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Published online March 27, 2006

Evolution of North American Dent Corn from Public to Proprietary Germplasm

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ABSTRACT

Current corn (*Zea mays* L.) hybrids are produced using proprietary inbred lines as parents. These proprietary lines are protected by U.S. Patent and/or the U.S. Plant Variety Protection Act (PVPA) and their use is restricted, but as protection expires these lines become available to the entire corn breeding industry. Our objectives were to gain understanding of this protected germplasm by utilizing pedigree information available in the U.S. Patent and PVPA records to enhance the use of this germplasm in new line development as the lines become publicly available. Ownership, derivation, and lineage of corn inbred lines protected by U.S. Patent or PVPA from 1980 to 2004 were surveyed. Thirty-three companies have protected 908 corn inbred lines and four of these companies: Dekalb Genetics (DK), Holden's Foundation Seeds (LH), Pioneer Hi-Bred (PH), and Syngenta (SG) originated 685 of them. We identified the most significant lines by their cumulative use as parents in the development of new lines. Much of today's germplasm originates from seven progenitor lines: B73, LH82, LH123, PH207, PH595, PHG39, and Mo17. The germplasm surveyed is grouped by pedigree lineage into Oh43, Lancaster, Oh07-Midland, Iodent, Stiff Stalk, Commercial hybrid derived, and Argentine Maiz Amargo backgrounds, with new diversity emerging from the two latter groups. Recycling elite inbred lines using two-parent crosses followed by pedigree breeding was the most prevalent method of new line development.

As parents of F1 corn hybrids have transitioned from public to private inbred lines, predominant sources of germplasm for new product development have shifted from public to private germplasm. A 1985 seed industry survey documented the accelerating use of private sector inbred lines and the concurrent rapidly diminishing role of public germplasm in commercial corn hybrids (Darrah and Zuber, 1986). Only the public inbred B73 still had significant use, but its role was declining. This is well illustrated in Smith (1988) and Smith and Smith (1991) who analyzed the diversity of key commercial dent corn hybrids of the mid-1980s. Smith, through isozyme and/or RFLP genomic markers, determined that commercial hybrids from most seed companies other than Pioneer Hi-Bred had a number of inbred parents in common. Foundation inbred lines, particularly those from Holden's Foundation Seeds, were becoming widely used in branded hybrids marketed by many seed companies. This was the transition period from public germplasm to private germplasm for many of these companies. B73, and to a lesser extent Mo17, were the only public inbreds used in hybrids. For most companies, with the exception of Pioneer Hi-Bred, inbreds from foundation seed companies allowed them to remain competitive during the transition from public to private germplasm. Smaller companies that do not have plant breeders still depend on foundation seed companies to supply inbreds as parents for their commercial hybrids. Today the effort in private companies for inbred line development and evaluation greatly exceeds that in the public sector.

North American dent corn is composed of multiple heterotic groups that when crossed together can optimize hybrid performance. The nomenclature of heterotic groups is somewhat subjective (Tracy and Chandler, 2005). Heterotic groups in dent corn have been subdivided into Iowa Stiff Stalk Synthetic (BSSS) and non-BSSS (Lu and Bernardo, 2001). A similar grouping consists of Reid Yellow Dent (includes BSSS), Lancaster, and miscellaneous heterotic groups (Gethi et al., 2002). Troyer (1999) divided corn into five genetic backgrounds: Reid Yellow Dent (Iodent Reid and BSSS), Minnesota 13 (W153R and SD105), Northwestern Dent (A48, A509, and A78), Lancaster Sure Crop (Mo17 and Oh43), and Leaming Corn (Oh07). The Reid Yellow Dent group is the largest group and made significant contributions to commercial hybrids. Smith and Smith (1989) constructed a more detailed list of dent corn pedigrees describing seven backgrounds. Their classification includes Pioneer Hi-Bred's proprietary germplasm base and identifies several new groups consisting of broad base Iodent, non–Stiff Stalk, and Stiff Stalk backgrounds.

To understand present day corn germplasm and its lineage through the past two decades, we examined the protected proprietary corn lines of Dekalb Genetics, Holden's Foundation Seeds, Pioneer Hi-Bred International, Inc., and Syngenta (includes through consolidation Novartis and Northrup King). Together these lines account for approximately 80% of protected germplasm and formulate approximately 90% of the commercial hybrid seed sold. Representative of the era of this study, U.S. corn hybrid market share of these four companies was estimated to be Pioneer Hi-Bred 42%, Holden's Foundation Seeds 35%, Dekalb Genetics 11%, and Novartis (now Syngenta) 8% (Fairley, 1998; Fritsch, 1997). An undetermined quantity of Holden's Foundation Seeds germplasm is present in its licensees Dekalb Genetics and Novartis market share. These protected registered corn inbred lines are traceable within the public domain through U.S. Patent and/or U.S. PVPA records. Seed of corn inbreds protected at the beginning of the patent and PVPA protection programs is now becoming available to all breeders as protection expires. These inbreds could be useful to broaden germplasm in

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Published in Crop Sci. 46:1193–1205 (2006).
Crop Breeding & Genetics
doi:10.2135/cropsci2005.10-0371
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Abbreviations: DK, Dekalb Genetics; LH, Holden's Foundation Seeds; NK, Northrup King; PD, Patent Database; PH, Pioneer Hi-Bred International; PVPA, Plant Variety Protection Act; SG, Syngenta Seeds.

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the public domain that over the last 20 yr has become increasingly constrained by the restrictions imposed through protection of corn inbreds. An understanding of the genetic relationships among these protected inbreds is essential to their effective use in breeding.

Our first objective was to gain a greater understanding of corn germplasm protected from 1980 to 2004 by: (i) querying the U.S. Patent database to identify the inbreds most often referred to in comparisons within patents of new lines, (ii) creating and querying our own proprietary pedigree database (PD) consisting of derivations of 685 protected inbred lines to identify those lines most often used in recombinant populations for the development of new inbreds, and (iii) using PD to identify the types of germplasm and parental populations used for line development. Our second major objective was to use the information gained from Objective 1 to describe today's germplasm as it has changed during the last four cycles of selection and group it by relation and novelty into informative family backgrounds. This greater understanding of the corn germplasm base and heterotic groups should assist plant breeders in using this material as it becomes available for unrestricted use when U.S. Patent and/or U.S. PVPA protection expires.

MATERIALS AND METHODS

In 1970 the U.S. Congress passed the PVPA to facilitate the protection of plant germplasm, but corn breeders rarely used it until the early 1980s. In 1985 the U.S. Patent and Trademark Office (internal decision) allowed the patenting of corn inbred lines and hybrids (Janis and Kesan, 2001). The onset of extensive use of U.S. PVPA and/or U.S. Patent protection of corn inbreds coincides with the transition of parentage of commercial seed corn hybrids from public to proprietary inbred lines. The protection of corn lines by PVPA and/or patent facilitates public access to their description, performance, and pedigree information. To study these lines we created a PD by mining both the U.S. PVPA certificates and U.S. Patent database for protected corn lines and their pedigree derivation. The PD contains the protected corn lines and their derivations from Dekalb Genetics (160 lines), Holden's Foundation Seeds (134 lines), Pioneer Hi-Bred International (336 lines), and Syngenta (55 lines from Syngenta, Novartis, and Northrup King), or, in sum, 685 lines. Surprisingly, not all protected lines have their pedigree derivation divulged; for example, some U.S. patented inbred lines do not declare their pedigree derivation. All lines protected by U.S. PVPA show the pedigree derivation of the protected line. The PD consists of only those lines that have their pedigree declared in either a PVPA certificate and/or a patent. Because some lines are protected by PVPA only, some by patent only, and some are dual protected, lines protected by patent were cross checked with those lines protected by PVPA, and vice versa, to ensure that each inbred was counted only once. In addition, transgenic and/or conventional trait isoline conversions of the original line were not counted. Not represented in our search are abandoned, withdrawn, and pending applications as these records are closed and not accessible to the public. Protected inbreds were counted and tabulated by originating company within patent and PVPA records.

Within the description of each U.S. patented inbred line are other inbred line(s) used for comparative purposes to establish the novelty of the newly patented line both as an inbred and/or in a hybrid formula. These comparative inbreds are typically the most commercially elite lines of appropriate maturity and usage to which the patent assignee has access. As commercial corn lines are sold as branded hybrids, there is no direct way to judge the merits and extent of use of these lines. To measure the relative importance of commercial lines, we queried the U.S. Patent Database for all of the known proprietary and public inbred corn lines of this era to determine the number of patents in which each line is used for phenotypic comparisons. We refer to these occurrences as patent hits. Inbreds with larger numbers of patent hits were inferred to be more commercially valuable or elite. The U.S. Patent Office database is web accessible (http://patft.uspto.gov/netahtml/search-bool.html) with a search engine built into the database interface; thus, it is ideal for performing queries. Unfortunately, the U.S. PVPA records are not in a digital database, but rather exist as papers filed at one restricted site and cannot be electronically queried. To determine the importance of these protected lines we used the cumulative number of patent hits for each line in the PD. For the lines identified with the most patent hits we show the family background, pedigree derivation, and estimated cycle of recombination.

A second determination of the importance of a line is the number of times it is recombined or occurred in the pedigree derivation of another line. The cumulative number of occurrences in the pedigree of other lines in the PD was summed for each inbred. Each line's family background, pedigree derivation, and estimated cycle of recombination was determined.

To facilitate an understanding of chronology of development of the inbreds we estimated their "age" by cycle of recombinant selection. Cycle 0 inbreds consist of the public and proprietary inbred corn lines available at the beginning of this time period (1980). Subsequent recombination of Cycle 0 lines creates Cycle 1 progeny, and recombination of Cycle 1 lines creates Cycle 2 progeny, and so forth. This paper covers corn inbred lines protected from 1980 through 2004 and spans approximately four cycles of recombination.

Pedigree lineages of inbred lines identified as most significant through U.S. Patent hits and recombination events were graphically linked together by descent. Results are presented in separate figures for Stiff Stalk, Lancaster/Oh07-Midland/Oh43, and Iodent related lines. Arrows originating at parent and pointing to progeny depict lineage of the inbred lines. A best effort was made to trace the lineages of the proprietary lines back to a public line or publicly recognized population or synthetic.

The preponderant pedigree backgrounds of the inbred lines are categorized and summarized. Criteria for grouping lines into pedigree background were their prevalent lineages by descent. Key founder lines for each lineage background are listed.

The types of populations from which PD lines were developed are categorized as: two parent inbred A × inbred B; backcross one (A × B) × B; backcross two or greater [(A × B) × B] × B; three parent (A × B) × C; four or more parents; synthetic or broad base population; synthetic or broad base population crossed to inbred(s); and commercial hybrid. If a commercial hybrid was crossed to an inbred it was considered a three-parent population. The overall composition of proprietary germplasm is summarized as to proportion of corn inbred lines originating from public, Pioneer Hi-Bred, Holden's Foundation, Dekalb Genetics, and Syngenta derived germplasm.

RESULTS AND DISCUSSION

For ease of presentation, the U.S. PVPA certificate number, U.S. Patent number, or other sources containing the derivation or description of origin of the inbreds mentioned in this paper either in a table, figure, or in the text are shown in Table 1.

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Table 1. Citations for corn inbred line backgrounds.

Line	Source of background†	Line	Source of background
Public		**Holden's Foundation Seeds (cont.)**	
A632‡	Gerdes et al., 1993	LH235	Pat. 5,639,942
A634	Gerdes et al., 1993	LH283	Pat. 5,773,683
B73	Gerdes et al., 1993	LH287	Pat. 6,281,414
CM105	Gerdes et al., 1993		
H93	Gerdes et al., 1993	**Pioneer Hi-Bred**	
Mo17	Gerdes et al., 1993	PH041	Smith and Smith, 1987
N22A	Gerdes et al., 1993	PH06B	PVPA 200100250, 200200190
W117	Gerdes et al., 1993	PH07D	PVPA 9700214
		PH09B	PVPA 9700218
		PH207	PVPA 8300144
Cornelius Hybrid Seed Company		PH24E	PVPA 9600204
CB59G	PVPA 9200250	PH581	PVPA 200100250
		PH595	PVPA 9800383
Dekalb Genetics		PH814	Smith et al., 1997
DK01IBH2	Pat. 6,855,877	PH848	Smith et al., 1997
DK2FACC	PVPA 9000016	PH8PG	PVPA 200200190
DK3AZA1	Pat. 5,910,25	PHAA0	PVPA 9400091
DK3IBZ2	PVPA 9100223	PHAC54	PVPA 8700214
DK3IIH6	PVPA 9300087	PHB09	Smith et al., 1997
DK4676A	PVPA 8600092	PHB47	PVPA 8300141
DK5B2C-A	PVPA 9100034	PHBE2	PVPA 9500200
DK78551S	PVPA 8800195	PHBW8	PVPA 9200079
DK87916W	PVPA 8800189	PHG29	PVPA 8600047
DKFBAB	PVPA 8700173	PHG35	PVPA 8300140
DKFBLL	PVPA 9100034	PHG39	PVPA 8300115, 9500208
DKHBA1	Pat. 4,594,810	PHG3BD2	Smith et al., 1997; PVPA 8300144
DKIBC2	PVPA 8700198	PHG3RZ1	Smith et al., 1997; PVPA 9700226
DKIBI	PVPA 8700197	PHG42	Smith et al., 1995
DKJ6	PVPA 8700196	PHG44	PVPA CN 9700226
DKMM402A	PVPA 9100222	PHG47	PVPA CN 8600131
DKMM501D	PVPA 9300085	PHG50	PVPA CN 8300143
DKPB80	PVPA 9100034	PHG69	Smith et al., 1997
DKRDBQ2	Pat. 6,037,531	PHG71	PVPA CN 8400157
DKZZZ38	PVPA 9100223	PHG84	PVPA CN 8600130
		PHG86	PVPA CN 8700170
Holden's Foundation Seeds		PHH93	PVPA 8800216
610	Gerdes et al., 1993; Pat. 5,773,683	PHHB9	PVPA 9300108
LH1	PVPA 7600047	PHJ40	PVPA 8600133
LH7	Gerdes et al., 1993	PHJ90	PVPA 9100093
LH24	Gerdes et al., 1993	PHK05	PVPA 8800001
LH51	PVPA 8200062	PHK29	PVPA 8700214
LH53	Gerdes et al., 1993	PHK42	PVPA 9100093
LH59	PVPA 8700213	PHK56	PVPA 9000247
LH74	PVPA 8200063	PHK76	PVPA 8800036
LH82	PVPA 8500037	PHKM5	PVPA 9400097
LH85	PVPA 8700088	PHKW3	PVPA 9500209
LH105	Pat. 5,457,275	PHM10	PVPA 8900312
LH117	Gerdes et al., 1993	PHMK0	PVPA 9300112
LH119	PVPA 8200064	PHN18	PVPA 9200086
LH122	Gerdes et al., 1993	PHN46	PVPA 9000249
LH123	PVPA 8400030	PHN82	PVPA 8900317
LH132	PVPA 8300148	PHP02	PVPA 8800212
LH146	PVPA 8700089	PHP38	PVPA 9000250
LH168	Pat. 5,457,275	PHR03	PVPA 9100097
LH172	Pat. 5,276,266	PHR25	PVPA 8800002
LH176	Pat. 5,491,296	PHR47	PVPA 8800213
LH181	Pat. 5,304,713	PHR61	PVPA 9100100
LH185	Pat. 5,491,294	PHRE1	PVPA 9300114
LH194	PVPA 9000125	PHT11	PVPA 9100101
LH195	Pat. 5,059,745; PVPA 9000047	PHTD5	PVPA 9400095
LH198	Pat. 5,304,717	PHV78	PVPA 8800003
LH200	Pat. 5,285,005	PHW52	PVPA 8800215
LH202	PVPA 9000126	PHZ51	PVPA 8600132
LH206	PVPA 9000126		
LH210	Pat. 5,276,262		
LH211	Pat. 5,387,743	**Syngenta and Novartis**	
LH212	Pat. 5,276,260	NK347	PVPA 8800152
LH213	Pat. 5,276,259	NK377	PVPA 8800152
LH216	Pat. 5,276,263	NKB386	PVPA 8800152
LH227	Pat. 5,633,429	SGH8431	PVPA 8800152

† PVPA refers to U.S. Plant Variety Protection Act (PVPA) certificate number and Pat. refers to U.S. Patent number.

‡ Public inbred lines are denoted by published prefix of origin. All other lines are prefixed as CB, DK, LH, NK, PH, SG are Cornelius Hybrid Seed Company, Dekalb Genetics, Holden's Foundation Seeds, Northrup King, Pioneer Hi-Bred, Syngenta (includes Novartis, Northrup King, and Ciba), respectively.

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Pedigrees of public and some of the foundation seed company, but not proprietary, corn inbred lines of this era have been published in sources such as Henderson (1983), Gerdes et al. (1993), and Mike Brayton Seeds Genetics LLC (Anonymous, 2003). In these sources the inbred derivation of known foundation seed company corn inbred lines is frequently gleaned from sales information and commonly does not name the specific inbreds in the derived lines pedigree. For example, in Gerdes et al. (1993) the derivation of LH195 is shown to be B37, B73 and in Mike Brayton Seed Genetics (Anonymous, 2003) its derivation is shown to be B73, LH1; whereas the actual derivation of LH195 is found to be LH117 × LH132 as per U.S. PVPA and patent records (Table 1). Establishing the correct pedigree derivation of LH195 allows its lineage to be established and therefore a greater understanding of its true background. The pedigree data assembled in this paper are from U.S. Patent and U.S. PVPA records and not from anecdotal and/or generic sales information. There is no previously published summary of proprietary lines of this era that discusses collectively their backgrounds, lineage, origin, and significance.

Thirty-three companies were identified that had inbred lines protected through U.S. Patent, PVPA, or both (Table 2). In total, 908 unique inbred lines were protected in the period of this study. Of these, 685 lines (78%) are in the PD. This database consists of lines and their pedigree derivations from Dekalb Genetics, Holden's Foundation Seeds, Pioneer Hi-Bred, and Syngenta. We focused on the inbred pedigrees from these four larger companies as they make up approximately 90% of U.S. corn hybrids and are continuously represented throughout this era.

Table 2. U.S. Patent and U.S. PVPA registration of corn inbred lines.

	Number of inbred lines		
Assignee	U.S. Patent	U.S. PVPA†	Nonredundant‡
Pioneer Hi-Bred International, Inc.	223	336	340
Dekalb Genetics Corp.	103	134	163
Holden's Foundation Seeds, LLC	75	134	134
Novartis AG	26	34	52
Advanta Technology, Ltd.	9	23	32
Syngenta Seeds AG	17	8	18
Asgrow Seed Company, LLC	15	4	17
United AgriSeeds, Inc.	0	15	15
Agrigenetics Inc.	14	2	14
J.C. Robinson Seed Company	9	14	14
Limagrain Genetics Corp.	7	7	14
NDSU Research Foundation	0	10	10
Standard Oil Company	1	10	10
Monsanto Technology, LLC	8	0	8
Zeneca Ltd.	8	0	8
FFR Cooperative	6	1	7
Illinois Foundation Seeds, Inc.	6	1	7
KWS Kleinwanzlebener Saatzucht AG	5	2	6
DowElanco	0	5	5
Wilson Hybrids, Inc.	0	5	5
Entities with 4 or fewer nonredundant lines§	28	13	29
Total	560	758	908

† United States Plant Variety Protection Act (PVPA).
‡ Nonredundant factors out lines that are double protected in both U.S. Patent and U.S. PVPA databases and ensure that each line is counted once.
§ Cargill Inc. (4 lines), Hogemeyer Hybrids (4), Rustica Prograin Genetique (4), Golden Seed Company, LLC (3), Lifaco Seed Corp. (3), Garst Seed Company (2), Iowa State University (2), Sandoz Ltd (2), Edward J. Funk (1), Funk Seeds International, Inc. (1), Mycogen Corp (1), Quality Research Associates (1), and Stine Seed Farms (1).

Important Lines

Of the 43 inbred lines identified as having the most patent hits, three are C0 or founder public inbred lines (Table 3) and in descending number of patent hits are: B73 (Stiff Stalk), A632 (early maturity Stiff Stalk), and Mo17 (Lancaster). B73 incurred the most patent hits of any inbred line, either public or proprietary, and is pivotal in the development of Stiff Stalk lines for all of the proprietary programs surveyed. The significance of Mo17 surely is underestimated due to the presence of Holden's Foundation Seed inbred LH51, which originated from a backcross recovery of Mo17 and is shown to be approximately 97% Mo17. Of the 43 inbreds identified as most elite by patent hits in Table 3, 20, or nearly half, are of Stiff Stalk backgrounds.

Significant lines identified in Tables 3 and 4 are shown graphically in Fig. 1–3 that group the lines by Stiff Stalk, Lancaster/Oh43/Oh07-Midland, and Iodent backgrounds, respectively. Additional lines from the PD were added to link together lines by pedigree derivation where necessary to unify the figures. When possible, the lineage of these lines is traced back to publicly recognizable ancestors.

We have formulated a grouping of lineage backgrounds to reflect how today's germplasm has evolved as a result of the past four cycles of recombination (Table 5). Seven major groups are designated: Oh43, Lancaster, Oh07-Midland, Iodent, Commercial hybrid derived, Maiz Amargo, and Stiff Stalk, as well as subgroups created from recombination between groups. Intergroup recombination has been successful between groups that each independently combines well opposite a common background in commercial hybrids. This essentially conserves combining ability of the derived group. For example the Oh43 × Lancaster subgroup is derived from two heterotic groups that each combine well with Stiff Stalk lines to make commercial hybrids. Thus, combining ability is preserved, but germplasm diversity is enhanced by the new recombinant subgroups. It is also true of the Iodent × Oh07-Midland group, as they both combine well with Stiff Stalk lines to produce commercial hybrids. The Stiff Stalk × Iodent subgroup works well in crosses to Oh43 lines, as both independently combine well with Oh43 lineage lines. With this in mind, we postulate that a Stiff Stalk × Oh43 derived subgroup may work well in commercial hybrid formulas opposite Iodent. The numerous subgroups within the Stiff Stalks are successful as they still maintain performance when crossed with Oh43, Lancaster, Oh07-Midland, commercial hybrid derived, or Iodent backgrounds to produce commercial hybrids. Thus, Stiff Stalk germplasm plays a significant role in many hybrids. Broadening the germplasm base of

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Table 3. Most referenced corn inbred lines for phenotypic comparisons in the U.S. Patent database.

Inbred	Hits†	Cycle‡	Background§	Derivation
B73¶	63	C0	SSS	Iowa Stiff Stalk Synthetic C5
LH185	63	C2	Pioneer Hybrid 3535	LH59 × LH123
LH132	60	C1	SSS	(H93 × B73) × B73
LH198	59	C2	SSS	(LH132 × B84) × LH132
LH51	54	C1	Lancaster	Mo17 backcross 5 recovery
LH195	48	C2	SSS	LH117 × LH132
PHP38	47	C1	Amargo/SSS	PHG39 × PHK29
PHP02	41	C2	Iodent	PHG44 × PHG29
PHRE1	40	C2	Amargo/SSS	PHJ40 × PHR47
LH172	38	C2	Pioneer Hybrid 3558/Pioneer Hybrid 3535	(LH82 × LH122) × LH82
LH200	37	C2	SSS	LH117 × LH132
PHN46	37	C2	Oh07-Midland	PHZ51 × PHV78
LH82	36	C1	Pioneer Hybrid 3558	Holden private line 610 × LH7
LH74	35	C1	SSS	A632 × B73
PHW52	34	C1	Amargo/SSS	B73 × PHG39
LH59	34	C1	Lancaster/OH43	(Mo17 × H99) × LH53
DKFBLL	33	C2	SSS	DK5B2C-A × DKPB80
LH212	33	C2	Pioneer Hybrid 3535/Lancaster	(LH24 × LH123) × LH123
PHR03	33	C2	Oh07-Midland	PHT19 × PHG84
PHTD5	33	C2	Iodent	PHH93 × PHR25
PH24E	32	C3	Iodent	PHP02 × PHN82
LH216	30	C3	Lancaster/Pioneer Hybrid 3535	[(LH51 × LH123) × LH51] × LH51
DK3IIH6	29	C2	Pioneer Hybrid 3737	Pioneer Hybrid 3737
A632	27	C0	SSS	[(Mt42 × B14) × B14] × B14
PHHB9	27	C2	Amargo/SSS	PHG86 × PHW52
LH210	27	C2	Lancaster	LH51 × BS11
PH09B	26	C3	Amargo/SSS	PHP38 × PHHB9
PHK56	26	C2	Oh07-Midland/Oh43	PHG47 × PHG35
LH202	26	C1	SSS	[(A662 × B73) × B73] × B73
PHAA0	25	C2	SSS	PHW03 × PHJ40
LH176	25	C2	Pioneer Hybrid 3558	Pioneer Hybrid 3704 × LH82
Mo17	25	C0	Lancaster	C.I.187–2 × C103
LH168	24	C2	Pioneer Hybrid 3558/Oh43	LH82 × LH105
DK2FACC	24	C2	SSS	DK4676A × DKPB80
DK01IBH2	24	C2	Pioneer Hybrid 3737	Pioneer Hybrid 3737
LH119	23	C1	SSS	(H93 × B73) × B73
LH146	22	C1	SSS	(B73 × CM105) × CM105
LH235	22	C3	SSS	LH194 × LH195
PHBE2	21	C3	Oh07-Midland	PHR03 × PHN46
LH85	21	C1	unknown	Pioneer Hybrid 3978
LH213	21	C2	Pioneer Hybrid 3535/Lancaster	LH123 × LH51
PHR25	21	C1	Iodent	PHB83 × PH207
LH227	20	C2	SSS	(LH145 × LH146) × LH119

† Hits are the cumulative number of references for a given line in the patents of other corn inbred lines in the U.S. Patent database.
‡ Cycles of recombination are estimated cycles of recombination past the base genetics available when pedigrees began to be published through U.S. Plant Variety Protection and U.S. Patents.
§ Background shown is an estimate of the most predominant background. The derivation of some inbred lines can be from a commingling of several backgrounds. Backgrounds are Oh43, Lancaster, Oh07-Midland, Iodent, Commercial hybrid (Pioneer Hybrid 3737, 3558, and 3535 derived), Maize Amargo (Amargo), and Stiff Stalk (SSS) derived. Some lines are significantly derived from multiple backgrounds that are shown separated by a "/" with the predominant background shown first.
¶ Corn inbred lines are prefixed with DK (Dekalb Genetics), LH (Holden's Foundation Seeds), and PH (Pioneer Hi-Bred International) proprietary lines. All other lines are public inbred corn lines and are denoted by conventional recognized format.

Stiff Stalk lines would have an immediate effect on expanding the diversity of commercial hybrids. Diversity among Stiff Stalk lines may have decreased with the emergence of B73 lineage as the dominant Stiff Stalk source along with concurrent loss of purebred B14 and B37 lineages.

Overall, in all programs hybrids have been improved as a result of intercrossing within heterotic groups, introgression of exotic germplasm, and tapping germplasm from other programs and using it in unfamiliar ways. During this period, increased hybrid diversity originated from the new groups derived from Maiz Amargo and Commercial Hybrid derived (germplasm from Pioneer Hi-Bred hybrids 3737, 3535, and 3558).

Oh43 Background

The Oh43 group has over the last several cycles of recombination lost its purebred identity. This lineage played a role in the development of numerous significant inbred lines through recombination with Oh07-Midland and Lancaster groups in Pioneer Hi-Bred and Holden's Foundation Seeds germplasm, respectively. An Oh43 progenitor within Pioneer Hi-Bred is the inbred line PH041 that is derived from Oh43 × (Iodent × WF9). It is broad based in origin, but is one-half Oh43 derived (Smith and Smith, 1987). Although the line PH041 was only found to be a parent of three new lines in our study, one of its direct progeny, PHG47, was found to be recombined 11 times in the development of new protected corn lines. PHG47 is derived from PH041 × MKSDTE Cycle 10. The background of MKSDTE is unknown, but is presumed to be a broad-based population. PHG47 was recombined primarily with Oh43 and Oh07-Midland, but also Stiff Stalk and Iodent, derived lines to develop new corn lines. It was through recombination of PHG47 with the Oh07-Midland derived line PHG35 that the significant line PHK56 was developed.

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Table 4. Most recombined corn inbred lines within the pedigree database.†

Title	Number of times used as parent‡	Cycle§	Background¶	Derivation
B73#	33	C0	SSS	Iowa Stiff Stalk Synthetic C5
DKFBLL	22	C2	SSS	DK5B2C-A × DKPB80
PHR03	21	C2	Oh07-Midland	PHT19 × PHG84
PH207	17	C0	Iodent	PHG3BD2 × PHG3RZ1
PHP02	16	C2	Iodent	PHG44 × PHG29
LH51	15	C1	Lancaster	Mo17 backcross 5 recovery
PHW52	15	C1	Amargo/SSS	B73 × PHG39
LH123	14	C1	Pioneer Hybrid 3535	Pioneer Hybrid 3535
PHJ40	14	C1	SSS	PHB09 × PHB36
DK3IIH6	14	C2	Pioneer Hybrid 3737	Pioneer Hybrid 3737
Mo17	13	C0	Lancaster	C.I.187–2 × C103
LH132	13	C1	SSS	(B73 x H93) × B73
LH82	13	C1	Pioneer Hybrid 3558	Holden line 610 × LH7
PHG39	12	C0	Amargo	A33GB4 × A34CB4
DK01IBH2	12	C2	Pioneer Hybrid 3737	Pioneer Hybrid 3737
DK2FACC	12	C2	SSS	DK4676A × DKPB80
PHHB9	12	C2	Amargo/SSS	PHG86 × PHW52
PHG47	11	C1	Oh43	PH041 × MKSDTE Cycle 10
PHP38	11	C1	Amargo/SSS	PHG39 × PHK29
PHK29	10	C0	SSS	PHB47 × PHAC54
LH74	10	C1	SSS	A632 × B73
DK3IBZ2	10	C2	unknown	DKIBC2 × DKZZZ38
LH59	9	C1	Lancaster/Oh43	(Mo17 × H99) × LH53
PHR25	9	C1	Iodent	PHB83 × PH207
PH595	8	C0	Oh07-Midland	Fem Comp, Oh07, Midland OP#
DKMM501D	8	C2	unknown	LH38 × DK88121A
PHN46	8	C2	Oh07-Midland	PHZ51 × PHV78
PHRE1	8	C2	Amargo/SSS	PHJ40 × PHR47
PHTD5	8	C2	Iodent	PHH93 × PHR25
PHK76	7	C0	unknown	PHAD18 × PHB02
DK87916W	7	C1	SSS	[(DKW37–2 × B73) × B73] × B73
SGH8431	7	C2	SSS	(NK377 × NKB386) × NK347
LH194	7	C2	SSS	LH117 × LHE137
LH195	7	C2	SSS	LH117 × LH132
PHN82	7	C2	Iodent	PHG29 × PHHD38
CB59G	6	C0	SSS	[(B14A × R168) × B59] × B59
DKHBA1	6	C1	unknown	Pioneer Hybrids 3195 × 3199
DKMM402A	6	C1	unknown	LH38 × DKMANS
PHG50	6	C1	Iodent	PH848 × PH207
PHKM5	6	C1	unknown	PHK70 × PHG96
LH213	6	C2	Pioneer Hybrid 3535/Lancaster	LH123 × LH51
PHBW8	6	C2	Amargo/SSS	PHJ40 × PHW52
LH38	6	??	unknown	unavailable
DK3AZA1	5	??	unknown	DKAQA3 × DKQFAR
CM105	5	C0	SSS	(V3 × B14) × B14
PH814	5	C0	Lancaster	Broad base Lancaster
DK78551S	5	C1	unknown	DK78060A × LH38
DKFBAB	5	C1	SSS/Lancaster?	B14 × LH23
DKIBC2	5	C1	Lancaster	DKJ6 × Mo17Ht
LH85	5	C1	unknown	Pioneer Hybrid 3978
PHG29	5	C1	Iodent	(PH207 × PH806) × PH207
PHN18	5	C1	unknown	PHDK6 × PHNN2
PHT11	5	C1	Amargo/SSS	PHG39 × PHG69
LH210	5	C2	Lancaster	LH51 × BS11
PH09B	5	C2	Amargo/SSS	PHP38 × PHHB9
PHKW3	5	C3	Iodent	PHN82 × PHN63
A634	4	C0	SSS	{[(Mt42 × B14) × B14] × B14} × B14
W117	4	C0	Minnesota 13	643 × Minnesota 13
DKIBI	4	C1	unknown	Pioneer Hybrid 3901
LH119	4	C1	SSS	(H93 × B73) × B73
PHG35	4	C1	Oh07-Midland/Iodent	PHG3BD2 × PH595
PHK05	4	C1	Flint	CM7 × PH051
PHM10	4	C1	Iodent/Amargo	PHG39 × PH207
LH172	4	C2	Pioneer Hybrid 3558/ Pioneer Hybrid 3535	(LH82 × LH122) × LH82
LH181	4	C2	Pioneer Hybrid 3535/Lancaster	LH58 × LH122
LH198	4	C2	SSS	(LH132 × B84) × LH132
LH211	4	C2	Pioneer Hybrid 3535/Lancaster	LH58 × LH123
LH212	4	C2	Pioneer Hybrid 3535/Lancaster	(LH24 × LH123) × LH123
PH07D	4	C2	Amargo/SSS	PHMK0 × PHR61
PHJ90	4	C2	Iodent	PHG50 × PHK42

† Pedigree database (PD) consists of all of the protected corn lines protected in the U.S. Patent and U.S. Plant Variety Protection Act with known pedigree derivations. These lines were from Dekalb Genetics, Holden's Foundation Seeds, Pioneer Hi-Bred International, and Syngenta (Syngenta, Novartis, and Northrup King) or in sum 685 lines. Lines are prefixed as CB, DK, LH, PH, SG are Cornelius Hybrid Seed Company, Dekalb Genetics, Holden's Foundation Seeds, Pioneer Hi-Bred, Syngenta (includes Novartis, Northrup King, and Ciba), respectively. All other lines are public inbred lines denoted by published prefix.

‡ Number of times used as parent is the cumulative number of times within the PD that a line is cited as a parent in the pedigree of another line.

§ Cycles of recombination are estimated number of cycles of recombination past the base genetics available at the beginning of this era (approximately 1980).

¶ Background shown is an estimate of the most predominant background. The derivation of some inbred lines can be from a commingling of several backgrounds. Backgrounds are Oh43, Lancaster, Oh07-Midland, Iodent, Commercial hybrid (Pioneer Hybrid 3737, 3558, and 3535 derived), Maize Amargo (Amargo), Stiff Stalk (SSS), Flint, and Minnesota 13 derived. Some lines are significantly derived from multiple backgrounds that are shown separated by a "/" with the predominant background shown first.

Pioneer Female Composite is a proprietary composite of Pioneer Hi-Bred, Midland is an Open Pollinated variety.

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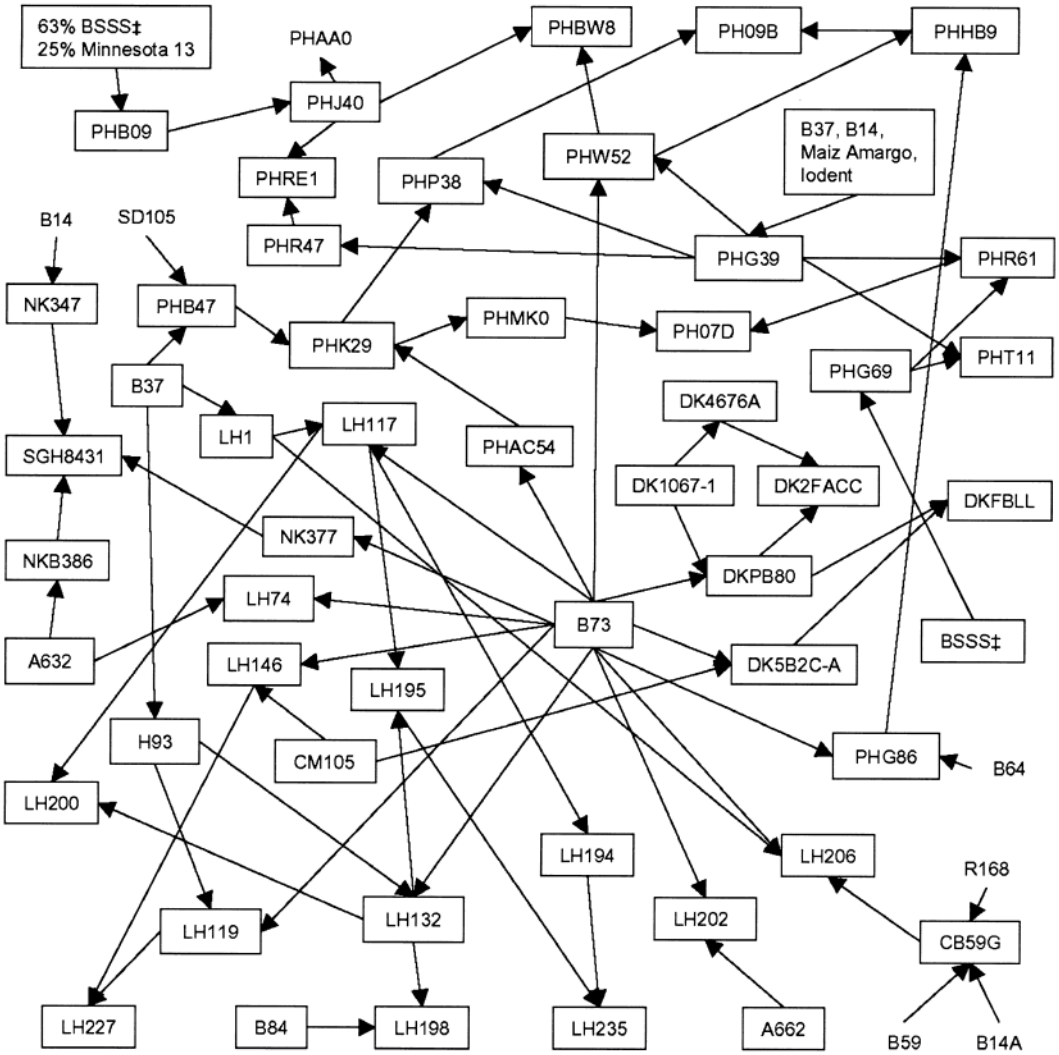

Fig. 1. Lineage of elite Stiff Stalk corn inbred lines. Figure illustrates the lineage of corn inbred lines by descent as depicted by arrows originating from parents and pointing to its progeny. Proprietary inbreds are noted by the following prefixes: CB, Cornelius Hybrid Seed Co.; DK, Dekalb Genetics; LH, Holden's Foundation Seeds; NK, Northrup King (now owned by Syngenta); PH, Pioneer Hi-Bred International; and SG, Syngenta. Public inbred lines are noted by standard published nomenclature. BSSS, Iowa Stiff Stalk Synthetic.

Within Holden's Foundation Seeds Oh43 germplasm is present in LH59 and LH168, which were derived from recombination of Oh43 derived lines with Lancaster and Pioneer hybrid 3558 (LH82) derived backgrounds, respectively.

Lancaster Background

The public line Mo17 is the founder line that along with LH51 (itself a C1 Mo17 derivative and near Mo17 isoline) is the predominant lineage of Lancaster germplasm outside of Pioneer Hi-Bred. Mo17 and LH51 were widely used in new line development within Holden's Foundation Seeds and its licensees. Thus it was used by nearly all seed companies in the USA (Smith, 1988; Smith and Smith, 1991). Recombination of LH51 led to the development of 15 C2 lines that include the elite lines LH210, LH213, and LH216 (Table 4). Lancasters were recombined with lines from Lancaster, Oh43, and Commercial Hybrid derived backgrounds to create new commercial corn lines. Nowhere in the U.S. PVPA records or U.S. Patent database was a Pioneer Hi-Bred (336 Pioneer Hi-Bred lines) line found that was directly developed from Mo17 or LH51. However, PH06B, an unprotected line derived from the three-parent cross (Mo17 × PHN82) × PHR03 or generalized by background as (Lancaster × Pioneer Iodent) × Pioneer Oh07-Midland is the parent of two protected lines, PH581 and PH8PG, as divulged in their PVPA certificates (Table 1). PH06B is a line that Pioneer Hi-Bred did not register by U.S. PVPA or U.S. Patent and is presumed not to have been a commercially used line but is the only known carrier of Mo17 into Pioneer Hi-Bred germplasm.

The Lancaster germplasm background was present in Pioneer Hi-Bred, composing approximately 4.5% of a set of U.S. central Corn Belt commercial hybrids during this period (Smith et al., 2004). The Lancaster background in Pioneer came from several sources. The Lancaster strain that is the progenitor of Mo17 was nearly

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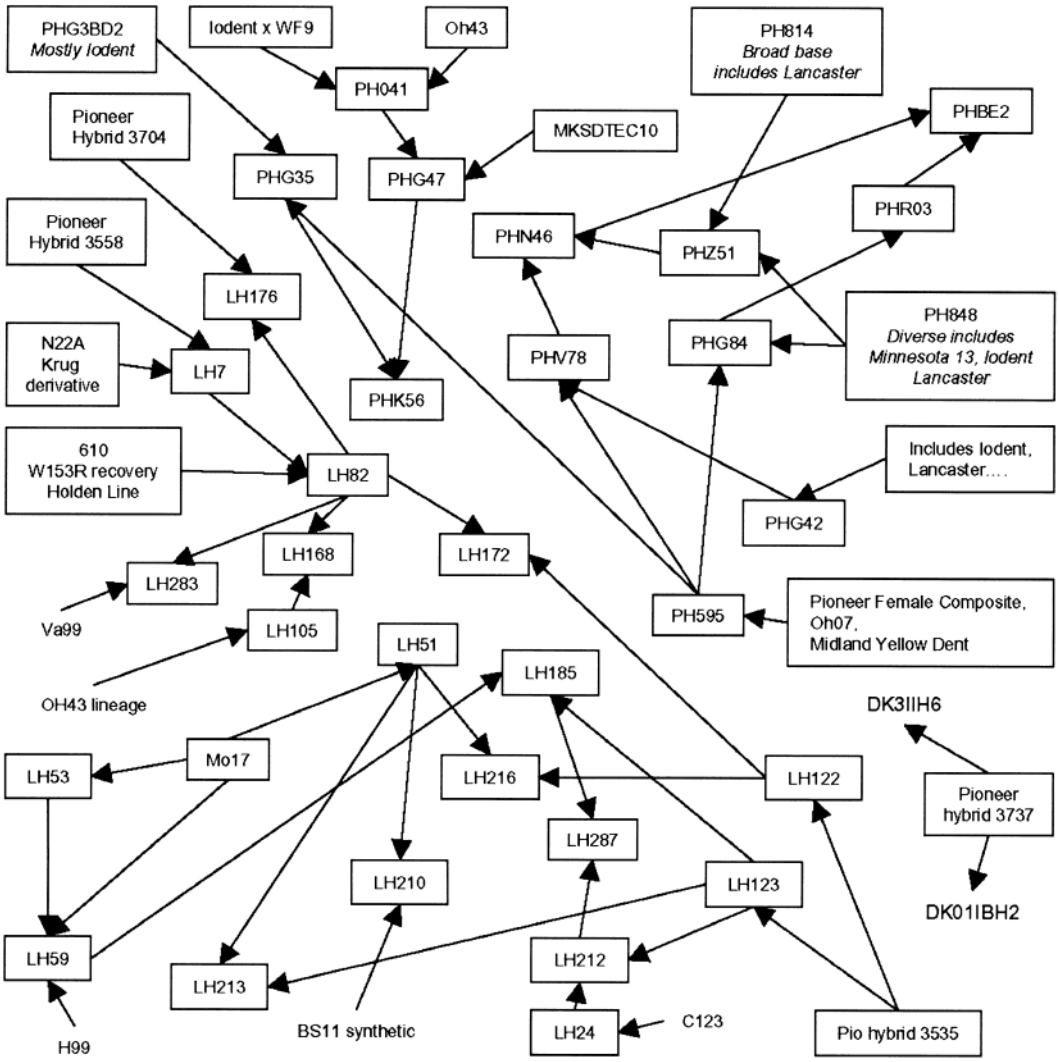

Fig. 2. Lineage of elite Lancaster, Oh07-Midland, and Oh43 corn inbred lines. Figure illustrates the lineage of corn inbred lines by descent as depicted by arrows originating from parents and pointing to its progeny. Proprietary inbreds are noted by the following prefixes: DK, Dekalb Genetics; LH, Holden's Foundation Seeds; and PH, Pioneer Hi-Bred International. Public inbred lines are noted by standard published nomenclature.

absent in a set of Pioneer U.S. central Corn Belt hybrids of this era (1980 to 2004) (Smith et al., 2004). The presence of Lancaster in Pioneer's germplasm during this era was commingled within the PHG71 related Stiff Stalk lineage and the non–Stiff Stalk PH814 and PH848 related lineages (Smith and Smith, 1989).

Oh07-Midland Background

The core of Pioneer non–Stiff Stalk, non-Iodent germplasm traces to PH595 which has a diverse background consisting of 50% Female Composite (Pioneer Hi-Bred proprietary population), 25% Oh07, and 25% from a line described as from a Midland Yellow Dent background (Table 1). Oh07 is derived from Illinois Long Ear × Illinois Two Ear (Gerdes et al., 1993). Troyer (1999) describes Oh07 as being derived from the Leaming Corn background. This background was not found anywhere else in the PD, thus Oh07 is unrelated to current germplasm. The same is true for Midland Yellow Dent. The background of Female Composite is unknown, but presumed to be genetically broad based and may or may not contain Lancaster. The best descriptive notation for the background of PH595 is Oh07-Midland. Recombination of PH595 led to the development of C1 lines PHG35, PHV78, and PHG84 and these C1 lines were recombined to develop the C2 lines PHK56, PHN46, and PHR03. All of these PH595 derived C2 lines are presumed elite, as measured by both patent hits and recombination events in this study. The most recombined Pioneer Hi-Bred proprietary line is PHR03, which is a direct progenitor of over 21 protected C3 corn lines. Non–Stiff Stalk, non-Mo17, and non-pure Iodents are characteristic of three groups of Pioneer germplasm that contain Lancaster and/or Oh07 (Smith and Smith, 1989). These are grouped into the PH814, PH848, and PH595 backgrounds. As seen in Fig. 2, the contributions of PH814 and PH848 are less than that of PH595. PH595 is at the center of several key lineages within Pioneer Hi-Bred line pedigrees. Through recombination, the PH595 lineage

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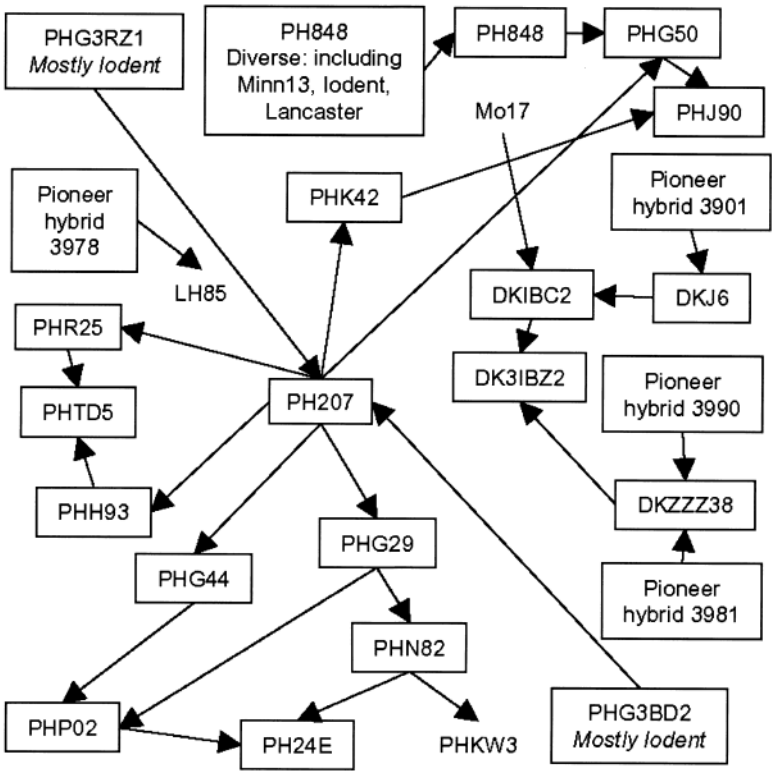

Fig. 3. Lineage of elite Iodent corn inbred lines. Figure illustrates the lineage of corn inbred lines by descent as depicted by arrows originating from parents and pointing to its progeny. Proprietary inbreds are noted by the following prefixes: DK, Dekalb Genetics; LH, Holden's Foundation Seeds; and PH, Pioneer Hi-Bred International. Public inbred lines are noted by standard published nomenclature.

has established itself as the major non–Stiff Stalk non-Iodent group. With that being said, the recombination of PH814 and PH848 either with each other, with PH595, or with Iodent lineages has originated significant lines, but, as a result, purebred PH814 and PH848 lineages were lost. As would be expected, the inbred lines of the PH595 lineage were crossed to Stiff Stalk lines to produce commercial hybrids.

Iodent Background

The Iodent group is important and unique to Pioneer Hi-Bred and this background made up approximately 15% of the composition of a set Pioneer Hi-Bred U.S. central Corn Belt hybrids during the period of this study (Smith et al., 2004). Troyer (1999) presented an excellent overview of the origin of the Iodents. As a result of many cycles of selection Pioneer Hi-Bred optimized the performance of Iodents. In addition to Iodent, this group also has in its background a smaller proportion of Long Ear Open Pollinated Variety and Minnesota 13 (Smith and Smith, 1989; Smith et al., 1997). Much of the Iodent background of this era traces back to the founder line PH207 that was a parent in the development of 17 registered corn lines during this era. Significant C1 progeny of PH207 include the inbreds PHG29, PHG50, and PHR25 and the C2 inbreds PHJ90, PHN82, PHP02, and PHTD5. The lineage of Iodents and the role of PH207 as the main progenitor of Iodent germplasm within Pioneer Hi-Bred germplasm are shown in Fig. 3. Iodent germplasm may have been introduced into other proprietary programs through selfing and recombination from Pioneer Hi-Bred commercial F1 hybrids. Iodents have been crossed to lines from Oh43, Stiff Stalk, and Flint backgrounds to produce commercial F1 hybrids. Iodents have been recombined with lines from Iodent,

Table 5. Grouping of dent corn inbred backgrounds based on pedigree lineage.

Background†	Main progenitor line(s)‡
Oh43 related	
Oh43	PH041 and PHG47
Oh43 × Lancaster	LH59
Lancaster related	Mo17 and LH51
Oh07-Midland related	PH595
Oh07-Midland × Oh43	PHK56
Iodent related	
Iodent	PH207
Iodent × Midland/Oh07	PHG35
Iodent × stiff stalk	PHG71 and PHM10
Commercial hybrid derived	
Pioneer hybrid 3737	DK3IIH6 and DK01IBH2
Pioneer hybrid 3535	LH123
Pioneer hybrid 3558	LH82
Maiz Amargo 41.2504b	PHG39
Maiz Amargo 41.2504b × B73	PHW52
Stiff Stalk related	
B14	CM105 and A632
B37	PHB47
B37 × B73	LH117 and PHK29
B73	B73
B73 × B14	LH74 and LH202

† Backgrounds are subjectively grouped on the basis of prevalence of pedigree lineage. Public inbred lines are noted in published format, Dekalb Genetics (DK), Holden's Foundation Seeds (LH), and Pioneer Hi-Bred International (PH).
‡ Main progenitor lines are those which play an important founder lines in the lineages of each background.

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Lancaster, and to a lesser extent Stiff Stalk backgrounds for new line development. Iodents and Stiff Stalks both trace back to Reid Yellow Dent and yet, although related in origin, crosses between them can produce commercially acceptable hybrids.

Commercial Hybrid Derived Background

During the era of this study new diversity has emerged from Argentine Maiz Amargo and Commercial Hybrid derived germplasm. These new sources of germplasm either originated within or were refined by Pioneer Hi-Bred. Commercial Hybrid germplasm sources were derived from Pioneer hybrids 3737, 3535, and 3558 and appear to be different from any established heterotic backgrounds within Pioneer Hi-Bred and these lines are typically crossed to Stiff Stalk lines to produce commercial F1 hybrids.

The Pioneer 3737 derived germplasm is represented by two Dekalb Genetics inbreds, DK3IIH6 and DK01IBH2, which were highly recombined within the Dekalb germplasm pool (Table 4). The Pioneer 3535 and Pioneer 3558 derived germplasm groups were developed by Holden's Foundation Seeds.

The Pioneer Hi-Bred hybrid 3558 group is represented by the line LH82 that was derived by Holden's Foundation Seeds from the lines LH07 and Holden line 610 (Table 1). LH07 is 75% Pioneer Hybrid 3558 and 25% public line N22A that is Krug derived. Holden line 610 is a W153R recovery presumed to be approximately half W153R (Gerdes et al., 1993). Thus, LH82, the progenitor line of the Pioneer 3558 group, is composed, in decreasing proportions, of Pioneer Hybrid 3558, W153R, and Krug. Holden's Foundation Seeds, in the patent of LH168 (U.S. Patent 5457,275), state that "LH82 is considered a family unto itself," which reinforces the novelty of the LH82 background. The C1 line LH82 was recombined to develop the C2 lines LH168, LH172 and LH283. The derivatives of LH168 and LH172 involve recombination of LH82 with the Oh43 and Pioneer 3535 backgrounds, respectively. In the derivation of LH283, LH82 was recombined with the public inbred line Va99. It is worth mentioning that Va99 is derived from the cross Oh07B × Pa91 or the backgrounds Leaming Corn × Wf9 (Gerdes et al., 1993). This is a rare example of Oh07 (Leaming Corn) background outside of Pioneer Hi-Bred germplasm.

The Pioneer Hi-Bred hybrid 3535 group is represented by the line LH123 that was derived directly from selfing Pioneer Hybrid 3535 by Holden's Foundation Seeds and was a progenitor in the lineages of the lines LH185, LH211, LH212, LH213, and LH287. The Pioneer 3535 and 3558 groups have maintained their integrity by recombination within each group, although, on occasion, they have been crossed with each other, and with Lancaster derived lines (Fig. 2).

Other than for a few lines, the Lancaster lineage has not advanced as a purebred group during the most recent cycles of recombination. This has coincided with the emergence of the unique germplasm groups derived from the Commercial Hybrid (Pioneer Hi-Bred hybrids 3737, 3558, and 3535) derived group. Hybrid diversity has increased from interchanging these numerous Commercial Hybrid derived inbred corn lines in hybrid formulas with Stiff Stalk lines to produce new commercial hybrids. All three of these Commercial Hybrid derived groups introduced new unrelated sources of germplasm to companies outside of Pioneer Hi-Bred. Being derived from commercial F1 hybrids they also may be unique by being a composite of the known family groups within Pioneer Hi-Bred.

Maiz Amargo Background

Argentine Maiz Amargo is an exotic germplasm source whose introduction was instrumental in the creation of a unique germplasm within Pioneer Hi-Bred. This group emerged in the 1980s, with no significant use before 1980 (Smith et al., 2004). Maiz Amargo quickly established itself and with subsequent recombination within Pioneer Hi-Bred germplasm became a key component of their Stiff Stalk germplasm. Maiz Amargo was introduced through recombination with the public corn lines B96 and B64 that are 100 and 12.5% Maiz Amargo 41.2504B, respectively (Table 1). Though both PHG39 and PHG86 are Maiz Amargo recombinant lines, the PHG39 lineage is most significant in the introgression of Maiz Amargo into Pioneer Germplasm. PHG39 was a parent in the development of 12 protected corn lines. The background of PHG39 contains in decreasing proportions B37, B14, B96 (Argentine Maiz Amargo 41.2504B), and Iodent (U.S. PVPA 9500208). Notable first cycle recombinant lines from PHG39 are PHP38, PHR61, PHT11, and PHW52. These C1 lines are considered commercially significant because of the large number of reference hits in the U.S. Patent database (Table 3) and/or recombination events in the PD (Table 4). Significant second cycle recombinant lines of PHG39 include PHBW8, PHHB9, PHRE1, and PH07D. The Maiz Amargo lineage was perpetuated through the C1 derivative PHP38 that was a parent of 11 C2 lines and the C2 line PHHB9 that was the parent of 12 C3 corn lines (Table 4). Many Maiz Amargo derived lines were ultimately either directly or indirectly recombined with B73 and this facilitated a significant introgression of B73 concurrently with Maiz Amargo into Pioneer Hi-Bred germplasm. In fact, approximately 35% of Pioneer's U.S. central Corn Belt hybrids during this era were of Stiff Stalk (BSSS) background (Smith et al., 2004). Although the presence of Maiz Amargo is predominantly within Pioneer Hi-Bred it may have been serendipitously introduced into other proprietary germplasm sources through selfing and recombination of Pioneer Hi-Bred commercial hybrids or through using public lines such as B64, B68, or B96. However, the lineages of this era did not indicate a significant introduction of Maiz Amargo outside of Pioneer Hi-Bred through recombination of public lines. The U.S. PVPA protection of PHG39 has expired and the line is readily available for freedom-to-operate use.

Stiff Stalk Background

During the period covered by this study, improvement of Stiff Stalk inbreds was achieved largely through

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recombination either directly with the C0 inbred B73, its C1 derivatives DKPB80, LH74, LH119, LH132, LH146, LH202, LH206, PHG86, and PHW52, or its C2 derivatives DKFBLL, DK2FACC, LH194, LH195, LH198, LH200, LH227, PHBW8, PHHB9, and SGH8431. The public founder line B73 was universally recombined within all proprietary programs to develop 33 protected C1 corn lines during this period. Therefore the lineage of most present day Stiff Stalk lines traces back to B73 (Fig. 1). The Stiff Stalk line DKFBLL was a parent of 22 new corn lines and played a key role in Dekalb Genetics Stiff Stalk germplasm. Early maturity Stiff Stalks were derived from recombination of the C0 B14 founder lines A632, A662, CB59G (Cornelius Hybrid Company), and CM105. Many of the B14 derivatives were recombined with B73 derived Stiff Stalks in subsequent cycles such as in the derivation of LH74 and LH202. Inbred lines derived directly from the B37 include LH1 and PHB47 and no instances in later cycles of recombination were found that preserved the B37 lineage (Fig. 1). The lineages of Stiff Stalks (B14, B37, and B73) are commingled as shown by recombination of B73 lineages with B37 and B14 derived lines. Presumably, the loss of purebred B14 and B37 lines is because of agronomic performance that was inferior to B73.

Breeding Methodology

Selfing in two-parent hybrid populations followed by pedigree selection was used in 77% of the 685 derivations in PD (Table 6). In most cases, two-parent inbred populations involved the recycling of elite, often related, inbred lines. Among proprietary breeding programs there were differences in magnitude of two-parent population use. Pioneer Hi-Bred used 90% two-parent populations, but Holden's and Syngenta used only approximately 50% two-parent populations (Table 5). Two-parent backcross one populations, followed by three-parent, and commercial hybrid are the next most common types of populations used in inbred development. Using commercial hybrids as germplasm was prevalent within Syngenta, Dekalb, and Holden's. Synthetics or Open Pollinated varieties either used separately or crossed to inbred(s) were rarely used.

PVPA or patent protected lines are commercially elite lines that warranted protection and their derivations are primarily found to be from the recycling of elite lines. Of course, for every line protected, there were hundreds if not thousands of lines developed and evaluated that failed during evaluation and consequently were not protected. For these failures, the type of recombinant breeding methods or germplasm is not known.

Pioneer Hi-Bred during the period of this study was a self-sustaining closed system using only its own germplasm and a very small number of public lines. The only public line Pioneer used more than once was B73, which was used in the development of 7 inbred lines. During this era, Holden's Foundation Seeds and Syngenta (Syngenta, Novartis, and Northrup King) used public inbreds in the derivation of nearly one fourth of their new inbred lines. Frequently used public lines in Holden's populations were B73 (10 times), Mo17 (9), CM105 (5), A662 (2), A665 (2), B84 (2), H99 (2), and ND246 (2). For Syngenta, frequently used public inbreds in line development are B73 (7), W117 (4), B37 (3), Mo17 (3), and B14 (2). Dekalb Genetics primarily used the two public Stiff Stalks B73 (9) and A634 (4) in their successful inbred line development projects. Overall, B73 and Mo17 were the public inbred lines used most extensively in line development.

Table 6. Types of recombinant populations used in developed of corn inbred lines from 1980 to 2004.

	Pioneer Hi-Bred Int.		Holden's Foundation		Dekalb Genetics		Syngenta/Novartis		Combined Average	
Population†	No. lines‡	%§	No. lines	%	No. lines	%	No. lines	%	No. lines	%
Two-parent	303	90	73	54	126	79	26	47	528	77
BC1 (2 inbreds)	17	5	17	13	18	11	11	20	63	9
BC2+ (2 inbreds)	4	1	6	4	1	1	0	0	11	2
Three-parent	7	2	16	12	5	3	3	5	31	5
Four or more different parents	0	0	10	7	1	1	4	7	15	2
Synthetic	2	1	1	1	1	1	0	0	4	1
Synthetic × inbred	3	1	5	4	1	1	3	5	12	2
Commercial Hybrid	0	0	6	4	7	4	8	15	21	3
Total	336	100	134	100	160	100	55	100	685	100
Germplasm source¶										
Public	14 of 336	4	34 of 134	25	12 of 160	8	15 of 55	27	75 of 685	11
Pioneer Hi-Bred	333 of 336	99	13 of 134	10	31 of 160	19	12 of 55	22	389 of 685	57
Holden's Foundation	0		111 of 134	83	18 of 160	11	12 of 55	22	141 of 685	21
Dekalb Genetics	0		0		145 of 160	91	0		145 of 685	21
Syngenta/Novartis	0		0		0		35 of 55	64	35 of 685	5

† Population types: two-parent, inbred A × inbred B; backcross one, (A × B) × B; backcross two or more, [(A × B) × B] × B; three-parent (A × B) × C; four-parent or more (A × B) × (C × D); synthetic or broad base population; synthetic or broad base population crossed to inbred(s); and commercial hybrid. If commercial hybrid was crossed to an inbred corn line it was considered a three-parent population.

‡ Number of lines derived from each respective population type.

§ Percentage of total published pedigrees derived from each respective population.

¶ Population composition shows representation of public, Pioneer Hi-Bred, Holden's Foundation, Dekalb Genetics, and Syngenta (including Novartis, Northrup King, and Ciba) germplasm. Germplasm source used was inbred corn lines, except for Pioneer Hi-Bred germplasm which used as corn inbred lines in Pioneer's breeding program, but was used in the form of Pioneer Hi-Bred commercial hybrids in Dekalb Genetics, Holden's Foundation Seeds, and Syngenta breeding programs.

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Examination of the PD for the role of public lines in development of new inbreds from 1980 through 2004 shows 45% during 1980 to 1988 (dates are the years for PVPA filing), 10% from 1989 to 1996, and 2% from 1997 to 2004 of new lines having public inbred parent(s). Thus the number of new lines derived from public inbred parentage decreased from nearly half during the first third of this era to a minimal 2% during the last third of this era. Of the 55 elite public inbred lines of the late 1970s identified by Smith et al. (1985), only 11 were used more than once and only two (B73 and Mo17) were used more than 10 times in the derivations of the 685 lines in the PD. The role of these public lines was most significant at the beginning of this era (1980s) and quickly diminished in the 1990s. During the transition of decreased use of public inbreds in new inbred development projects, the use of Holden's Foundation inbred lines as a key source of germplasm was common in Dekalb, Syngenta, and nearly all other commercial seed companies, except for Pioneer Hi-Bred.

Another major source of germplasm used in development of new lines during this era for Holden's Foundation, Dekalb Genetics, Syngenta, and others was recombination of Pioneer Hi-Bred commercial hybrids. They were used either by direct selfing or by crossing the Pioneer commercial hybrid to inbred parents before selfing and selection. In a few cases, as noted in the pedigree derivation of Dekalb inbred DKRDBQ2, a Pioneer Hi-Bred inbred is stated as being used rather than the actual F1 commercial hybrid in development of a new line (U.S. Patent 6037,531). Pioneer hybrids used most often in inbred development were 3737 (used in eight new inbred line developments), 3394 (5), 3378 (5), 3901 (4), 3535 (2), and 3475 (2). The use of Pioneer commercial hybrids as germplasm constituted 8% of new lines (non–Pioneer Hi-Bred lines) developed from 1980 through 1988 (dates are the years for PVPA filing), 22% of new lines from 1989 through 1996, and 10% of new lines from 1997 through 2004. The decrease in the third period is most likely a result of restrictions from the onset of U.S. Patent protection of both corn hybrids and inbreds.

CONCLUSIONS

Review of the pedigree derivations in this study suggests that plant breeders have been most successful in developing new products when they recombine the most elite material available. The propensity of breeders to work elite related material in recycling of inbred lines may over the long-term decrease genetic diversity. During the years of this study new diversity, within particular companies, emerged from exotic (Argentine Maiz Amargo) or diverse (Commercial Hybrid derived that contain multiple backgrounds in the hybrid formula) sources rather than from recycling closely related inbred lines.

During the period evaluated, proprietary corn inbred development programs have become closed systems due to the diminishing contribution of public inbreds in new inbred development projects. Intellectual property protection through U.S. Patent and U.S. PVPA has further restricted germplasm access. However, over time, patents and/or PVPA certificates expire and previously protected germplasm becomes available for general use Protection for some lines already has expired and the lines are presently available with no restrictions: LH123 (Pioneer 3535 background); LH82 (Pioneer 3558 background); and PHG39 and PHG86 (Maiz Amargo background). In addition, the Iodent lines PH207, PHG29, and PHG50; Oh07-Midland lines PHG35, PHG84, and PHZ51; Oh43 line PHG47; Lancaster line LH51; and Stiff Stalk lines LH74, LH119, LH132, PHB09, PHB47, and PHJ40 have had their protection expire and are publicly available. Seed of PVPA protected lines is available from the North Central Regional Plant Introduction Station in Ames, IA, and seed of U.S. patented lines is available from the American Type Culture Collection in Manassas, VA. Hopefully, results from this study will assist corn breeders in understanding this germplasm and provide insight into its effective use in developing new corn inbreds. These previously protected lines may be a useful source of new germplasm, but the caveat is that these lines are antiquated by four cycles of recombination and selection. The challenge to breeders who have not previously had access to these lines is to find new ways to use this germplasm to generate unique germplasm that will within a cycle or two of recombination and selection create competitive, genetically diverse, commercially successful hybrids.

Although access to this germplasm provides new genetic resources to the companies to whom access was previously not permitted, it does not increase diversity of the total corn germplasm pool. We suggest two critical issues exist which need to be addressed to enhance diversity of corn germplasm. First, to continue to make gains in performance and diversity corn germplasm needs to be broadened through concerted efforts of both private and public research programs. Fortunately, such an effort is underway through the Germplasm Enhancement for Maize (GEM) program (Pollak, 2003). This program is a partnership of government and private researchers to increase diversity by identifying exotic corn germplasm and adapting it by crossing it with adapted elite private corn germplasm. Second, a measure of the diversity currently available to corn producers in the USA is needed. With the growing availability of formerly protected proprietary inbred corn lines, a molecular marker survey of those lines and current dent corn hybrids, done by a public agency or disinterested third party, could provide a measure of current genetic diversity and of shifts in diversity since the beginning of protection of lines. Such a survey might also be useful in identifying genomic regions in today's germplasm that have been conserved from key progenitor lines through multiple cycles of recombination and selection. These regions may contribute to increased performance stability and be valuable for use in future marker assisted selection projects.

ACKNOWLEDGMENTS

We wish to thank Robert Lambert and Richard Johnson for reviewing this manuscript and their suggestions for its improvement and Dennis Butler for assistance with our literature

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search. The assistance of Janice Strachan at the Plant Variety Protection Office for facilitating and providing copies of corn inbred PVPs is greatly appreciated. We thank the Roy J. Carver Biotechnology Center of the University of Illinois at Urbana-Champaign for financing the publication of this research.

REFERENCES

Anonymous. 2003. Genetic handbook. 30th ed. MBS Genetics, LLC., Story City, IA.

Darrah, L.L., and M.S. Zuber. 1986. 1985 United States farm maize germplasm base and commercial breeding strategies. Crop Sci. 26:1109–1113.

Fairley, P. 1998. Let the bidding begin. Chem. Week 160(7):9.

Fritsch, P. 1997. Monsanto to buy seller of corn seed. Wall Street Journal 7 Jan. 1997; A:3.

Gerdes, J.T., C.F. Behr, J.G. Coors, and W.F. Tracy. 1993. Compilation of North American maize breeding germplasm. CSSA, Madison, WI.

Gethi, J.G., J.A. Labate, K.R. Lamkey, M.E. Smith, and S. Kresovich. 2002. SSR variation in important U.S. maize inbred lines. Crop Sci. 42:951–957.

Henderson, C.B. 1983. Maize research and breeders manual. No. IX (Suppl.). Illinois Foundation Seeds, Champaign, IL.

Janis, M.D., and J.P. Kesan. 2001. Designing an optimal intellectual property system for plants: A U.S. Supreme Court debate. Nat. Biotechnol. 19:981–983.

Lu, H., and R. Bernardo. 2001. Molecular marker diversity among current and historical maize inbreds. Theor. Appl. Genet. 103: 613–617.

Pollak, L.M. 2003. The history and success of the public-private project on Germplasm Enhancement of Maize (GEM). Adv. Agron. 78:45–87.

Smith, J.S.C. 1988. Diversity of United States hybrid maize germplasm; isozymic and chromatographic evidence. Crop Sci. 28:63–69.

Smith, J.S.C., E.C.L. Chin, H. Shu, O.S. Smith, S.J. Wall, M.L. Senior, S.E. Mitchell, S. Kresovich, and J. Ziegle. 1997. An evaluation of the utility of SSR loci as molecular markers in maize (*Zea mays* L.): Comparisons with data from RFLPs and pedigree. Theor. Appl. Genet. 95:163–173.

Smith, J.S.C., D.N. Duvick, O.S. Smith, M. Cooper, and L. Feng. 2004. Changes in pedigree backgrounds of Pioneer brand maize hybrids widely grown from 1930 to 1999. Crop Sci. 44:1935–1946.

Smith, J.S.C., M.M. Goodman, and C.W. Stuber. 1985. Genetic variability within U.S. maize germplasm. II. Widely-used inbred lines 1970 to 1979. Crop Sci. 25:681–685.

Smith, J.S.C., and O.S. Smith. 1987. Associations among inbred lines of maize using electrophoretic, chromatographic, and pedigree data. 1. Multivariate and cluster analysis of data from 'Lancaster' Sure Crop derived lines. Theor. Appl. Genet. 73:654–664.

Smith, J.S.C., and O.S. Smith. 1989. The description and assessment of distance between inbred lines of maize: I. The use of morphological traits as descriptors. Maydica 34:141–150.

Smith, J.S.C., and O.S. Smith. 1991. Restriction fragment length polymorphisms can differentiate among U.S. maize hybrids. Crop Sci. 31:893–899.

Tracy, W.F., and M.A. Chandler. 2005. The historical and biological bases of the concept of heterotic patterns in 'Corn Belt' maize. Forty-First Annu. Illinois Corn Breeders School, Urbana, IL. University of Illinois, Urbana-Champaign.

Troyer, A.F. 1999. Background of U.S. hybrid corn. Crop Sci. 39: 601–626.

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