Published October 4, 2013
JOURNAL OF PLANT REGISTRATIONS
CULTIVAR

'Billings' Wheat Combines Early Maturity, Disease Resistance, and Desirable Grain Quality for the Southern Great Plains, USA

Robert M. Hunger, Jeffrey T. Edwards, Robert L. Bowden, Liuling Yan, Patricia Rayas-Duarte, Guihua Bai, Gerald W. Horn, James A. Kolmer, Kris L. Giles, Ming-Shun Chen, Yue Jin, Roger D. Osburn, Melanie B. Bayles, Bradford W. Seabourn, Arthur R. Klatt, and Brett F. Carver*

ABSTRACT

Selection pressure for earliness, resistance to multiple pathogens, and quality attributes consistent with the hard red winter (HRW) wheat (*Triticum aestivum* L.) market class is tantamount to, or can obscure, selection for yield potential in lower elevations of the U.S. southern Great Plains. The decline in acreage of 'Jagger' (PI 593688) only impelled this inclination as producers searched for substitutes in the Jagger maturity and yield range but with improved disease protection and similar quality attributes to which end users had become accustomed. Our objective was to certify those very strengths in the HRW wheat cultivar Billings (Reg. No. CV-1089, PI 656843), released in 2009 by the Oklahoma Agricultural Experiment Station. The cross from which Billings was selected, OK94P597/N566, underscores a historically important dual breeding objective of the Oklahoma State University wheat improvement program: to identify improved fungal disease resistance in, and capitalize on the perceived heterotic pattern among, progeny derived from Great Plains × eastern European crosses. Billings is the bulked descendent of an $F_{4:5}$ line and was tested as experimental line OK03522. Large kernel size and superior yielding ability reflect Billings' resistance to diseases prevalent in Oklahoma and surrounding states. Its favorable dough strength is expressed as exceptional recovery of isolated gluten fractions from compressive deformation.

Journal of Plant Registrations 8:22–31 (2014).
doi: 10.3198/jpr2012.11.0053crc
Freely available online through the author-supported open-access option.
Received 28 Nov. 2012. Registration by CSSA.
5585 Guilford Rd., Madison, WI 53711 USA
*Corresponding author (brett.carver@okstate.edu)

Early maturity is a leading criterion used by breeders and farmers when developing or choosing cultivars for winter wheat (*Triticum aestivum* L.) production in the southern Great Plains. Driving this preference is the greater likelihood of drought stress as grain filling progresses, as well as the likelihood of lower ambient temperatures, and subsequently lower evaporative demand, during grain fill of early-maturing cultivars than for later-maturing cultivars (Edwards, 2009). Contemporary cultivars are generally regarded as reaching anthesis earlier than their predecessors (Austin et al., 1980; Cox et al., 1988; Khalil et al., 1995). Preference for early wheat maturity carries over to a double-cropping management system, in which earlier sowing of the following crop improves the probability of its success.

Popularity of the hard red winter (HRW) wheat cultivar Jagger (PI 593688) (Sears et al., 1997) in the southern and central plains can be largely attributed to its early maturity. Acreage of Jagger in Oklahoma exceeded 25% as recently as 2009 (Oklahoma Field Office, 2011), with numerous offspring already in commercial production in Kansas and Oklahoma. Three Jagger derivatives in particular, 'Jagalene' (PI 631376),

R.M. Hunger and K.L. Giles, Dep. of Entomology and Plant Pathology, Oklahoma State Univ., Stillwater, OK 74078; J.T. Edwards, L. Yan, M.B. Bayles, A.R. Klatt, and B.F. Carver, Dep. of Plant and Soil Sciences, Oklahoma State Univ., Stillwater, OK 74078; R.L. Bowden, G. Bai, and M.-S. Chen, USDA–ARS, Hard Winter Wheat Genetics Research Unit, Kansas State Univ., 4008 Throckmorton Hall, Manhattan, KS 66506; P. Rayas-Duarte, Dep. of Biochemistry and Molecular Biology, Food and Agricultural Products Center, Oklahoma State Univ., Stillwater, OK 74078; G.W. Horn, Dep. of Animal Science, Oklahoma State Univ., Stillwater, OK 74078; J.A. Kolmer and Y. Jin, USDA–ARS, Cereal Disease Lab., 1551 Lindig St., Univ. Minnesota, St. Paul, MN 55108; R.D. Osburn, Oklahoma Crop Improvement Assoc., 2902 West 6th Ave., Stillwater, OK 74074; B.W. Seabourn, USDA–ARS, Center for Grain and Animal Health Research, 1515 College Ave., Manhattan, KS 66502. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the authors and do not necessarily reflect the view of the USDA.

Abbreviations: BYD, barley yellow dwarf; BYDV, *Barley yellow dwarf virus*; ELISA, enzyme-linked immunosorbent assay; FHS, first hollow stem; GS, glutenin subunits; HMW, high molecular weight; HRW, hard red winter; LMW, low molecular weight; OET, Oklahoma Elite Trial; OSGVPT, Oklahoma Small Grains Variety Performance Tests; OSU, Oklahoma State University; RGON, Regional Germplasm Observation Nursery; SBWMV, *Soilborne wheat mosaic virus*; SRPN, Southern Regional Performance Nursery; WSBM, wheat soilborne mosaic; WSSM, wheat spindle streak mosaic; WSSMV, *Wheat spindle streak mosaic virus*.

‘OK Bullet’ (PI 642415, Carver et al., 2006a), and ‘Overley’ (PI 634974), offered considerable promise in a comparable maturity range, yet in each case their fugacious tenure was caused by gradual or abrupt shifts in reaction to diseases as more virulent races increased in frequency. These diseases (and causal organisms) principally included leaf rust (*Puccinia triticina* Eriks.) and stripe rust (*Puccinia striiformis* Westend. f. sp. *tritici* Eriks.), but their susceptible reaction to powdery mildew [*Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici*] was another weakness in years when powdery mildew infection was high. Further shift toward *Yr17*-virulent races in 2010 compromised the value of even more cultivars with Jagger lineage (Fang et al., 2011).

Subsequent to the release of OK Bullet in 2005, special attention was placed in the Oklahoma State University (OSU) wheat improvement program on identifying candidates in the Jagger maturity and yield range but with divergent lineage and acceptable disease reactions. Other attributes relevant to Jagger and essential to cultivar release were acid-soil tolerance and acceptable end-use quality. This research culminated in the HRW wheat cultivar Billings (Reg. No. CV-1089, PI 656843). Our objective herein is to demonstrate Billings’ similarity in maturity and other agronomic traits to Jagger or appropriate descendants, but with improvement in grain yield and disease reaction, while maintaining marketable end-use quality.

Billings was developed cooperatively by the Oklahoma Agricultural Experiment Station (OAES) and the USDA–ARS with the experimental designation OK03522 and released by the OAES in 2009. The cultivar is licensed exclusively to Oklahoma Genetics, Inc. (Stillwater, OK), a producer-operated organization that manages the distribution of registered and certified seed classes. Billings’ namesake is a town in north-central Oklahoma, an area where Billings is well adapted and home to the late Henry Bellmon, a wheat farmer, a former Oklahoma governor and U.S. senator, and an OSU graduate.

Methods

Parentage, Breeding History, and Line Selection

From a total of 220 accessions originating in the wheat breeding program of the Plant Breeding and Genetics Institute (Odessa, Ukraine), 10 were chosen for desirable expression of resistance to barley yellow dwarf (BYD) caused by *Barley yellow dwarf virus* (BYDV) and the wheat soilborne mosaic (WSBM)/wheat spindle streak mosaic (WSSM) complex caused by *Soilborne wheat mosaic virus* (SBWMV)/*Wheat spindle streak mosaic virus* (WSSMV). Other traits included winterhardiness, green-leaf retention, maturity, plant height and straw strength, grain yield, and kernel size. Field evaluations occurred at Lahoma and Stillwater, OK, in 1994–1995. Mixograph results were kindly provided by the USDA–ARS (Lincoln, NE), which managed the exchange and distribution of the Odessa materials among U.S. wheat breeders. One of the 10 chosen accessions, N566, showed exceptional yielding ability (120% of local check cultivars), above-average green-leaf retention, a heading date 3 d earlier than the medium-early check cultivar, ‘Custer’ (F29-76/‘TAM 105’ [CItr 17826]//‘Chisholm’ [PI 486219]), and acceptable mixing tolerance.

In 1996, N566 was crossed with the OSU experimental line OK94P597 to produce the F_1 seed generation. N566 is ‘Eritrospermum 2755-91’/’Odisseya’, and OK94P597 is HBY359A/‘Fundulea 133’//‘TAM 200’ (PI 578255, Worrall et al., 1995). HBY359A was an experimental line produced in the former HRW wheat breeding program of Pioneer Hi-Bred International, Inc., and has the pedigree unknown spring wheat/Centurk//Sturdy/3/PL145(=Newton sib)/Sage. The F_2 seed generation was produced by harvesting 15 F_1 plants in bulk.

The F_2, F_3, and F_4 generations were advanced as bulk populations during harvest years 1998 to 2000. Bulked seed progeny were harvested in a dual-purpose managed environment at the Expanded Wheat Pasture Unit (EWPU) near Marshall, OK. Population evaluation occurred simultaneously at two grain-only sites in north-central and southwestern Oklahoma, but breeder seed was harvested solely from the dual-purpose site. The dual-purpose system provided a selection environment for derivation of lines from bulk populations expected to be equally adapted to dual-purpose or grain-only systems (Thapa et al., 2010). From the F_4 bulk population in Billings’ lineage, about 100 heads were selected from plants with desirable maturity and shorter stature.

Line derivation for Billings occurred originally as a single $F_{4:5}$ headrow selected in 2001 from population OK011158047. An unusually late November planting date for the headrow nursery allowed selection among and within headrow populations for rapid emergence and spring tillering capacity. Other targeted traits included uniformity of phenotype at physiological maturity, spike size, kernel size, and kernel morphology. Across all headrow populations, 65% of the harvested lines were advanced based on seed quality. All 14 lines harvested from population OK011158047 were advanced; hence seed quality was considered exceptional for this population.

The 14 $F_{4:6}$ headrow progenies were evaluated in a two-location, single-replicate observation nursery during the 2001–2002 season. This nursery was managed as a simulated dual-purpose environment at Stillwater, OK (planted 5 Sept. 2001, mechanically clipped continuously from 9 Nov. 2001 to 6 March 2002) and as a grain-only environment at Lahoma, OK (planted 8 Oct. 2001). In a concerted effort to select against precocious winter dormancy release, forage clipping continued at Stillwater beyond the initial stem elongation phase for the earliest breeding lines and the check cultivar Jagger. Billings traced back to a single $F_{4:6}$ progeny that produced acceptable forage ratings throughout the vegetative phase, average regrowth following forage removal, early heading date (similar to Jagger), exceptional canopy stay-green, shattering tolerance, grain yield of about 10% above the surrounding checks ‘Ok101’ (PI 631493, Carver et al., 2003) and ‘Ok102’ (PI 632635, Carver et al., 2004), and acceptable grain volume weight. Wheat protein content, kernel hardness index, kernel weight and diameter, flour extraction, and mixing tolerance were within acceptable values for all traits.

Billings was first entered into replicated yield trials within the OSU wheat improvement program in 2003 with the experimental designation OK03522. These trials were conducted as a randomized complete block design with an increasing number of environments (3 to 11) per year and two or three replicates per environment across years, with no more than 40 entries per block.

Seed Purification and Increase

Each year following isolation of the headrow, OK03522 was advanced in bulk without further selection within the line. Harvest occurred manually with a walk-behind binding reaper to prevent admixtures during years 2002 to 2004, and with a combine preceded by cleanout thereafter. The breeder-seed increase occurred during harvest years 2005 and 2006 at Stillwater, OK, and 2007 at Goodwell, OK. The breeder-seed increase in 2007 produced approximately 225 kg.

Foundation seed was first produced in 2008 near Newkirk, OK, followed by a second generation in 2009 near Newkirk and McCloud, OK, totaling 95 t (approximately 3500 bu), using foundation seed harvested in 2008. Billings was observed to be uniform and stable in the F_9–F_{13} generations. Variants are limited to plants with bronze glume color at a frequency of <1 in 2000.

Final Evaluation in Replicated Yield Tests

Billings was evaluated in the statewide Oklahoma Elite Trial (OET) nursery as an experimental line from 2006 to 2008 and as a check cultivar from 2009 to 2011. These tests featured either grain-only or dual-purpose experiments without the use of a starter fertilizer, seed treatment, or foliar fungicide. Soil fertilization followed soil-test recommendations for a preplanting yield goal of approximately 3000 to 6700 kg ha^{-1} and was adjusted for grain yield history at a specific site and for residual N in a 0- to 46-cm soil test.

The OSU-directed Oklahoma Small Grains Variety Performance Tests (OSGVPT) provided the majority of agronomic data reported here, including reactions to leaf rust and to BYD. Each year featured a representative sample of conventional-till and no-till tests, dual-purpose and grain-only tests, and tests featuring a single application of a foliar fungicide between Feekes growth stages 9 and 10. All tests were conducted as a randomized complete block design with four replicates. Grain yield and volumetric weight data were reported here from test sites representing the primary target region of Billings in Oklahoma, which spans the northern half of the state, extending to irrigated regions of the panhandle. The complete reports are available at http://wheat.okstate.edu/varietytesting/index.htm (accessed 15 July 2012). Other details in experimental design and procedures of the OSGVPT and the OET were provided by Edwards et al. (2012).

Evaluation of Agronomic, Disease, and Insect Characteristics

A unique objective of the OSGVPT is to collect data in nonreplicated plots on phenology, physiology, and disease incidence and severity for all wheat cultivars tested within a given year. Plots were sown at Stillwater or El Reno in early to mid-September at 135 kg ha^{-1} and comprised eight rows spaced 15 cm apart and 3.4 m (Stillwater) or 6.7 m (El Reno) long. In-furrow fertilizer (9–23–0) was applied as $(NH_4)_2HP0_4$ at seeding. The plots were not mowed or grazed and were checked for occurrence of first hollow stem (FHS) in a manner similar to that described by Edwards and Horn (2010) approximately every 3 d beginning in mid-February and continuing until all cultivars had reached the FHS stage of growth (about Feekes Stage 5), defined as when the average length of hollow stem present in a 10-plant subsample was ≥1.5 cm (Edwards et al., 2012).

Heading dates were collected from the same plots as FHS date at Stillwater, and from dual-purpose experiments at Marshall, OK, as described further by Edwards et al. (2012). Heading date was determined as the day of year by which 50% of the spikes in a plot had emerged completely from the boot (Feekes Stage 10.3). Plant height was measured as the distance from ground level to the spike tip, excluding awns, and recorded in single-replicate plots from the 2009, 2010, and 2012 OSGVPT. As an indicator of straw strength, lodging scores were collected from the OSGVPT (same years as plant height) on a scale of 0 (no lodging) to 10 (severe lodging) only in environments subject to moderate or severe lodging. The majority of data came from 2012, when lodging was most evident in Oklahoma since Billings' release in 2009. Visual ratings of acid-soil tolerance were collected from replicated yield trials or single-replicate observation nurseries conducted at naturally low pH field sites near Enid, OK (soil-water pH, 4.3–4.7, 65–75 mg kg^{-1} KCl-extractable aluminum [Al] concentration, >10% Al saturation) from 2008 to 2010, and near Braman, OK, in 2009 (soil-water pH 4.7). These tests were included in the OET or the Uniform Wheat Variety Trials coordinated by Texas AgriLife Research. Two ratings were reported here in a juvenile plant stage (Feekes Stage 3.0) and during ripening stages (Feekes Stages 11.1–11.4) on a scale of 0 (no apparent symptoms caused by low pH) to 5 (highly susceptible response).

Reactions to WSBM and WSSM were monitored by a dual approach of visual symptomatology and detection of the respective viruses using the enzyme-linked immunosorbent assay (ELISA) (Hunger et al., 1991). Using observation nurseries grown in the field near Stillwater from 2007 to 2011, we recorded symptoms of both diseases during Feekes Stages 5.0 to 7.0 on a scale of 1 (resistant) to 4 (highly susceptible). Testing for the presence of each virus and interpretation of the ELISA data were described in Edwards et al. (2012).

Stripe rust reactions were obtained from single readings in each of 3 yr in the field near Rossville, KS, at approximately Feekes Stage 10.5.4: 23 May 2009, 22 to 24 May 2010, and 31 May 2011. Supplemental inoculations were made with race PST-100 in 2009 and 2010. In 2011, four isolates were used, including those used in 2009 and 2010, plus isolates with putative *Yr17* virulence collected in 2010. These two additional isolates were subsequently identified as PSTv-46 (X. Chen, personal communication, 2012). Field evaluation protocols were further described in Edwards et al. (2012). Infection type was scored on a 1-to-9 scale (Line and Qayoum, 1991), and disease severity was scored as a percentage of flag leaves infected. Replicated data for stripe rust and viral disease reactions were obtained by multiple inclusions of Billings and relevant check cultivars in 8 to 21 OSU entry sets across years.

Barley yellow dwarf reactions were evaluated at Lahoma, OK, in 2010 and 2011 using replicated experiments of the OSGVPT arranged in a split-plot design, with or without a single application of a foliar fungicide as the whole-plot treatment. Ratings represented the percentage of the plot showing symptoms of flag leaf or penultimate leaf discoloration after flowering was complete, or immediately following Feekes Stage 10.5.3. In 2012, Billings and the same check cultivars were evaluated for BYD reaction in a similar manner in nonreplicated observation nurseries at Stillwater, but using a scale of 1 (resistant) to 4 (highly susceptible).

Field reactions to leaf rust were collected in 2009, the last year in which natural disease pressure sufficiently supported objective ratings in Oklahoma. Data were collected from the OSGVPT at Lahoma, OK, as mentioned for BYD reactions, and reported on a scale of 1 (resistant) to 9 (highly susceptible). Greenhouse seedling tests were further conducted in 2012 using a bulk of urediniospores collected at Stillwater in 2011, as described by Martin et al. (2003). The avirulence/virulence formula for this bulk was Lr17 19 26/1 2a 2c 3 3ka 9 10 11 13 14 16 18 24 30 TAM110 DNE CSM. Reactions to powdery mildew were reported from greenhouse seedling tests described by Y. Chen et al. (2009b). All other disease evaluations were performed at the USDA–ARS Cereal Disease Laboratory (St. Paul, MN) and the USDA–ARS Center for Grain and Animal Health Research (Manhattan, KS).

Reactions to Hessian fly (*Mayetiola destructor* Say) were performed in the greenhouse by the USDA–ARS Center for Grain and Animal Health Research. The Hessian fly population was derived from field collections in Scott County, KS, containing primarily biotype GP, with a small portion virulent to cultivars containing various resistance genes (M.S. Chen et al., 2009). Reactions to greenbug Biotype E [*Schizaphis graminum* (Rondani)] and to Russian wheat aphid (*Diuraphis noxia* Kurdjumov) were performed in the greenhouse by the USDA–ARS Wheat, Peanut and Other Field Crops Research Unit (Stillwater, OK).

Evaluation of End-Use Quality

Grain samples with no detectable preharvest moisture damage or postharvest insect damage were collected from OET experiments conducted in harvest years 2006 to 2011. Evaluations were conducted at the OSU Wheat Quality Laboratory, which included wheat protein and kernel hardness by near-infrared reflectance spectroscopy, milling quality by the Perten single kernel characterization system, physical dough tests, sedimentation volume adjusted for actual protein percentage in the flour, straight-dough baking quality, and identification of high-molecular-weight (HMW) and low-molecular-weight (LMW) glutenin subunits (GS), as previously described (Edwards et al., 2012).

Compression-recovery tests were conducted according to procedures described by Chapman et al. (2012) on gluten fractions of flour samples obtained from four locations of the 2011 OET. Compression-recovery curves were generated from data averaged across the four environments. As a measure of gluten elasticity, gluten recovery index was determined from three subsamples per environment for each cultivar.

Statistical Analyses

Cultivar means for agronomic, disease, and quality characteristics were compared using a two-tailed, two-sample *t* test with equal sample size and equal variance if appropriate or with unequal sample size and equal variance. Grain yield and grain-volume weight data from the OSGVPT were analyzed using a mixed-model ANOVA within years or pooled across years for only the reported cultivars. All effects except for cultivars were considered random. Mixed-model analyses were conducted using the MIXED procedure of SAS version 9.2 (SAS Institute), from which the least squares cultivar means were computed. The LSD values were calculated from standard error estimates generated from pairwise comparisons in the MIXED output. The CV was derived from an ANOVA using a general linear model in SAS. All tests of significance were conducted at the nominal 0.05 level unless otherwise indicated.

Characteristics

The coleoptile of Billings lacks anthocyanin pigment and has a mean length of 7.9 ± 0.3 cm (n = 25) at 15°C, which is intermediate to 'Duster' (PI 644016) (7.3 ± 0.1 cm, n = 30) and 'Endurance' (PI 639233) (9.0 ± 0.2 cm, n = 30) and similar to Overley (7.9 ± 0.1 cm, n = 30). Billings exhibits a semidecumbent vegetative growth habit across seeding rates and vegetative growth stages, similar to Endurance (Carver et al., 2006c) in growth habit but more coarse in canopy texture. At the boot stage, flag leaves of Billings are green, recurved, and twisted and have a waxy bloom. Spikes of Billings are inclined at harvest maturity, strap shaped, and mid-dense with white awns. The glumes are white, nonpubsescent, and long and wide, with square shoulders of medium width and acuminate beaks of medium width. Kernels are hard textured, red, and elliptical, with a narrow, shallow crease, rounded cheeks, and a large germ. The brush is not collared and short in length. Billings exhibits visual kernel characteristics conforming to the HRW wheat market class (M. Eustrom, USDA Grain Inspection, Packers & Stockyards Administration, personal communication, 2008).

Results

Maturity and Other Agronomic Traits

In the southern plains of the United States, timing of the transition from vegetative to reproductive development is a key component of cultivar selection by breeders and producers. Knowledge of this growth stage for a given cultivar permits optimal management decisions for irrigation and nutrient application and for grazing termination in a dual-purpose system. Cultivars that initiate stem elongation (FHS stage) relatively early tend to initiate heading relatively early (Edwards et al., 2007). Billings represents an early developmental pattern from the FHS stage to heading (Table 1), as it reached the FHS stage at the same time as Jagger and 'Fuller' (PI 653521) but 6 d earlier than OK Bullet and 14 d earlier than Endurance ($P < 0.01$). Cultivar differences were compressed at heading but consistent with FHS data, as Billings headed 5 d earlier than OK Bullet and Endurance. By subtraction, Billings maintained a longer interval between FHS and heading than Endurance (42 d vs. 33 d, respectively). A longer interval is intuitively associated with greater opportunity to accumulate biomass favorable for

Table 1. Occurrence of the first hollow stem and heading stages for Billings and four check cultivars in central Oklahoma, 2007–2012.†

Cultivar	Across years					
	First hollow stem (n = 8)			Heading (n = 8)		
	Mean	SD	Range	Mean	SD	Range
	d after 31 Dec.	——— d ———		d after 31 Dec.	——— d ———	
Billings	58	8.1	24	100	8.1	22
Jagger	55	10.9	33	100	7.1	20
OK Bullet	64**	7.1	20	105*	7.3	19
Fuller	56	7.0	21	102	7.5	19
Endurance	72**	6.1	18	105*	7.5	19

* Significant at the 0.05 probability level for the difference between Billings and the given check cultivar.

** Significant at the 0.01 probability level for the difference between Billings and the given check cultivar.

† First hollow stem data included measurements at Stillwater and El Reno, OK. Heading date was recorded at Stillwater and Marshall, OK.

grain production; on the other hand, an earlier FHS stage is unfavorable for extending the grazing season in a dual-purpose system. Overley was not reported in Table 1 as a check cultivar for the lack of 2012 data, but prior to 2012 Overley and Billings showed no difference in arrival at FHS or heading.

This early developmental pattern observed in the field was inconsistent with allele identities at three loci of known flowering genes previously shown to influence developmental phase variation in winter wheat (Y. Chen et al., 2009a, 2010). Given the *a* allele confers accelerated development at *VRN-A1* on chromosome 5A and *VRN-D3* on chromosome 7D but delayed development at *PPD-D1* on chromosome 2D, Jagger and Overley have allele *a* at all loci. Billings and Endurance have allele *b* at all loci, as does the moderately late-FHS cultivar Duster (Edwards et al., 2012). Hence, one or more additional loci must account for the distinctively earlier maturity pattern of Billings relative to Endurance and Duster.

Billings is an intermediate semidwarf (*RhtB1b*), equal in plant height (73 cm, n = 27) to Fuller (74 cm, n = 33), Duster (72 cm, n = 36), and Jagger (71 cm, n = 36) but shorter than Endurance (74 cm, n = 36, P < 0.05) and OK Bullet (78 cm, n = 33, P < 0.01). Straw strength of Billings is intermediate to moderately weak, as indicated by a mean rating of 3.7 (n = 11) on a scale of 0 to 10, where increasing values represent decreasing strength. Billings exhibits no greater straw strength (P > 0.05) than Duster (4.9, n = 11), Jagger (4.0, n = 11), and Endurance (3.0, n = 11) and lower strength than OK Bullet (1.6, n = 10, P < 0.05).

Visual ratings of juvenile or adult plants indicated a high level of field tolerance to acid-soil conditions. From 17 ratings collected in 3 yr on a scale of 0 to 5 (increasing values represent decreasing tolerance), Billings had a mean juvenile score of 1.7, slightly higher than those of Endurance (1.1) and Duster (1.1). Its mean adult-plant score (0.7) was equivalent to Endurance (0.7) and Duster (0.3). To confirm its tolerance to Al toxicity, Billings produced a slightly lower root tip staining score (4 on a scale of 1 to 5) than Atlas 66 (CItr 12561, Heyne, 1958), when Al-treated (0.36 mM Al) root tips were exposed to a solution of 0.2% (w/v) hematoxylin and 0.02% (w/v) KIO_3. Molecular marker ALMT1-UPS4 amplified the same fragment in Billings (720 bp) as in Atlas 66. Because *ALMT1-UPS4* is from the promoter region of *ALMT1*, it is considered a diagnostic marker for a functional *ALMT1* allele. Billings, however, contained different alleles than Atlas 66 at four additional SSR marker loci on 4DL, designated *Xssr3a*, *Xssr3b*, *Xwmc331*, and *Xgdm125*.

Disease and Insect Resistance

During the 5- to 8-yr period of line development and testing, diseases that typically occur in OSU breeding nurseries under natural infection include leaf rust, stripe rust, WSBM, WSSM, BYD, and powdery mildew. A severely unfavorable reaction to any one of those diseases would likely preclude cultivar release. Since Billings' release in 2009, the southern plains has experienced two dramatic shifts in predominant strains of the stripe rust pathogen. Billings' reaction to stripe rust remained essentially unchanged from 2009 to 2011 under field conditions in Kansas, where inoculated stripe rust screening nurseries were conducted with heavy disease pressure (Table 2). The most recent observations collected in 2012 also indicated a resistant reaction based on infection type (1 to 3, n = 3) or severity of infection (0.0–0.1%, n = 3) in Kansas, and a similar rating in Oklahoma on a scale of 0 (resistant) to 5 (highly susceptible) (mean = 0.0, n = 10). Additional ratings were collected for seedling (growth chamber tested) and adult plant (field) reactions in 2007 and 2008. The race used in the growth chamber in 2008 was PSTv-46 (PST-100). Seedling reaction averaged 5.6 (scale of 1–9, n = 5), and adult plant reaction in the field averaged 1.6 for incidence (scale of 0–9) and 3.0 for severity (0–100%) (5 ratings), indicating a strong level of adult-plant resistance to stripe rust.

Multiyear observations of leaf rust reaction in breeding trials up to Billings' release indicated a resistant reaction with natural infection in Oklahoma, generally producing scores of 1 to 2 on a scale of 1 (resistant) to 9 (highly susceptible) from 2006 to 2009. Subsequent testing in the OSGVPT produced objective data only in 2009 for comparison with contemporary cultivars, where leaf rust ratings in north-central Oklahoma for Billings were significantly better than Jagger, OK Bullet, and Overley but no different than Fuller or Endurance, with or without the addition of a foliar fungicide (Table 3). In OSU greenhouse seedling tests in December 2011, Billings showed a resistant reaction to a bulk collection of urediniospores from susceptible experimental lines grown at Stillwater, OK, in spring 2011. However, leaf rust ratings collected in 2012 at Castroville, TX (severity, 15%; infection type, 9), and at Hutchinson, KS (severity, 2%; infection type, 6), indicate that other virulent races currently exist at low frequency that may eventually compromise Billings' leaf rust

Table 2. Responses of Billings and selected hard red winter wheat check cultivars to field infection by stripe rust at Rossville, KS (2009–2011) and visual ratings for reactions to wheat soilborne mosaic and wheat spindle streak mosaic diseases at Stillwater, OK (2007–2011).†

Entry	Stripe rust reaction 2009–2011			Virus visual ratings 2007–2011			ELISA interpretation‡									
							SBWMV					WSSMV				
	Comparisons	Infection type	Severity	Comparisons	Early March	Mid-March	2007	2008	2009	2010	2011	2007	2008	2009	2010	2011
	no.	1–9§	%	no.	– 1–4¶ –											
Billings	10	2.2	2	16	1.2	1.3	R	R	R	MR	R	R	S	I	R	R
Endurance	13	5.2**	61**	12	1.5	1.6	R	R	R	R	R	R	S	I	MS	R
Fuller	7	7.6**#	29**#	8	1.3	1.5	–	R	R	MR	R	–	R	R	MR	R
Duster	21	4.0**	48**	16	1.1	1.1*	R	R	R	R	R	R	R	R	R	R

* Significant at the 0.05 probability level for the difference between Billings and the given check cultivar.

** Significant at the 0.01 probability level for the difference between Billings and the given check cultivar.

† Quantitative data are means across multiple nurseries and years for the given number of comparisons.

‡ ELISA, enzyme-linked immunosorbent assay; SBWMV, *Soilborne wheat mosaic virus*; WSSMV, *Wheat spindle streak mosaic virus*; R, resistant; MR, moderately resistant; I, intermediate; and S, susceptible.

§ 1 = resistant; 9 = highly susceptible.

¶ 1 = resistant; 4 = highly susceptible.

\# Fuller's 2009 stripe rust reactions to race PST-100 inoculation were inconsistent with other years and excluded from mean.

resistance. Based on infection types of *P. triticina* virulence phenotypes, Billings is postulated to have *Lr17* and *Lr24*, to which race MFPS is virulent.

Visual ratings in the field indicated an effective level of resistance for Billings to the WSBM–WSSM complex (Table 2). Reaction to WSSM was less consistent than to WSBM based on ELISA interpretation of the ratings, similar to the pattern observed for Endurance. Duster's more consistent ELISA-based WSSMV scores conferred a slight advantage to the WSBM–WSSM complex.

From ratings of the incidence of BYD across field plots in the OSGVPT in central Oklahoma, Billings showed an intermediate reaction that was similar to OK Bullet, Overley, and Fuller, but less susceptible than Jagger ($P < 0.05$) and more susceptible than Endurance ($P < 0.01$) (Table 3). This intermediate reaction was confirmed in 2012 from multiple inclusions of Billings in breeder nurseries evaluated in Stillwater, OK, under natural infection of BYDV. On a scale of 1 (resistant) to 4 (susceptible), mean ratings were 2.6 ± 0.2 for Billings ($n = 19$) versus 3.5 for Jagger and Fuller ($n = 2$) and 2.5 ± 0.3 for Endurance ($n = 4$).

Through cooperative evaluations of the USDA Regional Nursery Program, Billings showed a moderately resistant to resistant reaction in the seedling stage to stem rust races QFCSC (the predominant race in the Great Plains), QTHJC, RCRSC, TPMKC, RKQQC, TTTTF, TTKSK (Ug99), and TTTSK. Combined with its susceptible reaction to race TTKST, the *Sr24*-virulent form of TTKSK, and confirmation of the presence of *Lr24*, Billings is postulated to contain *Sr24*. It does not contain *Sr2* according to susceptible alleles detected by markers Stm559 (no amplification in Billings) and csSr2.

Field evaluations near Goodwell, OK, in the 2008 SRPN indicate that Billings is moderately resistant to *High Plains virus*. Field evaluations near Hays, KS, in the 2006 RGON show that Billings is susceptible to *Wheat streak mosaic virus*. Multiple seedling evaluations in the greenhouse since 2005 indicate a moderately susceptible to susceptible reaction to tan spot, caused by *Pyrenophora tritici-repentis* (Died.) Drechsler. On the basis of field observations to natural infection of powdery mildew in Oklahoma in 2012 ($n = 19$), Billings is moderately susceptible, with a mean rating of 3.1 ± 0.2 on a scale of 0 (resistant) to 4 (susceptible). Greenhouse seedling tests produced a susceptible reaction to inoculum of *B. graminis* collected in the Stillwater area.

Billings is susceptible to endemic Hessian fly biotypes in north-central and southwest Oklahoma. Across a 5-yr period (2006–2011) Billings ranked 14th in grain yield among 30 to 32 entries in OET experiments conducted at sites prone to Hessian fly infestation. Fly intensities averaged 2.6 flies per tiller in field plots. Similarly, Endurance, which is also susceptible to Hessian fly, ranked 19th in grain yield and fly intensities averaged 2.8 flies per tiller. According to Alvey (2009), wheat yield is significantly reduced and economic losses occur when fly intensities exceed 1 per tiller. Duster, which is resistant to endemic Hessian fly biotypes, ranked first in grain yield, and fly intensities averaged 0.2 flies per tiller. In greenhouse seedling-screening tests, Billings is susceptible to Hessian fly populations collected in Kansas. Billings is also susceptible to greenbug Biotype E and to Russian wheat aphid.

Table 3. Responses of Billings and selected hard red winter wheat check cultivars to field infection by leaf rust at Lahoma, OK (2009), and to *Barley yellow dwarf virus* (BYDV) at Lahoma and El Reno (2009–2011).

Entry	Leaf rust reaction, 2009			BYDV Reaction	
	Comparisons	No fungicide	With fungicide	Comparisons	2010–2011
	n	1–9†		*n*	%
Billings	4	1.3	1.3	12	55
Jagger	4	7.8**	2.8**	12	80*
OK Bullet	4	6.3**	2.3*	12	62
Overley	4	7.8**	3.3**	12	56
Fuller	4	2.0	1.3	12	66
Endurance	4	1.5	1.0	12	19**

* Significant at the 0.05 probability level for the difference between Billings and the given check cultivar.

** Significant at the 0.01 probability level for the difference between Billings and the given check cultivar.

† 1 = resistant; 9 = highly susceptible.

Comparisons of Grain Yield and Volume Weight

Regionwide estimates of yield potential were extracted from the 2007 and 2008 SRPN containing advanced experimental lines from cooperative hard winter wheat breeding programs (http://www.ars.usda.gov/Research/docs.htm?docid=11932). Across 27 sites, Billings was the sixth-highest-ranking entry in 2007 (4190 kg ha^{-1}) and similar to 'Armour' (PI 655955) (4010 kg ha^{-1}) and 'Everest' (PI 659807) (4400 kg ha^{-1}). Across 31 sites in 2008, Billings was the eighth-highest-ranking entry (3920 kg ha^{-1}) and again similar to Armour (4030 kg ha^{-1}) and Everest (3900 kg ha^{-1}). Across all environments, grain yield of Billings represented a 77 to 80% improvement over the long-term check 'Kharkof' (PI 5641), compared with a 66 to 67% improvement for the nursery mean. A more meaningful estimate of yield improvement, however, that is relevant to areas where a cultivar is likely to be adopted may be derived strictly from environments in the target region. Among Oklahoma test sites alone in the 2007 and 2008 SRPN, Billings showed a 132 to 144% improvement over the long-term check.

The OSGVPT included Billings as an experimental line or as a released cultivar from 2008. Restricting yield comparisons to regions of Oklahoma where Billings is currently positioned, its mean grain yield either exceeded or equaled that of cultivars Billings was intended to replace or complement (Table 4). An exception is reflected in the yield comparison of Billings to Endurance in northern Oklahoma, where Billings' vulnerability was exposed by a late winter freeze event in 2009 and by season-long drought stress in 2011. Across a 5-yr period of the OSGVPT, the grain volume weight of Billings (741 kg m^{-3}) was exceeded by OK Bullet, a cultivar with superior test weight patterns (Carver et al., 2006a), but greater than that for Jagger, Fuller, and Endurance.

End-Use Quality

A distinguishing characteristic of Billings' physical grain quality is its high grain volume weight coupled with large kernel size. Two SKCS attributes, kernel weight and diameter, were significantly ($P < 0.01$) greater than those for Endurance and Duster (Table 5). Both attributes combined, Billings exceeded Duster in kernel size by a mean of 16%. Billings

Table 4. Least-squares means for grain yield and grain volume weight of Billings and five hard red winter wheat check cultivars in northern locations and in irrigated trials of the Oklahoma Small Grains Variety Performance Tests, 2008–2012.†

Cultivar	Northern Oklahoma locations							Irrigated trials, OPREC				
	Grain yield						Grain vol. wt.	Grain yield				Grain vol. wt.
	2008	2009	2010	2011	2012	2008–2012		2010	2011	2012	2010–2012	
	kg ha^{-1}						kg m^{-3}	g ha^{-1}				kg m^{-3}
Billings	4430	2540	2870	2730	3570	3190	741	4520	2390	4350	3760	730
Jagger	3530	2720	2240	2630	3110	2850	721	3700	2150	2760	2870	700
OK Bullet	3640	2560	2220	2690	3020	2820	745	3910	2180	–	–	–
Overley	4070	2450	2310	2670	–	–	–	3380	–	–	–	–
Fuller	4740	2780	2290	2830	3330	3160	734	4060	2020	–	–	–
Endurance	4130	3190	2910	2960	3020	3200	723	3800	2490	2770	2870	700
LSD (0.05)	260	180	150	180	260	100	4	420	NS	560	360	10
CV%	9.0	10.8	8.6	11.0	14.3	11.5	1.7	7.7	23.4	12.2	14.0	1.6
No. of observations‡	96	120	90	138	120	489	435	24	20	12	36	36
Notable yield-limiting factors	leaf rust	spring freeze, leaf rust	stripe rust	chronic, severe drought stress	severe stripe rust				chronic severe drought stress			

† Northern locations included 25 trials in north central and northeastern Oklahoma; all irrigated trials conducted were at the OPREC, Oklahoma Panhandle Research and Extension Center, near Goodwell, OK.

‡ Summed number of cultivars (as listed), trials, and replicates per cultivar trial.

Table 5. Comparisons of Billings versus hard red winter wheat check cultivars Endurance and Duster for wheat milling, dough rheology, and bread-baking characteristics during harvest years 2006–2011 in Oklahoma.

Trait (unit of measurement)	Comparisons	Billings	Endurance	Duster
Wheat protein (g kg^{-1})	37	130	124**	126**
NIR hardness index (score)	37	74	67**	75NS
SKCS† kernel hardness (score)	37	70	66**	79**
SKCS kernel weight (mg)	37	31.7	28.5**	25.8**
SKCS kernel diameter (mm)	37	2.55	2.41**	2.35**
Flour extraction (g kg^{-1})	37	625	632NS	626NS
Mixograph peak time (min.)	37	4.5	4.1*	4.8NS
Mixograph tolerance rating‡	37	3.7	2.8**	3.7NS
Mixograph bandwidth (mm)	37	17.1	13.6**	17.5NS
Mixograph stability	37	6.3	8.0*	4.4*
Adjusted sedimentation vol. (mL)	37	7.1	6.2**	6.3**
Loaf volume (cm^3)	7	858	814NS	801*
Bake water absorption (g kg^{-1})	7	647	652NS	649NS
Crumb grain score‡	7	4.0	4.4NS	4.4NS
Gluten recovery index (%)§	12	78.1	71.2*	64.7**

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† SKCS, single kernel characterization system.

‡ Based on scale of 0 = poor to 6 = excellent.

§ Gluten recovery index determined in 2011 alone at 4 locations.

exceeded both check cultivars in protein quantity (0.5% points greater in Billings) and protein quality measured by sedimentation tests adjusted for flour protein concentration. The mixograph curve for Billings reflected moderately high dough strength, similar to Duster but superior to Endurance. These empirical results indicated Billings' bread-making acceptability relative to dough rheological attributes, loaf volume, and visual crumb properties.

The moderately high dough strength of Billings was corroborated by examination of isolated gluten fractions for recoverability from compressive deformation. Greater recovery indicates greater elasticity, which is conferred by a combination of polymer characteristics such as molecular weight, cross-linking of molecular chains, and physical entanglements along the polymer chains (Singh and MacRitchie, 2001). The gluten network of Billings recovered faster from compressive deformation, indicated by a steeper rise of the compression-recovery curve in Fig. 1, and it regained more of its original state via elastic recovery (height of the curve, Fig. 1) than Endurance or Duster. Billings produced a greater recovery index than did Endurance or Duster (Table 5). The gluten recovery index of Billings reported here (78%) is high relative to other estimates reported in HRW wheat (Chapman et al., 2012).

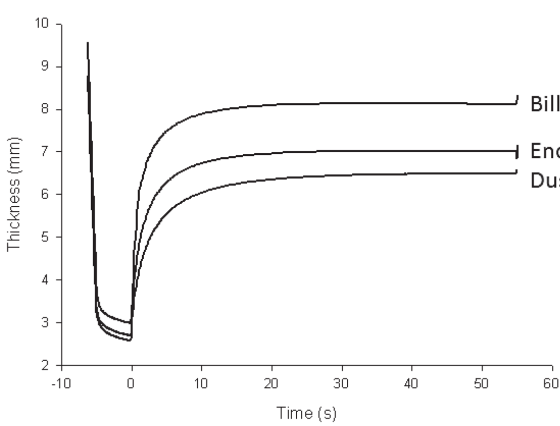

Fig. 1. Compression-recovery curves for gluten fractions isolated from Billings, Endurance, and Duster, in which gluten thickness (mm) vs. time (s) was recorded during 5-s compression at constant force of 8 N and 55-s recovery.

Billings does not contain either the T1BL-1RS or T1AL-1RS translocation. At the HMW-GS loci, Billings contains alleles *Glu-A1a* (subunit 1), *Glu-B1c* (subunits 7+9), and *Glu-D1d* (subunits 5+10). At the LMW-GS loci, only a faint SDS-PAGE band was detected corresponding to allele *Glu-A3b*, suggesting the encoded subunit may be present in low quantity. Other alleles present are *Glu-B3f* and *Glu-D3b*, although *Glu-D3d* could not be eliminated in the absence of a standard cultivar and the challenges of differentiating *Glu-D3* alleles with current protein separation methods (Liu et al., 2010).

Discussion

The cross from which Billings was selected, OK94P597/N566, underscores a historically important dual breeding objective of the OSU wheat improvement program: to identify improved fungal disease resistance in and to capitalize on the perceived heterotic pattern among progeny derived from southern Great Plains × eastern European crosses. Oklahoma cultivars developed previously with the same objective were 'Deliver' (PI 639232, Carver et al., 2006b), Custer, 'Tonkawa' (F29-76/TAM 105//Chisholm), and 'Pete' (PI 656844), each featuring parents or grandparents from Bulgaria, Romania, or Ukraine. Billings and Pete were the first in this group to derive one-half of their parentage from eastern European germplasm.

Another milestone reached with Billings was its earlier maturity, equivalent to Jagger and popular descendants such as Fuller and Overley. Adding significance was that Billings' earliness was achieved in a breeding program where selection pressure, either directly or indirectly, favored an extended vegetative period fit for dual-purpose management systems; not surprisingly, its earliness precludes Billings from widespread use in dual-purpose systems common to the southern plains. Billings accounted for 2% of the wheat acreage in Oklahoma in 2012, after first appearing on measurable acreage in 2011 (Oklahoma Field Office, 2012). Research is underway to identify gene(s) responsible for the early maturity pattern of Billings, currently unexplained by alleles present at *VRN-A1*, *VRN-D3*, and *PPD-D1*.

Throughout its development and commercialization, Billings maintained a resistant reaction to stripe rust during three major epidemics in 2005, 2010, and 2012. Although Billings exhibits a low level of race-specific seedling resistance, it is not effective against the newer races. Thus, adult-plant resistance to stripe rust is apparently strong, but this form of resistance may also be race-specific based on limited field data from Mt. Vernon, WA, in 2008, where Billings produced ratings of 8 for infection type (1-to-9 scale) and 30% severity. Continuation of Billings' grain yield superiority in environments unprotected by a fungicide will depend on the effectiveness of resistance genes for which their postulation is being pursued.

In contrast, the basis of resistance to leaf rust is well known in Billings, postulated as *Lr17* + *Lr24*, but may be in greater jeopardy moving forward. Survey data from 2009 and 2011 indicated isolates with virulence to both *Lr17* and *Lr24* accounted for 5 and 12% of all isolates in the United States, respectively (http://www.ars.usda.gov/Main/docs.htm?docid=10493). Only three races possessed this combination of virulence, and one was race MFPS. Among hard winter wheat cultivars released before 2011, only three possess the same gene combination ('Stanton' [PI 617033], 'Trego' [PI 612576], and 'NuDakota' [PI 643089]), and none of those have appeared on variety surveys conducted in Oklahoma.

Large kernel size and superior yielding ability of Billings are logically linked to its resistance to diseases prevalent in the southern Great Plains. In a forward breeding approach involving Billings as a foundation germplasm, efforts are now focused on incorporating known durable sources of leaf rust and stripe resistance, particularly *Lr34*/*Yr18*, to stabilize and extend those strengths of Billings while maintaining its desirable milling and baking properties. Billings also provides a worthy platform for further yield improvement, if kernel size can be sustained while incorporating complementary sources of high tillering capacity.

Availability

Oklahoma Foundation Seed Stocks, Inc. (OFSS, Inc., 2902 West Sixth Ave., Stillwater, OK 74074-1555) provides foundation seed of Billings to members of Oklahoma Genetics, Inc., to whom the cultivar is licensed and by whom a research and development fee is assessed on all registered and certified seed sales. Billings is protected under the U.S. Plant Variety Protection Act with the Certification Only option (PVP 20100098). The Oklahoma Agricultural Experiment Station maintains breeder seed production. Seed of Billings has been deposited with the USDA–ARS National Plant Germplasm System. Requests for small quantities of seed (<5 g) may be forwarded to the corresponding author during the period of PVP protection.

Acknowledgments

Billings was developed and characterized by financial support of the Oklahoma Wheat Commission, the Oklahoma Wheat Research Foundation, the Oklahoma Agricultural Experiment Station, and the Oklahoma Cooperative Extension Service. Research at the Wheat Pasture Research Unit near Marshall, OK, was supported in part by USDA–CSREES Special Research Grants from 1997 to 2010, with the final grant numbered 2010-34198-20812. Molecular characterization was supported in part by USDA–NIFA T–CAP Grant no. 2011-68002-30029 and the Oklahoma Center of Advanced Science and Technology (OCAST, PAS07-002). We are grateful for the assistance of Jeff Wright and Margaret Collins (OFSS, Inc.) in breeder seed increase and foundation seed multiplication and maintenance of Billings. The technical assistance of Brian Olson, Richard Austin, Tina Johnson, Connie Shelton, Nathan Stepp, Rich Kochenower, Roger Gribble, Ray Sidwell, Mike Hogg, Lawrence Bohl, Erich Wehrenberg, and Wayne Whitmore is specially acknowledged. The wheat breeding programs of the Plant Breeding and Genetics Institute and Pioneer Hi-Bred International, Inc., are gratefully acknowledged for providing germplasm that led to the development of Billings.

References

Alvey, D.P. 2009. Evaluation of the impact of Hessian fly (*Mayetiola destructor*) on Oklahoma winter wheat systems. Master's thesis, Oklahoma State Univ., Stillwater.

Austin, R.B., J. Bingham, R.D. Blackwell, L.T. Evans, M.A. Ford, C.L. Morgan, and M. Taylor. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci. 94:675–689. doi:10.1017/S0021859600028665

Carver, B.F., R.M. Hunger, A.R. Klatt, J.T. Edwards, W.D. Worrall, D.R. Porter, P. Rayas-Duarte, B.W. Seabourn, G.-H. Bai, F.E. Dowell, and B.C. Martin. 2006a. Registration of 'OK Bullet' wheat. Crop Sci. 46:2322–2324. doi:10.2135/cropsci2006.04.0268

Carver, B.F., E.G. Krenzer, R.M. Hunger, D.R. Porter, E.L. Smith, A.R. Klatt, J. Verchot-Lubicz, P. Rayas-Duarte, A.C. Guenzi, G. Bai, and B.C. Martin. 2004. Registration of 'Ok102' wheat. Crop Sci. 44:1468–1469. doi:10.2135/cropsci2004.1468

Carver, B.F., E.L. Smith, R.M. Hunger, D.R. Porter, A.R. Klatt, P. Rayas-Duarte, J. Verchot-Lubicz, B.C. Martin, E.G. Krenzer, J.T. Edwards, and B.W. Seabourn. 2006b. Registration of 'Deliver' wheat. Crop Sci. 46:1819–1820. doi:10.2135/cropsci2006.01-0016CRC

Carver, B.F., E.L. Smith, R.M. Hunger, D.R. Porter, A.R. Klatt, P. Rayas-Duarte, J. Verchot-Lubicz, B.C. Martin, E.G. Krenzer, J.T. Edwards, and B.W. Seabourn. 2006c. Registration of 'Endurance' wheat. Crop Sci. 46:1816–1818. doi:10.2135/cropsci2005.12-0452CRC

Carver, B.F., E.L. Smith, E.G. Krenzer, R.M. Hunger, D.R. Porter, A.R. Klatt, J. Verchot-Lubicz, P. Rayas-Duarte, A.C. Guenzi, B.C. Martin, and G. Bai. 2003. Registration of 'Ok101' wheat. Crop Sci. 43:2298–2299. doi:10.2135/cropsci2003.2298a

Chapman, S.J., S.J. Mulvaney, R. Chinnaswamy, P. Rayas-Duarte, and B. Allvin. 2012. Large deformation stress relaxation and compression-recovery of gluten representing different wheat classes. J. Cereal Sci. 55:366–372. doi:10.1016/j.jcs.2012.01.012

Chen, M.S., E. Echegaray, R.J. Whitworth, H. Wang, P.E. Sloderbeck, A. Knutson, K.L. Giles, and T.A. Royer. 2009. Virulence analysis of Hessian fly (*Mayetiola destructor*) populations from Texas, Oklahoma, and Kansas. J. Econ. Entomol. 102:774–780. doi:10.1603/029.102.0239

Chen, Y., B. Carver, S. Wang, S. Cao, and L. Yan. 2010. Genetic regulation of developmental phases in winter wheat. Mol. Breed. 26:573–582. doi:10.1007/s11032-010-9392-6

Chen, Y., B.F. Carver, S. Wang, F. Zhang, and L. Yan. 2009a. Genetic loci associated with stem elongation and dormancy release in winter wheat. Theor. Appl. Genet. 118:881–889. doi:10.1007/s00122-008-0946-5

Chen, Y., R.M. Hunger, B.F. Carver, H. Zhang, and L. Yan. 2009b. Genetic characterization of powdery mildew resistance in U.S. hard winter wheat. Mol. Breed. 24:141–152. doi:10.1007/s11032-009-9279-6

Cox, T.S., J.P. Shroyer, L.B. Hui, R.G. Sears, and T.J. Martin. 1988. Genetic improvement in agronomic traits of hard red winter wheat cultivars from 1919 to 1987. Crop Sci. 28:756–760. doi:10.2135/cropsci1988.0011183X002800050006x

Edwards, J.T. 2009. Systems-based wheat management strategies. In: B.F. Carver, editor, Wheat: Science and trade. Wiley-Blackwell, Ames, IA. p. 75–87.

Edwards, J.T., B.F. Carver, and M.E. Payton. 2007. Relationship of first hollow stem and heading in wheat. Crop Sci. 47:2074–2077. doi:10.2135/cropsci2007.01.0057sc

Edwards, J.T., and G.W. Horn. 2010. First hollow stem: A critical wheat growth stage for dual-purpose producers. Fact Sheet PSS 2147. Okla. State Univ. Coop. Ext. Serv., Stillwater, OK. http://osufacts.okstate.edu/docushare/dsweb/Get/Document-6693/PSS_2147web.pdf (accessed 31 Mar. 2011).

Edwards, J.T., R.M. Hunger, E.L. Smith, G.W. Horn, M.-S. Chen, L. Yan, G. Bai, R.L. Bowden, A.R. Klatt, P. Rayas-Duarte, R.A. Osburn, J.A. Kolmer, Y. Jin, D.R. Porter, K.L. Giles, B.W. Seabourn, M.B. Bayles, and B.F. Carver. 2012. 'Duster' wheat: A durable, dual-purpose cultivar adapted to the southern Great Plains of the USA. J. Plant Reg. 6:37–48. doi:10.3198/jpr2011.04.0195crc

Fang, T., K.G. Campbell, Z. Liu, X. Chen, A. Wan, S. Li, Z. Liu, S. Cao, Y. Chen, R.L. Bowden, B.F. Carver, and L. Yan. 2011. Stripe rust resistance in the wheat cultivar Jagger is due to *Yr17* and a novel resistance gene. Crop Sci. 51:2455–2465. doi:10.2135/cropsci2011.03.0161

Heyne, E.G. 1958. Registration of improved wheat varieties, XXI. Agron. J. 50:396. doi:10.2134/agronj1958.00021962005000070014x

Hunger, R.M., J.L. Sherwood, E.L. Smith, and C.R. Armitage. 1991. Symptomatology and enzyme-linked immunosorbent assay used to facilitate breeding for resistance to wheat soilborne mosaic. Crop Sci. 31:900–905. doi:10.2135/cropsci1991.0011183X003100040011x

Khalil, I.H., B.F. Carver, and E.L. Smith. 1995. Genetic gains in two selection phases of a wheat-breeding programme. Plant Breed. 114:117–120. doi:10.1111/j.1439-0523.1995.tb00774.x

Line, R.F., and A. Qayoum. 1991. Virulence, aggressiveness, evolution, and distribution of races of *Puccinia striiformis* (the cause of stripe rust of wheat) in North America, 1968–87. USDA Tech. Bull. 1788. USDA, Washington, DC.

Liu, L., T.M. Ikeda, G. Branlard, R.J. Peña, W.J. Rogers, S.E. Lerner, M.A. Kolman, X. Xia, L. Wang, W. Ma, R. Appels, H. Yoshida, A. Wang, Y. Yan, and Z. He. 2010. Comparison of low molecular weight glutenin subunits identified by SDS-PAGE, 2-DE, MALDI-TOF-MS and PCR in common wheat. BMC Plant Biol. 10:124–148. doi:10.1186/1471-2229-10-124

Martin, J.N., B.F. Carver, R.M. Hunger, and T.S. Cox. 2003. Contributions of leaf rust resistance and awns to agronomic and grain quality performance in winter wheat. Crop Sci. 43:1712–1717. doi:10.2135/cropsci2003.1712

Oklahoma Field Office. 2011. Oklahoma wheat variety. USDA National Agricultural Statistic Service. http://www.nass.usda.gov/Statistics_by_State/Oklahoma/Publications/Oklahoma_Crop_Reports/2011/ok_wheat_varieties_%202011.pdf (accessed 13 Nov. 2012).

Oklahoma Field Office. 2012. Oklahoma wheat variety. USDA National Agricultural Statistic Service. http://www.nass.usda.gov/Statistics_by_State/Oklahoma/Publications/Oklahoma_Crop_Reports/2012/ok_wheat_varieties_%202012.pdf (accessed 12 Nov. 2012).

Sears, R.G., J.M. Moffatt, T.J. Martin, T.S. Cox, R.K. Bequette, S.P. Curran, O.K. Chung, W.F. Heer, J.H. Long, and M.D. Witt. 1997. Registration of 'Jagger' wheat. Crop Sci. 37:1010. doi:10.2135/cropsci1997.0011183X003700030062x

Singh, H., and F. MacRitchie. 2001. Application of polymer science to properties of gluten. J. Cereal Sci. 33:231–243. doi:10.1006/jcrs.2000.0360

Thapa, R., B.F. Carver, G.W. Horn, and C.L. Goad. 2010. Genetic differentiation of winter wheat populations following exposure to two management systems in early inbreeding generations. Crop Sci. 50:591–601. doi:10.2135/cropsci2009.05.0234

Worrall, W.D., E.C. Gilmore, Jr., K.B. Porter, M.E. McDaniel, and L.W. Rooney. 1995. Registration of 'TAM-200' wheat. Crop Sci. 35:1223–1224.