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Pedigrees and genetic base of flax cultivars registered in Canada

Frank M. You, Scott D. Duguid, Irene Lam, Sylvie Cloutier, Khalid Y. Rashid, and Helen M. Booker

Abstract: Flax is an important oilseed crop with industrial, animal, and human nutrition uses. Breeding programs for linseed and fibre flax were initiated in Canada in the early 1900s. A total of 82 flax cultivars have been registered in Canada since 1910, including 24 cultivars introduced from foreign countries and 58 cultivars developed by Canadian breeders. This study collated pedigree data of Canadian flax cultivars and quantified their genetic base via pedigree analysis and coefficient of parentage (CP). A fairly high mean CP of 0.14 was observed between all registered cultivars; this value was even higher (0.23) when only the 46 cultivars released from 1981–2015 were considered. The registered cultivars traced back to 46 ancestors; 72% originated from foreign countries and contributed 83% of the genetic base of all cultivars, illustrating the dominant role played by foreign germplasm in the genetic improvement of Canadian flax. The top 11 ancestors contributed 70–93% of the genetic base of modern flax cultivars released in the last three decades and formed the core gene pool of Canadian flax cultivars. The genetic base of Canadian cultivars is relatively narrow, although it has gradually expanded, especially in the last two decades. Broadening the genetic base through the introduction of new exotic germplasm is needed to invigorate the gene pool of Canadian flax breeding programs.

Key words: flax, cultivar, pedigree, ancestor, genetic base, Canada.

Résumé : Le lin est un important oléagineux utilisé à des fins industrielles ainsi que pour l'alimentation humaine et animale. Les premiers programmes d'hybridation visant à accroître la production de graines et de fibres de cette culture remontent au début du vingtième siècle. Quatre-vingt-deux variétés de lin ont été homologuées au Canada depuis 1910, ce qui comprend 24 cultivars de l'étranger et 58 créés par des améliorateurs canadiens. Cette étude rassemble les données généalogiques sur les variétés canadiennes et en quantifie la base génétique d'après leur ascendance et leur coefficient de parenté (CP). Les auteurs ont relevé un CP moyen relativement élevé (0,14) entre les variétés homologuées; le CP est encore plus élevé (0,23) quand on ne tient compte que des 46 cultivars homologués entre 1981 et 2015. Les variétés homologuées ont 46 ancêtres. Soixante-douze pour cent ont pour origine des pays étrangers et représentent 83 % de la base génétique des cultivars, signe du très grand rôle que le matériel génétique exotique a joué dans l'amélioration du lin canadien. Les onze principaux ancêtres ont fourni de 70 à 93 % de la base génétique des variétés de lin contemporaines, homologuées au cours des trois dernières décennies, et constituent le principal réservoir de gènes des cultivars canadiens. Les variétés canadiennes de lin se caractérisent par une base génétique assez étroite, bien que celle-ci se soit graduellement élargie, surtout au cours

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Abbreviations: AAFC, Agricultural and Agri-Food Canada; ALA, α -linolenic acid; CDC, Crop Development Centre, University of Saskatchewan; CFIA, Canadian Food Inspection Agency; CP, coefficient of parentage; CPS, Crop Production Services, Saskatoon; CZBS, Cebeco Zaden Breeding Station in Lelystad, The Netherlands; GC, genetic contribution; GRIN, the Germplasm Resources Information Network; MAES, Minnesota Agricultural Experimental Station; MAGIC, multi-parent advanced generation intercross; MAS, marker-assisted selection; NDAES, North Dakota Agricultural Experiment Station; NDES, North Dakota Experiment Station; NLIRA, North Linen Industry Research Association, Ireland; PBRO, Plant Breeders' Rights Office; PBS-MANI, Plant Breeding Station of the Ministry of Agriculture for Northern Ireland; U of S, University of Saskatchewan; USDA-ARS, the United States Department of Agriculture, Agricultural Research Service.

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des vingt dernières années. L'élargissement de cette base par l'utilisation de germoplasme exotique est nécessaire pour vivifier le pool génétique des programmes canadiens d'amélioration de lin. [Traduit par la Rédaction]

Mots-clés : lin, cultivar, généalogie, ancêtre, base génétique, Canada.

Introduction

Flax (*Linum usitatissimum*) is an important oilseed and fibre crop with industrial uses and has proven benefits for animal nutrition and human health (Singh et al. 2011). Nearly every above-ground component of this crop can be utilized for industrial or food use. For example, oil obtained from the seeds is used in the production of paints, stains, coatings, and floorings, while the high nutritional value of seed constituents, such as alpha (α)-linolenic acid (ALA), lignan, protein, dietary fiber, and phenolic compounds make flax seed a valuable addition to food products (Oomah 2001; Duguid 2009; Flax Council of Canada 2015). Disease prevention and health benefits have been associated with flaxseed consumption; for example, Health Canada (2014) approved a claim that consumption of whole ground flaxseed reduces blood cholesterol levels in humans. For many centuries, flax fibers have been used to produce linen. While Europe mainly produces fiber flax for fabric manufacturing, Canada has been the largest global producer of linseed (oilseed flax) since 1994 (Flax Council of Canada 2015).

Flax was initially introduced to Canada in 1617 by Louis Hébert to New France (later the Province of Quebec) (Kenaschuk and Rowland 1995; Flax Council of Canada 2015). The market for linseed increased when the demand for industrial oil increased, particularly during the Second World War (Kenaschuk and Rowland 1995; Flax Council of Canada 2015). By the 1950s, flax products were distributed and utilized globally. This boom also marked the beginning of active flax breeding in Canada. Today, flax production in Canada is mainly concentrated in the Western provinces of Saskatchewan, Manitoba, and Alberta (Kenaschuk and Rowland 1995; Flax Council of Canada 2015).

The three major flax breeding programs in Western Canada are (i) the Agriculture and Agri-Food Canada (AAFC) program located at the Morden Research and Development Centre in Morden, Manitoba; (ii) the Crop Development Centre (CDC) program located at the University of Saskatchewan in Saskatoon, Saskatchewan; and (iii) the Saskatoon R and D facility of Crop Production Services Canada Inc. (CPS), previously known as the Viterra program, located at the Alberta Research Council site in Vegreville, Alberta (Duguid 2009; Flax Council of Canada 2015). Since 2000, CÉROM (Centre de recherche sur les grains), located in Saint-Mathieu-de-Beloeil in the province of Québec, has maintained a breeding program targeting flax for crop diversification (Flax Council of Canada 2015).

Canadian flax cultivars are usually developed for their oil quantity and quality. The goals vary among breeding programs but most aim to maximize grain yield while maintaining high seed oil (>45%) and ALA content (>50%), lower genetic susceptibility to diseases, increase lodging resistance, and shorten time to maturity (Duguid 2009; Hall et al. 2016; Flax Council of Canada 2015). Flax cultivar development is a continuing process using germplasm created by the cumulative efforts of flax breeders and researchers over many years. However, selection for improved genetic material can be attained only when useful genetic variation exists in the germplasm, requiring careful selection of parental lines with diverse genetic backgrounds for crossing to generate new genotypes with superior qualities (Hall et al. 2016).

Canadian flax breeding programs were initiated in the early 1900s, with flax cultivars released since 1910. We collated 82 flax cultivars registered in Canada between 1910 and 2015 and retrieved their pedigree information. Of these, 58 were developed by Canadian breeders and 24 are introductions from foreign countries that were registered for production in Canada (Table 1). A total of 6, 12, 18, and 23 cultivars were released from 1910–1950, 1951–1980, 1981–2000, and 2001–2015, respectively. Of the total registered cultivars, 72 are linseed, four (J.W.S., Liral Prince, Stormont Motley, and Weira) are fiber types, and six have uncertain end-uses.

In the early stages of Canadian flax breeding (especially before the 1960s), most registered cultivars were directly introduced from foreign countries (Table 1; Kenaschuk and Rowland 1995). The 24 cultivars directly introduced, field tested, and released for production in Canada between 1926 and 2000 are Winona (1926), Bison (1930), Buda (1930), J.W.S. (1930), Redwing (1934), Dutch White Blossom (1940), Liral Prince (1944), Viking (1945), Victory (1946), Dakota (1947), Sheyenne (1947), Valuta (1949), Stormont Motley (1949), Redwood (1951), Scorpion (1951), Cascade (1952), Marine (1952), B-5128 (1953), Norland (1955), Weira (1956), Arny (1961), Bolley (1964), Culbert (1978), and Taurus (2000) (Table 1). Cultivars developed in the early 1900s by Canadian breeders include Diadem (1910), Ottawa 770B (1910), Ottawa 829C (1910), and Novelty (1910).

In 1890, flax wilt was recognized as a problem in production areas of Canada (Kenaschuk and Rowland 1995). The first Canadian-bred cultivars (e.g., Crown and Diadem) were all susceptible to flax wilt. Cultivars Bison and Redwing, resulting from wilt-resistance breeding programs in the United States, were then introduced to Canada (Table 1; Kenaschuk and Rowland 1995). Many

Table 1. Flax cultivars registered in Canada between 1910 and 2015.

No.	Cultivar	Used names	Registered year	Breeding program ^a	Use type ^b	BA ^c	SC ^d	Oil (%)	IOD ^e	ALA (%) ^f	FW ^g	PM ^h	PA ⁱ	NA ^j	NC ^k	ND ^l	Reference ^m
1	Crown	C.I.327	1910		U	U								0	0	1	Fu et al. 2003
2	Diadem		1910	CEFO	Oil	U	B	42.9	184.5	53.3				0	0	0	Fu et al. 2003
3	Novelty	C.I.140	1910	CEFO	Oil	U	B	41.3	192.0	56.7	S	MR		0	0	0	Fu et al. 2003
4	Ottawa 770B		1910	CEFO	Oil	U	Y	42.4	194.1	59.3	MR			0	0	34	Fu et al. 2003
5	Ottawa 829C		1910	CEFO	Oil	U	Y	40.3	200.8	62.0				0	0	0	Fu et al. 2003
6	Winona	C.I.481	1926		U	U	B							0	0	0	CFIA 2015b
7	Buda	C.I. 2249	1930		U	U	B	41.7	187.0	54.5				0	0	6	CFIA 2015b
8	J.W.S.		1930		Fibre	U	B	41.6	192.3	59.3				0	0	43	CFIA 2015b
9	Bison		1930	NDES	Oil	S	B	40.6	185.7	51.7	R	MR	S	0	0	54	McGregor 1953
10	Redwing		1934	MES	Oil			39.0	193.3	56.2	MS	MR	S	0	0	51	McGregor 1953
11	Royal	C.I. 848	1939	U of S	Oil	S	B	40.5	185.8	54.6	MR		S	1	1	0	Army 1944
12	Dutch White Blossom		1940		U	U								0	0	0	CFIA 2015b
13	Liral Prince		1944	NLIRA	Fibre	CBS								2	1	0	CFIA 2015b
14	Viking		1945	NDES	Oil	CBS	Y				R	S	S	2	1	0	McGregor 1953
15	Victory	C.I. 1045	1946	NDES	Oil	U	B	40.6	191.9	58.0	S		S	3	2	1	McGregor 1953
16	Rocket		1947	AAFC	Oil	CBS	B	41.1	193.4	57.9	MR		S	4	3	0	Culbertson 1957
17	Dakota	C.I. 1071	1947	NDES	Oil	CBS	B	39.3	192.7	52.2	R		MT	2	1	44	Army 1949
18	Sheyenne	C.I. 1073	1947	NDES	Oil	CBS	LB							2	1	5	Culbertson 1952
19	Valuta	C.I. 2640	1949		Oil	CBS								0	0	3	CFIA 2015b
20	Stormont Motley		1949	PBS-MANI	Fibre	U								0	0	0	CFIA 2015b
21	Scorpion		1951		U	CBS								0	0	0	CFIA 2015b
22	Redwood	C.I. 1130	1951	MAES	Oil	CBS	B	41.2	193.0	46.0	R	MR	T	4	2	38	Culbertson 1952
23	Marine		1952	NDES	Oil		B	40.2	195.1		R		T	4	2	3	McGregor 1953
24	Cascade	Cascade Fiber, C.I. 1818	1952		Fiber	U	B	40.9	189.6	55.2				0	0	0	CFIA 2015b
25	B-5128	C.I. 980	1953	NDAES	Oil	CBS					MS		S	2	1	39	Culbertson 1961
26	Raja		1954	AAFC	Oil	CBS	B	41.4	184.8	53.1	MR			2	1	41	Culbertson 1957
27	Norland	C.I. 1176	1955	NDAES	Oil	S						MR		3	3	0	Culbertson 1961
28	Weira	C.I. 1602	1956		Fibre	S								2	1	0	CFIA 2015b
29	Cree	R.L. 219	1961	AAFC	Oil	CBS	B				MR		T	4	2	0	Tyson and Martin 1962
30	Army	C.I. 1559	1961	MAES	Oil	CBS					R		T	3	2	0	Culbertson 1961
31	Bolley	C.I. 1478	1964	NDAES	Oil	CBS	Y				MR		MT	5	4	0	Culbertson 1961
32	Noralta	F.P. 381	1965	AAFC	Oil	CBS	MB	39.4	191.0	55.7	MR	S	MR	2	2	15	Kusch et al. 1966
33	Redwood 65	F.P. 342	1965	CDC	Oil	X	B	41.6	189.0	55.6	R	MR	T	4	3	35	Larter et al. 1965
34	Linott	Ott. 4262-C9, F.P. 364	1966	AAFC	Oil	CBS	B	42.6	188.0	55.3	MR	MS		7	5	28	Kenaschuk 1980

(continued).

Table 1. (concluded).

No.	Cultivar	Used names	Registered year	Breeding program ^a	Use type ^b	BA ^c	SC ^d	Oil (%)	IOD ^e	ALA (%) ^f	FW ^g	PM ^h	PA ⁱ	NA ^j	NC ^k	ND ^l	Reference ^m
35	Dufferin	F.P. 597	1975	AAFC	Oil	CBS	B	43.1	189.0	55.1	MR	MR		8	5	17	Kenaschuk 1977
36	Culbert	CI 2776	1978	MAES	Oil	CBS	B	43.9	197.2	59.3	MR	MR		7	6	12	Comstock and Ford 1977
37	McGregor	F.P. 692	1981	AAFC	Oil	CBS	B	43.0	188.0	48.8	MR	MR		7	4	28	Kenaschuk and Hoes 1986a
38	NorLin	F.P. 698	1982	AAFC	Oil	CBS	B	42.6	187.4	55.2	MR	MS		10	6	16	Kenaschuk and Hoes 1986b
39	NorMan	M 109, F.P. 707	1984	AAFC	Oil	CBS	B	43.7	183.0		MR	S		10	6	9	Kenaschuk and Hoes 1986c
40	Vimy	S279, FP800	1986	CDC	Oil	CBS	B	44.6	187.0	58.0	MR	S		8	6	11	Rowland and Bhatti 1987
41	Andro	FP846	1988	CDC	Oil	TC	B	43.6	190.0		MS			7	5	0	Rowland et al. 1989
42	Somme	F82183, FP855	1989	CDC	Oil	CBS	B	43.6	188.0	57.0	MR	S		13	8	0	Rowland et al. 1990b
43	Flanders	F82033, FP859	1989	CDC	Oil	CBS	B	45.0	186.0	56.1	MR	MR		9	6	10	Rowland et al. 1990a
44	AC Linora	M1353, FP862	1991	AAFC	Oil	CBS	B	44.6	189.3	56.6	MR	S		10	7	2	Kenaschuk and Rashid 1993
45	AC McDuff	M2112, FP900	1993	AAFC	Oil	CBS	B	47.0	184.7	54.4	MR	MR		13	8	4	Kenaschuk and Rashid 1994
46	Linola™ 947	FP 947	1993	CPS/Viterra	Oil	CBS	Y	47.6		2.4	MR	MR		9	7	0	Dribnenki and Green 1995
47	AC Emerson	M2305, FP935	1994	AAFC	Oil	CBS	MB	44.2	196.5	58.9	MR	MR		9	7	6	Kenaschuk et al. 1996
48	CDC Normandy	F86343, FP966	1995	CDC	Oil	TC	B	44.7	192.6	58.0	MR	S		7	5	0	Rowland et al. 2002d
49	Linola™ 989	90-7921, FP 989	1995	CPS/Viterra	Oil	CBS	Y	48.4	145.4	2.6	MR	MR		9	7	3	Dribnenki et al. 1996
50	CDC Triffid	FP967, FP968	1996	CDC	Oil	T	B	44.3	191.0	57.4	MR	MR		10	7	0	McHughen et al. 1997
51	CDC Valour	F88121, FP980	1996	CDC	Oil	CBS	B	45.0	192.0	57.6	MR	S		11	7	0	Rowland et al. 2002c
52	AC Watson	M2859, FP974	1997	AAFC	Oil	CBS	B	45.7	195.0	58.5	MR	MR		14	9	3	Kenaschuk and Rashid 1998
53	AC Carnduff	M2993, FP 998	1998	AAFC	Oil	CBS	MB	45.3	193.4	57.8	MR	MR		10	9	0	Kenaschuk and Rashid 1999
54	CDC Bethune	FP91109, FP1026	1998	CDC	Oil	CBS	B	45.6	187.6	54.2	MR	MR		13	9	4	Rowland et al. 2002b
55	CDC Arras	FP1171, FP1030	1998	CDC	Oil	CBS	B	45.2	188.6	55.8	MR	S		9	7	0	Rowland et al. 2002a
56	Linola™ 1084	92-8678, SP 1084	1999	CPS/Viterra	Oil	CBS	LY	46.1		2.1	MR	MR		11	7	1	Dribnenki et al. 1999
57	Taurus		2000	CZBS	Oil	CBS					MR	MR		12	7	0	CFIA 2015a
58	Lightning	M4165, FP 1069	2001	AAFC	Oil	CBS	B	46.6	189.4	54.6	R	MR		14	10	0	Duguid et al. 2003b
59	Hanley	M 4119, FP 1094	2001	AAFC	Oil	CBS	B	43.7	195.4	57.5	R	MR		13	8	0	Duguid et al. 2003a
60	AC Nugget	FP 2002	2002	AAFC	Oil	CBS					MR	MR		10	7	0	PBRO 2015
61	CDC Mons	FP95346, FP2044	2002	CDC	Oil	CBS	B	44.8	193.0	57.3	MR	MR		11	9	2	Rowland et al. 2003
62	Linola™ 2047	94-54-F ₅ -244-2, SP 2047	2002	CPS/Viterra	Oil	CBS	DY	47.4		2.1	MR	MR		11	8	1	Dribnenki et al. 2003
63	Macbeth	M 4080, FP 1096	2002	AAFC	Oil	CBS	B	46.7	190.8	56.8	MR	MR		11	8	1	Duguid et al. 2003c
64	Linola™ 2090	93-6019-F ₁₀ -108-1, SP 2090	2003	CPS/Viterra	Oil	CBS	MY	47.2		1.9	MR	MR		10	8	0	Dribnenki et al. 2004
65	CDC Gold ⁿ	SP2100	2003	CDC	Oil	CBS	Y	43.3	153.2	<5.0	MR	MR		8	8	0	CFIA 2015b
66	Prairie Blue	M4455, FP2024	2003	AAFC	Oil	CBS	B	45.9	191.0	56.8	MR	MR		14	9	0	Duguid et al. 2004
67	Linola™ 2126	95-25-F ₉ -127-3, SP 2126	2004	CPS/Viterra	Oil	CBS	LY	47.2		1.4	MR	MR		15	11	0	Dribnenki et al. 2005
68	CDC Sorrel	FP2141	2005	CDC	Oil	CBS	B	44.2	195.0	58.8	MR	MR		15	9	1	CFIA 2015a

(continued).

Table 1. (concluded).

No.	Cultivar	Used names	Registered year	Breeding program ^a	Use type ^b	BA ^c	SC ^d	Oil (%)	IOD ^e	ALA (%) ^f	FW ^g	PM ^h	PA ⁱ	NA ^j	NC ^k	ND ^l	Reference ^m
69	Linola™ 2149	97-1014-F6-128-2, SP 2149	2005	CPS/Viterra	Oil	CBS	LY	47.6		2.2	MR	MR		12	9	0	Dribnenki et al. 2007
70	Prairie Thunder	FP2137, M6413	2006	AAFC	Oil	CBS	B	44.4	196.5	58.9	MR	R		15	10	0	Duguid et al. 2014b
71	Prairie Grande	FP2161, M6954	2007	AAFC	Oil	CBS	B	49.0	194.3	57.8	R	MR		17	10	0	Duguid et al. 2013a
72	Shape	FP2188, M7308	2008	AAFC	Oil	CBS	B	50.2	196.8	59.1	MR	MR		18	11	0	Duguid et al. 2013b
73	VT 50	NuLin™ VT 50	2009	CPS/Viterra	Oil	CBS	Y	48.8	210.3	67.8	MR			12	9	0	CFIA 2015a
74	CDC Sanctuary	FP2242	2009	CDC	Oil	CBS	B	45.3	188.2	56.2	MR	MR		14	10	0	CFIA 2015a
75	Prairie Sapphire	FP2214, M7471	2009	AAFC	Oil	CBS	B	49.0	194.3	57.8	MR	MR		20	11	0	Duguid and Rashid 2013
76	AAC Bravo	FP2270, M7970	2010	AAFC	Oil	CBS	B	46.8	196.0	60.9	MR	MR		10	7	0	Duguid et al. 2014a
77	CDC Glas	F06012, FP2300	2012	CDC	Oil	CBS	B	47.4	196.0	58.4	MR	MR		14	10	0	Booker et al. 2014b
78	CDC Neela	F07085, FP2314	2012	CDC	Oil	CBS	B	46.5	198.3	60.7	MR	MR		16	10	0	Booker et al. 2014a
79	WestLin 70		2013	CPS/Viterra	Oil	U	B	46.8	198.4	60.8	MR	MR					CFIA 2015b
80	WestLin 71	06-44-F6-368, FP2347	2013	CPS/Viterra	Oil	CBS	B	47.4	199.2	61.2	MR	MR		14	10	0	CFIA 2015b
81	WestLin 72	FP2376	2014	CPS/Viterra	Oil	U	B	47.4	199.2	61.2	MR	MR					CFIA 2015b
82	CDC Plava	FP2385	2015	CDC	Oil	CBS	B	47.0	195.8	57.8	MR	MR		15	11	0	CFIA 2015b

^aAAFC, Agricultural and Agri-Food Canada; CDC, Crop Development Centre, University of Saskatchewan; CEFO, Central Experimental Farm in Ottawa; CPS, Crop Production Services, Saskatoon; CZBS, Cebezo Zaden Breeding Station in Lelystad, The Netherlands; MAES, Minnesota Agricultural Experimental Station; MES, Minnesota Experimental Station; NDAES, North Dakota Agricultural Experiment Station; NDES, North Dakota Experiment Station; NLIRA, North Linen Industry Research Association, Ireland; PBS-MANI, Plant Breeding Station of the Ministry of Agriculture for Northern Ireland; U of S, University of Saskatchewan.

^bU, unknown.

^cBA, breeding approach; CBS, crossing/backcrossing followed by selection; S, selection; TC, tissue culture; X, X-irradiation; T, transgenic; U, unknown.

^dSC, seed color; B, brown; MB, medium brown; LB, light brown; Y, yellow; LY, light yellow; MY, medium yellow; DY, dark yellow.

^eIOD, iodine value.

^fALA, α -linolenic acid.

^gFW, resistance to Fusarium wilt; R, resistant; MR, moderately resistant; S, susceptible; MS, moderately susceptible; T, tolerant; MT, moderately tolerant. These abbreviations are also applicable to the PM and PA columns.

^hPM, resistance to powdery mildew.

ⁱPA, resistance to pasmo.

^jNA, the number of ancestors.

^kNC, the number of cycles of crossing/backcrossing and selection.

^lND, the number of derived cultivars.

^mCFIA, Canadian Food Inspection Agency; PBRO, Plant Breeders' Rights Office.

ⁿThe oil content, IOD value, and ALA content for CDC Gold were calculated based on the averages of four years at two locations in the core collection (unpublished data).

of these early registered cultivars, such as Ottawa 770B (1910), J.W.S. (1930), and Bison (1930), were frequently used as core parents and contributed to the genetic base of later-developed modern flax cultivars.

Flax rust became a problem in the late 1930s when wilt resistant but rust susceptible Bison was widely grown in Canada and the United States (Kenaschuk and Rowland 1995). Royal, a wilt resistant selection from Crown and developed by the University of Saskatchewan in 1939, was resistant to rust and later replaced Bison in the prairie provinces (Table 1; Kenaschuk and Rowland 1995). Rust resistance breeding by Agriculture Canada led the way for the development of cultivar Rocket in 1947. Dakota and Sheyenne were rust resistant introductions from the United States (Table 1), but by 1948 resistance had broken down in these cultivars as new races of rust evolved (Kenaschuk and Rowland 1995). These susceptible cultivars were replaced by resistant cultivars Marine, Rocket, and Sheyenne (Table 1; Kenaschuk and Rowland 1995). An outbreak of new virulent rust (race 300) appeared in 1962, overcoming the rust resistance L gene of Cree, Marine, and Sheyenne (Kenaschuk and Rowland 1995). Cultivar Raja, developed by Agriculture Canada, and Bolley and Redwood, introduced from the United States, replaced susceptible cultivars (Kenaschuk and Rowland 1995). The last outbreak of new rust races occurred in 1973 when races 370 and 371 appeared and overcame the N¹ resistant gene in susceptible cultivars Norlata and Redwood 65, which were quickly replaced by Linott and Dufferin (Table 1; Kenaschuk and Rowland 1995). Disease resistance to rust and wilt continue to be emphasized in breeding programs to keep these problems under control.

The breeding program at Agriculture Canada, in place since the 1950s, produced important cultivars Linott, Raja, and Rocket (Table 1; Kenaschuk and Rowland 1995). In Alberta, breeding was conducted at Agriculture Canada's Fort Vermillion Experiment Station and the Beaverlodge Research Station in the 1960s and produced cultivar Noralta, which because of its early maturity became predominant in northern Alberta and Saskatchewan in the 1970s and 1980s (Table 1; Kenaschuk and Rowland 1995). Since 1951, a total of 61 cultivars have been registered, 46 of which date to the last 35 years (Table 1).

The three major breeding programs of AAFC, the CDC, and CPS/Viterra have released 18, 16, and 11 cultivars, respectively, since 1981. Breeding programs in the 1980s focused on development of NuLin™ (high ALA) and Solin (low ALA), two special linseed types with ALA higher than 65% or less than 5%, respectively. The CPS/Viterra cultivars were trademarked as NuLin™ and Linola™, respectively. One Nulin (NuLin™ VT 50) and seven Solin (Linola™ 947, 989, 1084, 2047, 2090, 2126, and 2149) cultivars have been released. The Solin

cultivars have low ALA content of 1.4%–2.6% while Nulin VT 50 has as much as 67.8% ALA (Table 1). Moreover, the Crop Development Centre of the University of Saskatchewan in co-operation with the Saskatchewan Wheat Pool registered CDC Gold in 1987 as a Solin cultivar for production in Canada (Table 1; Kenaschuk and Rowland 1995). Solin oil has higher solidification temperatures suitable for the margarine industry. However, the markets for these specialty linseed cultivars remain undeveloped, and, as a consequence, all Solin cultivars have been deregistered in Canada and their production has ceased. Yellow seeded cultivars were exclusive to the Solin type. The deregistration of all Solin cultivars means that new cultivars can be developed or commercialized in Canada with either a yellow or a brown seed coat regardless of ALA content (Flax Council of Canada 2015). The CDC breeding program released CDC Bethune and CDC Sorrel in 1998 and 2005, respectively, and these brown linseed cultivars are predominant in current production (Table 1; B. Siemens, personal communication, 2016, Canadian Grain Commission). Cultivar CDC Bethune garnered the Seed of the Year West award for its importance to the seed industry and cultivar development in Western Canada (T. Hyra, personal communication, 2012, SeCan).

The objectives of this study were to collate the flax cultivars registered in Canada and their pedigree data and quantify their genetic base via a pedigree analysis, to calculate coefficients of parentage (CP), and to estimate the genetic contribution (GC) of each ancestor to understand the genetic base and diversity of historical and current Canadian flax cultivars. This data will serve to inform the selection of parental material for future genetic improvement of flax in Canada.

Materials and Methods

Registered cultivars and pedigree data

Information on the flax cultivars registered in Canada was collected from six sources: (1) the database of cultivars registered in Canada (CFIA 2015a); (2) scientific journals — Canadian cultivars released before 1961 were usually published in the *Journal of Agronomy* and then in *Crop Science*, and since 1980, all registered flax cultivars have been published in the *Canadian Journal of Plant Science*; (3) the Germplasm Resources Information Network (GRIN) database (<http://www.ars-grin.gov/npgs/index.html>), a part of the National Genetic Resources Program (NGRP) of the United States Department of Agriculture, Agricultural Research Service (USDA-ARS), as well as the Canadian GRIN database (GRIN-CA) of Agriculture and Agri-Food Canada's Plant Gene Resources of Canada (http://pgrc3.agr.gc.ca/index_e.html); (5) the database and website of the Flax Council of Canada (<http://flaxcouncil.ca/>); and (6) personal communications with flax breeders. For all flax cultivars registered in Canada, we traced their

parentage to the oldest known ancestors or any most remote variety or breeding line for which parentage information was available. An ancestor was defined as the ultimate variety, landrace, or breeding line from which a cultivar was derived and where further parentage was unknown or untraceable from available pedigree records. Some direct or indirect parents were also considered ancestors when complete pedigree records were lacking.

Genetic contribution of ancestors to genetic base

The GC of an ancestor to a flax cultivar was determined as the genetic proportion in the flax cultivar that could be traced to an ancestor via pedigree analysis (Gizlice et al. 1994). CP was used to estimate this contribution. The CP between two genotypes was defined as the probability that a random allele at a random locus in one genotype is identical by descent to a random allele at the same locus in another genotype (Kempthorne 1957; Malécot 1969). In flax, we assume all ancestors, cultivars, and parental breeding lines are homozygous. All ancestors are assumed to be independent, i.e., the CP between any pair of ancestors is '0'. A cultivar or a breeding line derived from crossing of two parents obtains half of its genome from each parent. Several breeding approaches, such as direct selection of natural variants from germplasm, artificial mutants, tissue culture-derived somaclonal variants, and transgenic technique generated cultivars, feature almost the same genetic background except for minor genetic changes in some gene loci for specific traits. To simplify the CP calculation, we assumed that the cultivars developed using these approaches obtained all genetic material from their progenitor, i.e., the CP between the progenitor and the essentially derived cultivars is equal to 1. In theory, the GC of different ancestors to a derived cultivar is defined as the relative genetic constitution of the ancestors in the derived cultivar but, in practice, it is estimated using the CPs of the ancestors and the derived cultivars. The sum of CPs of all ancestors of a cultivar must be equal to 1, i.e., $\sum_{i=1}^n CP_i = 1$, where n is the total number of ancestors of a derived cultivar. The sum of the mean CPs of ancestors across all or selected cultivars must also be equal to 1, i.e., $\sum_{i=1}^n \sum_{j=1}^m CP_{ij} / m = 1$, where n is the number of ancestors of all or selected cultivars and m is the number of all or selected cultivars. These two conditions can be used to validate CP calculations. The algorithm to calculate CPs is described in detail elsewhere (Cui et al. 2000). All pedigree analyses were programmed using a custom Perl script, which is available upon request.

Cluster analysis of registered cultivars

Based on the distance (1-CP) among flax cultivars, a hierarchical cluster analysis was performed using the *hclust* function with the Ward method in R (<http://www.cran.r-project.org>).

Results

Pedigree relations of flax cultivars

Pedigree information was sought for all registered flax cultivars; however, records for the recent CPS/Viterra cultivars WestLin 70 and WestLin 72 and for several cultivars registered before the 1950s could not be obtained and are therefore not presented. The pedigree records for several direct or indirect parents were also not available, so these parents were considered ancestors. Based on available pedigree records, individual pedigree trees for all registered cultivars were drawn and merged to build a chart with an overall Canadian flax cultivar pedigree tree (Fig. 1). Of the 82 cultivars, 72 group into a single tree, illustrating the extent of the common genetic base among Canadian flax cultivars. The other cultivars group into several smaller pedigree trees or singletons as a consequence of the unavailability of their pedigree records or because they were not used as parents for breeding.

We calculated the CPs among all registered cultivars, as well as the mean CPs among cultivars released in different years and within/among the cultivars released by different breeding programs. The mean CPs among all 82 registered cultivars and among the 46 cultivars released from 1981 to 2015 are 0.14 and 0.23, respectively, indicating the narrowness of the Canadian flax cultivars, especially those recently developed. Among the 46 cultivars released from 1981 to 2015, only one out of 946 pairs of cultivars (VT 50 vs. Vimy) has no pedigree relation; all other pairs have CPs ranging from 0.01 to 1. On average, any two cultivars share 23% of their genetic base.

Comparison of the CPs between cultivars released by different breeding programs (Table 2) shows the cultivars developed by the CDC have the closest pedigree relation (mean CP of 0.30) vs. those from the AAFC and CPS/Viterra programs (0.24). Comparing cultivars across breeding programs also indicates fairly high percentages of genetic similarity (0.16–0.25) (Table 2).

A cluster analysis was performed based on the distance (1-CP) among the cultivars. The dendrogram of registered cultivars and their major ancestors (Fig. 2) clearly depicts the pedigree relation of the flax cultivars and their parents or ancestors. Cultivars merging at a 1-CP value of 0 are indicative of cultivars obtained via direct selection (e.g., Royal from Crown), tissue culture (Andro and CDC Normandy from McGregor), irradiation (Redwood 65 from Redwood), or transgenic technique (e.g., CDC Triffid from Norlin). CDC Triffid was deregistered in 2001 by the Canadian Food Inspection Agency (CFIA) due to concerns by the European market about the production of transgenic flax and the use of transgenic technology as such by European consumers. In the cluster analysis, cultivars with no pedigree relation were excluded. The remaining 64 cultivars and their major ancestors grouped into three major clusters (Fig. 2). Cluster I represents the 14 major ancestors and

Fig. 1. Pedigrees of flax cultivars registered in Canada from 1910 to 2015. The major ancestors of Canadian flax cultivars are underlined.

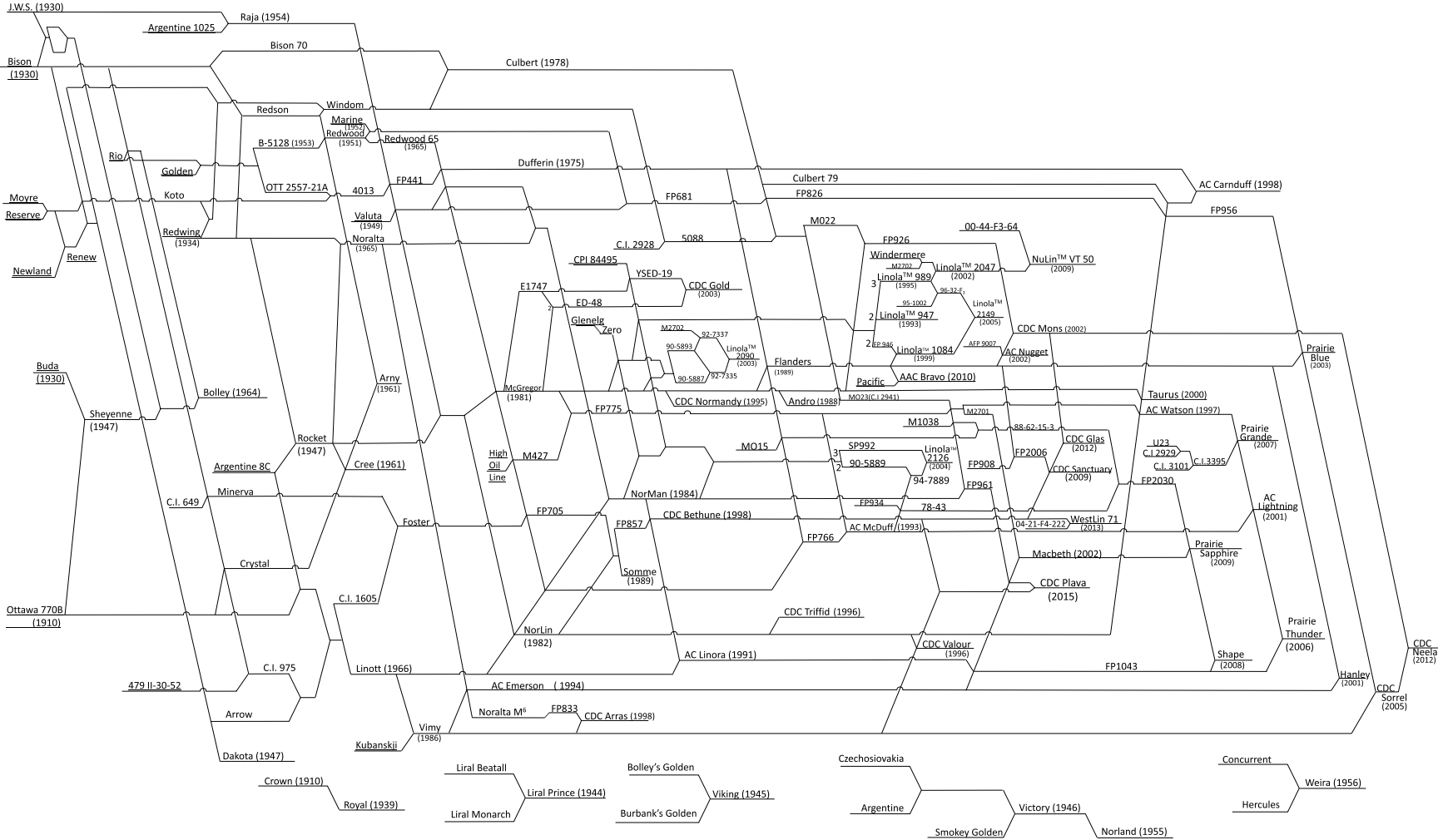


Table 2. Mean CPs of cultivars released from 1981 to 2015 by the three major breeding programs in Canada.

Program	No. of cultivars	AAFC	CDC	CPS/Viterra
AAFC	18	0.24	0.25	0.16
CDC	16		0.30	0.19
CPS/Viterra	9			0.24

Note: WestLin 70 and 72 released by CPS/Viterra were not included in the analysis. The diagonal values represent the mean CPs of cultivars released by different breeding programs.

some early registered cultivars. Because most cultivars in this cluster are ancestors that had no pedigree relation, the mean CP among the cultivars in Cluster I is relatively small (0.04); the mean CPs of cultivars between Cluster I and the other two clusters represent the mean genetic contribution of each ancestor to the derived cultivars in Clusters II and III (0.06–0.08) (Table 3). Clusters II and III contain most of the modern flax cultivars derived from some Cluster I ancestors. The cultivars within Clusters II and III share 24% and 34% of their genetic base, respectively (Table 3). Clusters II and III cultivars share 15% of their genetic base. Three ancestors, Argentine 8C, Redwing, and Kubanksij, cluster together into a sub-cluster of Cluster II (Fig. 2), suggesting these three cultivars contribute more to the cultivars in Cluster II than Cluster III.

Ancestors of flax cultivars

Of the 82 registered cultivars, eight (Diadem, Novelty, Ottawa 829C, Winona, Dutch White Blossom, Stormont Motley, Scorpion, and Cascade) have no derived cultivars and two (WestLin 70 and WestLin 72) have no pedigree records, and were thus excluded from ancestor analysis. The 72 remaining registered cultivars trace back to 46 ancestors (Table 4), of which 18 are breeding lines without pedigree records. These ancestors originate from Canada (28%), the USA (15%), Europe (20%), Australia (4%), and unknown geographical origins (33%), corresponding to 17%, 40%, 15%, 3%, and 25% of the GC to the flax cultivars, respectively (Table 5). As the 15 ancestors of unknown geographical origins are non-Canadian lines, they were considered foreign germplasm, which therefore accounts for a total of 72% of the 46 ancestors and explains 83% of the genetic base of the Canadian flax cultivars.

The cultivars released in the periods 1910–1950, 1951–1980, and 1981–2000 have 16, 19, and 18 ancestors, respectively. In the past two decades, new germplasm has been introduced into Canadian flax breeding programs, such as Pacific, Windermere, and other improved breeding lines. This is reflected in the increased number of ancestors for cultivars released from 2001 to 2015, which is almost twice (36) that of the previous period. Likewise, the number of ancestors per cultivar has gradually

increased, especially over the last 35 years (Fig. 3). The mean number of ancestors per cultivar released from 1910–1950, 1951–1980, 1981–2000, and 2001–2015 is 2.3, 4.1, 10.1, and 13.6, respectively. Cultivars, such as Prairie Sapphire released in 2009, have up to 20 ancestors in their genetic makeup (Table 1).

Of the original 46 ancestors, the top 11 in Table 4 contribute 28.6%, 81.0%, 92.5%, and 69.6% of the genetic base to the cultivars developed during 1910–1950, 1951–1980, 1981–2000, and 2000–2015, respectively (Table 4). These ancestors contribute the majority of the genetic base to cultivars released between 1981 and 2015 and form the core gene pool of Canadian flax cultivars. Redwing, Bison, and Argentine 8C alone contribute 34–46% of the genetic base to cultivars registered since 1951 and more than 40 flax cultivars are derived from each of them (Table 4).

Discussion

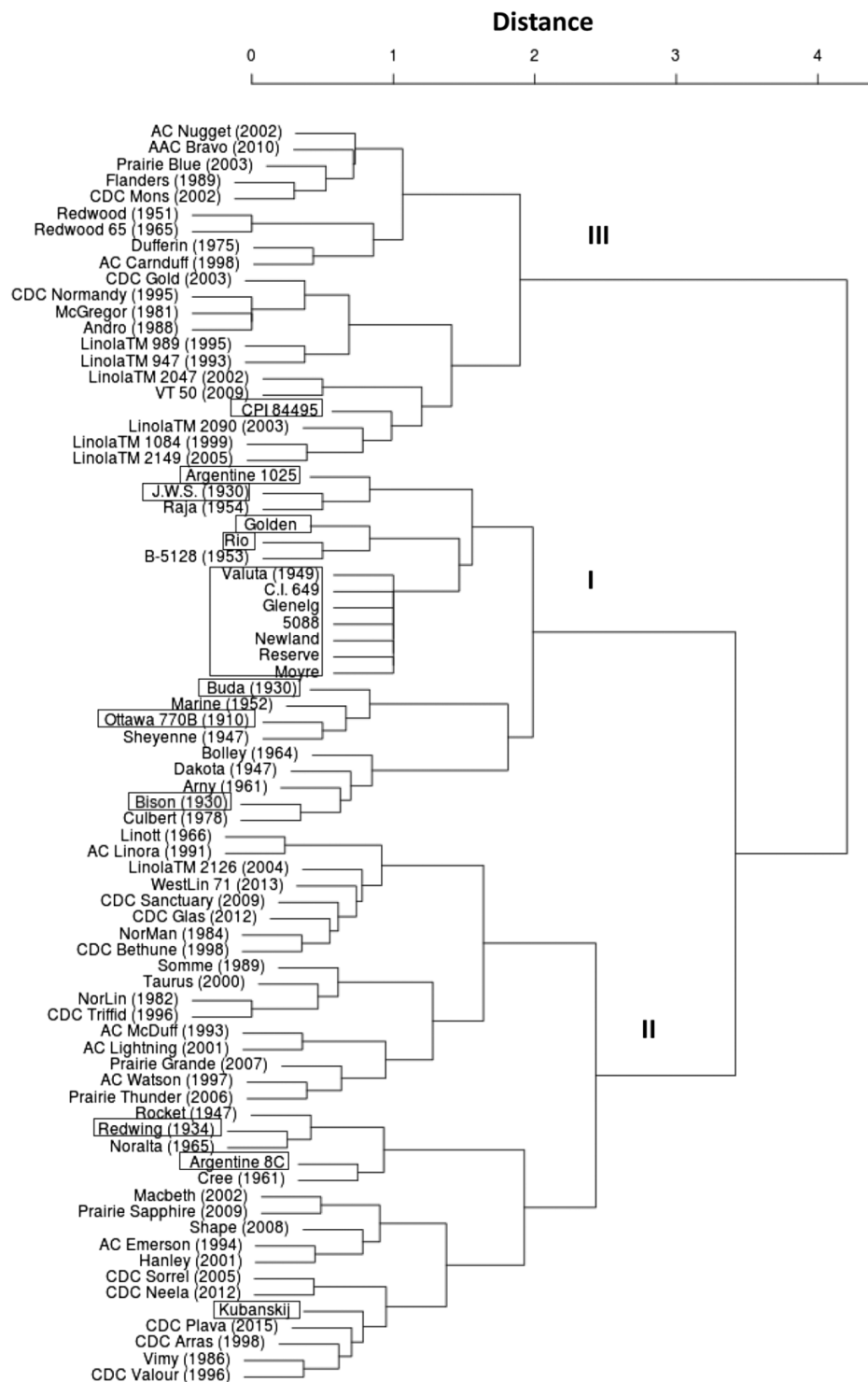
Germplasm preservation and evaluation to assist expansion of the genetic base

Increasing reliance on relatively few cultivars as parents in most breeding programs has led to the loss of genetic diversity and narrowing of the genetic base, which may reduce tolerance to the effects of climate change, new pests, and diseases. The higher number of ancestors of recent cultivars is an indication that breeders are paying attention to the consequences of the narrow genetic base. Moreover, focused breeding efforts for brown as well as yellow linseed development, the demand from industry for higher oil and ALA content flaxseed and from flax producers for improved agronomic traits associated with yield production in the Northern Prairies have resulted in the necessity to introduce novel germplasm into breeding programs for crop improvement. It is imperative that flax breeders continue to consider suitable breeding strategies for expanding the genetic base and increasing the genetic diversity of future flax cultivars.

Of the 82 registered cultivars, 25 were directly introduced for production from foreign countries (e.g., USA, Germany, and Australia) and 72% of the ancestors originated from foreign germplasm, indicating the potential adaptability and importance of foreign germplasm as a source of genetic diversity and elite alleles. Expansion of the genetic base in recent decades is primarily attributed to imported germplasm. Thus, the introduction, evaluation, and utilization of new exotic germplasm should continue to be an efficient approach to further broaden the genetic base of Canadian flax cultivars.

There are approximately 48 000 flax accessions in the *ex situ* world collections (Diederichsen 2007), whereas the Canadian national plant germplasm repository, Plant Gene Resources of Canada (PGRC), preserves a collection of 3252 accessions of *Linum usitatissimum* L. and 76 accessions of other species of the genus *Linum*,

Fig. 2. Dendrogram of flax cultivars released in Canada and their major ancestors (boxed) based on the 1-CP distance among cultivars. Fifteen cultivars (Cascade, Crown, Diadem, Dutch White Blossom, Novelty, Ottawa 829C, Royal, Scorpion, Stormont Motley, Victory, Viking, Weira, WestLin8 70, WestLin 72, and Winona) were not included because they have no pedigree relation with other cultivars or no pedigree records.



originating from 72 countries and representing all historical and present cultivation regions for linseed or fibre production (Diederichsen and Fu 2008). In the last two decades, most of these Canadian collections

(over 90%) have been resampled to be characterized and evaluated for morphologic, phenological, and agronomic characters such as plant height, seed color, seed weight, seed oil content, fatty acid profile, seed

Table 3. Mean CPs of cultivars across the three clusters generated by the cluster analysis in Fig. 2.

Cluster	No. of cultivars	Cluster		
		I	II	III
I	22	0.05	0.05	0.06
II	34		0.24	0.15
III	21			0.33

coat mucilage content, fiber content, adaptation to dry growing conditions, disease resistance, seed vigour, seed lignin content, and so on (Diederichsen 2001; Diederichsen and Raney 2006; Diederichsen and Fu 2008; Diederichsen et al. 2008; Diederichsen and Ulrich 2009). Molecular markers of randomly amplified polymorphic DNA (RAPD) have also been used to evaluate the genetic variation and geographic patterns of more than 2700 flax accessions and cultivars (Fu et al. 2002, 2003; Fu 2005, 2006; Diederichsen and Fu 2006). Large-scale characterization and evaluation demonstrate a wide range of diversity of economically relevant traits within and among accessions is a valuable source of genetic variation for breeding (Diederichsen and Fu 2008). This variation exists largely within geographical regions because only a small portion (8.2%) of the RAPD variation in the flax accessions can be explained by the geographical regions (Fu 2005). Comparison with Canadian cultivars indicates that the wide variation in agro-botanical characters of flax germplasm is useful for flax breeding (Diederichsen 2001). The weak correlation between fibre content and other agronomic traits in the flax germplasm demonstrates that the variation in fibre content of flax germplasm is useful for identifying germplasm relevant for breeding dual purpose flax (Diederichsen and Ulrich 2009).

Due to the redundancy in the Canadian whole flax collection and breeding demands, a subset of 381 accessions plus 26 later appended Canadian cultivars, named the core collection (which includes most of the core ancestors identified in this study, their derived cultivars, and exotic germplasm) has been assembled to include most of the genetic variation present in the whole collection of 3378 accessions and current flax cultivars (Diederichsen et al. 2013). Molecular evaluation via 448 microsatellite markers has demonstrated that the core collection has abundant genetic diversity and a weak population structure, making it suitable for association mapping of agronomic and quality traits in flax (Soto-Cerda et al. 2013b). Important agronomic traits such as seed yield, oil content and quality, fiber traits, and disease resistance have been phenotyped at multiple locations and years (unpublished data). Thus, this core collection provides a realistic and useful germplasm for expanding the genetic base of future flax cultivars.

Pale flax (*Linum bienne* Mill.) is the wild progenitor of cultivated flax (Diederichsen and Hammer 1995; Fu and Peterson 2010). Pale flax and cultivated flax share the same chromosome number ($n = 15$) and their crosses generate fully fertile offspring, thus, it represents cultivated flax's primary gene pool (Diederichsen 2007). Genetic variation studies of the two species indicate that strong genetic differentiation exists between pale and cultivated flax and that pale flax is more genetically diverse (Diederichsen 2007; Uysal et al. 2010, 2012; Soto-Cerda et al. 2014a) and possesses favorable alleles with a potentially positive effect on improving seed yield through yield components (Soto-Cerda et al. 2014a). Therefore, pale flax provides another potential source of genetic variation to broaden the narrow genetic base of Canadian flax cultivars.

The genetic base of Canadian flax cultivars

The genetic base of all Canadian flax cultivars was estimated at both the population (all flax cultivars) and at the individual level (individual cultivars) using the number of ancestors and the genetic contribution of ancestors to all flax cultivars or individual cultivars included in this study. We identified 46 ancestors from all registered flax cultivars, of which 36 are from cultivars released in the last 35 years. The top 11 ancestors contribute as much as 70%–93% of the genetic base of modern flax cultivars. Although the genetic base of individual cultivars has greatly improved in the last two decades, flax cultivars share an average of 8.8 common ancestors, resulting in a mean CP of 0.23. These results suggest that Canadian flax cultivars have similar backgrounds, a relatively narrow genetic base, and low genetic diversity. This corroborates the results of Soto-Cerda et al. (2013a) that show all 31 Canadian cultivars present in a germplasm collection of 407 core collection flax accessions cluster together on the basis of 414 neutral DNA markers. While the entire core collection has 2202 alleles, the Canadian cultivars only have 1081. Even adjusted for sample size difference, the Canadian cultivars only comprise 2/3 of the genetic variability of the core collection, substantiating our findings regarding their narrow genetic base.

Ancestors of Canadian flax cultivars to assist parent selection

Flax is an autogamous crop plant and its breeding involves creating genetic variability via crossing, selecting the best recombinants, and fixing the desirable traits or genes by inbreeding (Hall et al. 2016). Crossing followed by selection is the predominant approach in Canadian flax breeding. Most cultivars (86%) released in the last 35 years were developed via this approach. Parental selection and crossing schemes to broaden the genetic base and generate variability in the breeding program material are key factors to the success of conventional hybridization breeding methodology. We

Table 4. Ancestors of registered flax cultivars, their number of derived cultivars, and their respective genetic contribution.

No.	Ancestor	Origin	1900–1950		1951–1980		1981–2000		2001–2015		Total		Cumulated
			ND	GC (%)	ND	GC (%)	ND	GC (%)	ND	GC (%)	ND	GC (%)	
1	Redwing	USA	1	7.14	9	14.29	20	17.86	23	13.64	51	14.44	14.44
2	Bison	USA	3	7.14	13	21.21	21	13.75	23	11.75	54	13.94	28.38
3	Argentine 8C	Unknown	1	7.14	4	5.36	21	15.03	23	8.98	48	9.96	38.33
4	Rio	USA	0	0.00	8	10.71	13	5.92	23	5.38	42	6.12	44.46
5	Ottawa 770B	Canada	1	7.14	6	8.04	14	6.32	15	3.55	35	5.80	50.26
6	Golden	USA	0	0.00	7	8.93	13	5.92	23	5.38	41	5.74	56.00
7	J.W.S.	Europe	0	0.00	3	5.36	18	7.81	23	5.32	44	5.56	61.56
8	Argentine 1025	Unknown	0	0.00	2	4.46	18	7.81	23	5.32	43	5.37	66.93
9	Kubanskij	Europe (Russia)	0	0.00	0	0.00	4	5.95	8	4.35	12	3.46	70.39
10	CPI 84495	Australia	0	0.00	0	0.00	3	2.98	6	4.08	9	2.40	72.79
11	479 II-30-52	Canada	0	0.00	3	2.68	14	3.16	15	1.82	31	2.24	75.03
12	Smoky Golden	Unknown	1	7.14	1	3.57	0	0.00	0	0.00	2	1.54	76.57
13	Crown	Canada	1	14.29	0	0.00	0	0.00	0	0.00	1	1.54	78.11
14	Newland	Unknown	3	3.57	5	0.67	14	1.64	16	1.00	33	1.41	79.52
15	Buda	Unknown	1	7.14	2	2.68	0	0.00	3	0.08	6	1.38	80.90
16	Glenelg	Australia	0	0.00	0	0.00	3	1.79	5	2.04	8	1.30	82.20
17	Moyre	Unknown	4	1.79	6	0.67	16	1.07	19	0.86	39	0.99	83.18
18	Reserve	Unknown	4	1.79	6	0.67	16	1.07	19	0.86	39	0.99	84.17
19	5088	Canada	0	0.00	0	0.00	1	0.60	8	2.17	9	0.96	85.13
20	M2702	Canada	0	0.00	0	0.00	0	0.00	3	2.72	3	0.96	86.09
21	High Oil Line	Canada	0	0.00	0	0.00	2	0.89	7	1.36	9	0.77	86.86
22	Argentine	Unknown	1	3.57	1	1.79	0	0.00	0	0.00	2	0.77	87.63
23	Czechoslovakian	Unknown	1	3.57	1	1.79	0	0.00	0	0.00	2	0.77	88.40
24	00-44-F3-64	Canada	0	0.00	0	0.00	0	0.00	1	2.17	1	0.77	89.17
25	04-21-F4-222	Canada	0	0.00	0	0.00	0	0.00	1	2.17	1	0.77	89.94
26	AFP 9007	Europe (Germany)	0	0.00	0	0.00	0	0.00	1	2.17	1	0.77	90.71
27	Bolley's Golden	Unknown	1	7.14	0	0.00	0	0.00	0	0.00	1	0.77	91.48
28	Burbank's Golden	Unknown	1	7.14	0	0.00	0	0.00	0	0.00	1	0.77	92.25
29	Concurrent	Europe	0	0.00	1	3.57	0	0.00	0	0.00	1	0.77	93.02
30	Hercules	Europe	0	0.00	1	3.57	0	0.00	0	0.00	1	0.77	93.78
31	Liral Beattall	Europe	1	7.14	0	0.00	0	0.00	0	0.00	1	0.77	94.55
32	Liral Monarch	Europe	1	7.14	0	0.00	0	0.00	0	0.00	1	0.77	95.32
33	Pacific	Europe	0	0.00	0	0.00	0	0.00	1	2.17	1	0.77	96.09
34	M023	Unknown	0	0.00	0	0.00	0	0.00	2	1.63	2	0.58	96.67
35	Windermere	Unknown	0	0.00	0	0.00	0	0.00	2	1.63	2	0.58	97.25
36	FP934	Canada	0	0.00	0	0.00	0	0.00	2	1.09	2	0.38	97.63
37	95-1002	Canada	0	0.00	0	0.00	0	0.00	1	1.09	1	0.38	98.02
38	FP908	Canada	0	0.00	0	0.00	0	0.00	1	1.09	1	0.38	98.40
39	FP961	Canada	0	0.00	0	0.00	0	0.00	1	1.09	1	0.38	98.78
40	C.I. 649	USA	0	0.00	1	0.00	2	0.45	4	0.24	6	0.23	99.01
41	M1038	Unknown	0	0.00	0	0.00	0	0.00	2	0.54	2	0.19	99.21
42	MO15	Unknown	0	0.00	0	0.00	0	0.00	2	0.54	2	0.19	99.40
43	U23	USA	0	0.00	0	0.00	0	0.00	1	0.54	1	0.19	99.59
44	Z2236	Canada	0	0.00	0	0.00	0	0.00	1	0.54	1	0.19	99.78
45	Valuta	Europe (Romania)	0	0.00	0	0.00	0	0.00	3	0.34	3	0.12	99.90
46	High Oil Line2	USA	0	0.00	0	0.00	0	0.00	1	0.27	1	0.10	100.00

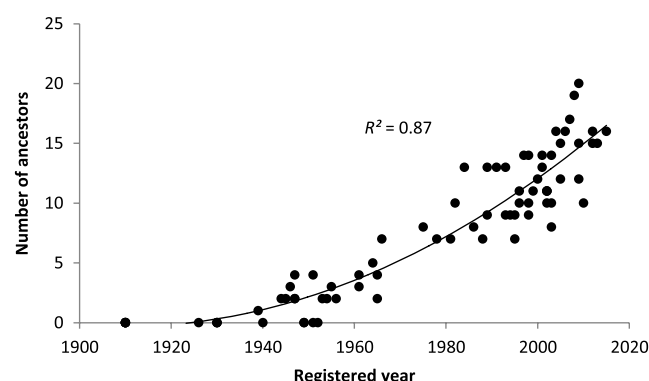
Note: ND, the number of derived cultivars; GC, genetic contribution.

identified 46 ancestors and 11 major ancestors that constitute the core gene pool of Canadian flax cultivars. These ancestors possess elite and adaptive alleles for economically important traits in flax. The genetic structure

of Canadian flax ancestors, if known, could reveal loci conditioning characters for improvement. For example, the majority of Canadian flax cultivars have the wilt resistant cultivar Bison as an ancestor. Understanding

Table 5. Numbers and mean GC percentages (in parentheses) of ancestors of flax cultivars registered from 1910 to 2015 classified by types and geographic origins.

Type	Origin					Total
	Canada	USA	Europe	Australia	Unknown	
Breeding line	11 (7.41)	2 (0.26)	1 (0.69)	1 (2.17)	3 (0.87)	18 (11.40)
Cultivar	2 (9.40)	5 (39.30)	8 (14.50)	1 (1.17)	12 (24.21)	28 (88.60)
Total	13 (16.81)	7 (39.57)	9 (15.20)	2 (3.34)	15 (25.08)	46 (100.00)

Fig. 3. Relationship between the number of ancestors of individual flax cultivars and their year of registration.

the major loci conditioning Bison's resistance to fusarium wilt would allow flax breeders to identify early generation lines with resistance loci, thereby increasing the efficiency of selection. Optimally, the selection of genetically diverse parents with complementary characteristics for the development of segregating populations should be chosen from two different clusters based on their CPs, the number of ancestors, and their common ancestors (Fig. 2).

Genomics-assisted breeding to assist expansion of the genetic base

Plant breeding pyramids elite complementary alleles from distinct parents using different approaches, such as conventional, mutation, transgenic, and, more recently, gene editing (Sauer et al. 2016) breeding techniques for crop improvement. Molecular breeding incorporates DNA molecular markers associated with specific traits to improve selection efficiency. Flax has a small to medium size genome of ~370 MB (Wang et al. 2012) that has been sequenced, assembled, and sorted to generate a chromosome-based pseudomolecule physical map based on CDC Bethune (Wang et al. 2012; You et al. 2015). With the rapid advances and application of next generation sequencing and high-throughput genotyping technologies, it is possible to affordably sequence and genotype sufficient numbers of individuals and readily use molecular breeding strategies for cultivar development, such as marker-assisted selection (MAS) and genomic selection (GS) (You et al. 2016). MAS and GS are strategies that use DNA markers to predict phenotypes, thus

increasing precision and efficiency and reducing the cost of offspring selection. Based on MAS, Peleman and van der Voort (2003) propose the "breeding by design" concept, which aims to bring together superior alleles for all genes of agronomic importance from potential germplasm resources to generate superior cultivars. This might be achieved through genome-wide high-resolution allele detection via precise quantitative trait loci (QTL) mapping of potential parental resources. In flax, some QTL associated with seed yield, oil content, ALA, and other important agronomic traits have been identified based on simple sequence repeat and single nucleotide polymorphism markers with bi-parental mapping populations (Cloutier et al. 2011; Kumar et al. 2015) and the Canadian flax core collection (Soto-Cerda et al. 2012, 2013c, 2014b). Utilizing the outcomes from the Total Utilization Flax Genomics (TUFGEN) project, the high-resolution chromosome haplotype map of the core collection has been generated (unpublished data). This information with the phenotyped traits have been used and will be further applied for precise assessment of the genetic basis of economically important traits, detection of allelic variations at these loci, and identification of superior genotypes for breeding. Thus, genome-wide genetic dissection of elite germplasm and modern genomics-assisted breeding strategies provide the knowledge to widen the genetic base of future flax cultivars not only through selection of multiple diverse elite lines as parents but also through the identification of recombinants with favourable alleles for the development of innovative, improved, and better adapted flax cultivars. Recent innovations in crossing schemes such as multi-parent advanced generation intercross (MAGIC) (Huang et al. 2015) may generate parental inbreds with a much broader genetic base if the constituent parents are chosen carefully from the pedigree tree (Fig. 1). Recently, an eight-parent derived wheat MAGIC-population was developed (Mackay et al. 2014) for further genetic enhancement and similar strategies can be applied in flax breeding using the diverse ancestors identified from the pedigree chart.

Conclusion

A total of 82 flax cultivars were registered in Canada from 1910 to 2015, including 24 from foreign countries and 58 developed by Canadian breeders, of which 46

date from the last 35 years. With the introduction of some foreign cultivars, crossing methodology is the predominant breeding approach in Canada and up to 11 cycles of crossing and selection are involved in Canadian flax improvement. Pedigree analysis indicates that Canadian flax cultivars have a narrow genetic base, although significant progress towards broadening the genetic base has been made in recent years. Great efforts have been made in the large-scale characterization and evaluation of the flax germplasm preserved at Plant Gene Resources Canada (PGR) and utilization of new exotic germplasm to the breeding programs should be further emphasized, besides exploiting the potential of multi-parent advanced generation intercross (MAGIC)-derived populations for expanding the genetic base of future cultivars. A broad range of genomic resources developed in flax during the last decade are available to mainstream the process to develop genetically diverse improved flax cultivars.

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