

Nitrogen Use and Biomass Distribution in Culms of Winter Wheat Populations Selected from Grain-Only and Dual-Purpose Systems

Charles T. MacKown* and Brett F. Carver

ABSTRACT

Beginning in late fall and ending at jointing in early spring, winter wheat (*Triticum aestivum* L.) crops in the southern Great Plains are often grazed by stocker cattle (*Bos taurus* L.) and then harvested for grain. Traditionally, dual-purpose (grazing plus grain) wheat cultivars are developed from a grain-only production system. Because culms of dual-purpose grown wheat may forfeit productivity gains for grain-only developed cultivars, we evaluated N and biomass traits at anthesis and maturity for 12 sets of subpopulations (each set a unique genetic background) to test benefits of making selections from a dual-purpose system. Sets came from F₂ sources and contained a "Base" F₃ bulk population and F₅ bulk populations mass selected from the F₂ within grain-only and dual-purpose production systems. The 12 sets of subpopulations were evaluated in grain-only and dual-purpose production systems in 2001–2002 and 2002–2003. At anthesis, main effects (year, system, genetic background, subpopulation selection environment) were significant for culm dry weight and N, and flag leaf dry weight. Among selections, differences for these traits were small (2.0–3.5%) with no difference between grain-only and dual-purpose selections; differences among genetic backgrounds, however, were large (21–30%). At maturity, differences (7.6–20%) for grain dry weight and kernel mass, harvest index (HI), N content, grain N, and N harvest index (NHI) of individual culms occurred among genetic backgrounds. Differences among subpopulations were smaller (1.4–4.5%) and significant for only culm and grain dry weight, kernel number and mass, and culm N content. Selections made from the dual-purpose environment performed similar to those from the grain-only environment when grown in either production system.

WINTER WHEAT planted in the southern Great Plains is grown extensively for forage as well as a grain-only crop. Depending on production goals and prevailing market conditions some producers graze the wheat with stocker cattle before harvesting a grain crop, while others graze-out the wheat crop entirely or cut it for hay or silage. About 40% of the wheat acreage in Oklahoma is grown as a dual-purpose crop (Hossain et al., 2004), and as much as 80% of the total wheat acreage in the southern Great Plains is grazed (Pinchak et al., 1996). Wheat producers choosing a dual-purpose management system have greater flexibility and additional economic advantages compared with those choosing to grow wheat as a forage-only or grain-only crop (Redmon et al., 1995),

but they need to follow system-specific management practices to optimize returns. Compared to grain-only wheat, dual-purpose wheat should be planted earlier (Hossain et al., 2003), be seeded more densely (Epplin et al., 2000), and have additional fertilizer N applied to account for N removal in consumed forage (Krenzer, 1991; Zhang et al., 1998).

Genotype by environment interactions (Krenzer et al., 1992) and genotype by production system interactions occur (Khalil et al., 2002) with wheat grown in the southern Great Plains. Wheat cultivars used for dual-purpose are derived nearly always on performance of selections in grain-only production systems. Even when adhering to recommended management practices, grain yields from early-planted wheat in the dual-purpose production system are typically less than those of later-planted grain-only production systems (24% less for 12 cultivars averaged across 3 yr, Khalil et al., 2002; 20% less for variety trials averaged across 11 environments, Carver, unpublished data, 2005). Consequently, if the two production systems favor different genetic adaptations among selections, then cultivar development based solely on selection in a grain-only production system could compromise gains in genetic improvement of wheat intended for dual-purpose production.

To justify the added complexity and expense of using livestock for the development of dual-purpose wheat cultivars, a better understanding of the possible benefits of this approach is needed. Because forage and grain yields of small-grain cereals are uncorrelated (Ud-Din et al., 1993) or only poorly correlated (Atkins et al., 1969), both forage and grain productivity traits need to be considered for dual-purpose wheat. We previously reported forage traits at the onset of fall grazing for two winter wheat nurseries each containing unique pedigrees of 12 sets of subpopulations representing an unselected F₃ bulk population and F₅ bulk populations mass selected from the same F₂ source for three consecutive generations with either a grain-only or dual-purpose production system (MacKown and Carver, 2005). We found that selections from the dual-purpose system offered equal or slightly less fall forage biomass without greatly changing forage total N and nitrate concentrations (MacKown and Carver, 2005).

In this study, we extended our previous work to determine the utility of developing bulk populations from grain-only or dual-purpose production systems by testing reproductive traits of these populations in both production systems. To determine if effects of selection environment on traits linked to grain yield of an individual culm differed, N use and biomass distribution patterns in wheat culms at anthesis and maturity were measured.

C.T. MacKown, USDA-ARS, Grazinglands Research Lab., 7207 W. Cheyenne St., El Reno, OK 73036; B.F. Carver, Dep. of Plant and Soil Sciences, 368 Ag Hall, Oklahoma State Univ., Stillwater, OK 74078. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture or Oklahoma State University. Received 16 May 2006.
*Corresponding author (charles.mackown@ars.usda.gov).

Published in *Crop Sci.* 47:350–358 (2007).
Crop Physiology & Metabolism
doi:10.2135/cropsci2006.05.0318
© Crop Science Society of America
677 S. Segoe Rd., Madison, WI 53711 USA

Abbreviations: HI, harvest index; NHI, nitrogen harvest index.

MATERIALS AND METHODS

Experimental Materials

The winter wheat subpopulations developed in this study (Table 1) were derived from hybridized single-cross and three-way crosses of released and experimental genotypes as previously described in detail (MacKown and Carver, 2005). The present study used the 12 sets of unique genetic backgrounds in Nursery 1 of the earlier study, which constituted a representative sample of crosses routinely made in the winter wheat cultivar development program at Oklahoma State University. In brief, the F₁ generation was grown in the greenhouse and each F₂ seedlot was divided and planted in field plots assigned to grain-only and dual-purpose production systems at the Wheat Pasture Center operated by Oklahoma State University and located 56 km west of Stillwater, OK. Seed harvested from plots in each system was planted in the same respective system for two subsequent generations, ending with the F₄ generation harvest in 2000. Generation advance was achieved by bulk harvesting each subpopulation (grain-only or dual-purpose production system); selection was driven only by environmental conditions inherent to each system. In addition to the system-derived pairs of subpopulations, seed from a subpopulation of the original F₂ generation was planted in 1999 and harvested in 2000 from an ungrazed seed-increase nursery located 56 km east of the Wheat Pasture Center. This single-generation increase (designated Base) offered a reasonable compromise for producing sufficient seed for field testing and maintaining genetic variability present in the original F₂ population, while restricting natural selection in a field environment to 1 yr.

Agronomic practices followed during the generation-advance stages (F₂–F₄) were consistent with those used by wheat producers in the southern Great Plains (Krenzer, 1991); full details reported previously (MacKown and Carver, 2005). All plots were harvested for grain on the same day, typically in early June. Each plot was 3 m long with five rows spaced 23 cm apart. The three middle rows were harvested with a rice binder to collect seed for advanced generations.

Evaluation of Experimental Materials

The 12 triplicate sets of the three subpopulations (Base, F₃; grain-only and dual-purpose selected, both F₃) were planted on Kirkland silt loam (fine, mixed, thermic Udertic Paleustoll) at the Wheat Pasture Center in adjacent fields corresponding to areas assigned to grain-only and dual-purpose production. Fertilizer N was applied as anhydrous ammonia and the amount was adjusted for residual mineral N in the top 60 cm of soil to achieve a grain yield goal of 3000 kg ha⁻¹ plus a dry forage yield of 3500 kg ha⁻¹. A cattle stocking rate of two steers per hectare was used to graze wheat plots in the dual-

purpose production field. For each production system a split-plot design with three complete blocks was used; the 12 sets were assigned to main plots, while the subpopulations within sets were assigned to split-plots. Experiments were established in the 2001–2002 and 2002–2003 cropping seasons and a different randomization of main-plots and split-plots for the two production systems was used each year. The same seed lots of the Base and the two production system selected subpopulations were used each year. Management practices in this population testing phase were similar to those used to derive subpopulations, except that planting dates were 10 Sept. 2001 and 24 Sept. 2002 for evaluations with dual-purpose production and 10 Oct. 2001 and 16 Oct. 2002 for evaluations with grain-only production. Each subplot was 3 m long with five rows spaced 23 cm apart.

Data Collection and Analyses

Samples were collected at anthesis (25 Apr.–2 May 2002; 28–30 Apr. 2003) and physiological maturity (3–12 June 2002; 27 May–3 June 2003) by clipping 20 culms from interior rows of the five-row plots. Each culm from a separate plant tagged at anthesis was clipped at a height of ≈4 cm above the soil surface. Flag leaf blades and spikes were separated from culms in the field and all plant parts dried to constant weight at 60°C and weighed. At maturity, grain was removed from the spikes and chaff recombined with the culms. All grain kernels were counted and all plant parts were dried at 60°C and weighed. Plant parts were ground (<1 mm) for total N analyses by automated flash combustion (CHN-1000; Leco Corp., St. Joseph, MI).

Statistical analyses of the genetic backgrounds and check cultivars were performed using ANOVA procedures. Years, genetic background, and cultivar were considered random effects and each data set was analyzed using mixed model procedures in the Fit Model platform of JMP software (SAS Institute, 2002).

RESULTS

For the 12 unique genetic backgrounds, ANOVA results for single culm traits measured at anthesis and maturity are summarized in Table 2. Nearly all of the higher order interactions and many of the two-way interactions were not significant ($P > 0.05$) for anthesis and mature traits. In contrast, main effects were often significant (production system and subpopulation) or always significant (genetic background) for anthesis and mature traits.

Anthesis Traits

Responses of the anthesis traits from the subpopulations averaged across grain-only and dual-purpose production system evaluations were not consistent among the genetic backgrounds (Fig. 1). The culm dry weight of several of the bulk subpopulations selected from a dual-purpose system were less than those of the Base (sets 5, 7, 10) and grain-only (set 7) selected bulk subpopulation, while set 3 Base subpopulation was less than both the grain-only and dual purpose subpopulations (Fig. 1A). The flag leaf blade dry weights of Base subpopulations for sets 5, 10, and 11 were greater than both the grain-only and dual-purpose selections of these sets and only the grain-only subpopulation of set 9 had a flag

Table 1. Genetic background of winter wheat bulk subpopulations used to evaluate anthesis and maturity traits in 2002 and 2003.

| Set | Genetic background |
|-----|---|
| 1 | 2180//Crr*2/CtyA-/3/Ogallala |
| 2 | Tkw//Karl 92*2/CtyA-/3/Hicokok |
| 3 | Platte//KS137-337/Wakefield |
| 4 | Plainsman V//OK79256 seln//FL302/3/Jagger |
| 5 | Custer//FL302//TAM 302 |
| 6 | KS92P0363-134//FL302//Ogallala |
| 7 | Jagger*2//FL302 |
| 8 | 2137//SW76-117C-4 |
| 9 | OK95G702//OK91P648 |
| 10 | OK95G703//2137 |
| 11 | OK95G703//OK92403 |
| 12 | OK95G704//OK91P648 |

Table 2. Significance ($P > F$) values from the ANOVA of selected dry weight and N traits of individual culms at anthesis and maturity for 12 sets of unique wheat subpopulations evaluated in grain-only and dual-purpose production systems for 2 yr.

| Source of variation | Anthesis traits | | | | Mature traits [†] | | | | | | | |
|------------------------|-----------------|-------------------------|-------------------|-----------|----------------------------|---------------|------------|-------------|-----|-----------|---------------|-----|
| | Culm dry wt. | Flag leaf blade dry wt. | Flag leaf blade N | N content | Culm dry wt. | Grain dry wt. | Kernel no. | Kernel mass | HI | N content | Grain N conc. | NHI |
| Year (Y) | * | *** | NS‡ | *** | NS | NS | ** | NS | NS | NS | ** | *** |
| Production system (PS) | *** | *** | * | *** | NS | NS | NS | ** | *** | NS | *** | *** |
| Y × PS | ** | NS | NS | NS | NS | NS | NS | NS | * | NS | NS | NS |
| Genetic background (G) | *** | *** | ** | *** | *** | *** | *** | *** | *** | *** | *** | *** |
| Y × G | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| PS × G | NS | NS | NS | NS | NS | NS | ** | * | NS | NS | * | ** |
| Y × PS × G | NS | NS | NS | NS | NS | * | * | NS | NS | NS | NS | NS |
| Subpopulation (S) | *** | *** | NS | ** | *** | ** | *** | * | NS | *** | NS | NS |
| Y × S | * | *** | NS | NS | NS | NS | NS | NS | NS | NS | NS | ** |
| PS × S | ** | * | NS | * | NS | NS | NS | NS | NS | NS | NS | NS |
| G × S | *** | *** | NS | ** | * | * | ** | ** | NS | NS | * | NS |
| Y × PS × S | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | ** | NS |
| Y × G × S | NS | NS | NS | NS | NS | NS | NS | * | NS | NS | NS | NS |
| PS × G × S | NS | NS | * | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| Y × PS × G × S | NS | NS | NS | *** | NS | NS | NS | NS | NS | NS | NS | NS |

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† HI, harvest index; NHI, nitrogen harvest index.

‡ NS, not significant.

leaf blade dry weight that was greater than that of the subpopulation selected from the dual-purpose system (Fig. 1B). Aboveground N content of the grain-only selection for set 8 was greater than the dual-purpose selection, while N content for the grain-only selection in set 6 was less than that of the dual-purpose subpopulation, and the Base subpopulations of sets 5 and 11 was greater than both the grain-only and dual purpose subpopulations (Fig. 1C).

Averaged across genetic backgrounds, values for traits measured at anthesis in dual-purpose production were unaffected by the source of the subpopulation and were consistently less than those from the grain-only production evaluations, except for flag leaf blade N concentration, which was unaffected by production system (Table 3). In the grain-only production system, culm and flag leaf blade dry weights and N content values from the Base subpopulation were often greater than those from the grain-only and dual-purpose subpopulations. The overall means for the grain-only and dual-purpose selected subpopulations were not significantly different ($P > 0.05$), whereas the overall production system evaluation means of the anthesis traits for the grain-only system were all greater than those of the dual-purpose system (Table 3). The overall mean flag leaf blade N concentration of culms in the grain-only production system was only 4% greater than that of culms from the dual-purpose system. Differences due to production system were greater for other anthesis traits of individual culms: dry weight was 15% greater, aboveground N content was 25% greater, and visually larger flag leaf blades that had 28% more dry weight than the anthesis traits of culms from the dual-purpose production system.

Mature Traits

Among the subpopulations, five of the 12 genetic backgrounds differed significantly ($P \leq 0.05$) in mature

culm dry weights averaged across both production systems that. Culm dry weight of the dual-purpose subpopulation in set 3 was greatest, while the Base subpopulations of sets 4, 7, and 10 had greater culm dry weight than the grain-only and dual-purpose subpopulation selections, and in set 11 the culm dry weight of the dual-purpose selection was less than the other two subpopulations (Fig. 2A). Differences in grain dry weights per culm among subpopulations within the genetic background (Fig. 2B) were generally consistent with differences in culm dry weights. Subpopulations within sets 3, 6, 7, and 10 differed in the number of kernels per culm with the Base subpopulations having greater than or equal kernel number as the grain-only and dual-purpose selected subpopulations (Fig. 2C). Three of the 12 sets of genetic backgrounds had individual kernel mass that differed among the three subpopulations with set 4 Base subpopulation kernel mass exceeding ($P \leq 0.05$) the weights of the other two subpopulations and the Base subpopulations of sets 3 and 5 having smaller kernel mass than the grain-only and dual-purpose selected subpopulations (Fig. 2D). There were no significant ($P \leq 0.05$) differences between kernel mass of grain-only and dual-purpose selections within a genetic background. Except for set 1, differences in grain N concentration of the grain-only and dual-purpose subpopulations within a set were not significant ($P \leq 0.05$), while the Base subpopulation of sets 4 and 10 had grain N concentrations less than the grain-only but not the dual-purpose selected subpopulation (Fig. 2E).

Except for culm dry weight, all mature trait averages across genetic background, production system, and years were not significantly ($P > 0.05$) different between the grain-only and dual-purpose selected subpopulations. The Base subpopulation culm dry weight, kernel mass, and aboveground N content exceeded and NHI (N harvest index, ratio of grain N to total aboveground N) in 2002 was less ($P \leq 0.05$) than those of the two selected

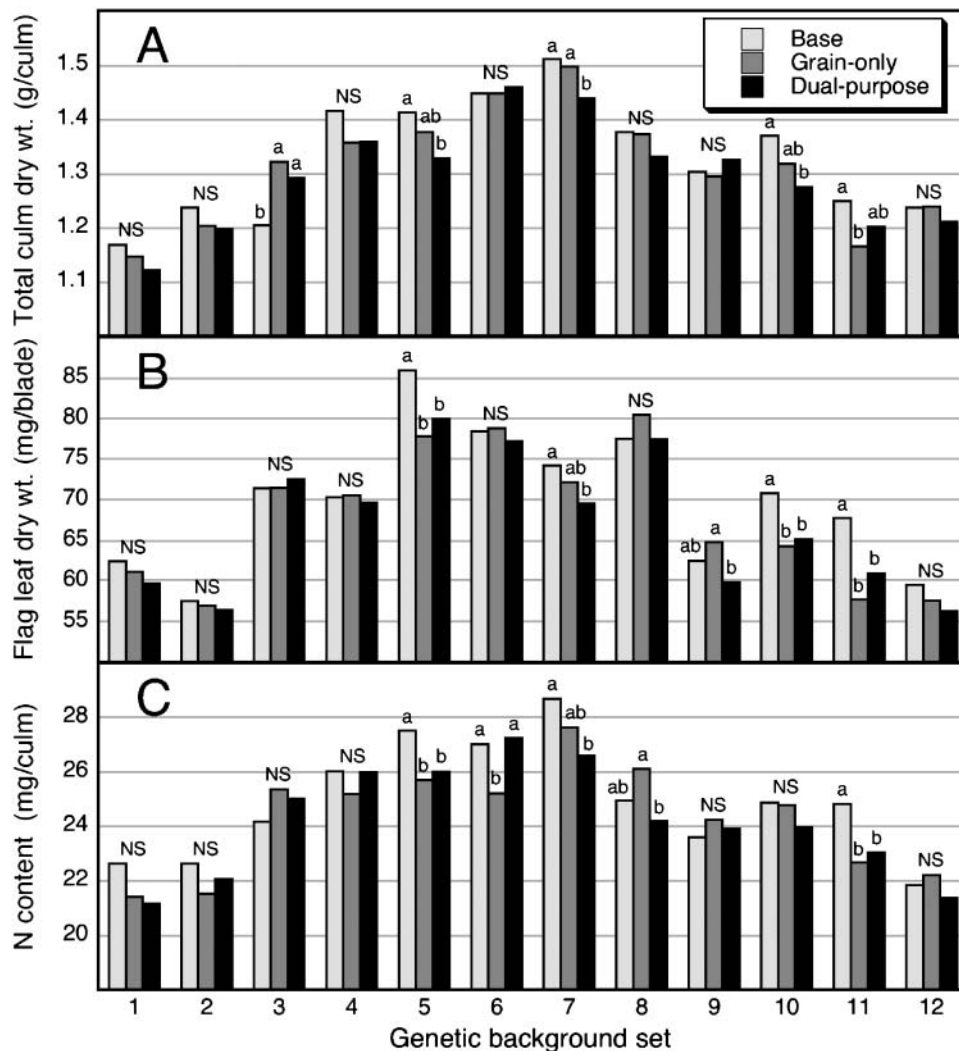


Fig. 1. Anthesis traits of bulk subpopulations (Base, grain-only, and dual-purpose) generated for 12 unique wheat genetic backgrounds. Values are least squares means ($n = 12$) of three replications across 2 yr and two production systems. Within a genetic background set, bars followed by the same letter are not significantly (NS) different at $P = 0.05$ using Student's t test.

subpopulations (Table 4). Among the three subpopulations, HI (harvest index, ratio of grain to total above-ground yield) and grain N concentrations were not significantly ($P > 0.05$) different and NHI values in 2003 exceeded those in 2002.

Among the genetic backgrounds there were small yet significant ($P \leq 0.05$) differences in HI and NHI averaged across subpopulations and years (Fig. 3). Sets 1, 4, 5, and 10 had HI values (≈ 0.43) that were less than sets 3 and 12 (≈ 0.46). For NHI, values for sets 5 and 10 (≈ 0.68) were less than those of sets 2, 6, 11, and 12 (≈ 0.73).

Overall means of culm dry weight, grain dry weight per culm, kernels per culm, and aboveground N content at maturity were not significantly ($P > 0.05$) different between the grain-only and dual-purpose production systems (Table 5). For the dual-purpose system, individual kernel mass, HI and NHI were greater and grain N concentrations were less than those of the grain-only system.

Between anthesis and maturity, the overall average loss of dry weight from nongrain culm tissue was 13.7%

of the anthesis dry weight. Effects of year, production system, genetic backgrounds, subpopulation selection environments, and their interactions were not significant ($P > 0.05$; data not shown).

DISCUSSION

During the grain filling development phase, grain dry weight accumulation coincides with substantial respiration of photosynthate (Hodges and Kanemasu, 1977; Gent and Kiyomoto, 1989; Gent, 1994). Photosynthate produced during grain filling and photosynthate reserves accumulated before grain filling are allocated for both processes (Pheloung and Siddique, 1991; Gent, 1994), with reserve photosynthate buffering fluctuations in current photosynthate (Kühbauch and Thome, 1989; Takahashi et al., 1994) and contributing proportionally more to grain dry weight in stressful environments (Schnyder, 1993; Gent, 1994) in response to shifts between source activity and sink demand (Bidinger et al., 1977; Willenbrink et al., 1998).

Table 3. Least squares means for total culm and flag leaf blade dry weights, flag leaf blade N concentration, and N content at anthesis as affected by production system and subpopulation (selection environment). Values are means across 12 unique wheat genetic backgrounds and 2 yr.

| Production system | Subpopulation | | | Avg. |
|---|---------------|------------|--------------|--------|
| | Base | Grain-only | Dual-purpose | |
| Culm dry wt., g culm⁻¹ | | | | |
| Grain-only | 1.43a† | 1.40ab | 1.37b | 1.40A‡ |
| Dual-purpose | 1.22c | 1.23c | 1.22c | 1.22B |
| Avg. | 1.33A | 1.31AB | 1.29B | |
| Flag leaf blade dry wt., mg blade⁻¹ | | | | |
| Grain-only | 78.9a | 76.0b | 74.5b | 76.5A |
| Dual-purpose | 60.8c | 59.6c | 59.6c | 60.0B |
| Avg. | 69.9A | 67.8B | 67.1B | |
| Flag leaf blade N, mg g⁻¹ | | | | |
| Grain-only | 41.0a | 41.0a | 41.3a | 41.1A |
| Dual-purpose | 39.7a | 39.9a | 39.6a | 39.7B |
| Avg. | 40.3A | 40.5A | 40.5A | |
| N content, mg culm⁻¹ | | | | |
| Grain-only | 27.9a | 26.9b | 26.7b | 27.2A |
| Dual-purpose | 21.9c | 21.8c | 21.8c | 21.8B |
| Avg. | 24.9A | 24.3B | 24.2B | |

† Subpopulation × production system trait values followed by the same lowercase letter are not significantly different according to Tukey-Kramer mean comparison test at $P = 0.05$.

‡ Averages in a column or in a row followed by the same uppercase letter are not significantly different according to Tukey-Kramer mean comparison test at $P = 0.05$.

Even though grain dry weight accumulation is affected proportionately less than expected when net photosynthesis is markedly reduced (Judel and Mengel, 1982; Takahashi et al., 1994), selections and genetic backgrounds that affect those culm traits associated with photosynthate production, storage, and use would be expected to have an effect on grain traits of a culm. During grain filling, kernel number per culm relates directly to demand for photosynthate. While there were marked differences in kernel number per culm among genetic backgrounds, four of the 12 genetic backgrounds evaluated had kernel numbers that differed due to the subpopulation selection environment. These differences in kernel number due to selection, however, were not consistently expressed. Furthermore, they did not correspond to differences in average kernel mass and only set 7 and partly set 4 corresponded to differences in total grain dry weight per culm (Fig. 2). The genetic background × subpopulation means of total culm dry weight at anthesis were strongly correlated (0.74, $P < 0.001$) with the means of grain dry weight per culm. Similarly, anthesis flag leaf blade dry weight and total N content, both linked to photosynthate production, were correlated (0.59 and 0.70, $P < 0.001$, respectively) with the means of grain dry weight per culm. The correlation for total N content was expected because it depends on total culm dry weight, which was strongly correlated with grain dry weight per culm.

Closer inspection of the grain dry weight results for the 12 sets of genetic backgrounds reveals only the dual-purpose selection subpopulation from set 3 had a significantly greater grain dry weight per culm than the grain-only subpopulation (Fig. 2). However, differences in anthesis flag leaf dry weight, total culm dry weight, and total N content (Fig. 1) or the relative losses in vegetative dry weight between anthesis and maturity were

not observed ($15 \pm 5\%$, dual-purpose subpopulation; $22 \pm 6\%$, grain-only subpopulation). The difference in culm grain dry weight of these two subpopulations from set 3 was not associated with any of these traits linked to photosynthate production but was consistent with subpopulation differences in kernel number per culm (sink demand). Similarly, Base subpopulations with a greater grain dry weight per culm than one or both of the selected subpopulations (e.g., sets 4 and 7) were not consistently associated with culm and flag leaf dry weight and N content at anthesis, but generally tracked differences in kernel number per culm of the subpopulations.

As we observed for forage traits at the onset of fall grazing (MacKown and Carver, 2005), trait differences among subpopulations were usually less than those differences among genetic backgrounds. Within the grain-only production system there were slight differences in anthesis traits among the subpopulations, while within the dual-purpose production system there were no differences (Table 3). Averaged across all genetic backgrounds and the three subpopulations, traits measured at anthesis were consistently greater in the grain-only system than the dual-purpose system (Table 4). A substantially larger flag leaf blade, culm dry weight, and N content at anthesis should favor greater photosynthate production and storage to support grain filling. However, when averaged across all genetic backgrounds and the three subpopulations, grain dry weight per culm was not different for grain-only and dual-purpose production systems. The absence of significant interactions of the subpopulations × production system for mature traits (Table 2) indicates that the small differences among subpopulations (Table 4; culm dry wt., grain dry wt., kernel number, kernel mass, and HI) was unaffected by production system.

Grain N is primarily derived from mobilization of N accumulated before grain filling commences (Austin et al., 1977; Van Sanford and MacKown, 1987; Heitholt et al., 1990), although wheat can readily absorb N and assimilate nitrate following anthesis (Austin et al., 1977; MacKown and Van Sanford, 1986). The amount of N absorbed after anthesis can be quite substantial when there is an adequate supply of soil mineral N and soil moisture is not limiting after anthesis (Wuest and Cassman, 1992). The potential for N uptake after anthesis is greater for plants with large spikes with numerous kernels (Mi et al., 2000), and the amount of N uptake after anthesis can be reduced when sink size is reduced (Pérez et al., 1989) particularly for cultivars that lack a compensatory kernel mass increase when 50% of the spikelets are removed at anthesis (Ma et al., 1996). At anthesis, the differences in flag leaf blade N concentration and N content associated with subpopulations were either not significant or small relative to the effects of genetic background and production system. The average amount of N at anthesis closely tracked the total culm dry weight when averaged across production systems (Fig. 2) indicating that overall tissue N concentrations were reasonably uniform across the subpopulations and genetic backgrounds. However, wheat from the dual-purpose production system had nearly 20% less N content at

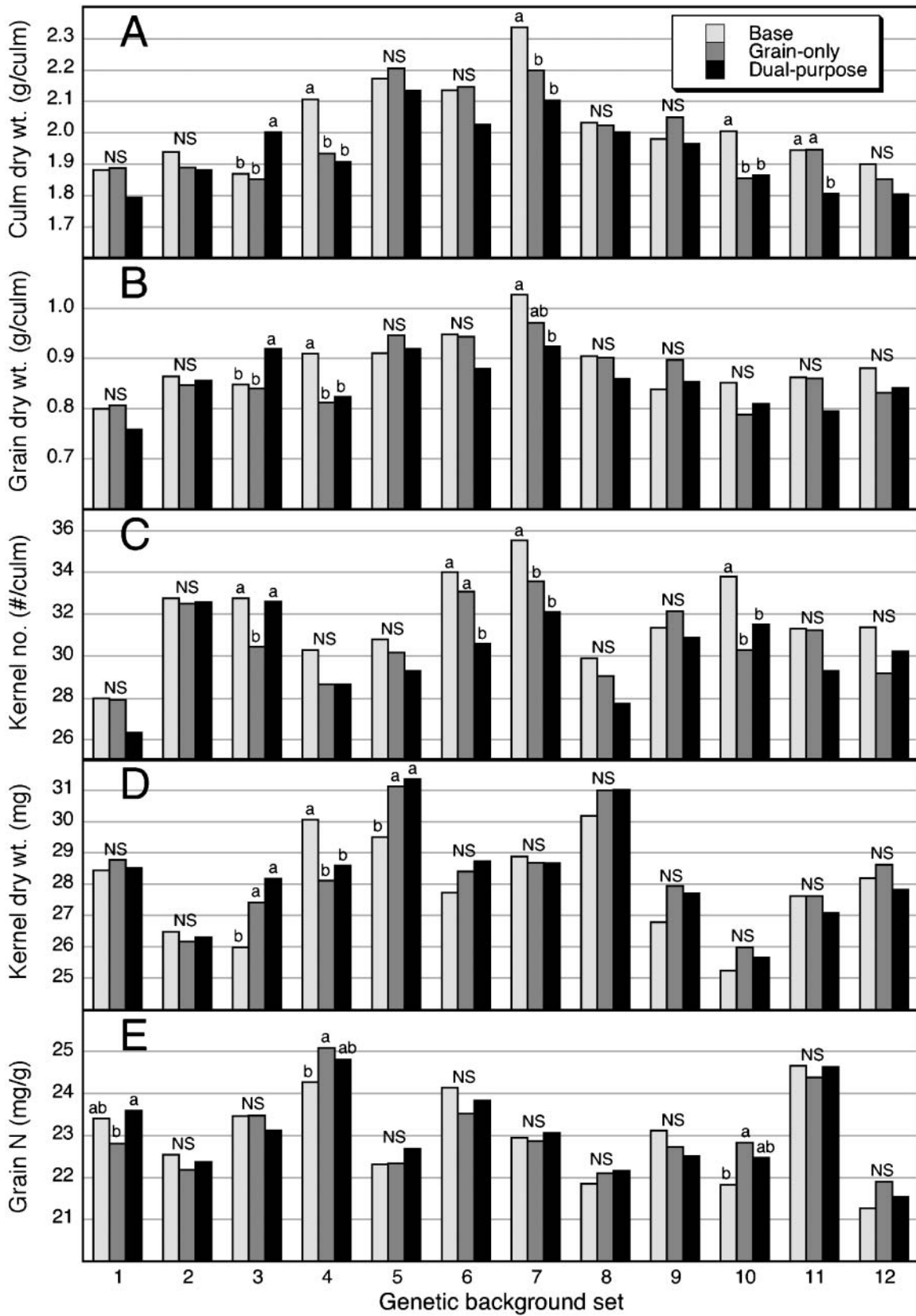


Fig. 2. Mature traits of bulk subpopulations (Base, grain-only, and dual-purpose) generated for 12 unique wheat genetic backgrounds. Values are least squares means ($n = 12$) of three replications across 2 yr and two production systems. Within a genetic background set, bars followed by the same letter are not significantly (NS) different at $P = 0.05$ using Student's t test.

Table 4. Subpopulation least squares means for mature wheat traits total culm, grain, and kernel mass, harvest index (HI), N content, grain N concentration, and N harvest index (NHI). Values are means across 12 unique wheat genetic backgrounds, two production systems, and 2 yr.

| Subpopulation | Culm dry wt. | Grain dry wt. | Kernel no. | Kernel mass | HI | N content | Grain N conc. | NHI | |
|---------------|----------------------|---------------|--------------------|-------------------------|-------|-----------------------|--------------------|--------|-------|
| | | | | | | | | 2002 | 2003 |
| | g culm ⁻¹ | | culm ⁻¹ | mg kernel ⁻¹ | | mg culm ⁻¹ | mg g ⁻¹ | | |
| Base | 2.02a† | 0.89a | 31.8a | 27.9b | 0.44a | 29.0a | 23.0a | 0.66C‡ | 0.74A |
| Grain-only | 1.98b | 0.87ab | 30.7b | 28.3a | 0.44a | 28.1b | 23.0a | 0.68B | 0.74A |
| Dual-purpose | 1.94c | 0.85b | 30.1b | 28.3a | 0.44a | 27.7b | 23.1a | 0.68B | 0.74A |

† Values in a column followed by the same lowercase letter are not significantly different according to Tukey–Kramer mean comparison test at $P = 0.05$.

‡ Year × selection environment HI values followed by the same uppercase letter are not significantly different according to Tukey–Kramer mean comparison test at $P = 0.05$.

anthesis than the grain-only wheat, while culm dry weight was only 13% less, resulting in an 8% lower overall tissue N concentration for wheat plants from the dual-purpose system. If the efficiency of plant N redistribution is similar for the two production systems, then less N content associated with wheat in the dual-purpose system could decrease grain N concentration of a culm, when N uptake during grain filling and grain dry weight of a culm are similar for the two production systems.

At maturity, the difference in N content due to production system had disappeared and corresponded to equivalent total culm dry weights of the individual culms from the two production systems. Accordingly, for this experiment postanthesis N uptake by plants evaluated in the dual-purpose production system was greater than that of plants evaluated in the grain-only production system. If postanthesis stress had limited N uptake during grain filling, then plants in the dual-purpose production system would be expected to have a lower grain N concentration (Van Sanford and MacKown, 1987). The range in N content at maturity among the subpopulation selections (Table 4, 27.7–29.0 mg culm⁻¹) was markedly less than the range among genetic backgrounds (25.4–31.5 mg culm⁻¹) and redistribution efficiency, as indicated by NHI, was only slightly different (0.66–0.68 in 2002) or equivalent (0.74 in 2003) among the subpopulations. The range in NHI among the genotypes (0.68–0.74) was narrower than the range for a

set of cultivars evaluated within a grain-only production system in the southern Great Plains (0.65–0.78, Heitholt et al., 1990). Because of the similar NHI values among the subpopulations, the slight differences in N content and grain dry weight (0.85–0.89 g culm⁻¹) did not cause a significant difference in grain N concentration (23.0 mg g⁻¹). Among the genetic backgrounds, however, there was a diversity in grain N concentrations (21.6–24.7 mg g⁻¹) as was observed for the other mature traits, but grain N concentration was not correlated with any of the other mature traits. For these genetic backgrounds, achieving a desired grain N concentration was independent of the selection environment and should be made directly on this trait itself. Selections made in either the grain-only or dual-purpose production system could have slightly lower grain N concentrations when grown in a dual-purpose system (22.5 mg g⁻¹) than the grain-only system (23.6 mg g⁻¹), but this decrease is not expected to alter end use of the flour.

Culm biomass and N traits measured at anthesis and maturity for subpopulations of 12 genetic backgrounds selected from grain-only and dual-purpose production systems revealed that differences in culm traits were often greater due to genetic background than selection environment of the subpopulations. Consequently, selections made from the dual-purpose environment performed similarly to those from the grain-only environment when grown in either production system. The relative impact of these factors on the anthesis and mature traits

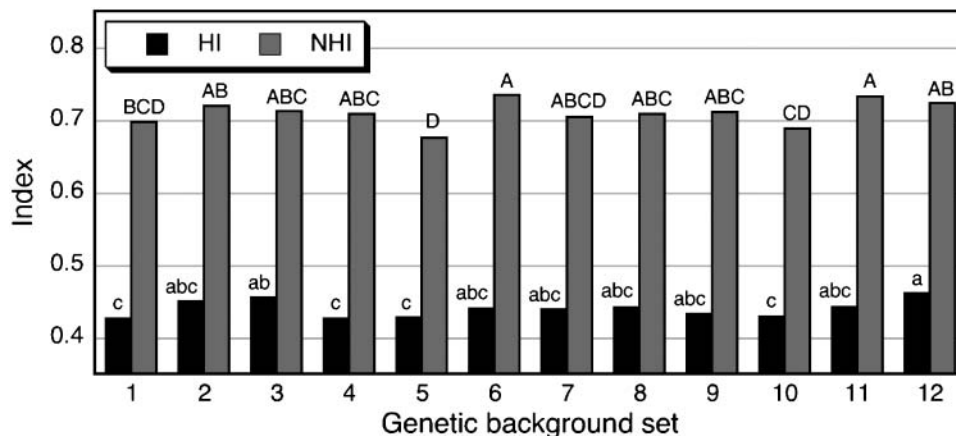


Fig. 3. Harvest index (HI) and nitrogen harvest index (NHI) of wheat culms for 12 unique wheat genetic backgrounds. Values are least squares means ($n = 36$) of three replications across 2 yr, two production systems, and three subpopulations. The HI bars with the same lowercase letters and the NHI bars with the same uppercase letters are not significantly different according to Tukey–Kramer mean comparison test at $P = 0.05$.

Table 5. Production system least squares means for total culm, grain, and kernel mass, and harvest index (HI), N content, grain N concentration, and N harvest index (NHI). Values are means across three subpopulations of 12 unique wheat genetic backgrounds evaluated in 2002 and 2003.

| Production system | Culm dry wt. | Grain dry wt. | Kernel no. | Kernel mass | HI | N content | Grain N conc. | NHI |
|-------------------|----------------------|---------------|--------------------|-------------------------|-------|-----------------------|--------------------|-------|
| | g culm ⁻¹ | | culm ⁻¹ | mg kernel ⁻¹ | | mg culm ⁻¹ | mg g ⁻¹ | |
| Grain-only | 1.98a [†] | 0.82a | 30.7a | 26.8b | 0.42b | 28.6a | 23.6a | 0.68b |
| Dual-purpose | 1.98a | 0.92a | 31.0a | 29.5a | 0.46a | 27.9a | 22.5b | 0.74a |

[†] Means within columns followed by the same letter are not significantly different ($P = 0.05$).

of individual culms is similar to what we observed for the forage traits of these subpopulations (MacKown and Carver, 2005). The marginal responses of individual culms to selection environment needs to be considered with caution, particularly when considering grain yield, because the number of kernels per unit area is a primary contributor to grain yield. For the plots used in this study, whole plot grain yields were enhanced for the dual-purpose subpopulations grown in both the dual-purpose (7.4%) and grain-only (5.8%) environments (Carver and MacKown, 2005). From a separate random sampling of 15 spikes at maturity, the dual-purpose subpopulations had similar kernels per spike and individual kernel mass, but more spikes per unit area than the grain-only subpopulations. Consequently, the dual-purpose selection environment favored the development of selections that produced a greater number of tillers with spikes when evaluated with both production systems. While individual culms from the subpopulations exhibited only minor differences, yield benefits can accrue through the use of a dual-purpose production system for development of favorable selections for both dual-purpose and grain-only production systems in the southern Great Plains.

ACKNOWLEDGMENTS

Assistance with collection, processing, and analyses of samples was provided by Jeff Weik and Kory Bollinger of the USDA-ARS Grazinglands Research Laboratory. Generation of crosses and development of bulk subpopulations was made possible by personnel of Oklahoma State University including Wayne Whitmore, Dr. Gerald Horn, and Dr. Eugene Krenzer.

REFERENCES

Atkins, I.M., O.G. Merkle, and P.E. Pawlisch. 1969. Visual estimates and clipping plot size for evaluating the forage potential of small grain varieties. *Agron. J.* 61:88–91.

Austin, R.B., M.A. Ford, J.A. Edrich, and R.D. Blackwell. 1977. The nitrogen economy of winter wheat. *J. Agric. Sci.* 88:159–167.

Bidinger, F., R.B. Musgrave, and R.A. Fischer. 1977. Contribution of stored preanthesis assimilate to grain yield in wheat and barley. *Nature* 270:431–433.

Carver, B.F., and C.T. MacKown. 2005. Selection responses in winter wheat induced by grain-only and dual-purpose management systems. 229–4. *In* 2005 Agronomy abstracts. ASA, Madison, WI.

Epplin, F.M., I. Hossain, and E.G. Krenzer, Jr. 2000. Winter wheat fall-winter forage yield and grain yield response to planting date in a dual-purpose system. *Agric. Syst.* 63:161–173.

Gent, M.P.N. 1994. Photosynthate reserves during grain filling in winter wheat. *Agron. J.* 86:159–167.

Gent, M.P.N., and R.K. Kiyomoto. 1989. Assimilation and distribution of photosynthate in winter wheat cultivars differing in harvest index. *Crop Sci.* 29:120–125.

Heitholt, J.J., L.I. Croy, N.O. Maness, and H.T. Nguyen. 1990. Nitrogen partitioning in genotypes of winter wheat differing in grain N concentration. *Field Crops Res.* 23:133–144.

Hodges, T., and E.T. Kanemasu. 1977. Modeling daily dry matter production of winter wheat. *Agron. J.* 69:974–978.

Hossain, I., F.M. Epplin, G.W. Horn, and E.G. Krenzer, Jr. 2004. Wheat production practices used by Oklahoma grain and livestock producers. Oklahoma Agric. Exp. Stn. B-818 [Online]. Available at osuxtra.okstate.edu/pdfs/B-818.pdf (verified 11 Dec. 2006). Oklahoma State Univ., Stillwater, OK.

Hossain, I., F.M. Epplin, and E.G. Krenzer, Jr. 2003. Planting date influence on dual-purpose winter wheat forage yield, grain yield, and test weight. *Agron. J.* 95:1179–1188.

Judel, G.K., and K. Mengel. 1982. Effect of shading on nonstructural carbohydrates and their turnover in culms and leaves during the grain filling period of spring wheat. *Crop Sci.* 22:958–962.

Khalil, I.H., B.F. Carver, E.G. Krenzer, C.T. MacKown, and G.W. Horn. 2002. Genetic trends in winter wheat yield and test weight under dual-purpose and grain-only management systems. *Crop Sci.* 42:710–715.

Krenzer, E.G., Jr. 1991. Wheat for pasture. OSU Ext. Facts 2586. Oklahoma State Univ. Ext. Serv., Stillwater, OK.

Krenzer, E.G., Jr., J.D. Thompson, and B.F. Carver. 1992. Partitioning of genotype × environment interactions of winter wheat forage yield. *Crop Sci.* 32:1143–1147.

Kühbauch, W., and U. Thome. 1989. Nonstructural carbohydrates of wheat stems as influenced by sink-source manipulations. *J. Plant Physiol.* 143:243–250.

Ma, Y.-Z., C.T. MacKown, and D.A. Van Sanford. 1996. Differential effects of partial spikelet removal and defoliation on kernel growth and assimilate partitioning among wheat cultivars. *Field Crops Res.* 47:201–209.

MacKown, C.T., and B.F. Carver. 2005. Fall forage biomass and N composition of winter wheat populations selected from grain-only and dual-purpose environments. *Crop Sci.* 45:322–328.

MacKown, C.T., and D.A. Van Sanford. 1986. Postanthesis nitrate assimilation in winter wheat. *In situ* flag leaf reduction. *Plant Physiol.* 81:17–20.

Mi, G., L. Tang, F. Zhang, and J. Zhang. 2000. Is nitrogen uptake after anthesis in wheat regulated by sink size? *Field Crops Res.* 68:183–190.

Pérez, P., R. Martínez-Carrasco, I.M. Martín del Molino, B. Rojo, and M. Ulloa. 1989. Nitrogen uptake and accumulation in grains of three winter wheat varieties with altered source-sink ratios. *J. Exp. Bot.* 40:707–710.

Pheloung, P.C., and K.H.M. Siddique. 1991. Contribution of stem dry matter to grain yield in wheat cultivars. *Aust. J. Plant Physiol.* 18:53–64.

Pinchak, W.E., W.D. Worall, S.P. Caldwell, L.J. Hunt, N.J. Worall, and M. Conoly. 1996. Interrelationships of forage and steer growth dynamics on wheat pasture. *J. Range Manage.* 49:126–130.

Redmon, L.A., G.W. Horn, E.G. Krenzer, Jr., and D.J. Bernardo. 1995. A review of livestock grazing and wheat grain yield: Boom or bust? *Agron. J.* 87:137–147.

SAS Institute. 2002. JMP statistics and graphics guide. Version 5.0. SAS Inst., Cary, NC.

Schnyder, H. 1993. The role of carbohydrate storage and redistribution in the source-sink relations of wheat and barley during grain filling—A review. *New Phytol.* 123:233–245.

Takahashi, T., N. Tsuchihashi, T. Takaku, and K. Nakaseko. 1994. Grain filling mechanisms in spring wheat. III. Effects of shadings on dry matter accumulation in grain and culm. *Japan. J. Crop Sci.* 63: 313–319.

Ud-Din, N., B.F. Carver, and E.G. Krenzer, Jr. 1993. Visual selection for forage yield in winter wheat. *Crop Sci.* 33:41–45.

Van Sanford, D.A., and C.T. MacKown. 1987. Cultivar differences in

- nitrogen remobilization during grain fill in soft red winter wheat. *Crop Sci.* 27:295–300.
- Willenbrink, J., G.D. Bonnett, S. Willenbrink, and I.F. Wardlaw. 1998. Changes of enzyme activities associated with the mobilization of carbohydrate reserves (fructans) from the stem of wheat during kernel filling. *New Phytol.* 139:471–478.
- Wuest, S.B., and K.G. Cassman. 1992. Effects of variation in soil water potential, depth of nitrogen placement, and cultivar on postanthesis nitrogen uptake by wheat. *Plant Soil* 143:45–53.
- Zhang, H., G.V. Johnson, W.R. Raun, N.T. Basta, and J.A. Hattey. 1998. OSU soil test interpretations. Oklahoma Coop. Ext. Serv. and Oklahoma Agric. Exp. Stn. F-2225 [Online]. Available at osueextra.okstate.edu/pdfs/F-2225web.pdf (verified 11 Dec. 2006). Oklahoma State Univ., Stillwater, OK.