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Genealogy of Contemporary North American Lettuce

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Abstract. **To determine the genealogy of cultivated lettuce in the United States, a survey was conducted on the pedigree of proprietary and publicly developed lettuce cultivars registered from 1970 through 2004. This was facilitated through information furnished by the U.S. Plant Variety Protection Act, U.S. patent, and journal publication of registered cultivars. In total, there were 328 registered cultivars of which 90.5% (297 cultivars) were from proprietary and 9.5% (31) from public breeding programs. The lettuce cultivars of this era are 61.6% crisphead, 19.5% loose leaf, 13.7% cos/romaine, 4.9% butterhead, and 0.3% latin lettuce types. To facilitate an understanding of current U.S. lettuce germplasm, the most recombined and putatively elite cultivars in the development of new cultivars were identified. The 10 most recombined cultivars were 'Salinas' (parent of 28 new cultivars), 'Calmar' (27), 'Vanguard' (22), 'Vanguard 75' (13), 'Vanmax' (13), 'Prize Head' (12), 'Parris Island Cos' (12), 'Empire' (11), 'Great Lakes 659' (11), and 'Red Coach 74' (10). The types of breeding populations used for new cultivar development during this era were two-parent (52% of new cultivars), within cultivar selection (31%), three-parent (7%), backcross two or greater (5%), backcross one (2%), four or more parents (2%), and interspecific cross (1%).**

Lettuce (*Lactuca sativa*) is the most commonly consumed of fruits or vegetables in the United States as determined by a mid-1990s survey (Hu et al., 2005; Johnston et al., 2000). Lettuce is a contributor of dietary vitamins A and C as well as lesser amounts fiber, iron, and calcium (Thompson, 1951; USDA, 2005). Lettuce grown in the United States is crisphead, cos/romaine, loose leaf (leaf), and butterhead types (Cook, 2002; Ryder, 1986a; Whitaker, 1974). The USDA National Agricultural Statistics Service estimates that crisphead (74,907 ha), romaine (34,196 ha), and leaf lettuce (25,778 ha) accounted for the 134,881 ha of U.S. commercial lettuce production in 2005 (Anonymous, 2006). Proportionately, crisphead lettuce was 56%, romaine 25%, and leaf lettuce 10% of U.S. lettuce production area. A 5-year trend (2000 through 2005) shows romaine lettuce production hectarage increasing 66% and leaf lettuce increasing by 26%, whereas crisphead lettuce production has remained relatively constant. For example, U.S. lettuce production was 90% crisphead in 1986, 80% in 1994, and 56% in 2005 (Anonymous, 2006; Ryder, 1986a; Waycott and Ryder, 1994). Contributing to the increasing use of romaine lettuce is the popularity of the Caesar salad and of precut bagged salads in grocery stores (Dunne, 2005; Ryder, 1986a). Home gardeners in the United States commonly grow leaf, butterhead, and romaine lettuce but have less success with the environmentally sensitive crisphead varieties. Worldwide, other types of lettuce are also popular, including latin and stem lettuce (Ryder, 1986a; Thompson, 1951).

Public and private breeding programs have worked diligently to improve lettuce through recombination and selection focusing on cultivar improvement for yield, environmental adaptability, quality, disease and insect resistance. Improvement of lettuce has largely been accomplished from recombination of cultivars within *L. sativa* but on occasion from recombination with related noncultivated wild *Lactuca* species such as *L. serriola*, *L. saligna*, and *L. virosa* (Lebeda et al., 2004; Whitaker and Provvidenti, 1983). The proprietary breeding efforts in lettuce cultivar development are increasing. Legal protection of proprietary cultivars is accomplished by registration either through the Plant Variety Protection Act (PVPA) enacted in 1970 or through utility patents of seed-propagated plants from the U.S. Patent and Trademark Office after 1985 (Janis and Kesan, 2001). Both PVPA and patent offer protection that prevents direct commercial use of a registered cultivar without permission of the originator (Mikel, 2006). Whereas U.S. patents prevent the use of registered material for breeding without assignee permission, PVPA registration does allow the use of protected material for breeding. Because PVPA and patent registration documentation is in the public domain, pedigrees and characteristics of these proprietary lettuce cultivars are publicly available.

The objective of this study was to understand contemporary North American lettuce germplasm by surveying public and proprietary cultivars of 1970 to 2004 by: 1) identifying the most elite progenitor cultivars by tabulating the cumulative number of times each cultivar has been used as a parent in breeding a new registered cultivar; 2) tracing the lineage and origin of these elite cultivars; and 3) summarizing the breeding methodology used in the development of the registered varieties of this era.

Materials and Methods

For the era of this study (1970 to 2004), the most important progenitor cultivars were determined for the 328 registered lettuce cultivars surveyed. This was accomplished by tabulating the cumulative number of times each parental cultivar was used in the development of a newly registered cultivar. U.S. PVPA, U.S. Patent, or publication in *HortScience* provided the pedigrees of the lines. Lettuce breeders are extremely knowledgeable regarding the performance of lettuce cultivars and devote much of their breeding effort into recombining those cultivars they determine to be most elite. Thus, elite progenitor or founder lettuce cultivars were identified as those lines that breeders have recombined the most frequently in the development of new registered commercial cultivars. In addition, lettuce type (crisphead, romaine/cos, leaf, or butterhead), year of release, and originator were determined for each progenitor line.

The categories of breeding populations from which the 328 lettuce varieties of this era were developed consisted of: A) within cultivar selection; B) two-parent "cultivar A × cultivar B"; C) three-parent "(A × B) × C"; D) four or more parents; E) backcross one "(A × B) × B"; F) backcross two or greater; and G) cross involving other *Lactuca* species (*L. serriola*, *L. virosa*, *L. saligna*). The category of breeding population was determined for each of the registered lettuce cultivars. Breeding population formulation consists of cumulative recombination before the onset of selfing.

An overall summary of the relationship of the previously identified elite lettuce cultivars is shown graphically through tracing the lineage of each cultivar for as many generations as possible (Fig. 1). The progenitor cultivars identified earlier by recombination frequency are shown as shaded boxes. Complex crosses used in the development of new cultivars are simplified as much as possible. Furthermore, uses of strain and plant numbers during inbreeding were omitted unless

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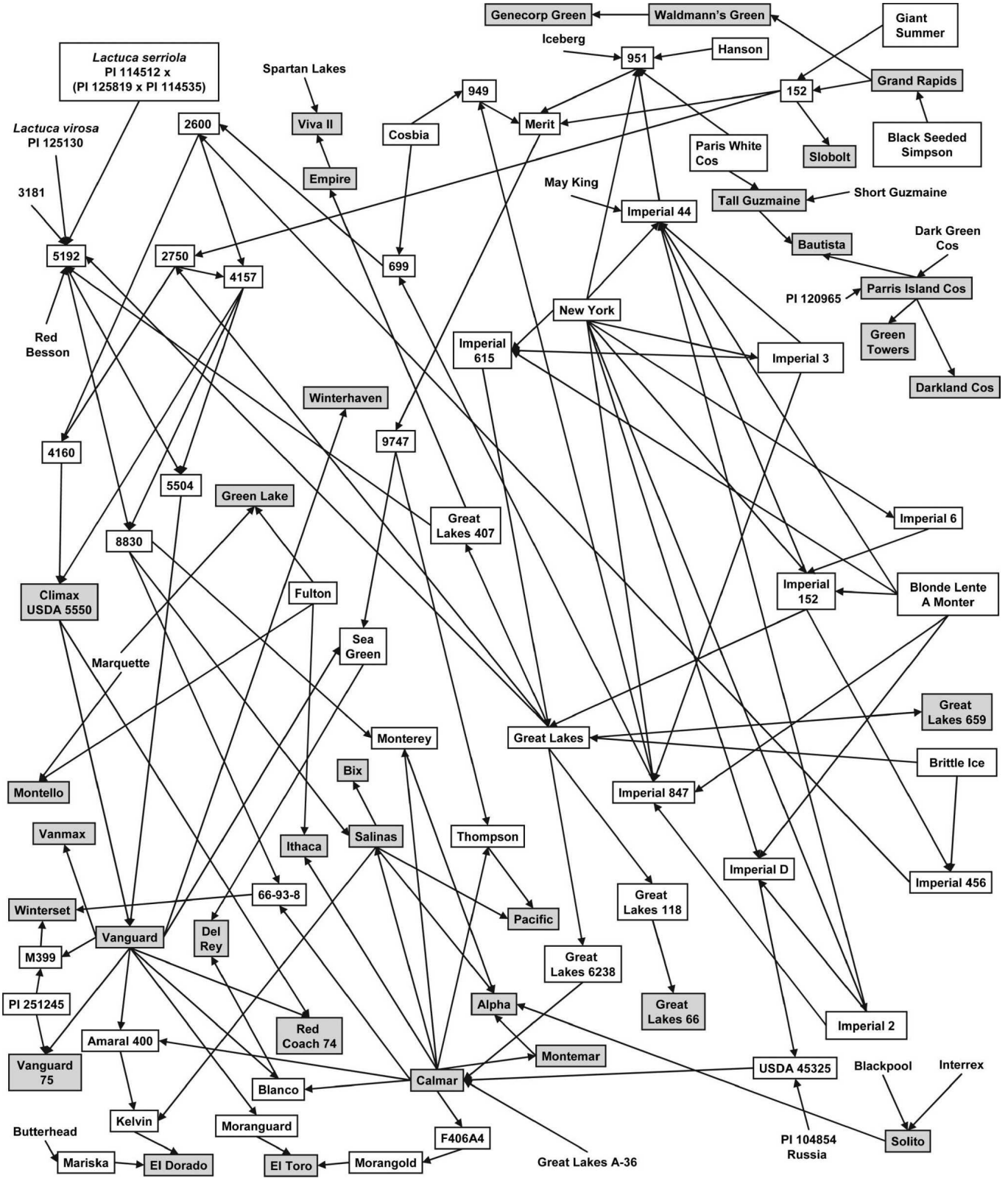

Fig. 1. This figure illustrates the lineage of each lettuce cultivar by descent as depicted by arrows originating from parent and pointing to their progeny. Derivations are furnished in Table 2 for those varieties depicted in shaded boxes. Breeding lines '152', '699', '949', '951', '2600', '2750', '4157', '4160', '5504', and '5192' and cultivar 'Merit' have their pedigree derivation shown in Thompson and Ryder (1961). Derivation of 'Imperial D', 'Imperial 2', 'Imperial 3', 'Imperial 6', 'Imperial 44', 'Imperial 152', 'Imperial 615', and 'Imperial 847' are described by Jagger et al. (1941). References are as shown for the pedigree derivation of 'Winterset', 'M399', and '66-93-8' (Ryder, 1986b); 'Salinas' and '8830' (Ryder, 1979a); 'Vanguard 75' (Ryder 1979b); 'Great Lakes' and 'Imperial 456' (Bohn and Whitaker, 1951); 'Pacific', 'Thompson', and '9747' (Ryder and Robinson, 1991); 'Sea Green' (Ryder, 1981); 'USDA 45325' (Compositdb, 2006); 'Great Lakes 407' (Anonymous, 1956); 'Great Lakes 118' (Anonymous, 1958); 'Great Lakes 6238' (Anonymous, 1965); and 'Monterey' (Lower, 1973). Pedigree derivation are from Plant Variety Protection Act (PVPA) certificates for 'Morangold' (PVPA 7600039), 'F406A4' (PVPA 7600039 and PVPA 7400014), 'Blanco' (PVPA 7800062), 'Kelvin' (PVPA 8700182), 'Amaral 400' (PVPA 7800083), and 'Mariska' (PVPA 9300014).

information is gained from their use. Cultivar names are used rather than experimental and breeding line designations whenever possible. For example, if a breeding line is used that is later renamed with a cultivar name designation, then its cultivar name was used for clarity.

Results and Discussion

The pedigrees of a total of 328 surveyed lettuce cultivars were registered and made public from 1970 through 2004 through U.S. PVPA, U.S. Patent, or publication in *HortScience*. There is frequently a hiatus of 2 to 3 years from the date of application for PVPA or patent registration until completion of review. During this time, the application is not publicly available. Overall, 90.5% and 9.5% of lettuce cultivars of this era were from proprietary and public programs, respectively (Table 1). Two thirds of the cultivars were developed or acquired by the following: Seminis Vegetable Seeds 32% (106 cultivars), Harris Moran 10% (33), Progeny Advanced Genetic 6% (21), Paragon Seed 6% (20), U.S. Department of Agriculture (USDA) 5% (17), Enza Zaden Beheer B.V. 4% (13), and Rijk Zwaan 4% (13). Format of lettuce cultivar registration is through U.S. PVPA (294 cultivars), *HortScience* (30), and U.S. patent (9). All cultivars from proprietary programs were registered through U.S. Patent or PVPA. Five proprietary cultivars were double-protected by both U.S. Patent and U.S. PVPA. Publicly developed cultivars, either academic or USDA, were described in their publication of release in *HortScience* but were not registered by PVPA or patent. During the first half of this era (1970 to 1986), proportionately more cultivars were registered by public programs than during the second half (1987 to 2004), 18% versus 6%, respectively. Nonetheless, despite their small numbers, the publicly developed lines played a pivotal role in the development of today's germplasm base. Apparently, commercial growers tended to rely on publicly developed lettuce cultivars as opposed to varieties developed independently by the private sector both for production and breeding of new cultivars (Dunne, 2005). For example, in the United States, the most produced lettuce of the 1960s and 1970s were the crisphead varieties 'Calmar' and 'Vanguard' that were developed at the University of California and USDA, respectively (Ryder, 1991). These two varieties were later replaced with the USDA developed cultivar 'Salinas', which quickly became the most produced lettuce cultivar of the 1980s (Ryder, 1979a). This validates the criterion described herein in which 'Salinas', 'Calmar', and 'Vanguard' were also determined to be elite progenitor cultivars (Table 2). Of the progenitor cultivars in Table 2, breeders at public institutions developed 13 and proprietary research programs developed 18 cultivars. Ten of these progenitors of today's lettuce germplasm were developed before 1960.

Nearly two thirds of new cultivars from this era were crisphead (61.6%) followed by leaf (19.5%), romaine (13.7%), butterhead (4.9%), and latin (0.3%) lettuce types. Concomitant with increasing use of leaf and romaine lettuce was an increase in the development of these types. The proportion of new leaf lettuce cultivars increased from 13% to 22%, and romaine types increased from 3% to 18% of new cultivars between the first half (1970 to 1986) and the second half (1987 to 2004) of this era, respectively (Table 1).

A generalization of the development of today's crisphead lettuce varieties features essentially three cycles of recombination: 'New York' type (Cycle 0), 'Imperial' type (C1), and 'Great Lakes' type (C2), leading to the crisphead varieties of today (C3). The development of the 'Imperial' type (C1) was primarily through recombination of 'New York' with 'Blonde Lente A Monter' or from selection within 'New York' for improved disease resistance. The 'Imperial' cultivars exhibited greatly improved resistance to the disease brown blight and were better adapted to the southwestern United States (Whitaker, 1974). The second cycle resulted in 'Great Lakes' type varieties primarily from recombination of 'Imperial' type cultivars with 'Brittle Ice'. 'Great Lakes' cultivars were stress-tolerant, resistant to the physiological disorder of tipburn, and widely adapted (Whitaker, 1974). Within cultivar selection was common within 'Great Lakes', which optimized the environmental adaptation of 'Great Lakes' and created many commercial varieties such as 'Great Lakes A-36', 'Great Lakes 66', 'Great Lakes 118', 'Great Lakes 407', 'Great Lakes 428', 'Great Lakes 6238', and 'Pacific Lakes'.

'Salinas', 'Calmar', 'Vanguard', 'Vanguard 75', and 'Vanmax' are the most prevalent progenitors in the background of today's crisphead lettuce varieties (Table 2). The latter three are close 'Vanguard' types derived through either selection within 'Vanguard' ('Vanmax') or backcross isoline conversion of 'Vanguard' ('Vanguard 75'). The varieties 'Salinas', 'Vanguard', 'Vanguard 75', and 'Vanmax' have the common progenitor PI 125130 (*L. virosa*). The original objective for the introgression of *L. virosa* into crisphead lettuce (*L. sativa*) was to breed for robust root system and decreased leaf drop. The genealogy of current crisphead cultivars can be split into two groups. The first group is comprised of cultivars developed from *L. virosa* through the breeding line '5192' (PI 125130, *L. virosa* derived) from either direct progeny of '5192', through the breeding line '8830' (lineage of cultivars 'Salinas', 'Winterset', and 'Monterey'), or by way of the breeding line '5504' (lineage of cultivars 'Vanguard', 'Vanguard 75', 'Vanmax', and 'Red Coach 74'). The second group is not *L. virosa* derived and consists of 'Calmar' and its progeny 'Ithaca' and 'Montemar'. 'Calmar' is a remarkable cultivar of 'Great Lakes' group, which remained the industry standard for 15 years since its release in 1960. 'Salinas' resulted from recombination between these two groups. Also not *L. virosa* derived are 'Montello', 'Green Lake', 'Empire', and 'Viva II' (Fig. 1). 'Montello' and 'Green Lake' are recombinant lines developed from the cultivar 'Fulton'. Cultivars 'Empire' and 'Viva II' are in the 'Great Lakes 407' derived lineage.

Other interspecies crosses with *L. sativa* for new cultivar development include crosses with *L. saligna* and *L. serriola*. The cultivar 'Salad Bibb' was developed through a series of crosses with *L. saligna* with several *L. sativa* cultivars (PVPA 8500060). The cultivars 'Calrey' and 'Calrico' were derived from crossing *L. sativa* cultivars with *L. serriola* (PI 91532), a source of downy mildew resistance (Wehner, 1999).

Lettuce breeders have increased genetic diversity and achieved disease resistance through breeding cultivated lettuce with noncultivated or wild lettuce types. Recombination of 'Great Lakes' varieties with PI 104854, a downy mildew-resistant Russian wild-type lettuce, resulted in the development of 'Calmar'. Wild Egyptian lettuce (PI 251245) was used to introduce lettuce mosaic virus (LMV) resistance in 'Vanguard' by backcross breeding resulting in 'Vanguard 75' and later through recombination additional lettuce mosaic-resistant varieties. Breeding of cultivated lettuce with other *Lactuca* species and wild-type lettuce germplasm has significantly contributed to the genetic makeup of today's lettuce varieties.

Leaf type lettuce cultivars were recombined primarily with each other. The most recombined leaf type lettuce is 'Prize Head' followed by 'Waldmann's Green' (Table 2). The loose leaf lettuce 'Grand Rapids' has contributed to the development of today's crisphead cultivars through the presence of a small proportion of 'Grand Rapids' in the

Table 1. Type and origin of registered U.S. lettuce cultivars.

	1970 to 1986		1987 to 2004		Overall	
Lettuce type	Number	Percent	Number	Percent	Number	Percent
Crisphead	72	80	130	55	202	61.6
Loose Leaf	12	13	52	22	64	19.5
Cos/Romaine	3	3	42	18	45	13.7
Butterhead	3	3	13	5	16	4.9
Latin	0	0	1	0	1	0.3
Total	90		238		328	
Developed by						
Proprietary program	74	82	223	94	297	90.5
Public program	16	18	15	6	31	9.5
Total	90		238		328	

Table 2. Most recombined lettuce cultivars in development of U.S. registered lettuce cultivars 1970 to 2004.

Cultivar	Pedigree derivation[z]	Type	Year of release	Citation	Originator[y]	Recombinant frequency[x]
Salinas	'Calmar' × '8830'	Crisphead	1975	Ryder, 1979a	USDA	28
Calmar	'Great Lakes A-36' × ('Great Lakes 6238' × USDA '45325')	Crisphead	1960	Anonymous, 1965	Univ. of Calif.	27
Vanguard	'5550' × '5504'	Crisphead	1958	Thompson and Ryder, 1961	USDA	22
Vanguard 75	'Vanguard' BC6 × PI 251245	Crisphead	1975	Ryder, 1979b	USDA	13
Vanmax	'Vanguard' Selection	Crisphead	1971	PVPA 7100096	Harris Moran	13
Prize Head	Unknown	Loose leaf	prior 1870	Compositdb, 2006		12
Parris Island Cos	PI 120965 × 'Dark Green'	Cos	1951	Compositdb, 2006	S.C. AES	12
Empire	Complex Hybrid × 'Great Lakes 407'	Crisphead	1957	Anonymous, 1960	USDA	11
Great Lakes 659	'Great Lakes' selection	Crisphead	1944	Compositdb, 2006	Dessert Seed Co.	11
Red Coach 74	'Climax' × 'Vanguard'	Crisphead	1974	PVPA 7400010	Koninklijke Zaaizaadbedrijven	10
Waldmann's Green	'Grand Rapids' Selection	Loose leaf	1958	Compositdb, 2006	John Waldmann	8
Darkland Cos	'Parris Island Cos' selection	Cos	1990	PVPA 9000137	Central Valley Seeds	8
Climax	'4157' × '4160'	Crisphead	1958	Thompson and Ryder, 1961	USDA	7
Ithaca	'Calmar' × 'Fulton'	Crisphead	1969	Compositdb, 2006	New York AES	7
El Toro	'Morangold' × 'Moranguard'	Crisphead	1982	PVPA 8200027	Harris Moran	7
Tall Guzmaine	'Short Guzmaine' × 'Paris White'	Cos		Compositdb, 2006		7
Montello	'Marquette' × 'Fulton'	Crisphead	1978	Compositdb, 2006	Univ. of Wis.	6
Bautista	'Parris Island Cos' × 'Tall Guzmaine'	Cos	1991	PVPA 9100259	Royal Sluis	5
El Dorado	'Kelvin' BC4 × 'Mariska'	Crisphead	1993	PVPA 9300014	Royal Sluis	5
Great Lakes 66	'Great Lakes 118' selection	Crisphead	1953	Compositdb, 2006; Anonymous, 1958	Associated Seed Growers	5
Pacific	'Thompson' × 'Salinas'	Crisphead	1986	Ryder and Robinson, 1991	USDA	5
Slobolt	'152' Selection	Loose leaf	1944	Thompson and Ryder, 1961	USDA	5
Winterhaven	'Vanguard' Selection	Crisphead	1974	PVPA 7400015	Harnish-Brinker Seed	5
Green Towers	'Parris Island Cos' selection	Cos	1986	PVPA 8600135	Harris Moran	5
Alpha	[('Montemar' × 'Monterey') × 'Solito'] × 'Salinas' BC1	Crisphead	1990	PVPA 9000055	Harris Moran	4
Bix	'Salinas' Selection	Crisphead	1986	PVPA 8600110	Seminis Vegetable Seeds	4
Dark Lollo Rossa	Unknown	Loose leaf		Compositdb, 2006		4
Del Rey	'Blanco' × 'Sea Green'	Crisphead	1992	PVPA 9200023	Royal Sluis	4
Gallega	Unknown	Cos		Compositdb, 2006		4
Genecorp Green	'Waldmann's Green' selection	Loose leaf	1984	PVPA 8400060	Seminis Vegetable Seeds	4
Grand Rapids	'Black Seeded Simpson'	Loose leaf	prior 1890	Compositdb, 2006	Eugene Davis	4
Green Lake	'Marquette' × 'Fulton'	Crisphead	1978	Compositdb, 2006	Univ. of Wis.	4
Malibu	Unknown	Loose leaf		Compositdb, 2006		4
Montemar	'Calmar' Selection	Crisphead	1971	PVPA 7100092	Harris Moran	4
Solito	'Blackpool' × 'Interrex'	Butterhead	1970s	Center for Genetic Resources, 2006		4
Viva II	'Empire' × 'Spartan Lakes'	Crisphead	1980	PVPA 8000043	Koninklijke Zaaizaadbedrijven	4
Winterset	'66-93-8' × 'M399'	Crisphead	1984	Ryder, 1986b	USDA	4

[z]Abbreviations are as follows: plant introduction (PI) and backcross (BC) such that BC1 is backcross 1 and so forth.
[y]Originators are U.S. Dept. of Agriculture (USDA), University of California (Univ. of Calif.), Harris Moran, S.C. Agriculture Experiment Station (AES), Dessert Seed Company, Koninklijke Zaaizaadbedrijven, John Waldmann, Central Valley Seeds, New York Agriculture Experiment Station (AES), University of Wisconsin (Univ. of Wis.), Royal Sluis, Associated Seed Growers, Harnish-Brinker Seed, Seminis Vegetable Seeds, and Eugene Davis.
[x]Recombination frequency is the cumulative number of times a cultivar is used in the development of a registered cultivar of this era.
PVPA = Plant Variety Protection Act.

pedigree of many crisphead varieties (Fig. 1). Development of new romaine lettuce varieties was accomplished mainly by recombination of cultivars within the type. The key component of today's romaine germplasm is the highly recombined 'Parris Island Cos'. For butterhead lettuce types, 'Solito' is the most recombined. Butterhead lettuce has limited use in the United States as a result of its poor shipping quality, but does have a presence in seasonal local markets.

Of the 328 registered lettuce varieties from 1970 to the present, half were derived directly from two-parent, 7% were derived from three-parent, and 2% from populations with more than three parents (Table 3). Backcross breeding was used in the derivation of ≈7% of lettuce cultivars, most predominantly backcross four or greater isoline conversions of existing cultivars for specific insect or disease resistance. Interestingly, nearly one third of new varieties were derived from selection within existing lettuce varieties. Thompson and Ryder (1961) noted that the cultivar 'Vanguard' was released as an F4 line whose unfixed genetic variation enabled seedsmen to select and fix through inbreeding better-adapted cultivars. To exploit this residual variation, breeders and seedsmen partnered in selection within existing cultivars. Of the three most recombined lettuce cultivars 'Calmar', 'Salinas', and 'Vanguard', each had five, four, and three new cultivars developed directly from within cultivar selection, respectively. In contrast, for dent corn breeding populations during the same era, Mikel and Dudley (2006) reported that the use of two-parent populations predominated in the development of 75% of new corn lines. No registered corn inbreds were developed from selection within inbred lines.

Lettuce breeding involves simultaneous improvement of numerous characters. Efforts in the United States have predominantly been in the development of crisphead varieties, but

Table 3. Breeding methodology for lettuce cultivar development.

Breeding method[z]	Number[y]	Percent
Two-parent	171	52
Selection within cultivar	101	31
Three-parent	24	7
Backcross 2 or more	15	5
Multiparent (greater than three-parent)	8	2
Backcross 1	5	2
Cross involving other *Lactuca* species	4	1
Total	328	

[z]Breeding methodologies are within cultivar selection; two-parent "cultivar A × cultivar B"; selection within cultivar; three-parent "(A × B) × C"; backcross 2 or greater; multiparent with four or more parents; backcross 1 "(A × B) × B"; and cross involving other *Lactuca* species (*L. serriola*, *L. virosa*, *L. saligna*).

[y]Number of registered cultivars from 1970 through 2004.

increased consumer demand for romaine and leaf lettuce is shifting the focus to improvement of these types, primarily for shipping quality and environmental adaptability. Lettuce breeders have access to a tremendous amount of diversity for cultivar improvement. The Center for Genetic Resources (2006) lists 1390 accessions of lettuce (*L. sativa*), of which only 15% are crisphead, the rest being a conglomeration of romaine, leaf, latin, butterhead, and stalk types (Jansen et al., 2006). A large collection of lettuce cultivars, PIs, breeding lines, and genetic stocks are preserved at 5 locations in the U.S. (Anonymous, 2004). These resources offer valuable germplasm for improvement of all types of lettuce. Use of interspecific crosses of *L. sativa* with other related lettuce species from throughout the world has been integral in development of the elite lettuce varieties of today. Novel sources of genetic diversity will be required for lettuce breeders to effectively meet the future needs of cultivar improvement for disease and insect resistance, nutritional value, horticultural quality, and environmental adaptability. The U.S. consumer continues to develop new preferences for lettuce types other than crisphead and lettuce breeders must concomitantly change their product models to adapt.

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