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Release of 19 Waxy Winter Wheat Germplasm, with Observations on Their Grain Yield Stability

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Abstract

“Waxy” wheats (*Triticum aestivum* L.) produce endosperm starch devoid, or nearly so, of amylose. Waxy starch consists only of amylopectin, imparts unique cooking properties, and serves as an efficient substrate for the production of modified food starches. To expand the genetic variation of waxy wheats useful to Great Plains breeding programs, the USDA-ARS, in cooperation with the University of Nebraska, developed and released 19 waxy winter wheats (Reg. No. GP-1003, PI 677864 to Reg. No. GO-1021, PI 677882) . Three of the waxy germplasm lines have soft endosperm texture; the remaining 16 lines have hard-textured grain. The grain yields of six of the waxy winter wheat germplasm lines were not significantly different from the highest yielding nonwaxy cultivar (‘Freeman’). All but four waxy germplasm lines had grain yields statistically equal to that of the waxy winter wheat cultivar Mattern. Grain yield stability (or response to changing environments) of the waxy germplasm lines demonstrated similar trends to those of the nonwaxy controls. Grain yield observations and responses to changing production potentials argue against any yield drag associated with waxy starch and indicate potential for the development of additional and competitive cultivars.

Hexaploid waxy wheats (*Triticum aestivum* L.) carry three nonfunctional (null) alleles (*Wx-A1b*, *Wx-B1b*, and *Wx-D1b*) at loci encoding the enzyme granule-bound starch synthase (EC 2.4.1.21) and produce endosperm starch nearly devoid of amylose (Nakamura et al., 1995). Waxy wheat starch may be used in the production of modified food starches and in other food and industrial applications (Graybosch, 1998; Van Hung et al., 2006; Graybosch and Hansen, 2016). Waxy flour, when added to typical, wild-type wheat flour, can improve the shelf life of baked goods (Bhattacharya et al., 2002), and amylose-free starch is more efficient in ethanol production than are wild-type (typical) starches (Zhao et al., 2009). Waxy wheat starch can serve as a more efficient substrate for the production of maltodextrins (Maningat et al., 2009). Waxy wheats also may be used to donate one or more waxy null alleles in wheat breeding programs. Evidence suggests the presence of one or more waxy null alleles, conditioning a reduced amylose or “partial waxy” condition, can improve texture and cooking properties of certain Asian noodle products (Epstein et al., 2002). The use of fully waxy lines as parental materials will increase the frequency of partial waxy segregants in derived breeding populations.

The absence of the granule-bound starch synthase eliminates one of the two major pathways in cereal endosperm starch synthesis. As starch represents the most abundant storage component of wheat grain, the question arises as to whether elimination of the granule-bound starch synthase reduces grain yield. Previous work (Graybosch et al., 2003) demonstrated grain yields of spring waxy wheats did not differ from the average grain yield of control cultivars. A secondary objective of the present work was to determine whether this observation held true for winter waxy wheats and whether such wheats differed in grain yield stability over multiple environments.

Waxy wheats were unknown to science until 1995 (Nakamura et al., 1995), and only two waxy wheat cultivars (Morris and King, 2007; Graybosch et al., 2014) have been released in North America

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to date. Only 'Mattern' (Graybosch et al., 2014) is adapted to Great Plains agro-ecological zones. To expand the range of available adapted genetic backgrounds, the USDA-ARS, in cooperation with the University of Nebraska, developed and released 19 Great Plains–adapted waxy winter wheat germplasm lines (Reg. No. GP-1003, PI 677864 to Reg. No. GP-1021, PI 677882).

Methods

Pedigrees, PI numbers, and USDA National Plant Germplasm System registration numbers of the 19 waxy winter wheat germplasm lines are listed in Table 1. Lines were developed via several rounds of phenotypic recurrent selection, commencing with Asian and North American donor lines of the *Wx* null alleles and passing through a series of winter-hardy, but lower-yielding waxy experimental lines developed by the USDA-ARS. The following parental lines were all waxy wheat breeding lines developed by the USDA-ARS at Lincoln, NE: 99 waxy bulk, NX04Y2066, 99Y1445, NX04Y2090, and NX03Y2115. The 99 waxy bulk population was an accidental mix of waxy wheats derived from the following crosses: VA94-52-25/'Norin 67' (PI 235238)//'BaiHuo', 'Cimarron'/'RioBlanco'//BaiHuo/'TAM200', Cimarron/TAM200//BaiHuo, Cimarron/TX93V5922//K94H115/BaiHuo, A92-3327//'Ike'/3/BaiHuo/KY88C-435-9, and BaiHuo/KY88C-435–9//Ike. NX04Y2066 was derived from N95L1229 (PI 608032)/99Y1442 (BaiHuo/'Kanto107'//Ike/3/96MD7413-10); 99Y1445 was selected from BaiHuo/Kanto107//Ike/3/96MD7413-10; NX04Y2090 was derived from a cross between 99Y1443 (BaiHuo/Kanto107//Ike/3/96MD7413-6) and SD97063 (ND8889/NE90574); NX03Y2115 was descended from (Cimarron/RioBlanco)//(BaiHuo/L910145)/3/('Colt'/'Cody')//('Stozher'/NE86582). Donors of the *Wx* null alleles in the above pedigrees included Cimarron (*wx-A1* null), RioBlanco and TAM200 (*wx-B1* null), BaiHuo (*wx-D1* null), and Ike (*wx-A1* and *wx-B1* nulls) (Graybosch et al., 1998). Additional parents (nonwaxy) used in the final mating cycles included 92201D5-2-29, a soft winter wheat breeding line developed by Purdue University; NI03418, a hard red winter wheat breeding line developed by the University of Nebraska-Lincoln; 'Wesley', a hard red winter wheat cultivar jointly developed by USDA-ARS and the University of Nebraska-Lincoln (Peterson et al., 2001); 'NuHorizon'(PVP 200100217), a hard white winter wheat cultivar developed by Monsanto; and 'NuDakota' (PVP 200600235), a hard white winter wheat cultivar developed by Syngenta Seeds.

The final cross of each pedigree was conducted in 2006. Populations were advanced, in-bulk, until the F_3 generation. A bulk sample of F_4 seed was then rapidly phenotyped using a single-kernel sorting device affixed with near-infrared reflectance (NIR) technology (Dowell et al., 2009) that facilitated identification of waxy seed and allowed development of >95% waxy F_4 seed samples. F_4 seed was used to plant bulk populations in fall 2009 at the University of Nebraska Agricultural Research and Development Center near Mead, NE. The following summer, single head selections were made from visually selected populations. A few seeds were removed from each head and stained with a dilute solution of I_2KI (5 g KI + 0.5 g I_2 in 250 mL H_2O, diluted 1:10 with H_2O before each use) which differentiates waxy and nonwaxy kernels (Fig. 1). Verified waxy selections were seeded at Mead, NE, as single 1-m head rows, and selections made on disease resistance and agronomic properties in 2011. Single heads were obtained from each selected row, a few seed of each stained with I_2KI, and remaining seed planted in single 2.5-m rows at Yuma, AZ. Yuma rows were each harvested in-bulk, and the resultant F_5–derived lines were assigned selection numbers. Forty-eight waxy winter wheat experimental lines were subsequently evaluated in multilocation replicated yield trials. Replicated trials were harvested from Mead, NE, and Aurora, SD, in 2013, and from Lincoln, Mead, Clay Center, North Platte, and Sidney, NE in 2014. The 48 waxy entries were planted along with control cultivars, 'Freeman', 'McGill', 'Infinity CL', 'Goodstreak', 'Overland', 'Camelot', 'Millennium', 'Settler CL', Mattern (waxy), 'Robidoux', and 'Pronghorn', and the breeding line NI08708. At each location, entries were seeded in four-row plots, trimmed to 3 m^2 before harvest, with three field replications (at Nebraska locations) using a randomized complete block design.

Table 1. Nineteen waxy wheat germplasm and pedigrees.

PI no.	Registration no.	Entry	Pedigree
PI 677864	GP-1003	NX12Y8174	92201D5–2-29/99 waxy bulk//NI03418
PI 677865	GP-1004	NX12Y8175	92201D5–2-29/99 waxy bulk//NI03418
PI 677866	GP-1005	NX12Y8176	92201D5–2-29/99 waxy bulk//NI03418
PI 677867	GP-1006	NX12Y8178	92201D5–2-29/99 waxy bulk//NI03418
PI 677868	GP-1007	NX12Y8186	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677869	GP-1008	NX12Y8187	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677870	GP-1009	NX12Y8188	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677871	GP-1010	NX12Y8189	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677872	GP-1011	NX12Y8190	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677873	GP-1012	NX12Y8205	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677874	GP-1013	NX12Y8209	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677875	GP-1014	NX12Y8210	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677876	GP-1015	NX12Y8212	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677877	GP-1016	NX12Y8213	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677878	GP-1017	NX12Y8214	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677879	GP-1018	NX12Y8215	NX04Y2066/Wesley//99Y1445/NuHorizon
PI 677880	GP-1019	NX12Y8221	NuDakota//NX04Y2090/NX03Y2115
PI 677881	GP-1020	NX12Y8222	NuDakota//NX04Y2090/NX03Y2115
PI 677882	GP-1021	NX12Y8223	NuDakota//NX04Y2090/NX03Y2115

Fig. 1. Endosperm of waxy and wild-type wheat stained with I_2KI. Waxy wheat kernels stain reddish-brown; wild-type kernels stain blue-black.

At Aurora, SD, entries were seeded in seven-row plots, trimmed to 6 m^2 before harvest, with two replications. The 19 waxy winter wheats described herein were selected from this larger sample of 48 breeding lines on the basis of field performance and purity of waxy seed. Experiment-wide LSD (0.05) values and means were calculated using all entries and are reported herein. Regression analysis (Eberhart and Russell, 1966) was used to evaluate grain yield stability across environments. Grain yields of each entry were used as dependent variables, and the average grain yield of all entries at each location was used as the independent variable (environmental index). Slopes (*b* values) of all entries were evaluated for statistical identity to that of McGill, the control cultivar with the highest *b* value (see below). Subsequent to harvest, the samples from Mead 2013 and 2014 were evaluated for grain and quality traits as per Graybosch et al. (2016). Disease responses were evaluated via the USDA-ARS coordinated 2016 Regional Germplasm Observation Nursery (USDA-ARS, 2016).

Characteristics

Grain yields, obtained from replicated yield trials in seven Nebraska and South Dakota environments over the 2013 and 2014 growing seasons, are presented in Table 2. The grain yields

Table 2. Mean grain yield, grain volume weight, and results of regression† of 19 waxy winter wheat lines (NX12Y8*xxx*) and control cultivars from seven Great Plains environments, 2013–2014.

Entry	Grain yield	Grain volume weight	R^2 regression	Slope (b)	P, slope vs. McGill slope
	kg ha^{-1}	kg hL^{-1}			
Freeman	4728	76.5	0.81	1.13	0.611
McGill	4698	78.9	0.98	1.26	
Infinity CL	4663	79.1	0.94	1.11	0.328
Goodstreak	4652	79.4	0.88	1.22	0.875
NX12Y8223	4644	76.0	0.89	1.03	0.200
Overland	4614	78.7	0.88	0.99	0.140
NX12Y8187	4561	77.0	0.98	1.22	0.776
NW07505	4528	77.8	0.95	1.03	0.089
Camelot	4515	78.3	0.89	1.19	0.733
NX12Y8189	4479	75.3	0.94	1.33	0.659
NX12Y8188	4457	77.0	0.95	1.22	0.785
NX12Y8221	4426	76.8	0.99	1.06	0.033
NX12Y8222	4412	75.4	0.91	1.00	0.118
NX12Y8215	4411	74.8	0.83	0.96	0.159
NX12Y8190	4391	76.1	0.96	1.09	0.167
Millennium	4390	78.6	0.87	1.13	0.549
Settler CL	4377	77.2	0.91	1.06	0.232
Mattern (waxy)	4313	76.4	0.76	1.14	0.708
Robidoux	4307	76.5	0.80	1.00	0.275
NX12Y8213	4294	74.0	0.96	1.02	0.051
NI08708	4262	77.1	0.88	1.12	0.495
NX12Y8209	4232	75.7	0.94	0.83	0.001
NX12Y8214	4224	74.4	0.87	0.78	0.002
NX12Y8205	4217	74.8	0.97	1.02	0.035
Pronghorn	4208	80.8	0.70	0.80	0.066
NX12Y8212	4197	73.9	0.89	0.84	0.006
NX12Y8210	4169	75.7	0.71	0.69	0.001
NX12Y8186	4157	74.5	0.88	1.28	0.775
NX12Y8174	3967	74.3	0.91	0.99	0.094
NX12Y8178	3958	71.5	0.82	1.03	0.320
NX12Y8175	3932	72.0	0.88	1.03	0.222
NX12Y8176	3805	73.0	0.69	0.80	0.078
Experiment mean	4027	75.3			
LSD	306	1.5			

† Regression of per location means of each entry against mean location mean (environmental index) of all trial entries.

of six of the waxy winter wheat germplasm lines were not significantly different from the highest-yielding nonwaxy cultivar (Freeman). All but four waxy germplasm lines had grain yields statistically equal to that of the waxy winter wheat cultivar Mattern. Grain volume weights were reduced in most waxy lines relative to nonwaxy controls. Grain volume weights of McGill and

Table 3. Mean grain yields of the five highest-yielding waxy wheat lines (NX12Y8*xxx*), based on overall results, compared with five high-yielding nonwaxy cultivars.

Entry	2013		2014				
	Mead	Aurora	Clay Center	Lincoln	Mead	North Plate	Sidney
	kg ha^{-1}						
Freeman	6752	4391	3470	4951	5914	3467	3688
McGill	6792	4657	3524	4139	5979	3152	4600
Infinity CL	6083	4371	3714	4482	6287	3040	4521
Goodstreak	6129	4966	3494	4458	6471	2755	4269
Overland	6182	4102	3986	4668	5778	3055	4233
NX12Y8223	5895	4085	3674	4511	6352	3365	4336
NX12Y8187	6694	4227	3628	3816	5764	3097	4604
NX12Y8189	6781	3578	3426	4350	5655	2689	4621
NX12Y8188	6312	3561	3334	4272	5738	2877	4883
NX12Y8221	6038	4395	3403	4136	5601	3002	4387
Experiment mean	5594	3798	3051	3654	5119	2804	4158
LSD (0.05)	887	605	417	1218	778	491	782

Table 4. Select grain and flour hardness characteristics of waxy wheat and nonwaxy wheat cultivars and breeding lines.

Entry	Grain hardness	Grain protein	Flour yield	Flour protein	Mixograph mix time	Mixograph tolerance	Gluten index
	hardness units	g kg^{-1}			min	mm	g kg^{-1}
Camelot	67.8	127.4	625.2	113.9	8.1	11.9	966.6
Freeman	75.7	122.0	638.3	106.8	16.8	6.0	987.1
Goodstreak	58.9	129.6	670.6	119.1	4.7	8.8	683.3
Infinity CL	63.3	119.7	639.3	104.9	14.3	8.9	988.8
Mattern	67.9	127.6	552.1	113.5	3.8	9.0	853.1
McGill	60.6	118.9	645.5	104.1	11.8	6.2	972.3
Millennium	65.8	126.9	664.8	112.0	6.8	10.9	941.1
NI08708	55.6	129.0	653.9	114.9	8.0	8.8	942.6
NW07505	72.8	124.7	620.0	109.1	13.6	10.9	990.1
NX12Y8174	38.9	118.1	510.8	107.9	2.5	3.6	610.3
NX12Y8175	38.3	124.0	519.8	114.0	4.1	10.3	770.8
NX12Y8176	57.2	120.9	606.3	113.8	3.9	8.5	820.7
NX12Y8178	25.5	126.0	455.8	112.6	4.3	10.9	900.2
NX12Y8186	70.0	133.4	542.0	121.8	3.2	9.0	815.5
NX12Y8187	62.7	124.6	609.0	113.7	9.6	20.9	803.5
NX12Y8188	64.8	130.2	593.1	118.3	8.4	21.1	946.0
NX12Y8189	61.2	132.4	617.9	120.0	8.3	22.6	957.5
NX12Y8190	65.7	123.1	601.6	111.9	9.4	22.3	931.4
NX12Y8205	50.8	126.3	610.8	116.1	5.6	14.0	911.8
NX12Y8209	52.1	128.4	609.3	117.3	5.4	14.3	927.7
NX12Y8210	56.2	132.0	599.9	121.4	10.1	21.4	944.9
NX12Y8212	54.7	131.9	611.8	120.8	5.3	13.4	898.5
NX12Y8213	51.7	126.1	603.3	115.8	5.2	14.9	916.3
NX12Y8214	50.9	125.5	599.9	114.5	5.7	14.4	929.5
NX12Y8215	55.7	121.7	612.6	112.0	6.8	18.9	945.5
NX12Y8221	63.3	122.7	597.6	112.7	4.6	10.9	810.5
NX12Y8222	66.2	125.1	593.8	116.8	4.3	12.6	867.7
NX12Y8223	64.1	122.6	607.5	113.9	4.3	11.1	836.4
Overland	67.1	126.3	666.6	109.5	4.9	8.2	751.1
Pronghorn	61.3	133.1	653.3	117.6	13.2	12.4	989.8
Robidoux	58.9	121.1	640.7	108.1	14.5	8.4	965.6
Settler CL	62.6	125.5	662.1	111.3	13.4	9.1	992.2
Experiment mean	59.2	127	600	116	6.8	11.9	888.0
LSD (0.05)	2.6	6.0	15.0	6.0	1.9	4.0	84.0

Pronghorn, the two highest observed in the nonwaxy controls, were statistically greater than the largest grain volume weights achieved by any of the waxy germplasm lines. Grain yield stability (or response to changing environments) of the waxy germplasm lines demonstrated (Table 2) similar trends to those of the nonwaxy controls. All waxy germplasm lines had slopes that differed from zero and increased with increases in the environmental index (mean location grain yield). Twelve of the waxy germplasm lines demonstrated slopes (*b* values) not significantly different from that of McGill, the control with the highest observed *b* value. In each environment, at least one of the five highest-yielding waxy wheats, based on grand means, did not differ significantly from the highest-yielding nonwaxy cultivar (Table 3). Grain yield observations and responses to changing production potentials argue against any yield drag associated with waxy (amylose-free) starch and indicate potential for development of additional and competitive cultivars.

Grain and flour quality evaluations from samples grown in two Nebraska production environments indicated a wide range of grain hardness and protein characteristics among the waxy wheat germplasm (Table 4). Based on assessment by a Perten (Hägersten, Sweden) single kernel characterization system, mean hardness scores identified three (NX12Y8174, NX12Y8175, and NX12Y8178) soft endosperm-textured (hardness units < 50) wheats, while the remaining 16 waxy wheats were classified as hard wheats. All of these waxy wheats breed true for red grain color. Gluten protein properties were extremely variable, with mixograph mix times ranging from 2.5 to 10.1 min. The only obvious quality deficiency of the waxy germplasm lines was that all had reduced flour yields relative to the nonwaxy controls. This effect seems to be universal among waxy wheats and was also observed in spring waxy types (Graybosch et al., 2003).

Based on observations from the 2016 USDA-ARS Regional Germplasm Observation Nursery, lines NX12Y8205, NX12Y8209, NX12Y8212, and NX12Y8213 demonstrated at least moderate resistance to KS and NC field races of stripe (yellow) rust (*Puccinia striiformis* Westend). Resistance genes to stem rust (*Puccinia graminis* Pers.:Pers. f. sp. *tritici* Erikss. & E. Henning) occur in NX12Y8186, NX12Y8187, NX12Y8188, NX12Y8189, and NX12Y8190 (all *Sr11*) and in NX12Y8205 and NX12Y8209 (*Sr7a*). No resistance was detected to Ug99 forms of stem rust.

Availability

Seed of all 19 waxy wheat germplasm lines has been deposited in the USDA National Plant Germplasm System, where it is available immediately. Until the end of calendar year 2018, small quantities of seed also will be available from R. Graybosch, USDA-ARS, University of Nebraska, Lincoln, NE, 68583. It is requested that the source of this material be acknowledged in future usage by wheat breeding and genetics programs.

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