PLEIOTROPIC EFFECTS OF AWN SUPPRESSION IN HARD RED WINTER WHEAT

By

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INTRODUCTION

Each chapter in this thesis conforms to the Publications Handbook and Style Manual of the American Society of Agronomy. Chapters will be submitted for publication in Crop Science, a Crop Science Society of America publication.

An appendix has also been provided at the end of the thesis. The appendix provides additional information concerning data analysis and results for various experiments but is not intended to be a part of either manuscript.

CHAPTER I

EFFECTS OF AWNS ON VARIOUS AGRONOMIC AND PHYSIOLOGICAL CHARACTERISTICS OF SMALL GRAINS: A LITERATURE REVIEW

INTRODUCTION

Hard red winter (HRW) wheat (*Triticum aestivum L.*) is a very important crop to Oklahoma and the southern Great Plains, ranking second only to beef cattle and calf production in agricultural income in Oklahoma (OK Dept. Ag., 1990). However, the dollar value of beef cattle is derived in part from wheat since beef cattle graze on wheat pasture in late fall, winter, and early spring. Throughout the southern Great Plains, awned wheat cultivars have traditionally prevailed. Awnless wheat could provide a source of highly palatable late season forage for this area, or it could be harvested for grain if the awnless characteristic was present in a desirable HRW background.

The wheat awn is a rudimentary leaf, of which little remains except the midrib. It is triangular in cross-section, and the two outer faces have many stomata (Lamb, 1967). The awns presumably compensate for reduced flag leaf photosynthesis during extreme drought stress or severe disease infections, and may contribute to water-use efficiency of the wheat plant. Awnless wheat cultivars have generally prevailed in the cooler, wetter regions of the U. S. such as the Pacific Northwest and the Southeast, while awned cultivars have prevailed in the hot, dry, southern Plains and Southwest. However, some producers in the southern Great Plains have recently preferred adapted awnless cultivars in graze-out situations where the wheat is grazed even past heading or harvested for hay. When the cattle graze wheat or eat wheat hay from awned plants, the awns may cause irritations to their mouth and eyes which, in turn, results in less forage consumption. Thus, many producers would prefer an awnless cultivar which could be utilized for cattle production without irritations and without grain yield loss if the field is left to mature.

Previous research on the relative attributes of awns has been concentrated in the cooler and wetter locations, and with spring and soft wheat. Also, comparisons of awned vs. awnless cultivars have often suffered confounding effects of genetic background. These investigations have given mixed results with respect to the value of the awned condition.

The uncertain effect of awnlessness in currently adapted hard red winter wheat varieties in the southern Great Plains prompted this investigation. Of primary concern are several agronomic traits, including grain yield, test weight, kernel weight, and quality characters like protein content and kernel hardness. Photosynthesis as well as season-long and instantaneous water-use efficiency, were also evaluated.

LITERATURE REVIEW

Awn Morphology and Genetic Control

Awn production in wheat has been widely studied for its physiological and agronomic contributions. The cereal awn is a rudimentary leaf of which little remains except the midrib (Lamb, 1967). The cereal awn contains many functional stomata on the outer two sides (Grundbacher, 1963; Lamb, 1967; Teare et al., 1972a), and are capable of fixing CO_2.

Teare et al. (1972a), while looking at stomatal frequencies on the inflorescences of *Triticum aestivum*, found wide variation in stomatal numbers per inflorescence among wheat lines. This difference was most profound between long-awned and short-awned or awnless cultivars. The long-awned cultivars had approximately 14,000 more stomata per inflorescence than short-awned cultivars, being mostly due to the awns. The contribution of awn stomata to total inflorescence stomata ranged from 222 for short-awned to 8441 per inflorescence for long-awned cultivars. They concluded that the total number of stomata per inflorescence ranged from 150,000 to 600,000, representing 3 to 16% as many stomata as the flag leaves.

A number of researchers have shown that awn stomata serve a photosynthetic function for the spike (Grundbacher, 1963; Evans and Rawson, 1970; Evans et al., 1972; Teare et al., 1972b; Johnson et al., 1975; Olugbemi et al., 1976b; Blum, 1985; Blum, 1986; Olugbemi and Bush, 1987;). Awns have also been shown to account for as much as 46% of the surface area of long-awned inflorescences (Teare, 1971).

Awns are relatively easy to select for in a breeding program since all three genotypes at a single locus can be visually distinguished in the classical 1:2:1 F_2

ratio. Atkins and Mangelsdorf (1942) reported that a single "awn-suppresser" gene displays incomplete dominance, such that the heterozygous individuals can be distinguished from either homozygote. Other researchers showed that segregation ratios in general showed a good fit expected for a single gene (Atkins and Norris, 1955; Molchan and Lezzhova, 1982; Knott, 1986).

Although when in the homozygous recessive state, full-length awns can be produced, there are also three partially epistatic awn-inhibitor genes which cause variation in the fully awned condition (Sears, 1944; Rao, 1981; Sridevi et al., 1991). These awn inhibitor genes are known as B1, B2, and Hd located on the proximal regions of chromosomes 5AL, 6BL, and 4BS, respectively (Rao, 1981). Rao (1981) estimated the genetic distance between the Hd (hooded) gene and the centromere on chromosome 4B to be 7.7±3.7%. Hd generally causes awns to be short and bent as in the variety 'Chinese Spring', while B2 is considered a dominant inhibitor of awns. B1 is a dominant inhibitor of awn production and also displays an inhibitory effect to a lesser extent in the recessive condition (Sears, 1944).

Molchan and Lezzhova (1982) found that by crossing the awned and awnless parents with the greatest differences between them, a greater proportion of awnless spikes in the F_2 would be obtained. When lines of minimal differences (semiawned X fully awned) were crossed, a deficit of awnless plants in the F_2 was observed. They also noted that the action of genes for awn development or awnlessness was stronger when these alleles were received from the female parent. This might imply a possible cytoplasmic influence on awn production. Also, drought conditions caused an increase in the number of awnless spikes in the F_2.

One can conclude that the awn trait is a highly heritable (e.g., either present or absent). Environmental factors, possibly cytoplasmic factors, and epistatic factors may also cause variation in the degree of expression of awns in wheat.

Agronomic Research

Historically, most HRW varieties have been awned in contrast to other classes. In 1919, 99.9% of the HRW varieties were awned in comparison to 32.8, 14.2, and 12.5% awned varieties for soft red winter (SRW), hard red spring (HRS), and white wheat market classes, respectively (Lamb, 1937). The proportion of awnless HRW varieties grown in Oklahoma has remained relatively constant, with the seeded acreage in 1990 being <1% awnless.

Field-based comparisons of awned versus awnless genotypes have been conducted by various researchers across the world. The results have varied widely depending upon the genetic background and experimental conditions. Experimental materials ranged from earlier studies of awned and awnless cultivars to more recent comparisons of near-isogenic or "true" isogenic lines. When comparisons were made among lines or populations with the same genetic background, the results have been consistent for certain traits while other traits have given mixed results and, in many cases, have been found to be genotype-dependent (Bayles and Suneson, 1940; Knott, 1986). Bayles and Suneson (1940) compared composites of HRW and HRS lines throughout the western US. They found that the effect on grain yield was dependent on parental genotypes, while trends for kernel and test weight were the same for both composites. Investigations by Knott (1986) also found in some locations in Canada that the awned HRS wheat lines yielded significantly more than awnletted lines, while in another location, the awnletted had significantly higher yields than the awned. His research also showed that awned lines had significantly heavier kernels at all locations. These findings are not unique. Atkins and Norris (1955) evaluated isogenic lines of wheat and found that the yield difference between awned and awnless types changed sign among certain strains during some years. They also concluded that kernel weight and test weight were significantly higher for awned lines each year. Similarly, Patterson et al. (1962) stated that advantages or disadvantages of awns were more consistently expressed in kernel weight and test weight than in grain yield.

Although these researchers found interactions with genetic background and environments, others have found grain yield to be increased by the presence of awns alone. Schaller et al. (1972) evaluated isogenic lines of barley which were either fully awned, half awned, quarter awned, or awnless. Upon evaluation of these lines at 22 locations throughout the western U. S. and Canada, they found that the awnless lines generally produced less grain weight. Although the fully awned genotype was not always more productive than the half or quarter awned, the fully awned was highest yielding in more productive environments and had the highest quality grain at all locations, regardless of yield level. They estimated the grain yield contribution of awns to be 35.6 kg ha^{-1} per cm of awn length. Similar to these results, Tandon and Dhillon (1970), when comparing 20 pairs of $F_{2:5}$ populations, found awns to influence kernel weight and grain yield consistently for all populations and years (average increase of 6.4 and 6.3%, respectively). Likewise, Acharya et al. (1991), concluded that awned spring wheat populations had higher kernel weights and yields than the awnless populations in India.

Initial conjecture was that awns were more advantageous in dry, warm climates, with little benefit in cooler, humid environments (Atkins and Norris, 1955; Grundbacher, 1963). Exceptions can be found, as indicated above for barley (Schaller et al., 1972). Patterson et al. (1962) found the greatest yield advantage of awned near-isogenic lines in an unusually cool and wet season, which was most favorable for wheat production. Although in these two instances the awns were most favorable in the cooler, more humid environments, the bulk of literature still supports the theory that awns increase productivity in drier environments.

A few studies have shown superiority of the awnless type for various traits. McKenzie (1972) evaluated awned and awnletted (contains tip awns) forms of 'Thatcher' and 'Lee' wheat in four years under irrigated and non-irrigated (moderately hot or dry) conditions of southern Alberta. The awnletted genotypes were consistently superior; the average yield increase of awnletted forms was 133 kg ha^{-1}. These findings were consistent with those of Olugbemi et al. (1976a) working with near-isogenic lines of winter wheat in Great Britain where there was little drought stress. In most crosses, awnless isogenics had slightly higher kernel weight and grain yield. Overall, awns decreased grain yield and kernel weight significantly. It must be noted that the experiments of Olugbemi et al. (1976a) and McKenzie (1972), occurred under conditions of adequate moisture regimes.

The differential performances of awned and awnless lines has generated various hypotheses for the causes of such responses, beyond photosynthetic factors. Schaller et al. (1972) found that awns provided protection for developing barley kernels from the foliar pathogen causing net blotch (*Drechslera teres sacc.*). Because in certain environments the quarter-awned genotype had higher yields than the fully-awned genotype, they also proposed a possible physiological competition between awns and floret development. This concept was supported by Rasmusson and Crookston (1977), who developed barley lines with multiple awns per floret. These lines produced lower grain yields than their normal awned counterparts. However, previous experiments for wheat conducted by Evans et al. (1972) and Olugbemi et al. (1976a) found no evidence that the awns on a normal fully awned inflorescence interfere with floret development. It is unclear to what extent the environmental factors may play in these differing opinions of competition between awn and floret development.

McKenzie (1972) proposed that awns were linked to a deleterious gene (or that plant vigor was linked to genes controlling the awnletted condition) in his experiments in which the awnletted genotype was superior. Another possible disadvantage of awns is that they provide for a greater spike surface area to trap rain and wind, and possibly increase the amount of lodging (Grundbacher, 1963; Lamb, 1967; Evans et al., 1972). In more humid environments such as northwestern Europe, lodging is often the main yield-limiting factor (Grundbacher, 1963). Pool and Patterson (1958) conducted experiments on the water relations of awned and awnless spikes. They found that during a wetting event, awned spikes took up moisture at a greater rate than awnless spikes but when in the drying phase, they dried out faster than the awnless spikes.

There are other potential advantages for awns, which might not always be clearly evident. Benci et al. (1973) experimented with the aerodynamic and energy balance effects of awned and awnless isogenic barley lines in Montana. They found that the canopy temperatures of awned lines were cooler than those of awnless lines. They noted that the air-sensible heat exchange with the atmosphere was higher for the full-awned canopy, causing it to be cooler, apparently because the complex geometry of the awned canopy dissipated heat better. This difference in heat dissipation was attributed to the tendency for higher turbulent air flow above the awned canopy.

Unlike the effects of more rapid heat exchange, Acreman and Dixon (1986) found awns to be advantageous for reduction of aphid (*Sitobion avenai*) infestations. In their experiments the aphid infestations were 33% less on awned plants than awnless. They also stated that awns are not a very suitable host for the aphids, causing them to be 22% less fecund. These results were due to both the combined effects of antibiosis of the awns and the self-cleaning effect of aphids wind-blown to the ground, with only 28% recolonizing the plants.

Photosynthesis and Physiological Research

By far one of the most important attributes of awns are their ability to conduct photosynthesis. Various experiments have been conducted to determine the photosynthetic attributes of awns and awned spikes. Results of such experiments have shown varying amounts of carbohydrates in the kernels supplied by the awns and spikes. In one of the earlier studies, Asana and Mani (1949) found, when shading spikes, that 15 to 59% of the carbohydrates in the grain was contributed by spike photosynthesis and that shading was mostly related to lower kernel weight, not fewer seeds per spike.

Saghir et al. (1968) conducted experiments in Lebanon where the awns of 'Ramona' wheat were clipped at and after anthesis. Like Asana and Mani (1949), they found the spike to be the most critical plant part in supplying photosynthate for kernel development. Clipping of awns at anthesis led to a 20.8 and 13.4% decrease in grain yield and 1000-kernel weight, respectively. Due to these decreases, they recommended varieties with large spikes and dense foliage in the upper canopy to increase grain yield and kernel weight.

Similar experiments on removal of plant organs were conducted by Duwayri (1984). Duwayri's experiments were conducted under dryland conditions in Jordan with one hexaploid and nine *Triticum durum* genotypes. Grain yield was reduced by removal of the flag leaf alone at heading , of awns alone, or both by 10.7, 15.9 and 21.2%, respectively. The corresponding decrease in kernel weight was 5.2% for awn removal and 11.3% with combination removal, but no significant decrease was found with removal of the flag leaf alone. Results of their experiment suggested that neither the awns nor the flag leaf was able to completely compensate for the removal of the other.

Due to physical modification of the growing environment by shading or by possible mechanical damage by clipping of the awns, more recent studies have been conducted using radiolabeled CO_2 or by infrared gas analysis. Olugbemi et al. (1976a) utilized ^{14}C techniques in Britain to study awned vs. awnless isogenic lines. Recall that in their field experiments awned lines had lower yields and kernels weights. They found that awns contributed an average of 12.2% to gross canopy photosynthesis but didn't increase overall canopy photosynthesis. Likewise, at 30 days post-anthesis, awns increased spike photosynthesis by 11% but, a decrease was noted for other organs by approximately the same amount. They also noted that under their conditions (no drought), the awns became yellow as early or earlier than the remainder of the ear, which was only slightly later than that of the flag leaf. This would tend to suggest that no overall benefit was gained from the awns.

Evans et al. (1972) included drought stress as an additional treatment to study photosynthate supply of spikes. The presence of awns doubled the net photosynthetic rate, and drought stress increased the proportion of spike-contributed photosynthesis from 13 to 24% in awnless spikes, and from 34 to 43% in awned spikes. Contrary to original thought, they also noted that spike photosynthesis rate in an awnless line was unaffected by drought, while spike photosynthesis rate of an awned line decreased by 25%. Although awns may posses a xeromorphic structure, they still may be affected by drought conditions. They found no clear relationship between activity from ear-assimilated ^{14}C per grain and awn length.

Although results have shown awns to be photosynthetically active, one must also consider the possibility of increased transpiration due to the increased spike surface area. Teare et al. (1972b) addressed this topic when evaluating isogenic wheat lines under greenhouse conditions. They found that the net (gross photosynthesis minus respiration) photosynthetic rates per unit area of the spikes were 20-26% of those for flag leaves. Respiration rates for awned and awnless spikes were 1.7 and 3.0 times greater than those of the flag leaves. Transpiration rates per awnless or awned head were 34 or 43% of flag leaf rates, with the awnless type having 20% greater water-use efficiency. While in their comparisons the awns added a 40% increase in photosynthetic capacity, the transpiration rate was doubled in the awned heads compared to the awnless. Thus, the authors found that the awnless type was more water-use efficient. They reasoned that greater canopy resistance and narrower boundary layer of the awned lines increased water loss from the plant.

Somewhat contrary to the results of Teare et al. (1972b) were the findings of Blum (1985; 1986) for carbon exchange rates (CER) and transpiration of wheat and barley lines. He found that over both species, awns contributed 40 to 80% of the total spike CER and only 10 to 20% of transpiration, while constituting 50 to 70% of the spike-surface area. He also found that awns had the largest transpiration ratio (photosynthesis/transpiration) of any other organ and concluded that the awn is a "water-use-efficient organ." Further experimentation by Blum (1986) with heat hardening of wheat plants showed that the temperature optimum of CER in awns was greater than that of the leaves or glumes. He also found that while whole-spike CER was negative at 30°C, the CER of the awns was positive.

It is quite clear, that this topic has been of concern worldwide and many researchers have attempted to explain the effects of awn removal in cereal grains. Also evident, is the wide variability of results obtained from such experiments. Inconsistent results have been obtained from both agronomic and physiological studies related to the awns. It is thus imperative that for consideration of awnletted varieties in areas where awned varieties have prevailed, experimental results with current cultivars and environmental conditions are needed.

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CHAPTER II

EFFECTS OF AWN SUPPRESSION ON AGRONOMIC AND QUALITY TRAITS IN HARD RED WINTER WHEAT

Effects of Awn Suppression on Agronomic and Quality Traits in Hard Red Winter Wheat

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ABSTRACT

Producers in the southern Great Plains, who utilize wheat for grain, hay, or late season grazing, would benefit from awnless wheat cultivars if yield potential is maintained relative to current awned cultivars. The uncertainty of the effects of awnlessness in currently adapted HRW varieties in the southern Great Plains prompted this investigation. The objectives of this research were to determine the average effects of awn suppression on certain agronomic and quality traits, and to determine the frequency of awnletted lines that differ in agronomic performance from their awned sister lines. Bulk populations of lines either homozygous awned or awnletted, but otherwise randomly distributed for other genes, were developed within 'TAM 107', 'Century', and 'Mustang' backgrounds, and evaluated in 11 environments. Homozygous awned and awnletted F_3-derived sib lines were also developed from the same three base populations and evaluated in four environments. No differences in grain yield were detected in the Mustang and Century bulk populations, while a significant decrease in yield was found for the awnletted TAM 107 population. Significant decreases in test weight were associated with the awnletted character in all backgrounds. The Century-awnletted population had longer spikes, greater spike harvest index and a greater number of kernels per spike than Century-awned. Awnletted sibs were found which yielded equally as well as their awned sibs, but higher yielding awned sibs were more frequent than higher yielding awnletted sibs. Thus, it appears possible to develop awnletted lines which are agronomically satisfactory, but greater attention must be placed on traits such as test weight than might ordinarily be given.

INTRODUCTION

Annually, about 2.8 million hectares in Oklahoma are planted to HRW wheat, of which 35 to 55% is used for grazing by stocker cattle through fall, winter, and early spring (Krenzer et al., 1992). Traditionally, the percentage acreage of awnless wheat has been very low (<1%), partly because the character has been available in less adapted SRW cultivars (OK Dept. Ag., 1991). Interest in awnless varieties for Oklahoma has recently increased with the advent of awnless HRW cultivars, 'TAM 109' and Agripro 'Longhorn'.

When wheat is planted in the fall, generally the decision has not been made on how to utilize the wheat. Such management decisions are often affected by government programs, producer preference (beef producer vs. beef and grain producer), weather conditions, and also by weed pressure (E.G. Krenzer, 1993, personal communication). Of the total area planted each fall, generally around 2.1 million hectares are harvested for grain leaving a difference between area planted and area harvested for grain of around 0.7 million hectares (OK Dept. Ag. 1991). Although the amount of wheat left for grain but remains unharvested is quite variable, the majority of this difference in area is utilized for graze-out or for haying operations. The use of awnless cultivars may provide added flexibility in managing this acreage for grain, graze-out, or hay since awnless HRW cultivars may reduce irritation suffered by livestock when grazing awned wheat. The grain produced by awnless SRW cultivars may be harvested but is difficult to market in the southern Great Plains.

Numerous agronomic experiments have been conducted using different genetic materials to evaluate the value of awns in small grains. Results of these experiments have varied. Atkins and Norris (1955) found awned isogenic lines of wheat to have higher test weights and kernel weights than awnless isogenic lines, while grain yield differences were inconsistent among years. Likewise, Bayles and Suneson (1940) found significant differences for grain yield between awned and awnless HRS composites, but not for grain yield of HRW composites. Kernel weights and test weights were significantly lower for awnless composites of both classes. Knott (1986) conducted a series of experiments with awned and awnletted (spikes containing tip awns or a few apical awns) lines of HRS wheat in Canada. Grain yield differences were inconsistent among locations. Kernels of awned lines were significantly heavier at all locations while quality differences were generally insignificant. Similarly, McNeal et al. (1969) found that awnletted spring wheat populations had lower test weights and lower grain yields in Montana. Awnletted populations in these experiments showed superior milling and baking characteristics and had greater number of spikelets per head.

In contrast, McKenzie (1972) reported higher grain yields of awnletted lines under irrigated and non-irrigated conditions in southern Alberta. Experiments conducted in Great Britain utilizing near-isogenic lines of winter wheat revealed no significant effect of awns on grain yield; the awnless lines had slightly heavier kernels and higher grain yields (Olugbemi et al., 1976).

These conflicting results, the recent development of high-yielding awnless HRW cultivars, and the limited research in the southern Great Plains prompted this investigation. The recent emergence of new HRW awnless cultivars casts doubt on the perceived yield advantage of awned cultivars held since the introduction of 'Turkey' in the 1870's. The aim of this study was to systematically evaluate the effect of awn suppression on agronomic traits in three contemporary HRW genetic backgrounds. Objectives were to compare agronomic performance (grain yield, test weight, and kernel weight) as well as spike and kernel development of awned and awnletted types, and to assess correlated changes in kernel protein and hardness.

MATERIALS AND METHODS

Bulk Population Experiment

The original plant material for this experiment consisted of F_2 populations of 'TAM107'*2/'McNair 1003', 'Mustang'*2/McNair 1003, and 'Century'*2/McNair 1003. The original F_1 seed were provided by Dr. Edward Smith, Oklahoma State University. TAM 107 (Porter et al., 1987), Mustang, and Century (Smith et al., 1989) are awned HRW wheat cultivars currently grown in the southern Great Plains. McNair 1003 is a SRW cultivar with large grain size, average test weight, and awnletted spikes (Newton et al., 1980). McNair 1003 has shown good yield potential when grown in Oklahoma (unpublished data). Backcross populations were used to provide genetic material applicable to HRW breeding programs. All homozygous dominant lines developed from these crosses contained tip awns and a few short awns on spikelets in the upper portion of the spikes. For this reason, and because the parent, McNair 1003 was originally described (Newton et al., 1980) as awnletted, all lines utilized in these experiments will be referred to as either awned or awnletted.

Single F_2 plants were grown during 1987-1988 in 23 by 31 cm hill plots. Population sizes were $\approx$ 250 plants per background. Seed from each plant were harvested and labeled according to its genotype: homozygous awnletted, heterozygous (intermediate expression), or homozygous awned. Bulk populations were formed in each background by combining equal amounts of seed from random F_2 plants in each homozygous class. Sixty plants were bulked to form the awned populations within each background, while 34, 48, and 25 awnletted plants were bulked to form the awnletted populations for TAM 107, Mustang, and Century, respectively. These populations were tested in the F_3, F_4, and F_5

generations during 1988-1989, 1989-1990 and 1990-1991, respectively.

To avoid possible inadvertent selection within these heterogeneous populations during testing, the bulks were reconstituted each year from equal amounts of seed derived from each line advanced in hill plots. Because some heterozygous plants were mistakenly identified as homozygous awnletted in the F_2, advance of individual lines allowed for elimination of awned plants from awnletted bulks. However, the proportion of awned plants in awnletted bulks never exceeded 5%, while awned bulks were 100% pure.

The six bulk populations and four parents were evaluated in 11 environments over the 3-yr period in the major wheat production areas of Oklahoma (Table 1). These locations represent diverse soil types, and also a broad range in precipitation during the growing season (Table 1). Experimental design was a randomized complete block with three replications per environment. Plots were 1.2 by 3.1 m and were seeded at a rate of 80.5 kg ha^{-1}, a common rate for wheat in Oklahoma. All plots were fertilized according to soil-test recommendations. Foliar diseases were not controlled in any of the environments. Plots were harvested with a Hege (H and N Equipment, Colwich, KS) small-plot combine. Grain yield, test weight, kernel weight (wt. per 1000 kernels), kernel hardness index, and grain protein were determined in all environments. Hardness and protein were measured by NIR spectroscopy using a Technicon (Tarrytown, NY) InfraAlyzer 400 according to approved methods 39-70 (AACC, 1983), and protein values were adjusted to 140 g kg^{-1} basis before data analysis. Spike length (base of spike to tip, excluding awns), harvest index of spike (grain wt./total spike wt.), and number of kernels per spike were determined on 20-spike samples taken from the center two rows of each plot in three environments.

After confirming error homogeneity, the data were combined across environments and analyzed using Statistical Analysis System procedures (SAS

Institute, 1985). Single-df orthogonal contrasts were used to determine differences between means of the awned and awnletted bulks within the same background. The error term used for these contrasts was the pooled interactions of awned vs. awnletted populations by environments. During analysis, environments were considered as random effects while genotypes were considered fixed.

Sib-Line Experiment

Twenty-six pairs of sib lines were derived from each of the same crosses as in the bulk experiment: TAM 107*2/McNair 1003, Mustang*2/McNair 1003, and Century*2/McNair 1003. One member of each pair was homozygous awnletted while the other member was homozygous awned. Each pair descended from an F_2 plant showing heterozygous expression of awn production in 1988. Progeny rows were planted in the greenhouse in 1988-1989, consisting of 10 F_3 plants per family. From each progeny row, one random pair of homozygous awned and awnletted plants was harvested. The following year, each sib pair was increased as $F_{2:4}$ lines, in two-row plots, 3.1 m in length, and verified for homozygosity of the awned or awnletted trait. Any sib pair showing segregation was not included in subsequent tests. Seed of each line were harvested in bulk for field evaluation. Sufficient seed increase allowed for testing of the same generation ($F_{2:5}$) in four environments.

Sib lines were evaluated at Stillwater and Lahoma, Oklahoma (soil types given in Table 1) during the 1990-1991 and 1991-1992 growing seasons. The experimental design was a replicates-in-sets design (three replications per environment) with a split-plot arrangement of sib lines. Sib pairs were assigned to whole plots consisting of four rows 0.3 by 3.1 m, while each awned and awnletted line was randomly assigned to split plots of two rows. Twenty-six sib pairs were evaluated in each genetic background, divided arbitrarily into two sets. Thus, each set consisted of 13 sib-pairs from each background, totaling 39 sib-pairs, plus four parents and two check cultivars ('Chisholm' and 'Cimarron'). Seeding rate was 80.5 kg ha^{-1} as in the bulk population experiment. Plots were managed for fertility and disease control as described above.

Plots were harvested at maturity with a two-row binder, retaining all above-ground biomass. Bundles were then weighed and threshed using a stationary thresher. Traits evaluated at all locations included grain yield, test weight, kernel weight, harvest index, kernel hardness, and grain protein percentage. Hardness and protein were measured by NIR spectroscopy as described above.

Means were determined across environments and single-df contrasts ($P = 0.05$) were performed within each pair and tested against the across environment analysis residual error. Those comparisons were grouped into one of the following categories; awned sib significantly greater than the awnletted sib, awned equal to awnletted, and awned significantly less than awnletted. Genetic correlations for test weight and yield were determined using multivariate analysis of variance across locations.

RESULTS

Bulk Population Experiment

The test sites in this experiment provided a broad spectrum of mean yield levels, ranging from 1575 kg ha^{-1} to 4066 kg ha^{-1} (Table 1). The intent was to test these populations in a wide range of environmental conditions. Historically, experiments conducted at Altus, Goodwell, and Perkins suffer from drought and/or heat stress during the reproductive period. Goodwell and Altus generally receive low amounts of rainfall while Perkins has the sandiest soil texture.

As would generally be expected, significant differences were found for certain traits including grain yield, among the three genetic backgrounds. The objective of this research was not to draw inferences with respect to a specific background but to evaluate differences which might occur between awned and awnletted populations within a representative set of HRW parents. These three HRW parents were used to determine whether the effects of awn suppression were consistent across backgrounds.

The number of spikes per square meter (spike density) was monitored in several environments to determine whether yield differences might be due to chance differences in tiller formation and survival. As expected, no differences were found between awned and awnletted populations within backgrounds for this trait. For grain yield across all environments, a significant decrease of 157 kg ha^{-1} (5.7%) was noted for the awnletted TAM 107 population (Table 2). In contrast, no significant difference was found for grain yield in either the Mustang or Century populations. With respect to individual environments, differences between the Mustang populations were significant in none of the eleven environments. The awnletted Century population tended to have a higher grain yield, although significant in only one environment, while the TAM 107 awned population tended to have higher yield in individual environments (significant in two environments). No significant relationship was found between the productivity level of the environment and the difference between awned and awnletted populations (Figure 1). Across all backgrounds, the yield advantage was in favor of the awned populations by 6 kg ha^{-1}.

Kernel weight was not affected by awn suppression in any background (Table 2). A consistent decrease in test weight was associated with the awnletted populations, averaging 10.3, 11.5 and 5.1 kg m^{-3} for the TAM 107, Mustang, and Century populations, respectively. Although awn suppression appears to clearly affect test weight, the reduction amounts to less than one pound per bushel. Awn suppression did not show a consistent effect on kernel texture and protein concentration. Hardness score was not changed in the TAM 107 populations, while there was a significant decrease of 5.3 and 16.1 units for the awnletted Mustang and Century populations. Protein content was decreased by the absence of awns in the Mustang background only.

Kernel and spike development was measured in more detail in a reduced number of environments (Table 3). No differences in spike length were found between awned and awnletted populations derived from TAM 107 and Mustang, while a significant increase of 0.8 cm per spike was found for the awnletted Century population. Harvest index of the spike was determined as the proportion of grain weight to total spike weight. Assuming awns constitute a negligible portion of total spike weight, an increase in spike harvest index might be expected in the awned populations if the awns contribute additional photosynthate to the developing kernels. Similar to spike length, however, no differences were detected for the TAM 107 or Mustang backgrounds. The awnletted Century population actually showed an increase in spike harvest index of 4.6 percentage units.

Inconsistent changes in kernels per spike were also observed (Table 3). Awned and awnletted populations in the Mustang background had similar kernel numbers. A decrease of 2.8 kernels per spike was associated with the awnletted TAM 107 population while an increase of 4.2 kernels per spike was associated with the awnletted Century population. This change in the number of kernels per spike closely follows the trend for yield differences. This factor appears to be the most likely cause of yield differences since neither spike density nor kernel weight differed between populations within any background.

Sib-Line Experiment

A total of 26 sib pairs per background were evaluated for various agronomic and quality characteristics. No differences in grain yield were found in approximately one-half of the comparisons (awned sib vs. awnletted sib) in any given background. The awned sib had a significantly higher grain yield than its corresponding awnletted sib in the remaining comparisons, with exception of two sib pairs where the awnletted sib was higher yielding (Table 4). In the overwhelming majority of comparisons, the awned sib had a significantly higher test weight than its corresponding awnletted sib (Table 4). Test weight differences between sibs ranged from 20 kg m^{-3} in favor of the awnletted to 56 kg m^{-3} in favor of the awned.

Contrary to the bulk populations, the awned sib usually had heavier kernels than the awnletted sib. The frequency in which there were no significant differences between sibs was greater for kernel weight than for test weight. However, in 84% of the comparisons where the awned sib had a significantly higher test weight, it also had a significantly higher kernel weight. Harvest index, measured as the proportion of grain weight to total above-ground biomass weight, was also affected by the presence or absence of awns in all backgrounds. When differences for harvest index occurred, they generally favored the awned sibs. Only one awnletted sib had a higher harvest index than its awned sib (Table 4).

Kernel hardness was least affected by awn suppression, with at least one-half of the sib pairs having the same hardness score. However, where differences occurred between sibs, the awned sibs tended to have higher hardness scores. Grain protein percentage was influenced in an opposite manner to most other traits. For those sibs which differed, the awnletted lines tended to be higher in grain protein percentage than their corresponding awned lines. This factor could be related to the reduced grain yield of some awnletted sibs. Other factors such as the lower kernel weights for awnletted lines may play a role in this phenomenon as well.

For the development of a commercially acceptable cultivar, the combination of various agronomic traits must be evaluated closely. The most agronomically important traits for HRW wheat include both grain yield and test weight. When looking at sib comparisons for grain yield versus test weight (Figure 2), in most comparisons the awned sib had both higher grain yield and higher test weight than the awnletted sib. However, several lines were identified which didn't differ significantly for either trait. Also, one awnletted line was developed within the TAM 107 background which had both a higher yield and test weight than its corresponding awned sib.

DISCUSSION

It is clear that there are negative effects of awn suppression in currently adapted HRW cultivars when grown in the southern Great Plains. Some previous investigations, such as Atkins and Norris (1955), indicate that awns are most favorable under extreme stress conditions while the differences become negligible under favorable conditions. Other researchers have found the greatest advantage of awns under the most favorable conditions (Patterson et al., 1962). This study showed no apparent pattern in superiority of either spike type with productivity level of the environment (Figure 1). Results of these experiments also indicate that the effects of awn suppression are genotype-dependent, as did the experiments of Bayles and Suneson (1940), as well as Knott (1986). Awnletted lines equal in yield to their awned counterparts were identified within all backgrounds while relatively high yielding awnletted lines (awnletted lines significantly greater than awned) were identified in each background except Mustang.

The decline in test weight with awn suppression might cause concern in developing commercially acceptable cultivars of awnless HRW wheat. The magnitude of test weight differences in the bulk experiment was equivalent to less than one pound per bushel; in the sib experiment, the difference in test weight required for significance was 11.3 kg m^{-3}, again amounting to less than one pound per bushel. Depending on the absolute level of test weight, this reduction may or may not reflect a decrease in market price.

Multivariate analysis of variance for yield and test weight among awnletted sibs produced a genotypic correlation coefficient of 0.86 for these two traits. This would indicate that selection for a high yielding awnletted line would not be expected to hinder efforts for improving test weight as well. When looking at the range in both grain yield and test weight for awnletted lines it appears that sufficient variation for both traits can be found within these backgrounds such that lines satisfactory for desirable traits could be identified in the breeding program. Also, the test weight for McNair 1003 was relatively low compared to the HRW parents. If another genetic source such as a currently adapted awnless HRW line with higher test weight was used as a source for awn suppression, part of the test weight concern may be somewhat alleviated.

Because test weight was generally lower for awnletted genotypes while kernel weight results varied, kernel morphological traits may also need to be evaluated to more closely monitor differences in test weight. Although this study was not aimed at evaluating the effects of awns on animal performance, it is clear that if a high yielding awnletted line with satisfactory test weight were developed, management concerns associated with livestock irritations caused by the awns could be eliminated.

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Table 1. Year of bulk population experiment, locations, soil types, rainfall during growing season, and mean grain yield of all entries.

Growing season	Location	Soil type†	Rainfall amount‡	Mean grain yield¶
			mm	kg ha^{-1}
1988-1989	Stillwater	Norge L, fine-silty, mixed, thermic	574	2134
	Lahoma	Pond Creek SiL, fine-silty, mixed, thermic	439	2632
1989-1990	Stillwater		681	1575
	Lahoma		366	2123
	Altus	Hollister CL, fine, mixed, thermic	439	2264
	Woodward	Carey L, fine-silty, mixed, thermic	231	4066
1990-1991	Stillwater		399	2438
	Lahoma		323	2696
	Goodwell	Richfield CL, fine, montmorillonitic, mesic	300	2876
	Woodward		340	2583
	Perkins	Teller L, fine-loamy, mixed, thermic	439	2147

†L = loam, SiL = silt loam, and CL = clay loam.

‡Rainfall between planting and harvest date only.

¶Mean yields represent the mean of all test entries at a given location.

Table 2. Bulk population means of agronomic and quality characteristics combined across 11 environments.

Background	Population	Yield	1000-Kernel wt.	Test wt.	Hardness score	Protein concentration
		kg ha^{-1}	g	kg m^{-3}		g kg^{-1}
TAM 107	Awned	2754*	27.5	710**	51.3	126
	Awnletted	2597	27.0	700	52.0	128
Mustang	Awned	2265	27.1	689**	31.1**	128*
	Awnletted	2301	27.1	677	25.8	125
Century	Awned	2508	24.2	701*	40.3**	131
	Awnletted	2610	23.8	696	24.2	129

*,** Contrasts of awned and awnletted means within a background significant at P=0.05, and 0.01, respectively, based on the F-test.

Table 3. Bulk population means of spike traits combined across three environments.

Background	Population	Spike length†	Harvest index of spike‡	Kernels per spike
		cm	%	no.
TAM 107	Awned	7.5	66.5	27.0*
	Awnletted	7.8	65.7	24.2
Mustang	Awned	7.1	64.7	25.9
	Awnletted	7.7	67.6	25.1
Century	Awned	7.6	64.7	26.0
	Awnletted	8.4*	69.3*	30.2**

*,** Contrasts of awned and awnletted means within a background significant at P= 0.05, and 0.01, respectively.

†Length of spike from base to tip, excluding awns.

‡Proportion of grain wt. to total spike weight.

Table 4. Comparison of awned vs. awnletted lines within and across sib pairs for six traits measured in four environments.†

	Sib-pair comparisons‡										
	Awned > Awnletted			Awned = Awnletted			Awned < Awnletted			Awned	Awnletted
Trait	T107	Cty	Mtg	T107	Cty	Mtg	T107	Cty	Mtg	mean	mean
					no.						
Grain yield, kg ha^{-1}	13	12	13	12	13	13	1	1	0	2080**	1880
Test weight, kg m^{-3}	22	24	23	4	1	3	0	1	0	671**	640
1000-kernel wt., g	17	22	22	9	3	4	0	1	0	26.2**	24.0
Harvest index, %	11	6	14	15	19	12	0	1	0	33.1**	32.0
Hardness score	5	5	10	19	17	13	2	4	3	35.4**	32.9
Protein conc., g kg^{-1}	0	1	2	12	11	17	14	14	7	127	134**

*,** Awned and awnletted means significantly different at P = 0.05, and 0.01, respectively.

†Differences greater than 217.8 kg ha^{-1} (grain yield), 11.3 kg m^{-3} (test weight), 1.01g (1000 kernel wt.), 1.51% (harvest index), 4.51 (kernel hardness score), and 5.3 g kg^{-1} (grain protein) were considered significant ($P < 0.05$) for individual sib comparisons.

‡T107 = TAM 107, Cty = Century, and Mtg = Mustang.

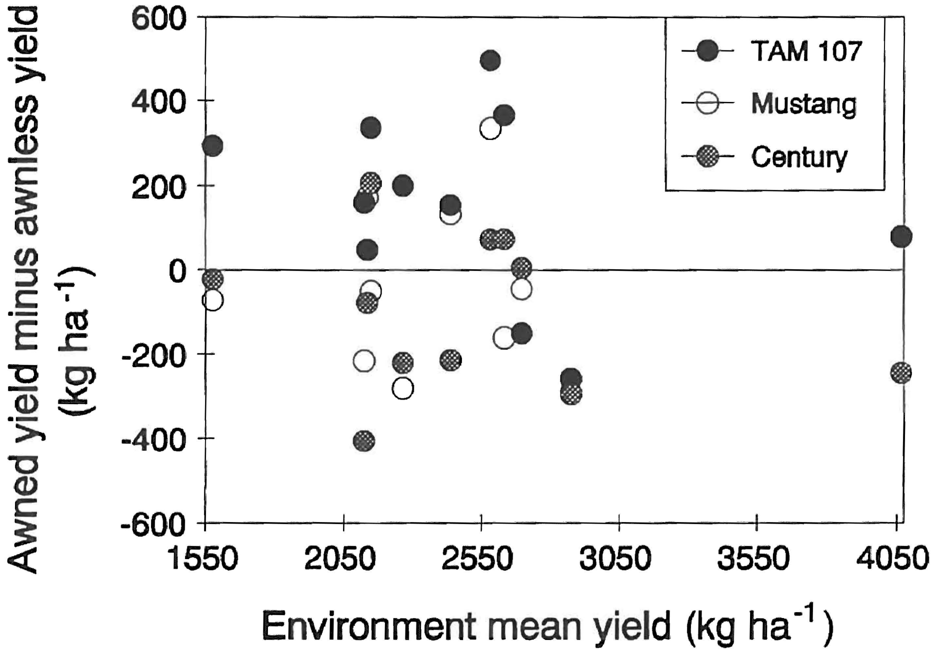

Figure 1. Difference in grain yield between awned and awnletted bulk populations vs. environment mean yield. Points above the horizontal line indicate where grain yield of the awned population exceeded the corresponding awnletted population.

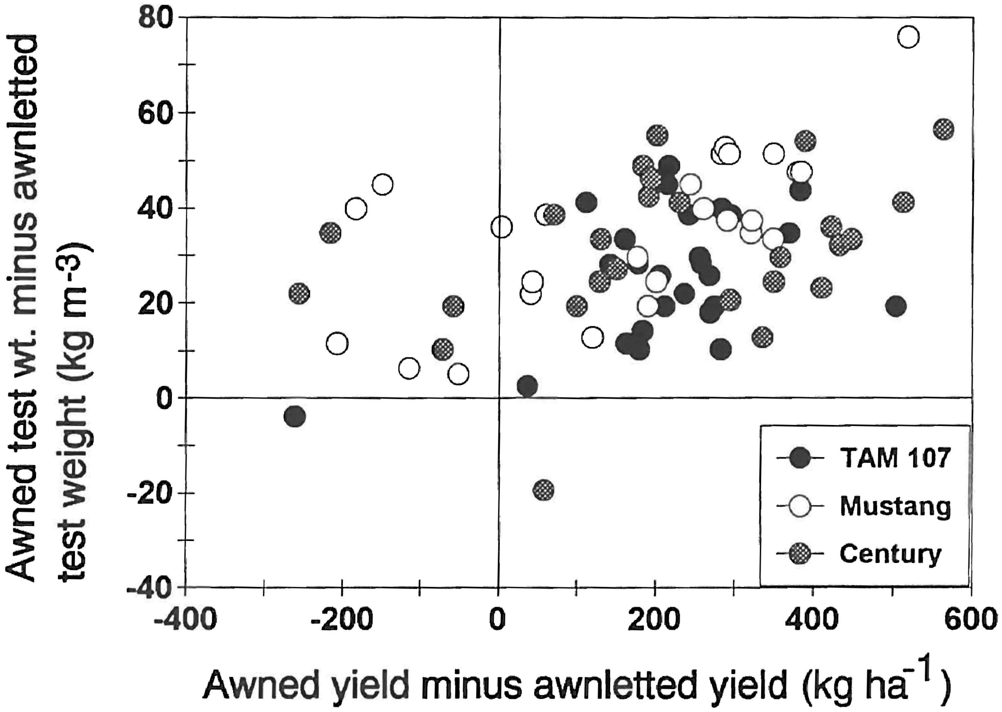

Figure 2. Difference between awned and awnletted sibs for test weight vs. grain yield in three HRW wheat backgrounds. Each point represents an individual sib pair comparison.

CHAPTER III

PHOTOSYNTHESIS AND WATER-USE EFFICIENCY OF AWNED AND AWNLETTED NEAR-ISOGENIC LINES IN HARD RED WINTER WHEAT

Photosynthesis and Water-Use Efficiency of Awned and Awnletted Near-Isogenic Lines In Hard Red Winter Wheat

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ABSTRACT

Awned wheat cultivars have traditionally prevailed in the drier areas such as the southern Great Plains. They are generally thought to be more water-use efficient and the awns may also compensate for reduced flag leaf photosynthesis which occurs during drought stress or severe disease infection. The aim of this study was to evaluate awned and awnletted near isogenic lines representing three diverse HRW backgrounds (TAM 107, Century, and Mustang). Plants were grown in a controlled environment chamber under both well watered and water-deficit stressed conditions. Photosynthetic rates of both inflorescences and flag leaves were taken at two stages of development and various other physiological characters such as season-long and grain water-use efficiency were calculated. Net photosynthetic rates for awnletted spikes were significantly lower than the awned for all backgrounds at 14 days after anthesis (DAA), while significantly lower for two backgrounds at 24 DAA. Under stress conditions, awned spike rates were significantly higher for Mustang and TAM 107 spikes at 14 DAA, while no differences were found at 24DAA. No differences were found for flag leaf photosynthesis between awned and awnletted lines at any measurements nor for season-long water-use efficiency. Generally, differences in agronomic characters were insignificant between awned and awnletted lines.

INTRODUCTION

The wheat awn is a rudimentary leaf, of which little remains except the midrib. It is triangular in cross-section and the two outer faces contain stomata (Lamb, 1967; Teare et al., 1972a). It is widely acknowledged that the cereal awn serves a photosynthetic function for the spike by providing carbohydrates to developing kernels (Grundbacher, 1963; Saghir et al., 1968; Evans and Rawson, 1970; Johnson et al., 1975; Olugbemi et al., 1976a; Blum, 1986; Olugbemi and Bush, 1987).

The contribution of awn photosynthesis, relative to leaf or canopy photosynthesis, has been determined by various methods. Olugbemi et al. (1976a) found that awns contributed 12% of gross canopy photosynthesis but didn't increase overall canopy photosynthesis. At 30 days post-anthesis, awns increased spike photosynthesis by 11%, but a decrease was noted for other organs by approximately the same amount. They also noted that under their conditions (no drought stress), the awns senesced as early or earlier than the remainder of the spike, which was only slightly later than that of the flag leaf. This would tend to suggest that no overall benefit was gained from the awns.

The presence of awns doubled the net photosynthetic rate, and drought stress increased the proportion of spike-contributed photosynthesis from 13 to 24% in awnless spikes, and from 34 to 43% in awned spikes (Evans et al., 1972). Contrary to original thought, spike photosynthesis rate of an awnless line was unaffected by drought, while spike photosynthesis rate of an awned line decreased by 25%. Awns may posses a xeromorphic structure, but they still may be affected by drought conditions.

The photosynthetic benefit of awns should be weighed against a potential increase in transpiration rate due to the increased spike surface area. Teare et al. (1972b) addressed this topic when evaluating isogenic wheat lines under greenhouse conditions. They found that the net photosynthetic rates per unit area of the spikes were 20 to 26% of those for flag leaves, while transpiration rates per awnless or awned head were 34 or 43% of flag leaf rates. While in their comparisons the awns resulted in a 40% increase in photosynthetic capacity, the transpiration rate was doubled when compared to the awnless spikes, resulting in a 20% lower water-use efficiency. In contrast, awns contributed 40 to 80% of the total spike carbon exchange rate (CER) and only 10 to 20% of the transpiration in wheat and barley, while constituting 50 to 70% of the spike-surface area (Blum, 1985; 1986). Further experimentation by Blum (1986) with heat hardening of wheat plants showed that the temperature optimum of CER in awns was greater than that of the leaves or glumes.

Data is limited on the photosynthetic capacity and water-use efficiency of awned and awnletted hard red winter (HRW) lines adapted to the southern Great Plains, where awned cultivars have traditionally prevailed. This study was conducted to evaluate the effects of awn suppression under controlled environmental conditions in near-isogenic lines representing three diverse HRW backgrounds. The objective was to compare spike photosynthetic rates, season-long water-use efficiency and related agronomic traits of awned and awnletted lines under both water-deficit stressed and well-watered conditions. Another objective was to determine whether leaf photosynthesis in the awnletted lines might compensate for a lower photosynthetic rate in the spike.

MATERIALS AND METHODS

Experimental materials consisted of backcross-derived awned and awnletted near-isolines from 'TAM 107'*5/'McNair 1003', 'Mustang'*5/McNair 1003, and 'Century'*5/McNair 1003. The original F_1 seed were provided by Dr. Edward Smith, Oklahoma State University. TAM 107 (Porter et al., 1987), Mustang, and Century (Smith et al., 1989) are awned HRW wheat cultivars currently grown in the southern Great Plains. McNair 1003 is an awnletted soft red winter cultivar with large grain size and average test weight (Newton et al., 1980). McNair 1003 has shown good yield potential when grown in Oklahoma (unpublished data). All homozygous dominant lines developed from these crosses contained tip awns and a few short awns on spikelets in the upper portion of the spikes. For this reason, and because the parent, McNair 1003 was originally described (Newton et al., 1980) as awnletted, all lines utilized in this experiment will be referred to as either awned or awnletted.

Seeds were placed in Styrofoam seed flats and allowed to germinate. At the three-leaf stage, plants were placed in a vernalization chamber at 4°C for six weeks. After vernalization, plants were slowly acclimatized to a temperature of 25°C. Plants were then transplanted (one per pot) into 1.5 L clay pots. The soil mix used was a 4:2:1:1 (v/v/v/v) Sphagnum peat moss (FaFard Peat Moss Co., Ltd., Shippegan, New Brunswick, Canada), mushroom compost (Green Country Soil Co., Miami, OK), sand, and Redi-Earth peat lite mix (Grace Sierra Co., Milpitas, CA). Each pot received 730 g of the soil mix and the initial pot weights plus soil were recorded. At transplanting, each pot received 6 g of Sierra 17-6-12 Plus Minors (Sierra Chemical Co., Milpitas CA) slow-release fertilizer. This approach was used so that each pot received the same amount of fertilizer regardless how much water would eventually be applied. Fertilizer was mixed in the upper 5 cm of the soil surface.

Pots were placed in a Conviron (Controlled Environments Ltd., Winnipeg, Manitoba, Canada) walk-in growth chamber with a day/night temperature regime of 20/15°C and a 12 h daylength. Relative humidity was not controlled but ranged from 63 to 81%. The water-holding capacity of the soil was calculated gravimetrically and was approximately equal to the soil weight. Pots were weighed to the nearest gram and watered to the nearest ml every third day. Each pot was maintained at 80% (well watered) or 50% (water deficit stressed) of the maximum gravimetric soil water content. All pots were well-watered (80% saturation) immediately following transplanting to avoid transplant shock. Control pots (without plants) within each treatment were utilized to monitor evaporation of water.

Approximately two weeks before heading, water deficit stress was imposed in one-half of the pots by reducing the amount of added water. The amount of added water for stressed plants was gradually reduced in increments of 10% saturation until they were watered to 50% saturation. To assess stress levels, relative water content (RWC) was measured on check plants which were watered to the same level of each treatment. Goal pot weights (weight of pot, soil, and water at the desired saturation level) were adjusted for plant growth by measuring the fresh weight of similar-sized border plants.

At 14 and 24 d post-anthesis (growth stages 74 [medium milk] and 81, [early dough development] respectively, Tottman, [1987]), gas-exchange characteristics were measured by infrared gas analysis on two intact flag leaves and their corresponding spikes, using an Li-6200 portable photosynthesis system (Li-Cor Inc., Lincoln, NE), with a 4 L chamber. Measurements were taken at 1800 μmol m^{-2} s^{-1} photosynthetically active radiation, 25°C, and ambient CO_2 concentrations. Spikes were measured simultaneously in the natural position. All measurements were made with the chamber inside of a three-sided box covered with reflective foil. This was done to provide adequate light to all sides of the spikes.

Net photosynthetic rates, stomatal conductance, transpiration rate, internal CO_2 concentration, and instantaneous water-use efficiency (WUE_i, ratio of photosynthesis to transpiration) were measured. Since flag leaves and spikes were measured more than once, they could not be removed for area measurements in the traditional manner. Therefore, surface areas were measured using BioScan OPTIMAS (BioScan, Inc., Edmonds, WA) two-dimensional computer image analysis program. It was assumed that each spike represented a rectangular parallelogram, with four sides and equal opposite sides. Therefore, anterior and lateral views were taken of each spike, and the areas were calculated and summed, then multiplied by two to adjust for the four sides of each spike.

Stress treatments were continued until harvest maturity. At maturity, the mean amount of water evaporated from control pots within a specific water treatment was subtracted from the amount of water given to each pot of the same treatment to derive the water used by each plant. The amount of water utilized by each plant was used in season-long water-use-efficiency (WUE) calculations. Whole plant weights, including spikes, foliage, and roots, were summed for WUE calculation also. Samples of five random spikes from primary tillers were taken to determine seed no. per spike and weight per thousand kernels (1000-KW). Other characters measured included, grain wt. per plant, spike harvest index (ratio of grain wt. to total spike wt.), and grain WUE calculated as the ratio of grain weight produced to water used. With regard to total water use calculations for season-long WUE, only the amount of water used by the plants from transplanting to harvest was considered. All dry weight was assumed to be produced after transplanting since dry weight of vernalized seedlings was negligible.

A completely randomized design was used for this experiment. All pots were randomly placed in a growth chamber and were moved weekly to guard against spatial differences in microclimate. Two separate runs of this experiment were conducted consecutively over time. Treatments consisted of well watered and a water-deficit stressed pots within each run of the experiment. Two pots per treatment by genotype combination were utilized for run 1 and three pots per combination were evaluated in run 2. Effects due to runs were considered random while effects of both treatments and genotypes were considered fixed. During analysis, error homogeneity between runs was confirmed and an analysis of variance was performed within each treatment combined across runs. Single-df contrasts were used to determine differences between awned and awnletted isolines within each treatment.

RESULTS AND DISCUSSION

Relative water content was monitored on check plants during the period in which photosynthetic measurements were made. While water-deficit stressed plants were maintained at a gravimetric soil water saturation content 30% lower than well-watered plants, RWC values averaged three percentage units lower. This provided a moderate stress level, which was observable as flag leaf wilting by the time additional water was supplied to the plants. When evaluating all genotypes within a treatment together, the stressed treatment showed a two-fold increase in the number of sterile spikes and overall decrease in biomass production of 20% versus the well-watered treatment. Spike photosynthesis rate of water stressed plants at 14 and 24 days after anthesis (DAA) was decreased by 51 and 40%, respectively

Clearly, one of the most important aspects of the cereal awn is its ability to conduct photosynthesis. Under well-watered conditions, photosynthetic rates of awnletted spikes at 14 DAA were significantly lower than those of awned spikes (Fig. 1). Rates of awnletted spikes were 20 to 34% of the awned rates depending on background. These results are consistent with previous investigations which have also shown awns to increase photosynthetic capacity of the spike (Evans et al., 1972; Olugbemi et al. 1976b; Blum, 1985; Olugbemi and Bush, 1987). Awnletted genotypes responded differently to water stress conditions at 14 DAA. Both Mustang and TAM 107 awnletted lines actually showed a net CO_2 evolution and were consequently lower than the awned isolines (Fig. 1). No difference, however, was found between Century isolines. At 24 DAA under well-watered conditions, both Mustang and TAM 107 awned spikes were still significantly higher than the corresponding awnletted spikes, while no difference was found between the Century isolines (Fig. 1). No significance was indicated for spike photosynthesis rates at 24 DAA under stressed conditions. Flag leaf rates were not different at 14 or 24 DAA for any background or water treatment (Fig. 2).

It is generally thought that awned cultivars are more water-use efficient and thus more suitable to drier climates than awnless cultivars (Grundbacher, 1963). That hypothesis was tested using season-long and instantaneous water-use efficiency (WUE) calculations. No significant differences were found between isolines for whole-plant WUE (Table 1). The values of season-long WUE are consistent with previously reported values for HRW cultivars grown under containerized conditions (Cai, 1992). Likewise, no differences between isolines were found for grain WUE with the exception of TAM 107 isolines under stress conditions. The stressed awnletted TAM 107 lines produced an additional 0.6 g grain per kg water used than the awned isoline.

Instantaneous measurements of WUE for spikes paralleled trends in spike photosynthetic rate. Awned spikes were generally more water-use efficient in CO_2 assimilation than awnletted spikes at 14 and 24 DAA (Table 1). Values were significantly in favor of the awned genotype in almost half of the isoline comparisons. Instantaneous flag leaf values indicated no relationship between leaf WUE and the presence or absence of awns, nor were they associated with the WUE values for spikes.

There was no treatment by genotype interaction for any of the traits evaluated, indicating that awned and awnletted isolines were affected similarly by water deficit stress. Because the aim of the experiment was to evaluate differences between awned and awnletted under both conditions, means of agronomic traits were compared within each treatment (Table 2). Differences were usually non-significant, except for the pair of isolines derived from TAM 107. The number of kernels per spike was increased by 7 and 9 kernels in the well-watered and water-stressed treatments, respectively. Schaller and Qualset (1975) suggested that with increasing awn length, the number of fertile florets decreases due to competition between awn and floret development. Consistent with this hypothesis, with only one exception, all awnletted lines were numerically higher in the number of kernels per spike than their corresponding awned isoline. The increased kernel number of awnletted TAM 107 was not offset by reduced kernel weight (Table 2). No differences between lines for kernel weight were detected within any of the three backgrounds.

Under water-deficit stress conditions, awnletted isolines of Mustang and TAM 107 deposited a significantly larger proportion of energy into grain relative to the total spike than their awned counterparts (Table 2), although total weight of awnletted Mustang spikes was reduced relative to the awned spikes (data not shown). Grain yield per plant was not reduced. Grain yield was actually higher for the awnletted TAM 107 isoline under water stress.

During rapid grain growth, awns appear to be a vital part in not only supplying needed photosynthate to the developing kernels but also during periods of water deficit for maintaining at least a positive carbon exchange rate. A popular school of thought that photosynthetic activity of the awns would be a significant factor later in kernel development during flag leaf senescence was not supported by this study. These results showed no significant advantage of awns to developing kernels during early dough development in a wide range of genetic backgrounds. Flag leaves showed no significant compensation for the reduced spike photosynthesis of awnletted lines.

Although a few point measurements indicated that awned spikes might be more water-use efficient than awnletted spikes, this was not translated into increased WUE at the whole-plant level. This is most likely due to the multitude of factors affecting WUE over development. Given the lack of significant isoline differences for agronomic traits, it would appear that increased photosynthesis rate of awned spikes does not greatly impact agronomic performance. Previous field experiments with the same genetic backgrounds gave mixed results as well with respect to yield for awned vs. awnletted comparisons.

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Table 1. Means of season-long and instantaneous water-use efficiency (WUE) for near-isogenic awned and awnletted pairs of lines under well-watered and water-stressed treatments.

					Instantaneous WUE			
			Season-long WUE		Spike		Flag leaf	
Treatment	Background	Spike type	Whole-plant†	Grain‡	14DAA§	24DAA	14DAA	24DAA
			g kg^{-1}	g kg^{-1}	----------------------µmol mmol^{-1}----------------------			
Well watered	Mustang	Awned	4.53	0.98	1.10**	0.83**	1.50	0.86
		Awnletted	4.81	1.02	0.20	-0.05	1.40	0.94
	Century	Awned	5.52	1.64	1.05	0.72	1.41	2.00
		Awnletted	5.86	1.78	0.41	0.57	1.11	0.99
	TAM 107	Awned	5.06	1.54	0.88	1.02**	1.49	1.30
		Awnletted	5.18	1.85	0.37	0.32	2.16	1.99
Water stressed	Mustang	Awned	4.85	1.18	0.70*	0.56	1.44	1.13
		Awnletted	4.78	1.03	-0.06	-0.13	1.00	1.18
	Century	Awned	5.38	1.59	0.67	0.57	1.62	0.72
		Awnletted	5.21	1.65	0.41	0.18	1.97	0.74
	TAM 107	Awned	4.39	1.08	0.79*	0.47	1.41	1.32
		Awnletted	5.13	1.71*	-0.17	0.42	1.36	2.12

*, ** Indicates significance between awned and awnletted lines within treatments and genotypes at $P < 0.05$, 0.01, respectively.

†Ratio of dry matter produced to amount of water used.

‡Ratio of grain weight produced to amount of water used.

§DAA = days after anthesis

Table 2. Means of seed yield and yield components for near-isogenic awned and awnletted pairs of lines under well-watered and water-stressed treatments.

Treatment	Background	Spike type	Kernels per spike	1000 kernel wt.	Harvest index of spike†	Grain yield per plant
			no.	g	%	g
Well watered	Mustang	Awned	28.0	24.7	59.3	5.1
		Awnletted	24.7	19.4	63.5	3.9
	Century	Awned	32.0	29.1	68.7	7.9
		Awnletted	32.3	24.7	71.1	8.3
	TAM 107	Awned	24.4	29.5	67.1	6.1
		Awnletted	30.9*	30.6	72.7	7.7
Water stressed	Mustang	Awned	27.6	24.4	62.5	4.2
		Awnletted	28.4	18.3	66.6*	3.5
	Century	Awned	29.1	30.8	69.8	6.5
		Awnletted	33.3	25.1	72.7	6.5
	TAM 107	Awned	19.6	27.7	62.6	3.4
		Awnletted	28.3*	29.9	72.2**	5.7*

*, **Indicates significance between awned and awnletted lines within treatments and genotypes at P = 0.05, 0.01, respectively.

†Ratio of grain weight to total spike weight.

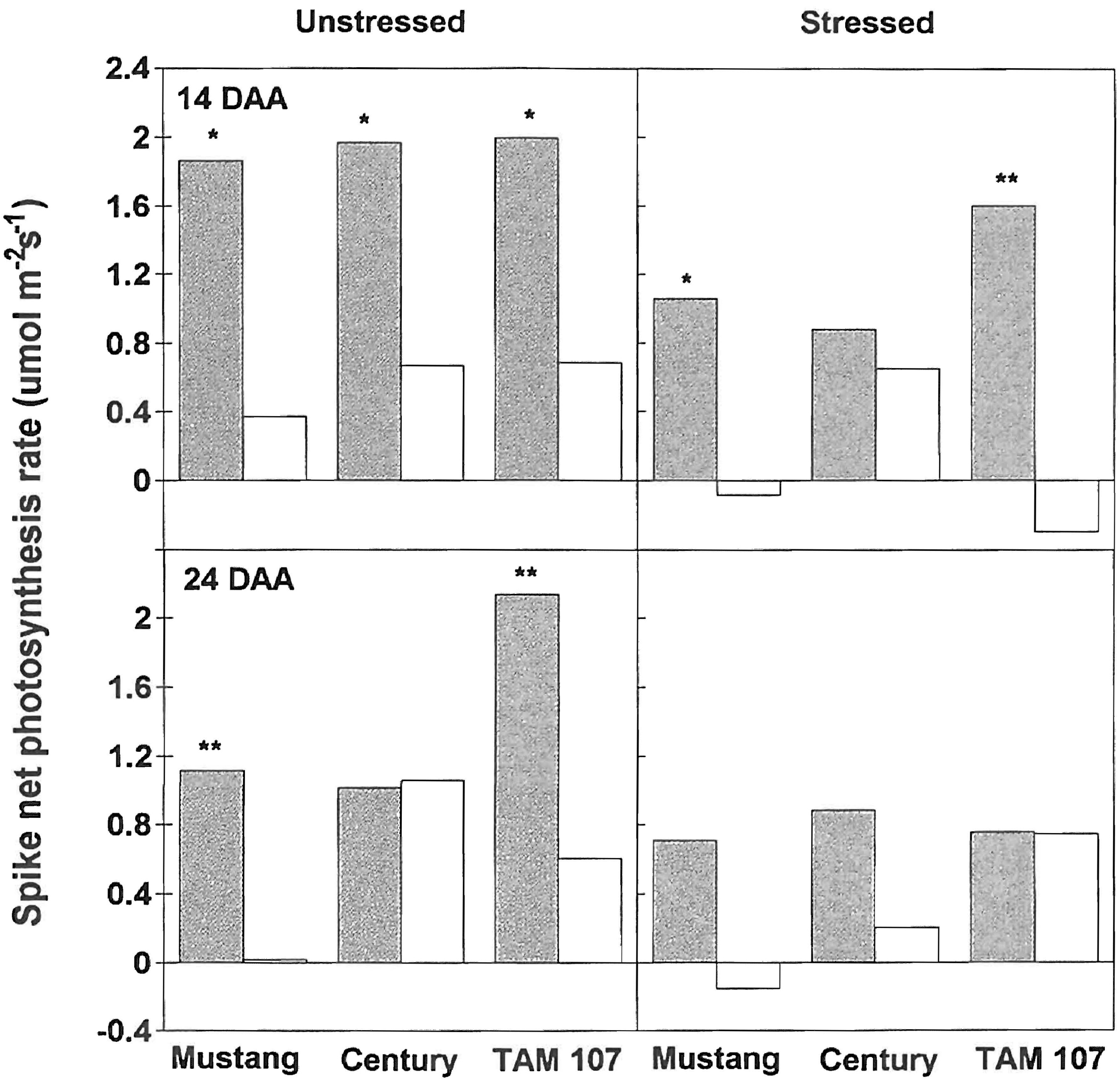

Figure 1. Spike net photosynthesis rate measured at 14 and 24 days after anthesis (DAA). *, ** indicates a significant difference between the awned (solid columns) and awnletted (white columns) near-isogenic line within a given treatment and background at $P = 0.05$, and 0.01, respectively.

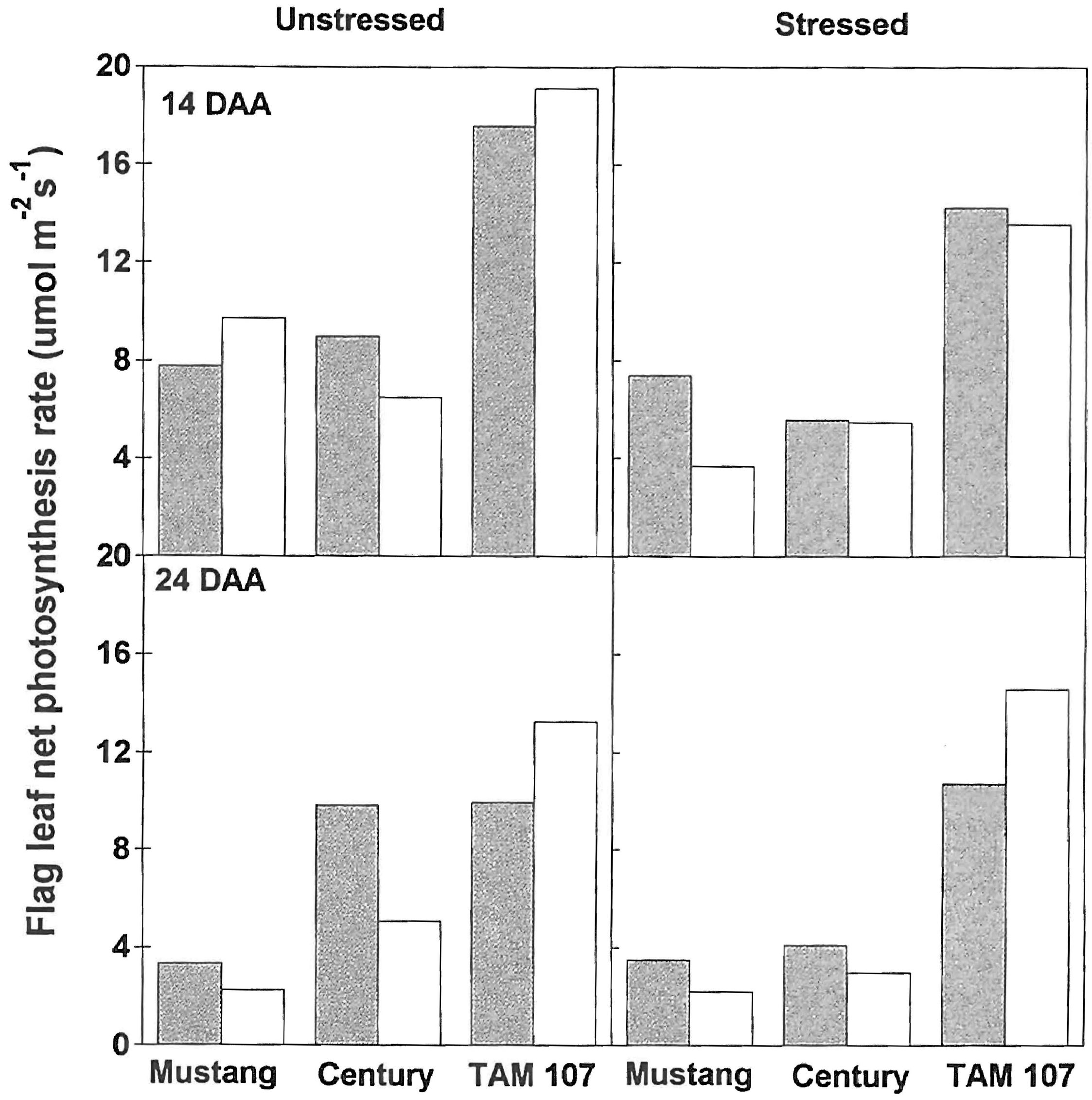

Figure 2. Flag leaf net photosynthesis rate measured at 14 and 24 days after anthesis (DAA). *, ** indicates a significant difference between the awned (solid columns) and awnletted (white columns) near-isogenic line within a given treatment and background at P = 0.05, and 0.01, respectively.

APPENDIX

SUPPLEMENTAL INFORMATION FOR BULK POPULATION, SIB-LINE AND NEAR ISOGENIC EXPERIMENTS

Table 1. Selected mean squares for agronomic and quality traits in the bulk population experiment

Source	df	Grain yield	1000 kernel wt.	Test wt.	Protein conc.	Hardness index
Environments	10	11,920,188**	439.4**	175.1**	19.468**	3,642.13**
Replications(Env)	22	154,674	2.7	2.0	0.288	31.68
Entries	9	931,566**	112.0**	57.2	1.953**	8,125.93**
TAM 107 Awned vs. Awnletted (T107)	1	404,085*	5.1	11.9**	0.794	8.51
Mustang Awned vs. Awnletted (Mtg.)	1	21,265	0.03	12.3**	0.982*	452.00**
Century Awned vs. Awnletted (Cty.)	1	172,242	3.2	4.0*	0.526	4,302.76**
Awned vs. Awnletted bulks	1	1,867	5.9	26.7*	0.227	2,348.42
McNair 1003 vs. HRW parents	1	29,920	218.4**	364.3**	4.737	46,204.56
Background	2	2,679,854**	229.2**	51.5**	2.873*	10,204.69**
Awngroup X Background	2	297,863	1.2	0.7	1.037**	1,207.38**
Entry X Environments	90	315,696**	4.3**	4.7**	0.512**	63.98**
T107 X Env.	10	74,214	2.4*	0.4	0.125	28.64
Mtg. X Env.	10	59,447	2.1	1.3	0.229	32.84
Cty. X Env.	10	52,665	0.6	0.9	0.328	55.97
Awned vs. Awnletted X Env.	10	112,236	2.4*	0.7	0.363	42.86
Background X Env.	20	495,995**	5.2**	8.3**	0.797**	117.40**
Awngroup X Background X Env.	20	37,045	1.3	0.9	0.160	37.30
Error	198	71,882	1.3	0.9	0.227	39.15
C.V. %		10.7	4.2	1.8	2.7	13.6

Table 2. Selected mean squares for spike traits in the bulk population experiment

Source	df	Spike density	Spike length	Spike harvest index	Seeds per spike
Environments	2	161,735*	6.1**	560.8**	802.0**
Replications(Env)	6	15,088	0.5	23.9	13.9
Entries	9	39,176**	5.9**	24.4	57.0**
TAM 107 Awned vs. Awnletted (T107)	1	1,743	0.6	2.8	33.7*
Mustang Awned vs. Awnletted (Mtg.)	1	15,880*	1.2	36.9	2.7
Century Awned vs. Awnletted (Cty.)	1	10,257	2.7*	110.6*	80.7**
Awned vs. Awnletted bulks	1	1,474	4.0	74.3	0.8
McNair 1003 vs. HRW parents	1	159,911**	37.6**	0.0	189.9**
Background	2	51,178**	1.7**	3.0	38.6
Awngroup X Background	2	13,203	0.2	38.0	58.2*
Entry X Environments	18	4,610	0.3	17.3	13.8
T107 X Env.	2	2,611	0.3	1.0	3.0
Mtg. X Env.	2	1,281	0.1	28.1	5.6
Cty. X Env.	2	2,324	0.3	4.1	1.6
Awned vs. Awnletted X Env.	2	372	0.2	6.0	4.3
Background X Env.	4	5,826	0.2	32.4	14.5
Awngroup X Background X Env.	4	2,922	0.3	13.6	3.0
Error	54	4,035	0.2	17.5	9.8
C.V. %	11.4	5.3	6.3	11.8	

Table 3. Selected mean squares for agronomic and quality traits in the sib-line experiment

Source	df	Grain yield	1000 kernel wt.	Test wt.	Harvest index.	Protein concentration	Hardness index
Environments (Env)	3	194,522,121**	12,239.3**	15,119.8**	36,701.7	434.63**	9,412.6**
Sets	1	4,471,977	45.1	152.8*	116.1	143.82**	2,763.3**
Env X Sets	3	2,716,933	96.0*	182.8**	147.7	135.84**	1,455.2**
Reps(Env. X Sets)	16	1,038,157	27.9	33.6	170.6	1.75	114.4
Sib pairs(Sets)	76	1,217,926**	81.7**	49.5**	83.1	6.21**	5,334.7**
Env X Sib pairs(Sets)	228	513,101**	10.1**	10.1**	23.4	4.07**	168.6**
Reps(Env X Sets) X Sib pairs	156	117,367**	2.9**	3.6**	14.9	0.48	31.5
Sibs (Sib pairs(Sets))	78	439,683**	37.2**	43.4**	18.4	9.13**	357.1**
Env X Sibs(sib pairs (Sets))	234	130,576**	2.5**	3.2**	11.8	6.50**	69.6**
Error	1076	74,101	1.6	1.2	3.6	0.44	31.8
C.V. %		13.7	5.0	2.2	5.8	5.8	13.1

Table 4. Means of spike and leaf photosynthesis rates for parents and isolines under well-watered and water-stressed treatments in the growth-chamber experiment.

			Net photosynthesis rate			
			Spike		Flag leaf	
Treatment	Background	Spike type	14DAA†	24DAA	14DAA	24DAA
			----------µmol m^{-2} s^{-1}----------			
Well watered	TAM 107	Awned	1.40	2.04	10.39	8.84
	Century	Awned	1.95	2.20	7.39	13.94
	Mustang	Awned	1.31	1.41	10.15	5.11
	McNair 1003	Awnletted	0.90	1.20**	10.90	9.06
	All isolines	Awned	1.94**	1.42**	11.45	7.71
	All isolines	Awnletted	0.57	0.53	11.94	7.13
Water stressed	TAM 107	Awned	1.51	1.15	11.74	7.86
	Century	Awned	0.46	1.33	8.56	13.62
	Mustang	Awned	1.20	1.08	6.31	5.49
	McNair 1003	Awnletted	-0.31**	0.95	8.69	6.99
	All isolines	Awned	1.18**	0.78	9.08	6.12
	All isolines	Awnletted	0.09	0.26	7.57	6.59

*, ** Indicates significance at $P < 0.05$, 0.01, respectively between McNair 1003 and the average of the awned parents, or between all awned and awnletted isolines within treatments .

†DAA = days after anthesis

Table 5. Means of season-long and instantaneous water-use efficiency (WUE) for parents and isolines under well-watered and water-stressed treatments in the growth-chamber experiment.

			Season-long WUE		Instantaneous WUE			
					Spike		Flag leaf	
Treatment	Background	Spike type	Whole-plant†	Grain‡	14DAA§	24DAA	14DAA	24DAA
			g kg^{-1}	g kg^{-1}	----------------------μmol mmol^{-1}----------------------			
Well watered	TAM 107	Awned	5.36	1.59	0.76	1.18	1.14	1.22
	Century	Awned	5.61	1.80	0.95	1.10	1.25	2.36
	Mustang	Awned	5.21	1.41	0.62	1.12	1.35	1.20
	McNair 1003	Awnletted	5.54	2.17*	0.45	0.67*	1.62	1.57
	All isolines	Awned	5.04	1.39	1.01**	0.85**	1.47	1.38
	All isolines	Awnletted	5.25	1.55	0.32	0.26	1.58	1.34
Water stressed	TAM 107	Awned	5.35	1.42	0.67	0.80	1.28	1.63
	Century	Awned	5.27	1.54	-0.03	0.90	1.42	1.73
	Mustang	Awned	5.01	1.35	0.54	0.81	1.16	1.13
	McNair 1003	Awnletted	5.57	2.01*	-0.38*	0.57	1.52	1.45
	All isolines	Awned	4.88	1.28	0.72**	0.53	1.49	1.06
	All isolines	Awnletted	5.04	1.47	0.06	0.16	1.44	1.34

*, ** Indicates significance at $P < 0.05$, 0.01, respectively between McNair 1003 and the average of the awned parents, or between all awned and awnletted isolines within treatments.

† Ratio of dry matter produced per amount of water used.

‡ Ratio of grain weight produced per amount of water used.

§ DAA = days after anthesis

Table 6. Means of seed yield and yield components for parents and isolines under well-watered and water-stressed treatments in the growth-chamber experiment.

Treatment	Background	Spike type	Kernels per spike	1000 kernel wt.	Harvest index of spike†	Grain yield per plant
			no.	g	%	g
Well watered	TAM 107	Awned	24.7	21.6	61.6	5.2
	Century	Awned	34.9	26.6	68.6	8.4
	Mustang	Awned	30.2	25.4	63.7	6.0
	McNair 1003	Awnletted	36.2*	30.5*	71.6	8.8*
	All isolines	Awned	28.1	27.7	65.1	6.4
	All isolines	Awnletted	29.2	25.1	69.1	6.6
Water stressed	TAM 107	Awned	24.2	26.3	65.5	4.6
	Century	Awned	31.9	30.3	69.7	6.0
	Mustang	Awned	25.7	29.2	63.8	4.9
	McNair 1003	Awnletted	34.4*	29.5	71.0	6.9
	All isolines	Awned	25.4	27.7	65.0	4.7
	All isolines	Awnletted	30.0*	24.5	70.5**	5.3

*, ** Indicates significance at $P < 0.05$, 0.01, respectively between McNair 1003 and the average of the awned parents, or between all awned and awnletted isolines within treatments.

†Ratio of grain weight to total spike weight.

VITA 2

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