.3	58.8	56.6	68.6	82.9	75.7	61.5	70.9	66.2
RA 1-5	52.8	57.0	54.9	70.5	65.8	68.2	61.7	61.4	61.5
RA 4-0	43.8	47.2	45.5	50.8	58.4	54.6	47.3	52.8	50.1
RA 16-5	61.3	66.2	63.7	89.7	91.8	90.7	75.5	79.0	77.2
RA 3-0	45.7	52.2	49.0	60.7	71.5	66.1	53.2	61.8	57.5
RA 3-5	68.2	65.7	67.0	76.4	88.9	82.7	72.3	77.3	74.8
TAM W-101	60.0	54.8	57.4	74.2	81.3	77.8	67.1	68.1	67.6
Sturdy	56.6	64.7	60.6	72.7	82.3	77.5	64.7	73.5	69.1

High or HI, Low or LO, and Random or RA:high-yield, low-yield selections,and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 14

AVERAGE STOMATAL CONDUCTANCE, LEAF AREA, AND RELATIVE WATER CONTENT OF TAM W-101, STURDY AND THEIR F4 (1987) PROGENY

	Stomatal conductance			Leaf area			Relative water content		
	Stress levels		Mean	Stress levels		Mean	Stress levels		Mean
	DRY	WET		DRY	WET		DRY	WET	
	mol/m^2s			cm^2			%		
Grand mean	0.031	0.122	0.077	20.16	21.31	20.73	83.2	86.1	84.7
Selection groups									
High	0.037	0.125	0.081	20.71	21.75	21.23	83.8	86.7	85.3
Low	0.030	0.125	0.077	20.39	20.40	20.40	82.6	85.3	83.9
Random	0.027	0.119	0.073	19.43	20.84	20.14	82.8	86.1	84.5
Parents	0.031	0.115	0.073	19.94	24.96	22.45	85.1	87.2	86.2
Individual lines									
HI 4-1	0.059	0.084	0.072	24.35	20.83	22.59	86.7	84.7	85.7
HI 17-4	0.036	0.165	0.101	17.66	25.29	21.48	84.1	86.5	85.3
HI 41-4	0.059	0.130	0.094	19.56	19.33	19.45	83.3	88.1	85.7
HI 8-4	0.034	0.091	0.062	19.26	20.77	20.02	83.8	90.9	87.3
HI 30-2	0.028	0.135	0.081	21.02	21.13	21.07	85.3	87.1	86.2
HI 14-4	0.031	0.112	0.071	22.42	22.84	22.63	82.2	86.4	84.3
HI 30-3	0.025	0.082	0.054	19.60	18.49	19.05	81.9	86.5	84.2
HI 44-3	0.024	0.203	0.114	21.78	25.34	23.56	83.5	83.3	83.4
LO 3-4	0.036	0.106	0.071	22.96	21.97	22.47	85.2	87.7	86.5
LO 16-3	0.043	0.090	0.066	17.70	19.96	18.83	80.1	86.5	83.3
LO 13-3	0.015	0.167	0.091	20.82	20.20	20.51	85.8	84.3	85.1
LO 43-2	0.045	0.147	0.096	21.89	19.53	20.71	80.0	84.4	82.2
LO 44-2	0.028	0.127	0.077	19.11	23.69	21.40	79.7	85.0	82.4
LO 27-4	0.026	0.125	0.075	22.13	22.93	22.53	85.5	85.2	85.3
LO 8-3	0.032	0.090	0.061	21.17	19.37	20.27	81.9	82.2	82.1
LO 16-1	0.014	0.145	0.080	17.35	15.58	16.46	82.8	86.7	84.7
RA 8-0	0.031	0.162	0.096	19.99	19.70	19.84	82.0	84.3	83.1
RA 13-0	0.034	0.152	0.093	17.05	16.54	16.80	83.0	85.7	84.4
RA 1-0	0.007	0.152	0.080	22.15	38.53	30.34	82.4	84.9	83.6
RA 1-5	0.034	0.066	0.050	19.86	18.68	19.27	85.4	87.9	86.6
RA 4-0	0.028	0.105	0.067	14.32	15.41	14.86	85.1	84.3	84.7
RA 16-5	0.038	0.106	0.072	23.59	22.34	22.96	82.8	88.0	85.4
RA 3-0	0.020	0.096	0.058	19.60	21.48	20.54	78.7	87.5	83.1
RA 3-5	0.024	0.115	0.070	18.92	14.09	16.50	83.1	86.6	84.8
TAM W-101	0.029	0.137	0.083	18.91	20.78	19.84	85.3	88.0	86.6
Sturdy	0.033	0.093	0.063	20.98	29.14	25.06	85.0	86.4	85.7

All data were taken from two out of four plants in a plot row at anthesis (April 27 to 29, 1987).
High or HI, Low or LO, and Random or RA:high-yield, low-yield selections,and random lines, respectively.
DRY and WET:drought-stressed and well-watered, respectively.

TABLE 15

AVERAGE STOMATAL CONDUCTANCE AND LEAF AREA OF TAM W-101, STURDY AND THEIR F4 (1987) PROGENY

	Stomatal conductance	Leaf area
	--mol/m^2s--	--cm^2--
Grand mean	0.060	16.53
Selection groups		
High	0.065	16.54
Low	0.063	16.58
Random	0.045	16.56
Parents	0.086	16.21
Individual lines		
HI 4-1	0.055	16.52
HI 17-4	0.092	16.37
HI 41-4	0.057	12.79
HI 8-4	0.043	17.08
HI 30-2	0.084	16.90
HI 14-4	0.045	18.07
HI 30-3	0.051	17.87
HI 44-3	0.093	16.71
LO 3-4	0.082	17.91
LO 16-3	0.071	15.70
LO 13-3	0.060	17.50
LO 43-2	0.080	14.18
LO 44-2	0.051	19.19
LO 27-4	0.071	14.22
LO 8-3	0.038	17.80
LO 16-1	0.050	16.13
RA 8-0	0.072	14.63
RA 13-0	0.018	16.62
RA 1-0	0.063	18.16
RA 1-5	0.022	15.72
RA 4-0	0.022	13.84
RA 16-5	0.072	23.89
RA 3-0	0.048	13.95
RA 3-5	0.045	15.69
TAM W-101	0.100	16.99
Sturdy	0.072	15.42

All data were taken from well-watered plots at mid grain fill (May 11 to 13, 1987). High or HI, Low or LO, and Random or RA:high-yield, low-yield selections, and random lines, respectively.

TABLE 16

PHENOTYPIC CORRELATION COEFFICIENTS BETWEEN PLANT MATURITY AND AGRONOMIC TRAITS, AND THEIR OBSERVED SIGNIFICANT LEVEL (OSL) VALUES (POOLED OVER STRESS LEVELS AND YEARS)

	HEAD	SCN	LFDR	HEIGHT	TTLWT	HVINDX	YLD	SPIKE	KNLSP	KNLWT
HEAD	1.00000	0.78538	-0.76233	0.23694	0.58328	-0.59885	0.42461	0.57901	-0.32041	0.03698
	0.0	0.0001	0.0001	0.2438	0.0018	0.0012	0.0306	0.0019	0.1105	0.8576
SCN	0.78538	1.00000	-0.19810	-0.25757	0.39511	-0.07654	0.38366	0.64527	-0.26111	-0.13981
	0.0001	0.0	0.3320	0.2040	0.0457	0.7102	0.0530	0.0004	0.1976	0.4958
LFDR	-0.76233	-0.19810	1.00000	-0.64448	-0.51050	0.86824	-0.27123	-0.24219	0.23436	-0.20474
	0.0001	0.3320	0.0	0.0004	0.0077	0.0001	0.1802	0.2332	0.2492	0.3157
HEIGHT	0.23694	-0.25757	-0.64448	1.00000	0.34788	-0.68598	0.14761	-0.20624	-0.25127	0.70681
	0.2438	0.2040	0.0004	0.0	0.0816	0.0001	0.4718	0.3121	0.2156	0.0001
TTLWT	0.58328	0.39511	-0.51050	0.34788	1.00000	-0.46259	0.95066	0.76866	0.02171	0.24834
	0.0018	0.0457	0.0077	0.0816	0.0	0.0173	0.0001	0.0001	0.9162	0.2212
HVINDX	-0.59885	-0.07654	0.86824	-0.68598	-0.46259	1.00000	-0.18694	-0.11790	0.25714	-0.30226
	0.0012	0.7102	0.0001	0.0001	0.0173	0.0	0.3605	0.5662	0.2048	0.1334
YLD	0.42461	0.38366	-0.27123	0.14761	0.95066	-0.18694	1.00000	0.80371	0.17536	0.13668
	0.0306	0.0530	0.1802	0.4718	0.0001	0.3605	0.0	0.0001	0.3915	0.5055
SPIKE	0.57901	0.64527	-0.24219	-0.20624	0.76866	-0.11790	0.80371	1.00000	-0.07386	-0.18242
	0.0019	0.0004	0.2332	0.3121	0.0001	0.5662	0.0001	0.0	0.7199	0.3724

TABLE 16 (Continued)

	HEAD	SCN	LFDR	HEIGHT	TTLWT	HVINDX	YLD	SPIKE	KNLSP	KNLWT
KNLSP	-0.32041	-0.26111	0.23436	-0.25127	0.02171	0.25714	0.17536	-0.07386	1.00000	-0.54376
	0.1105	0.1976	0.2492	0.2156	0.9162	0.2048	0.3915	0.7199	0.0	0.0041
KNLWT	0.03698	-0.13981	-0.20474	0.70681	0.24834	-0.30226	0.13668	-0.18242	-0.54376	1.00000
	0.8576	0.4958	0.3157	0.0001	0.2212	0.1334	0.5055	0.3724	0.0041	0.0

OSL values were determined under the null hypothesis that a correlation coefficient was 0.
HEAD:heading date, SCN:flag leaf senescence date, LFDR:flag leaf duration, HEIGHT:plant height at harvest, TTLWT:total plant weight at harvest, HVINDX:harvest index, YLD:grain yield per plant, SPIKE:spike number per plant, KNLSP:kernel number per spike, and KNLWT:kernel weight.

TABLE 17

PHENOTYPIC CORRELATION COEFFICIENTS BETWEEN PHYSIOLOGICAL AND AGRONOMIC TRAITS, AND THEIR OBSERVED SIGNIFICANT LEVEL (OSL) VALUES (POOLED OVER STRESS LEVELS IN 1987)

	CD_ANTH	LA_ANTH	RWC_ANTH	HEAD	SCN	LFDR	HEIGHT
CD_ANTH	1.00000	0.12624	-0.14281	0.02512	-0.21241	-0.21750	0.24247
	0.0	0.5389	0.4865	0.9030	0.2975	0.2858	0.2327
LA_ANTH	0.12624	1.00000	-0.03604	-0.43953	-0.41070	0.22571	0.22871
	0.5389	0.0	0.8613	0.0247	0.0371	0.2676	0.2611
RWC_ANTH	-0.14281	-0.03604	1.00000	0.07146	0.35143	0.21021	-0.17230
	0.4865	0.8613	0.0	0.7287	0.0783	0.3027	0.4000
HEAD	0.02512	-0.43953	0.07146	1.00000	0.65539	-0.75554	0.17893
	0.9030	0.0247	0.7287	0.0	0.0003	0.0001	0.3818
SCN	-0.21241	-0.41070	0.35143	0.65539	1.00000	-0.00039	-0.33906
	0.2975	0.0371	0.0783	0.0003	0.0	0.9985	0.0902
LFDR	-0.21750	0.22571	0.21021	-0.75554	-0.00039	1.00000	-0.53100
	0.2858	0.2676	0.3027	0.0001	0.9985	0.0	0.0053
HEIGHT	0.24247	0.22871	-0.17230	0.17893	-0.33906	-0.53100	1.00000
	0.2327	0.2611	0.4000	0.3818	0.0902	0.0053	0.0
TTLWT	0.02974	0.32593	0.12322	0.32228	0.34964	-0.12344	0.35092
	0.8853	0.1042	0.5487	0.1083	0.0800	0.5480	0.0788

TABLE 17 (Continued)

	CD_ANTH	LA_ANTH	RWC_ANTH	HEAD	SCN	LFDR	HEIGHT
HVINDX	-0.13031	-0.07675	-0.03285	-0.56170	-0.02478	0.72219	-0.54216
	0.5258	0.7094	0.8734	0.0028	0.9043	0.0001	0.0042
YLD	-0.03295	0.34961	0.13963	0.17952	0.37532	0.08784	0.20825
	0.8731	0.0800	0.4963	0.3802	0.0588	0.6696	0.3073
SPIKE	-0.14406	-0.08158	0.18755	0.32800	0.62462	0.10749	-0.21313
	0.4826	0.6920	0.3589	0.1019	0.0006	0.6012	0.2958
KNLSP	-0.09692	0.43542	0.10016	-0.03143	0.13150	0.15567	-0.12205
	0.6377	0.0262	0.6264	0.8789	0.5220	0.4476	0.5526
KNLWT	0.20831	0.19120	-0.17738	-0.16870	-0.44078	-0.15895	0.73292
	0.3072	0.3495	0.3860	0.4100	0.0242	0.4380	0.0001

TABLE 17 (Continued)

	TTLWT	HVINDX	YLD	SPIKE	KNLSP	KNLWT
CD_ANTH	0.02974	-0.13031	-0.03295	-0.14406	-0.09692	0.20831
	0.8853	0.5258	0.8731	0.4826	0.6377	0.3072
LA_ANTH	0.32593	-0.07675	0.34961	-0.08158	0.43542	0.19120
	0.1042	0.7094	0.0800	0.6920	0.0262	0.3495
RWC_ANTH	0.12322	-0.03285	0.13963	0.18755	0.10016	-0.17738
	0.5487	0.8734	0.4963	0.3589	0.6264	0.3860
HEAD	0.32228	-0.56170	0.17952	0.32800	-0.03143	-0.16870
	0.1083	0.0028	0.3802	0.1019	0.8789	0.4100
SCN	0.34964	-0.02478	0.37532	0.62462	0.13150	-0.44078
	0.0800	0.9043	0.0588	0.0006	0.5220	0.0242
LFDR	-0.12344	0.72219	0.08784	0.10749	0.15567	-0.15895
	0.5480	0.0001	0.6696	0.6012	0.4476	0.4380
HEIGHT	0.35092	-0.54216	0.20825	-0.21313	-0.12205	0.73292
	0.0788	0.0042	0.3073	0.2958	0.5526	0.0001
TTLWT	1.00000	-0.46584	0.95962	0.74766	0.31995	0.10306
	0.0	0.0165	0.0001	0.0001	0.1111	0.6164
HVINDX	-0.46584	1.00000	-0.21847	-0.18054	0.16293	-0.19477
	0.0165	0.0	0.2836	0.3775	0.4265	0.3403

TABLE 17 (Continued)

	TTLWT	HVINDX	YLD	SPIKE	KNLSP	KNLWT
YLD	0.95962	-0.21847	1.00000	0.76108	0.44160	0.03237
	0.0001	0.2836	0.0	0.0001	0.0239	0.8753
SPIKE	0.74766	-0.18054	0.76108	1.00000	0.14655	-0.34872
	0.0001	0.3775	0.0001	0.0	0.4750	0.0808
KNLSP	0.31995	0.16293	0.44160	0.14655	1.00000	-0.48412
	0.1111	0.4265	0.0239	0.4750	0.0	0.0122
KNLWT	0.10306	-0.19477	0.03237	-0.34872	-0.48412	1.00000
	0.6164	0.3403	0.8753	0.0808	0.0122	0.0

OSL values were determined under the null hypothesis that a correlation coefficient was 0.
Data from two out of four plants in a plot row were used for calculation.
CD_ANTH:stomatal conductance at anthesis (April 27 to 29, 1987), LA_ANTH:area of a flag leaf on which stomatal conductance at anthesis was estimated, RWC_ANTH:relative water content of a leaf on which stomatal conductance at anthesis was estimated, HEAD:heading date, SCN:flag leaf senescence date, LFDR:flag leaf duration, HEIGHT:plant height at harvest, TTLWT:total plant weight at harvest, HVINDX:harvest index, YLD:grain yield per plant, SPIKE:spike number per plant, KNLSP:kernel number per spike, and KNLWT:kernel weight.

TABLE 18

PHENOTYPIC CORRELATION COEFFICIENTS BETWEEN PHYSIOLOGICAL AND AGRONOMIC TRAITS, AND THEIR OBSERVED SIGNIFICANT LEVEL (OSL) VALUES (POOLED OVER REPS IN WELL-WATERED PLOTS IN 1987)

	CD_MGF	LA_MGF	RWC_MGF	HEAD	SCN	LFDR	HEIGHT
CD_MGF	1.00000	0.35554	0.01109	-0.27292	-0.25666	0.13870	0.36627
	0.0	0.0747	0.9571	0.1774	0.2056	0.4992	0.0657
LA_MGF	0.35554	1.00000	-0.10632	-0.22927	-0.22237	0.11077	0.24412
	0.0747	0.0	0.6052	0.2599	0.2749	0.5901	0.2294
RWC_MGF	0.01109	-0.10632	1.00000	-0.30359	-0.01617	0.38361	-0.21267
	0.9571	0.6052	0.0	0.1316	0.9375	0.0530	0.2969
HEAD	-0.27292	-0.22927	-0.30359	1.00000	0.64523	-0.75956	0.26256
	0.1774	0.2599	0.1316	0.0	0.0004	0.0001	0.1950
SCN	-0.25666	-0.22237	-0.01617	0.64523	1.00000	0.00684	-0.35196
	0.2056	0.2749	0.9375	0.0004	0.0	0.9735	0.0779
LFDR	0.13870	0.11077	0.38361	-0.75956	0.00684	1.00000	-0.64331
	0.4992	0.5901	0.0530	0.0001	0.9735	0.0	0.0004
HEIGHT	0.36627	0.24412	-0.21267	0.26256	-0.35196	-0.64331	1.00000
	0.0657	0.2294	0.2969	0.1950	0.0779	0.0004	0.0
TTLWT	0.25206	0.41281	-0.20280	0.44785	0.47452	-0.18219	0.31085
	0.2142	0.0361	0.3204	0.0218	0.0143	0.3730	0.1222

TABLE 18 (Continued)

	CD_MGF	LA_MGF	RWC_MGF	HEAD	SCN	LFDR	HEIGHT
HVINDX	-0.03740	-0.01928	0.24727	-0.63819	-0.16579	0.69417	-0.65182
	0.8561	0.9255	0.2233	0.0005	0.4183	0.0001	0.0003
YLD	0.26188	0.46316	-0.14482	0.24571	0.43418	0.04805	0.12818
	0.1962	0.0172	0.4803	0.2263	0.0267	0.8157	0.5326
SPIKE	-0.17568	0.03720	0.04964	0.35140	0.71823	0.15154	-0.26036
	0.3906	0.8568	0.8097	0.0784	0.0001	0.4599	0.1989
KNLSP	0.08445	0.47864	-0.51336	-0.08302	0.06366	0.16286	-0.13053
	0.6817	0.0134	0.0073	0.6868	0.7574	0.4267	0.5250
KNLWT	0.55025	0.18366	0.18846	-0.04072	-0.42892	-0.31187	0.67753
	0.0036	0.3691	0.3565	0.8434	0.0288	0.1209	0.0001

TABLE 18 (Continued)

	TTLWT	HVINDX	YLD	SPIKE	KNLSP	KNLWT
CD_MGF	0.25206	-0.03740	0.26188	-0.17568	0.08445	0.55025
	0.2142	0.8561	0.1962	0.3906	0.6817	0.0036
LA_MGF	0.41281	-0.01928	0.46316	0.03720	0.47864	0.18366
	0.0361	0.9255	0.0172	0.8568	0.0134	0.3691
RWC_MGF	-0.20280	0.24727	-0.14482	0.04964	-0.51336	0.18846
	0.3204	0.2233	0.4803	0.8097	0.0073	0.3565
HEAD	0.44785	-0.63819	0.24571	0.35140	-0.08302	-0.04072
	0.0218	0.0005	0.2263	0.0784	0.6868	0.8434
SCN	0.47452	-0.16579	0.43418	0.71823	0.06366	-0.42892
	0.0143	0.4183	0.0267	0.0001	0.7574	0.0288
LFDR	-0.18219	0.69417	0.04805	0.15154	0.16286	-0.31187
	0.3730	0.0001	0.8157	0.4599	0.4267	0.1209
HEIGHT	0.31085	-0.65182	0.12818	-0.26036	-0.13053	0.67753
	0.1222	0.0003	0.5326	0.1989	0.5250	0.0001
TTLWT	1.00000	-0.41937	0.93651	0.71361	0.31827	0.09898
	0.0	0.0330	0.0001	0.0001	0.1131	0.6305
HVINDX	-0.41937	1.00000	-0.09064	-0.06178	0.37109	-0.35897
	0.0330	0.0	0.6597	0.7643	0.0620	0.0717

TABLE 18 (Continued)

	TTLWT	HVINDX	YLD	SPIKE	KNLSP	KNLWT
YLD	0.93651	-0.09064	1.00000	0.74794	0.51606	-0.02638
	0.0001	0.6597	0.0	0.0001	0.0070	0.8982
SPIKE	0.71361	-0.06178	0.74794	1.00000	0.18837	-0.43619
	0.0001	0.7643	0.0001	0.0	0.3568	0.0259
KNLSP	0.31827	0.37109	0.51606	0.18837	1.00000	-0.42524
	0.1131	0.0620	0.0070	0.3568	0.0	0.0303
KNLWT	0.09898	-0.35897	-0.02638	-0.43619	-0.42524	1.00000
	0.6305	0.0717	0.8982	0.0259	0.0303	0.0

OSL values were determined under the null hypothesis that a correlation coefficient was 0. CD_MGF:stomatal conductance at mid grain-fill (May 11 to 13, 1987), LA_MGF:area of a flag leaf on which stomatal conductance at mid grain-fill was estimated, RWC_MGF:relative water content of a leaf on which stomatal conductance at mid grain-fill was estimated, HEAD:heading date, SCN:flag leaf senescence date, LFDR:flag leaf duration, HEIGHT:plant height at harvest, TTLWT:total plant weight at harvest, HVINDX:harvest index, YLD:grain yield per plant, SPIKE:spike number per plant, KNLSP:kernel number per spike, and KNLWT:kernel weight.

TABLE 19

VOLUMETRIC WATER CONTENT AT VARIOUS DEPTH IN THE SOIL PROFILE OF EXPERIMENTAL PLOTS UNDER A RAIN SHELTER

Year	Days	Stress levels	Depth (cm)							
			15	30	45	60	75	90	105	120
			%							
1986	77	Dry	33.9	38.1	38.0	38.4	38.1	38.8	38.3	38.2
	77	Wet	36.4	38.7	39.1	37.2	37.4	37.6	37.2	37.6
	86	Dry	24.5	35.5	36.4	37.0	37.6	38.5	38.2	38.2
	86	Wet	31.0	37.3	37.8	37.9	38.5	37.6	37.3	37.4
	99	Dry	21.4	33.2	34.0	35.9	37.0	38.4	39.3	39.5
	99	Wet	31.2	37.4	37.8	37.5	37.5	38.2	38.5	38.4
	107	Dry	17.4	31.7	32.5	33.4	35.7	37.2	37.4	38.0
	107	Wet	28.8	36.2	36.4	36.3	36.6	37.6	37.9	37.6
	121	Dry	17.0	30.1	30.5	31.9	33.3	35.6	36.8	37.3
	121	Wet	31.5	37.4	37.3	37.1	36.2	37.6	37.8	.
	128	Dry	16.7	29.0	30.0	30.3	32.5	34.8	36.1	37.1
	128	Wet	31.9	36.6	35.6	35.8	36.3	37.3	37.3	37.4
	142	Dry	15.8	29.1	29.8	31.0	32.6	34.9	36.5	37.8
	142	Wet	32.3	37.3	36.5	36.7	36.4	37.6	38.7	38.8
1987	132	Dry	21.0	26.3	25.8	26.1	28.0	30.9	32.9	.
	132	Wet	29.8	29.0	28.9	27.6	30.1	32.8	34.7	.

Days:days from January 1.
Dry and wet:drought-stressed and well-watered conditions, respectively

VITA

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