Chapter 4
Genetic Erosion Under Modern Plant Breeding: Case Studies in Canadian Crop Gene Pools

Yong-Bi Fu and Yi-Bo Dong

Abstract There is long-standing concern that modern plant breeding reduces crop genetic diversity. Such reduction may have consequences both for the vulnerability of crops to biotic and abiotic stress. To understand the impact of plant breeding on diversity, we conducted a series of genetic diversity analyses from 1999 to 2009 on existing Canadian gene pools of flax, oat, wheat, soybean, potato and canola. Here we summarize these analyses, highlight major findings, and discuss related issues. These gene pools displayed variable patterns and degrees of genetic diversity decline over the past 100 years of Canadian breeding efforts. Significant allelic loss and genetic shift were found in the wheat and oat gene pools. Such diversity declines underline the need for continuous efforts in conservation of improved crop germplasm and in the diversification of plant breeding materials for sustainable breeding programs.

Keywords Plant breeding · Canadian crop gene pool · Genetic diversity · Genetic erosion · Allelic change · Genetic shift · Genetic marker

4.1 Introduction

Concern has been frequently expressed that modern plant breeding reduces crop genetic diversity (National Research Council 1972; Duvick 1984; Vellve 1993; Clunier-Ross 1995; Tripp 1996; Tanksley and McCouch 1997), as modern crops have become phenotypically more uniform and genetically less heterogeneous (Duvick 1984; Brush 1999). The genetic vulnerability of crop uniformity has been well documented with the abundant history of epidemics such as the Irish potato

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blight in the 1840s and the U.S.A. corn blight in the 1970s (National Science Council 1972). The threat of the extremely virulent new race of stem rust Ug99 from East Africa to genetically uniform wheat is a current concern (Borlaug 2007). Theoretically, selective breeding within a narrow range of plant germplasm could eliminate rare alleles, change allele frequencies, reduce genetic diversity, and increase linkage disequilibrium (Allard 1999; Hedrick 2000).

Efforts have been made to assess genetic diversity changes in major agricultural crop species (Duvick 1984; Swanson 1996; Tripp 1996; Donini et al. 2000; Fu and Somers 2009). Early assessments were largely based on phenotypic (Rodgers et al. 1983) and pedigree data (e.g., Cox et al. 1985) and have their limitations either due to environmental influence or biased inference of parental contribution. Over the last two decades, more informative assessments have been made using molecular markers such as random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), and simple sequence repeats (SSRs) (Fu 2006). However, no consensus has been reached as to the overall impact of modern plant breeding on crop genetic diversity (Fu 2006; Rauf et al. 2010; van de Wouw et al. 2010).

From 1999 to 2009, we conducted a series of genetic diversity analyses of existing Canadian gene pools of flax, oat, wheat, soybean, potato, and canola, using different molecular markers, as part of the effort to monitor genetic erosion in crop gene pools and to understand the impacts of plant breeding on crop genetic diversity (Fu 2005; Fu and Gugel 2010). In this chapter, we summarize these diversity analyses, highlight the major findings, and discuss some key issues associated with these analyses. It is our hope that this summary helps to paint a clear picture of the genetic diversity changes in the Canadian crop gene pools established over the last 100 years of plant breeding.

4.2 Plant Breeding in Canada

Canada is a comparatively young country, but it is one of the few countries with a long-term, continuous, and complete modern plant breeding history (Campbell and Shebeski 1986). In 1874, the first agricultural college was established at Guelph, Ontario, to train professionals in agricultural science. In 1886, the act creating the system of federal experimental farms was passed and the first experimental farm was established at Ottawa. In 1888, William Saunders, the first director of the Central Experimental Farm, Ottawa, initiated a wheat breeding program and his son, Charles Saunders, released the famous cultivar Marquis in 1909. While plant breeding efforts were expanded in the federal department of agriculture, the provinces, universities, and private companies were slow to initiate cultivar development programs. After the Second World War, many veterans received training at agricultural colleges as professional breeders (Archibald 1949), and the breeding efforts accelerated with many cultivars released and more breeding programs were established across Canada. Rapeseed oil seed breeding was a good example of the modern plant breeding expansion in Canada with success to improve oil quality (Stefansson and Downey 1995). The legislation of Plant Breeders' Rights legislation in 1990 further enhanced the breeding efforts in Canada (Slinkard and Knott 1995).

The breeding efforts for the six crops are briefly summarized in Table 4.1. Some variation exists among different crops in breeding history, method, goal, and output; however, the breeding methods were similar, particularly before 1940s. The four basic breeding methods of introduction, selection, hybridization, and backcrossing, were widely applied. Introduction and selection within landraces played an important role in the early breeding efforts. Hybridization is a procedure of deliberate intraspecific or interspecific breeding to generate variability and was widely applied to develop new cultivars. Recurrent selection with backcrossing, since the 1940s, was successful in genetic improvement of disease resistance. Since the 1990s, biotechnology and marker-assisted selection has become available and used to a limited extent in cultivar development.

The major breeding targets of all crops were adaptability, yield, early maturity, disease resistance, and quality, but they varied among the different crops and changed over time (Table 4.1). For example, spring wheat breeding before 1928 was aimed at early maturity, yield, and baking quality. With the rust epidemic in 1920–1930, the breeding targets were shifted toward developing cultivars with disease resistance. Since then, breeding efforts for disease resistance has intensified, particularly in oat (McKenzie and Harder 1995). While yield has always been the primary goal of any breeding program since the 1950s, end-use quality traits have also been considered. For example, one of the main goals of rapeseed breeding was to decrease erucic acid content and improve rapeseed oil/meal quality for human consumption (Downey 1964). In wheat, there are many classes of eastern and western Canada wheat, respectively, to address requirements of the end-users (http://www.grainscanada.gc.ca/wheat-ble/classes/classes-eng.htm).

4.3 Case Studies in Canadian Crop Gene Pools

We have performed 10 genetic diversity analyses using different sets of molecular markers to monitor six crop gene pools (Table 4.2). The basic procedure for these analyses was to select representative cultivars from a germplasm collection held at Plant Gene Resources of Canada, sample seeds randomly from each cultivar, plant them in a greenhouse, collect leaf tissue, extract DNA, perform PCR using selected primers, collect marker data, and analyze marker data for various diversity components. These analyses may have differed in cultivar sampling, marker application, and diversity estimation. All of the analyses were centered on addressing a key question of the crop gene pool: Does modern plant breeding in Canada reduce allelic diversity at individual loci, shift the genetic background, or narrow the genetic diversity?

Table 4.1 Brief summary of breeding efforts before 1996 in Canada for the six crops analyzed in this chapter

Crop	Brief history	Breeding method	Primary breeding focus		Released cultivars (years)
			Agronomy/quality	Resistance	
Wheat	Wheat production as early as 1605; public breeding in 1886	Introduction; selection; hybridization; double-haploid; marker-assisted selection	Yield; early maturing; milling quality; protein	Rust; bunt; loose smut; *Fusarium*; stem sawfly; drought	89 (1845–1994)
Oat	Oat production as early as 1605; public breeding in the late 1800s	Introduction; selection; hybridization; backcrossing	Yield; early maturing; protein; milling quality	Smut; rust; BYDV	43 (1886–1992)
Flax	Flax cultivation as early as 1617; public breeding in early 1900s	Introduction; selection; hybridization; double-haploid; biotechnology	Yield; oil quality	*Fusarium* wilt; rust	34 (1910–1995)
Potato	Potato production in 1888; public breeding in 1934	Introduction; selection; hybridization; clonal propagation	Yield; disease-free stock; processing quality	Late blight; mosaic; common scab; leaf roll	59 (1888–1982)
Soybean	Public breeding in 1893	Introduction; selection; pedigree; backcrossing; modified single seed descent	Yield; early maturing; natto-type; tofu type; yellow hilum; protein	Root rot	191 (1923–1992)
Canola	Rapeseed production in 1939; public breeding in 1944	Recurrent selection; selfing, synthetic and half-seed techniques; male sterility	Yield; early maturing; oil quality	White rust; blackleg; triazine herbicide	15 (1954–1988)

Note The information in this table was largely obtained from Anstey (1986), Marshall (1989), and Slinkard and Knott (1995)

Table 4.2 List of 10 assessments from 1999 to 2009 on genetic diversity changes in six Canadian crop gene pools

Analysis	Crop[a]	Marker	Diversity change[b]	Allelic reduction	Shift[c]
Fu et al. 2005	Wheat, 75, 1845–2004	31 SSRs	R by AMOVA*, but M by similarity*	After 1970s*	GS
Fu et al. 2006	Wheat, 75, 1845–2004	37 EST–SSRs	R by AMOVA*	After 1990s*	GS
Fu et al. 2009c	Wheat, 75, 1845–2004	370 SSRs	R by AMOVA*	After 1930s*	GS
Fu et al. 2003a	Oat, 96, 1886–2001	30 SSRs	M by similarity*	After 1970s*	GS
Fu et al. 2004	Oat, 96, 1886–2001	442 AFLPs	M by PFL*	–	–
Fu et al. 2003b	Flax, 28, 1910–1998	84 RAPDs	M by PFL*	–	–
Fu et al. 2009a	Canola, 10 (*B. rapa*), 1940–2001	18 SSRs	R by similarity*	After 1960s	–
Fu et al. 2010	Canola, 10 (*B. napus*), 1943–1992	22 SSRs	R by similarity*	After 1960s	–
Fu et al. 2007	Soybean, 45, 1934–2001	37 SSRs	I by AMOVA*	–	NGS
Fu et al. 2009b	Potato, 68, 1919–2002	36 SSRs	M by AMOVA*	–	NGS

[a] The number of assayed cultivars is shown after the crop, followed by the period of cultivar release

[b] *R* reduction, *M* maintained, *I* increased, *AMOVA* analysis of molecular variance, and *PFL* proportion of fixed loci

[c] *GS* genetic shift and *NGS* no genetic shift

*Result with a statistical test of significance. – Result not available

4.3.1 Wheat

Wheat is the most important cultivated crop in Canada. Wheat breeding began in 1886, has so far released hundreds of cultivars, and has generated a significant impact on Canadian agriculture (DePauw et al. 1995). Briefly, breeding goals in wheat have changed from adaptation and quality before 1940, resistance to biotic and abiotic stresses such as rust from 1940 to 1990, to end-use quality such as increased grain protein after 1990. The accompanying breeding methods ranged from introduction, mass selection, hybridization, backcrossing, and double-haploidy to marker-assisted selection.

We selected 75 Canadian hard red spring wheat cultivars released from 1845 to 2004 and performed three diversity analyses using (1) 31 genomic SSR markers

(Fu et al. 2005), (2) 37 EST-derived SSR markers (Fu et al. 2006), and (3) 370 genomic SSR markers (Fu and Somers 2009). The assayed cultivars represented early introductions and those cultivars released over the more than 100 years from several main wheat breeding programs in Canada. To facilitate the diversity analyses, these cultivars were grouped based on their periods of release (prior 1910, 1911–1929, 1930–1949, 1950–1969, 1970–1989, and 1990–2004).

The diversity analyses revealed several patterns of genetic changes over time. First, significant allelic reduction started as early as the 1930s (Fig. 4.1). Considering 2010 SSR alleles detected in 20 of the earliest released cultivars, 38 % of them were retained, 18 % are new, and 44 % were lost in the 20 most recent cultivars. The net reduction of the total SSR variation in the 20 recent cultivars was 17 % (Fu and Somers 2009). Interestingly, allelic reduction occurred in every part of the wheat genome and a majority of the reduced alleles resided in only a few early cultivars. Second, a significant genetic shift was also observed in the gene pool in response to the long-term breeding pressure (Fig. 4.2a). Third, these allelic changes in the gene pool were associated with long-term wheat trait improvements (Fu and Somers 2011). Comparing results among three analyses revealed essentially the same patterns of genetic changes in the gene pool; however, the EST-derived SSR markers displayed smaller allelic changes than the genomic SSR markers (Fu et al. 2005, 2006) and the genome-wide sampling increased the resolution for assessing allelic changes over time (Fu and Somers 2009).

These patterns of genetic changes in the wheat gene pool are not surprising, as the breeding was largely limited to a narrow range of wheat germplasm with only three major introgressions as reflected in three ancestral families (Marquis in 1908; introduced Thatcher introduced in 1935; and Neepawa in 1969) and the selection was intensified over time to meet market class requirements of bread wheat (McCallum and DePauw 2008).

4.3.2 Oat

Oat breeding in Canada began in the late 1800s to meet the demand of the growing Canadian livestock industry (McKenzie and Harder 1995). Selection and hybridization from the 1900s to the 1930s generated several highly productive cultivars such as ‘Liberty’ and ‘Legacy.’ Backcrossing of rust resistant genes into ‘Rodney’ and ‘Pendek’ in the 1960s greatly improved rust resistance in cultivars such as ‘Harmon,’ ‘Dumont,’ and ‘Robert.’ Introduction of germplasm from other oat species than *Avenasativa* in the 1970s further enhanced the development of many cultivars with genes for resistance to both stem rust and crown rust. Overall, the breeding efforts have developed over 43 registered cultivars, many of which have made significant impacts on the economy of western Canada (McKinnon 1998).

We selected 96 Canadian oat cultivars released from 1886 to 2001 and performed two diversity analyses using 30 SSR (Fu et al. 2003a) and 442 AFLP markers (Fu et al. 2004), respectively. These cultivars were selected based on

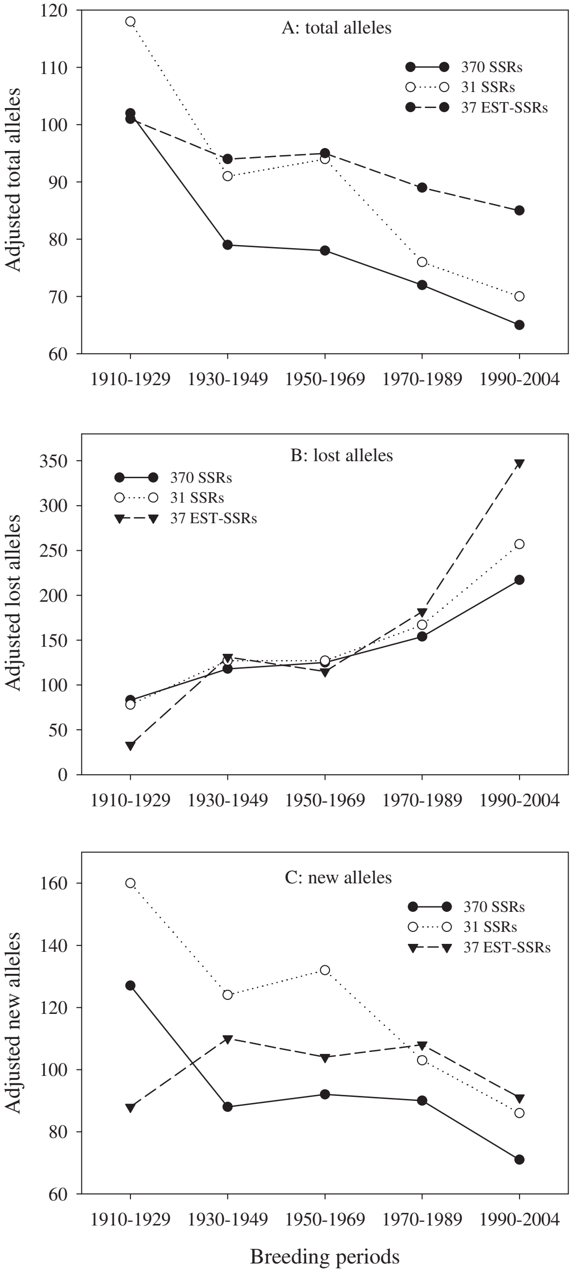

Fig. 4.1 Allelic changes in 75 Canadian hard red spring wheat cultivars released over the six breeding periods, as revealed by three genetic diversity analyses (see Fu et al. 2005, 2006; Fu and Somers 2009). For ease of diversity comparison among cultivar groups of variable size, the adjusted alleles are presented. They are calculated as the observed allele count adjusted by 100 over the expected allele count under a random scenario with a given group size, in which the expected allele count was obtained from 10,000 random permutations

pedigree, agronomic and economic importance, and representation of different eras of oat breeding in Canada. The cultivars were grouped based on their release periods (pre-1930, 1930s, 1940s, 1950s, 1960s, 1970s, 1980s, and 1990s) for diversity analyses.

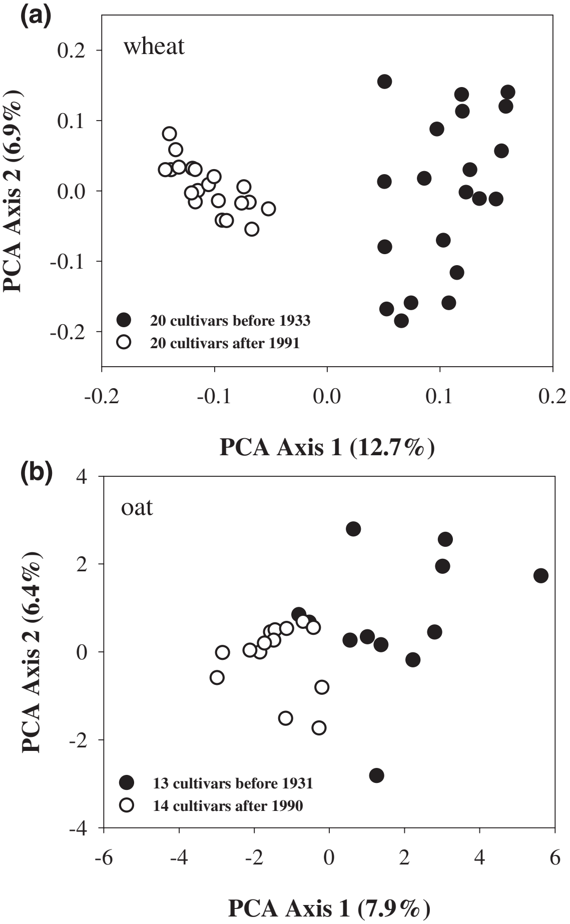

Fig. 4.2 Genetic shift detected from early to recent cultivars in the Canadian improved gene pools of wheat and oat, as illustrated in the principal component plots of respective SSR data (adapted from Fu et al. 2003a; Fu and Somers 2009)

The diversity analyses revealed three major findings. First, there were four marked patterns of allelic change detected at single loci over the past century of the Canadian oat breeding: Decreasing, Shifting, Increasing, and Random (Fig. 4.3). More loci with decreasing allelic pattern supported the reduction tendency of genetic diversity in the Canadian oat gene pool over years (Fu et al 2003a). Agenetic shift occurred in the oat gene pool (Fig. 4.2b), as evidenced with some loci (Fig. 4.3d). Second, a significant allelic reduction was found for the cultivars released after 1970 (Table 4.2; Fu et al 2003a). Third, the SSR analysis (Fu et al. 2003a) was more informative than the AFLP analysis in the assessment of diversity changes, and the allele-based diversity measure is more informative than those similarity-based diversity estimates (Fu et al. 2004).

The oat SSR analysis in 2003 revealed the first, clear-cut molecular evidence for the negative impacts of modern oat breeding on the oat genetic diversity. Genetic changes occurred at individual loci and allelic loss started after 1970. The evidence, along with those in the Canadian wheat gene pool (Fu and Somers 2009), supports the argument that modern plant breeding has reduced crop genetic diversity.

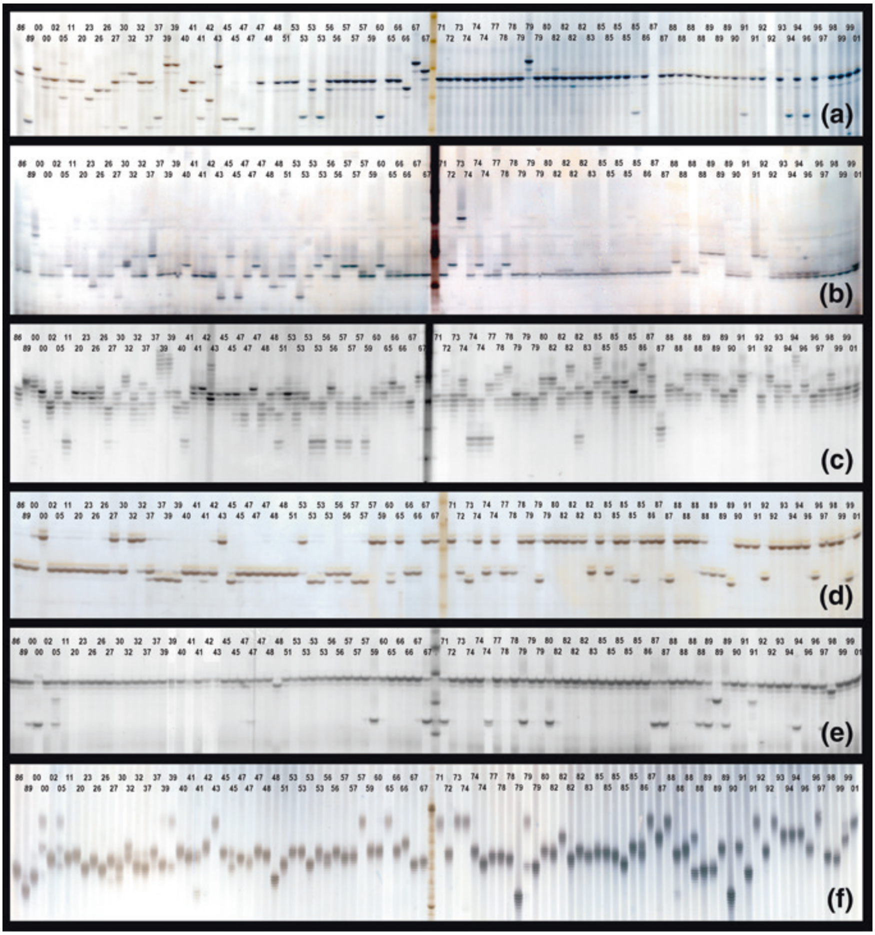

Fig. 4.3 Seven silver staining gels that illustrate four patterns of allelic change over the past 115 years of Canadian oat breeding. **a–c** Decreasing (detected by SSR primers AM31, AM38, AM1, respectively); **d** Shifting (by AM42); **e** Increasing (by AM102); and **f** Random (by AM3). In each gel, samples for 96 Canadian oat cultivars are arrayed from left to right in a chronological order, from 1886 to 2001; only the last two digits of the release year are given for each cultivar. The DNA ladder is shown between two cultivars released in 1967 and 1971 (adapted from Fu et al. 2003a)

4.3.3 Flax

Canadian flax breeding started in the early 1900s at the Central Experimental Farm, Ottawa, with release of three cultivars in 1910. The breeding effort was expanded into western Canada in the 1920s to develop cultivars with increased seed yield and improved oil quality. Introduction, selection and hybridization were among the major breeding methods applied to develop cultivars, although biotechnology was applied in the late 1990s to develop genetically modified flax.

The long-term breeding efforts toward increasing seed yield, improving oil quality, selecting for resistance to rust and wilt, and decreasing days to maturity, have produced more than 30 registered cultivars (Kenaschuk and Rowland 1995).

A RAPD analysis of 28 Canadian flax cultivars released from 1910 to 1998 was performed in 2002 (Fu et al. 2003b). The assayed cultivars represented the effort in three breeding periods: Period 1 for the cultivars released before 1932; Period 2 from 1932 to 1980; and Period 3 after 1980. However, these cultivars displayed only a trend of genetic erosion over the 90 years, measured by the proportion of fixed recessive RAPD loci. Specifically, the intensive selection for rust resistance after 1947 increased the average proportion of fixed recessive RAPD loci in the cultivars released later. In addition, the average RAPD similarity in the flax gene pool was continuously decreasing over the past century (Fu et al. 2003b). These findings suggest that genetic narrowing occurred in the Canadian flax gene pool.

4.3.4 Potato

Potato breeding in Canada began in 1888 with the goal to improve potato yield of early introductions (Turner and Molyneaux 2004). Since then, the breeding efforts have gone through several major stages from early selection and adaptation, selection for disease resistance, obtaining disease-free stock, to selection for processing quality (Anstey 1986). Substantial improvements have been made in traits associated with production, utilization, disease control, in vitro culture, and processing quality (Tarn et al. 1992). Hundreds of potato cultivars have been developed, many of which have had significant impacts on Canadian agriculture (Anstey 1986; Turner and Molyneaux 2004).

We assayed 114 Canadian and 55 exotic potato accessions released from 1910 to 2002 using 36 SSR primer pairs (Fu et al. 2009). It was found that the proportion of total SSR variation occurring between Canadian and exotic germplasm was 0.6 %; among the Canadian cultivars of four major breeding periods 2.7 %; among heirloom varieties, modern cultivars and elite breeding lines 4 %; and between tetraploid and diploid lines 3.7 %. Slightly more diversity was found for exotic, than the Canadian, germplasm. The modern cultivars displayed slightly more diversity than the heirloom varieties and the early cultivars revealed slightly more variation than the recent ones. The analysis with only the Canadian cultivars and breeding lines revealed only a trend of genetic erosion over the whole modern breeding history (Fu et al. 2009). These findings demonstrate the narrow genetic base of the Canadian potato germplasm. Interestingly, such genetic narrowing persists in spite of the use in breeding of Andean cultivated potatoes of groups Phureja, Andigena, and Tuberosum and as many as 14 wild species (Spooner and Salas 2006; Hirsch et al. 2013).

4.3.5 Soybean

Soybean breeding in Canada began in 1893 with the goal to improve forage yield of early introductions (Beversdorf et al. 1995). Since then, the breeding efforts have gone through several major stages from early selection and adaptation, to expansion and to commercialization. Substantial improvements have been made in disease control, maturity, seed yield, and quality traits (Morrison et al. 2000). So far, hundreds of soybean cultivars have been developed, many of which have had significant impacts on the economy of eastern Canada (Beversdorf et al. 1995).

We selected 45 Canadian soybean cultivars released from 1934 to 2001 and 37 exotic germplasm accessions as the comparison for a diversity analysis using 37 SSR markers (Fu et al. 2007). It was found that the proportion of total SSR variation residing between exotic and Canadian germplasm was 9 %; among the Canadian cultivars of three breeding periods 10 %; and between the cultivars of maturity groups 0 and 00 4 %. Greater allelic diversity was found for exotic, than the Canadian, germplasm. More diversity was observed in the cultivars of the recent, than the early, breeding period. More specifically, the cultivars released after 1990 had slightly more diversity than those prior to 1970. These results indicate that the Canadian soybean gene pool, although genetically narrow, maintained a broad degree of genetic diversity.

4.3.6 Canola

Canola, a low erucic acid, low glucosinolate form of rapeseed (Stefansson and Downey 1995), is a great achievement of modern plant breeding in Canada (Busch et al. 1994). Small-scale *Brassica napus* breeding efforts started in 1944, but it was expanded significantly in the 1960s to include other *Brassica* species (Stefansson and Downey 1995). The first Canadian licensed *B. napus* and *B. rapa* cultivars were Golden in 1954 and Echo in 1964, respectively. The public breeding programs released more than 15 cultivars before 1996. Since the 1990s, the canola breeding in private sector has accelerated and produced more than 100 herbicide-tolerant cultivars.

The rapeseed oilseed crop in western Canada has undergone extensive genetic modifications on oil quality traits through conventional breeding methods (Stefansson and Downey 1995); however, the developed rapeseed germplasm may have reduced genetic diversity. We selected 10 elite *B. napus* summer rape and 10 elite summer *B. rapa* cultivars from 1940 to 2001 for diversity analyses with 18–22 SSR markers, and found that the overall genetic diversity was largely unchanged over the years of cultivar release (Fu and Gugel 2009, 2010). However, significant decreases in the number of SSR alleles and average dissimilarities were found over the 60 years of breeding outcrossing *B. rapa*. Similarly, a trend of decline in SSR variation was also observed over the years of breeding self-compatible *B. napus*. These findings are aligned with the argument that the extensive selection in conventional canola breeding for oil quality traits could narrow the crop genetic diversity.

4.4 Limitation and Implication

Our genetic diversity analyses have revealed variable patterns and degrees of diversity decline in the six Canadian crop gene pools. How general are these findings with respect to other plant breeding programs? What can be learned from these diversity analyses? To answer these questions, we will discuss the related issues with our diversity analyses and their implications for future efforts.

4.4.1 Issues

Our diversity analyses have several major issues that may affect the interpretations of our research findings. First, these analyses applied different marker systems that would affect the comparison of genetic changes within and among different gene pools. For example, the SSR analysis of the oat gene pool showed a better resolution of genetic changes than the AFLP analysis (Fu et al. 2003a, 2004). The genomic SSR markers (Fu et al. 2005) were more sensitive for wheat genetic change assessment than the EST-derived SSR markers (Fu et al. 2006). Second, insufficient genome coverage with application of a limited number of markers may have diluted the diversity analyses. For example, the analysis of 370 wheat SSR markers that were widely distributed over all 21 wheat chromosomes (Fu and Somers 2009) was more informative in detecting the allelic changes than those with 31 genomic SSR (Fu et al. 2005) or 37 EST-SSR markers (Fu et al. 2006). Third, not all of the diversity measures used were equally informative, and the measure of allelic change was more informative than the similarity-based diversity measure. For example, a significant decrease in SSR alleles was found over the 60 years of breeding outcrossing *B. rapa*, but the overall genetic diversity was largely maintained in these assayed cultivars (Fu and Gugel 2009). Fourth, bias existed in cultivar representation and grouping for breeding periods, and unbalanced group sizes may have also introduced bias into the assessment of diversity changes.

Considering these issues, we would argue for the need to establish a standard procedure for a crop genetic diversity analysis of this nature to make the diversity comparison among crop gene pools more feasible. Ideally, allelic diversity should be measured and compared (Caballero and Rodríguez-Ramilo 2010), and a genome-wide sampling should be done with informative genetic markers such as SSR or single nucleotide polymorphism (Jiao et al. 2012; Hirsch et al. 2013; Fu et al. 2014). To make a crop genetic diversity analysis more informative, we may need to consider all the related issues discussed in detail by Fu (2006), minimize possible biases at every aspect, and focus on specific long-term breeding programs. With the advances in next generation sequencing, it is more feasible nowadays to perform a genome-wide diversity analysis of a crop gene pool through genotyping by sequencing (Fu and Peterson 2011; Poland and Rife 2012; Fu et al. 2014) for a better understanding of the diversity impacts of modern plant breeding.

4.4.2 Implications

Given that these limitations may have accounted for much variation in revealed patterns of diversity change, it is difficult to generalize these diversity patterns to other breeding programs in Canada, and even more challenging to do this for programs in other countries. However, several lines of reasoning for it are worth mentioning here. First, the six assayed crops represent cereals, oilseeds, and specialty crops, and the established gene pools should generally reflect the genetic consequences of the long-term breeding efforts in Canada. Second, the assayed gene pools largely represent self-fertilizing crops. The Canadian breeding efforts for these crops applied essentially the same breeding methods to reach similar goals, particularly before the 1990s. Thus, they should have similar breeding history and compatible genetic consequences, as revealed with the wheat and oat crops. Third, the breeding efforts and selection intensities varied among different crops over various breeding periods. Such variation may help to explain in part the variable patterns of diversity changes revealed from these analyses. Fourth, some of these diversity patterns may be found in the crop gene pools established in other developed countries, as the cereal breeding in Canada may not differ much in breeding method and goal from those in other countries such as the USA oat breeding program (Holland 1997).

The revealed patterns of genetic erosion are consistent with our common knowledge about the diversity reduction from modern plant breeding. These findings have significant practical implications for both plant germplasm conservation and genetic improvement. The need is obvious for continuous efforts to conserve released cultivars and germplasm from public breeding, especially older cultivars. Public gene banks like Plant Gene Resources of Canada have and will continue to play an important role in acquisition and conservation of elite germplasm released over the years. Substantial genetic variation still exists within some gene pools such as wheat and oat, even soybean, and selections within these gene pools are still possible, although it may be limited in the gene pools of canola and potato. Thus, it is important to widen the genetic bases of these breeding gene pools for sustainable agriculture. Fortunately, Canadian breeders have made some efforts to build more robust genetic bases, as an example, in the potato and soybean breeding programs (Fu et al. 2007, 2007).

4.5 Conclusions

Our genetic diversity analyses, although with some limitations, have revealed a new, clear picture that the Canadian crop gene pools displayed variable patterns and degrees of genetic diversity decline over the past 100 years of breeding effort. Substantial allelic reduction at individual loci was observed and genetic shift usually accompanying the reduction of genetic diversity was detected, particularly in the gene pools of wheat and oat. These patterns of genetic erosion support the argument that modern plant breeding reduces crop genetic diversity. The revealed erosions have significant practical implications for both plant germplasm conservation and genetic improvement. There is a need for ongoing efforts to conserve released cultivars and germplasm from public breeding programs, especially older cultivars, so that the purged alleles are protected. With such protected resources, plant breeders have the means required to widen the genetic base of the crop breeding gene pool for sustainable agriculture.

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References

Allard RW (1999) Principles of plant breeding, 2nd edn. Wiley, New York

Anstey TH (1986) One hundred harvests: research branch, agriculture Canada, 1886–1986. Res Branch Agr Canada 27

Archibald ES (1949) Hilgendorf memorial address 1949—the story of Canadian wheat. Experimental Farm Service, Agriculture Canada, Ottawa, Ontario

Beversdorf WD, Buzzell RI, Ablett GR, Voldeng HD (1995) Soybean. In: Slinkard AE, Knott DR (eds) Harvest of gold: the history of field crop breeding in Canada. University Extension Press, Saskatoon, pp 153–166

Borlaug N (2007) Sixty-two years of fighting hunger: personal recollections. Euphytica 157:287–297

Brush SB (1999) Genetic erosion of crop populations in centers of diversity: a revision. In: Proceedings of the technical meeting on the methodology of the FAO world information and early warning system on plant genetic resources, held at the Research Institute of Crop Production, Prague, Czech Republic, 21–23 June 1999 (http://apps3.fao.org/wiews/Prague/Paper5.jsp)

Busch L, Gunter V, Mentele T, Tachikawa M, Tanaka K (1994) Socializing nature: technoscience and the transformation of rapeseed into canola. Crop Sci 34:607–614

Caballero A, Rodríguez-Ramilo S (2010) A new method for the partition of allelic diversity within and between subpopulations. Conserv Genet 11:2219–2229

Campbell AB, Shebeski LH (1986) Wheat in Canada-past and present. In: Slinkard AE, Fowler DB (eds) Wheat production in Canada—a review. University of Saskatchewan, Saskatoon, pp 1–14

Clunier-Ross T (1995) Mangolds, manure and mixtures: the importance of crop diversity on British farms. Ecologist 25:181–187

Cox TS, Kiang YT, Gorman MB, Rodgers DM (1985) Relationship between coefficient of parentage and genetic similarity indices in soybean. Crop Sci 25:529–532

DePauw RM, Boughton GR, Knott DR (1995) Hard red spring wheat. In: Slinkard AE, Knott DR (eds) Harvest of gold: the history of field crop breeding in Canada. University Extension Press, Saskatoon, pp 5–35

Donini P, Law JR, Koebner RMD, Reeves JC, Cooke RJ (2000) Temporal trends in the diversity of UK wheat. Theor Appl Genet 100:912–917

Downey RK (1964) A selection of *Brassica campestris* L. containing no erucic acid in its seed oil. Can J Plant Sci 44:295

Duvick DN (1984) Genetic diversity in major farm crops on the farm and in reserve. Econ Bot 38:161–178

Fu YB (2005) Genetic erosion in the Canadian gene pools of flax, oat and wheat. CBD Technical Series No. 17:19–21

Fu YB (2006) Impact of plant breeding on genetic diversity of agricultural crops: searching for molecular evidence. Plant Genet Resour 4:71–78

Fu YB, Gugel RK (2009) Genetic variability of Canadian elite cultivars of summer turnip rape (*Brassica rapa* L.) revealed by simple sequence repeat markers. Can J Plant Sci 89:865–874

Fu YB, Gugel RK (2010) Genetic diversity of Canadian elite summer rape (*Brassica napus* L.) cultivars from the pre- to post-canola quality era. Can J Plant Sci 90:23–33

Fu YB, Peterson GW (2011) Genetic diversity analysis with 454 pyrosequencing and genomic reduction confirmed the eastern and western division in the cultivated barley gene pool. Plant Genome 4:226–237

Fu YB, Somers DJ (2009) Genome-wide reduction of genetic diversity in wheat breeding. Crop Sci 49:161–168

Fu YB, Somers DJ (2011) Allelic changes in bread wheat cultivars were associated with long-term wheat trait improvements. Euphytica 179:209–225

Fu YB, Peterson GW, Scoles G, Rossnagel B, Schoen DJ, Richards KW (2003a) Allelic diversity changes in 96 Canadian oat cultivars released from 1886 to 2001. Crop Sci 43:1989–1995

Fu YB, Rowland GG, Duguid S, Richards KW (2003b) RAPD analysis of 54 North American flax cultivars. Crop Sci 43:1510–1515

Fu YB, Kibite S, Richards KW (2004) Amplified fragment length polymorphism analysis of 96 Canadian oat cultivars released between 1886 and 2001. Can J Plant Sci 84:23–30

Fu YB, Peterson GW, Richards KW, Somers D, DePauw RM, Clarke JM (2005) Allelic reduction and genetic shift in the Canadian hard red spring wheat germplasm released from 1845 to 2004. Theor Appl Genet 110:1505–1516

Fu YB, Peterson GW, Yu JK, Gao LF, Jia JZ, Richards KW (2006) Impact of plant breeding on genetic diversity of the Canadian hard red spring wheat germplasm as revealed by EST-derived SSR markers. Theor Appl Genet 112:1239–1247

Fu YB, Peterson GW, Morrison MJ (2007) Genetic diversity of Canadian soybean cultivars and exotic germplasm revealed by simple sequence repeat markers. Crop Sci 47:1947–1954

Fu YB, Peterson GW, Richards KW, Tarn TR, Percy JE (2009) Genetic diversity of Canadian and exotic potato germplasm revealed by simple sequence repeat markers. Am J Potato Res 86:38–48

Fu YB, Cheng B, Peterson GW (2014) Genetic diversity analysis of yellow mustard (*Sinapis alba* L.) germplasm based on genotyping by sequencing. Genet Resour Crop Evol 61:579–594

Hedrick PW (2000) Genetics of populations, 2nd edn. Jones and Bartlett Publishers, Sudbury, MA

Hirsch CN, Hirsch CD, Felcher K, Coombs J, Zarka D et al (2013) Retrospective view of North American potato (*Solanumtuberosum* L.) breeding in the 20th and 21st centuries G3 (Bethesda) 3:1003–1013

Holland JB (1997) Oat improvement. In: Kang MS (ed) Crop improvement for the 21st century. Research Signpost, Trivandrum, pp 57–98

Jiao Y, Zhao H, Ren L, Song W, Zeng B, Guo J, Wang B, Liu Z, Chen J, Li W, Zhang W, Xie S, Lai J (2012) Genome-wide genetic changes during modern breeding of maize. Nat Genet 44:812–815

Kenaschuk EO, Rowland GG (1995) Flax. In: Slinkard AE, Knott DR (eds) Harvest of gold: the history of field crop breeding in Canada. University Extension Press, Saskatoon, pp 173–176

Marshall G (1989) Flax: breeding and utilisation. Kluwer Academic Publishers, Dordrecht

McCallum BD, DePauw RM (2008) A review of wheat cultivars grown in the Canadian prairies. Can J Plant Sci 88:649–677

McKenzie RIH, Harder DE (1995) Oat. In: Slinkard AE, Knott DR (eds) Harvest of gold: the history of field crop breeding in Canada. University Extension Press, Saskatoon, pp 98–112

McKinnon D (1998) Oat: Situation and outlook for 1998–1999. Biweekly Bull Agri Agri-Food Canada 11:1–4

Morrison MJ, Voldeng HD, Cober ER (2000) Agronomic changes from 58 years of genetic improvement of short-season soybean cultivars in Canada. Agron J 92:780–784

National Research Council (1972) Genetic vulnerability of major crops. The National Academy of Sciences, Washington DC

Poland JA, Rife TW (2012) Genotyping-by-sequencing for plant breeding and genetics. Plant Gen 5:92–102

Rauf S, Teixeira da Silva JA, Khan AA, Naveed A (2010) Consequences of plant breeding on genetic diversity. Int J Plant Breed 4:1–21

Rodgers DM, Murphy JP, Frey KJ (1983) Impact of plant breeding on the grain yield and genetic diversity of spring oats. Crop Sci 23:737–740

Slinkard AE, Knott DR (1995) Harvest of gold: the history of field crop breeding in Canada. University Extension Press, Saskatoon

Spooner DM, Salas A (2006) Structure, biosystematics and genetic resources. In: Gopal J, Khurana SMP (eds) Handbook of potato production, improvement, and postharvest management. Food Prod, Binghamton, pp 1–39

Stefansson BR, Downey RK (1995) Rapeseed. In: Slinkard AE, Knott DR (eds) Harvest of gold: the history of field crop breeding in Canada. University Extension Press, Saskatoon, pp 140–152

Swanson T (1996) Global values of biological diversity: the public interest in the conservation of plant genetic resources for agriculture. Plant Genet Res Newsl 105:1–7

Tanksley SD, McCouch SR (1997) Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277:1063–1066

Tarn TR, Tai GCC, de Jong H, Murphy AM, Seabrook JEA (1992) Breeding potato for long-day, temperate climates. Plant Breed Rev 9:217–232

Tripp R (1996) Biodiversity and modern crop varieties: sharpening the debate. Agr Hum Values 13:48–63

Turner S, Molyneaux H (2004) Agricultural science, potato breeding, and the Fredericton Experimental Station, 1912–1966. Acadiensis 33:1–25

van de Wouw M, van Hintum T, Kik C, van Treuren R, Visser B (2010) Genetic diversity trends in twentieth century crop cultivars: a meta analysis. Theor Appl Genet 120:1241–1252

Vellve R (1993) The decline of diversity in European agriculture. Ecologist 23:64–69