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Impact of plant breeding on genetic diversity of agricultural crops: searching for molecular evidence

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Abstract

There is a long-standing concern that modern plant breeding reduces crop genetic diversity, which may have consequences for the vulnerability of crops to changes in pests, diseases, climate and agricultural practices. Recent molecular assessments of genetic diversity changes in existing genepools of major agricultural crops may shed some light on the impact of plant breeding on crop genetic diversity. Reviewing published assessments revealed different impacts of plant breeding on improved genepools, not only narrowing or widening their genetic base, but also shifting their genetic background. In general, the genome-wide reduction of crop genetic diversity accompanying genetic improvement over time is minor, but allelic reduction at individual chromosomal segments is substantial. More efforts are needed to assess what proportion of lost alleles is associated with undesirable traits.

Keywords: allelic loss; cultivated plants; genetic diversity; genetic erosion; molecular markers; plant breeding

Introduction

Concern has often been expressed that modern plant breeding reduces crop genetic diversity (Duvick, 1984; Vellve, 1993; Clunier-Ross, 1995; Tripp, 1996; Tanksley and McCouch, 1997). This concern has some justification. First, many new cultivars are derived from crosses among genetically related modern cultivars and genetically more variable, but less productive, primitive ancestors are rarely included. These types of crosses, if continued over the long term, will eventually narrow the genetic base of breeding materials (De Koeyer *et al.*, 1999; Labate *et al.*, 1999; Yu and Bernardo, 2004; Hinze *et al.*, 2005). Second, with the extensive use of one or more closely related cultivars in large farm fields, crop uniformity in height, maturity and other phenotypic traits is evident (Cox *et al.*, 1986; van Esbroech *et al.*, 1998), strengthening the impression of genetic narrowing. Third, reducing genetic diversity of crops renders them more vulnerable to disease and insect epidemics and jeopardizes the potential for sustained genetic improvement over the long term (National Academy of Sciences, 1972; Clunier-Ross, 1995; Food and Agriculture Organization, 1998). This risk has been well demonstrated with the outbreak of Southern corn leaf blight in 1970 due to the extensive use of a single genetic male sterility factor genetically linked to disease susceptibility (Ullstrup, 1972). However, clear-cut evidence for the negative impact of plant breeding on the plant genome is largely lacking (Donini *et al.*, 2000), and an argument also exists for the role of plant breeding in widening crop genetic diversity (Witcombe, 1999).

Efforts have been made to provide some objective assessment of the changes that have occurred in genetic diversity of the major agricultural crop species (Duvick, 1984; Swanson, 1996; Tripp, 1996; Donini *et al.*, 2000). Earlier assessments were largely based on phenotypic (Rodgers *et al.*, 1983; Ortiz *et al.*, 2003) and pedigree data (Cox *et al.*, 1985; van Beuningen and Busch,

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1997). The substantial progress achieved in improving yield and other traits matches the shrinkage in the genetic basis of improved genepools (Duvick *et al*., 2004; Smith *et al*., 2004). However, pedigree assessments rely on a number of unrealistic assumptions, such as equal parental contributions, and do not positively identify genetic materials in the pedigree lineages, either qualitatively or quantitatively (Soleimani *et al*., 2002; Duvick *et al*., 2004), thus offering a limited resolution on the impact of plant breeding on the plant genome. Advances in molecular marker technology have made crop diversity assessments more attainable and informative than before. Molecular assessments of diversity have used markers such as random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs) and simple sequence repeats (SSRs). However, no consensus has been reached as to the overall impact of modern plant breeding on crop genetic diversity.

This paper represents a literature survey conducted to identify molecular evidence of the impact of modern plant breeding on crop genetic diversity. The findings are related to the following questions: (i) Does plant breeding affect overall (or genome-wide) genetic diversity of agricultural crops? (ii) Does plant breeding cause allelic reduction at individual loci? (iii) Does plant breeding shift the genetic background of an improved genepool? To facilitate future assessments, issues associated with the molecular analyses of genetic diversity change in improved genepools of cultivated plants are discussed.

Molecular evidence for the impact of plant breeding

The survey considered only applications of RAPDs, AFLPs and SSRs to assess genetic diversity change in improved genepools of cultivated crops, and comprised 23 articles published from 2000 to 2005 in eight journals (Table 1). While the survey attempted to be exhaustive, it is recognized that some relevant studies may not have been identified. The articles investigated the improved genepools of wheat, maize, barley, oat and flax in various countries over different breeding periods, including a maize genepool established in the USA since 1930. The approaches to assess genetic diversity changes were essentially common to all the studies. These involved the choice of a representative group of cultivars released over time from specific breeding efforts and/or regional breeding programmes, the genotyping of these cultivars using available molecular markers and a diversity analysis of these data using single or multiple diversity measures. However, there was a substantial degree of variation in the criteria applied for selecting genepools (i.e. cultivars from specific or regional breeding programmes), in the method for sampling diversity within cultivars (such as individual or bulked samplings), in analysing diversity changes (such as the use of a similarity coefficient or the enumeration of alleles) and in the statistical testing of diversity change. Because of these differences, generalizations are difficult to make. Thus, the findings have been summarized separately in an attempt to determine whether overall genetic diversity or allelic diversity in an improved genepool was maintained, increased or decreased over time. A further issue that could be addressed was whether there was any commonality between crop species in the pattern of genetic shift over time.

Overall genetic diversity

Changes in overall genetic diversity were reported in 19 studies, but various methods were applied to measure it, including (i) analyses of molecular variance (AMOVA) to calculate pairwise molecular differences of grouped cultivars; (ii) similarity methods to measure average similarities; (iii) the Rogers' modified method to estimate genetic distance; (iv) diversity indices to compare polymorphic information contents (PIC) of markers; (v) proportions of fixed marker loci (PFL) to analyse diversity trends; and (vi) principal coordinate analyses (PCO) to assess diversity change patterns. These measures may not be equally sensitive to plant breeding practice and thus are not necessarily equally informative. As it is difficult to properly weigh the findings of these studies, we simply assumed in this summary that each applied diversity measure truly reflected the genetic diversity of grouped cultivars.

Eleven studies showed that the overall genetic diversities of wheat, barley, maize and flax cultivars released over time remained relatively unchanged (Table 1); of these, nine assessments were supported by applied statistical tests. Four studies showed an increase of genetic diversity in several genepools of wheat either over the entire breeding effort or during some specific breeding periods; this increase was statistically significant in three of these studies. Seven studies demonstrated a reduction of genetic diversity in wheat and maize genepools over time, and in six of these studies the reduction was statistically significant. Thus, variable impacts of plant breeding on crop genetic diversity have been observed and appear to accord well with the changes reported in the genetic diversity of four major European crops (Reeves *et al*., 2004).

Major efforts have been made to assess the diversity changes in improved genepools of wheat established all over the world and different breeding programmes were reported to have had varying impacts on overall genetic diversity. It is not clear how general these

Table 1. List of 23 studies using RAPDs, AFLPs or SSRs to assess genetic diversity changes in improved genepools of cultivated wheat, maize, barley, oat and flax

Reference	Programme	Crop[a]	Marker	Diversity change[b]	Allelic reduction	Other[c]
Roussel *et al.*, 2005	Europe	480 wheats, 1840–2000	39 SSRs	–	18% after 1990s	–
Christiansen *et al.*, 2002	Nordic region	75 wheats, 1901–1993	47 SSRs	I before 1940/R after by AMOVA*	–	–
Donini *et al.*, 2000	UK	55 wheats, 1934–1994	84 AFLPs/14 SSRs	M by AMOVA*	–	GS
Roussel *et al.*, 2004	France	559 wheats, 1800–2000	42 SSRs	–	25%	NGS
Khlestrina *et al.*, 2004	Siberia	54 wheats, 1926–1994	23 SSRs	M by similarity	–	–
Khan *et al.*, 2005	Pakistan	20 wheats, 1933–2002	184 RAPDs	M by PFL*	–	–
Parker *et al.*, 2002	Australia	124 wheats	19 SSRs	I by AMOVA*	–	–
Hazen *et al.*, 2002	China	24 wheats, 1940s–1990s	6 SSRs	M by AMOVA*	–	–
Tian *et al.*, 2005	China	242 wheats, 1940s–1990s	245 AFLPs	R by diversity index	–	–
Fu *et al.*, 2005	Canada	75 wheats, 1845–2001	31 SSRs	R by AMOVA, but M by similarity*	After 1970s*	GS
Fu *et al.*, 2006	Canada	75 wheats, 1845–2001	37 EST-SSRs	R by AMOVA*	After 1990s*	GS
Reif *et al.*, 2005b	CIMMYT	253 wheats, 1950–1989	90 SSRs	R before 1990/I after by GD*	–	–
Manifesto *et al.* 2001	Argentina	105 wheats, 1932–1995	71 AFLPs/10 SSRs	M by PIC*	–	–
Maccaferri *et al.*, 2003	Italy	58 durum wheats, 1915–1998	70 SSRs	I by PCO	–	GS
Lu and Bernardo, 2001	USA	8 current/32 older maizes	83 SSRs	M by GD*	35%*	–
Duvick *et al.*, 2004	USA	55 maizes, 1930–2001	100 SSRs	–	12%	–
Reif *et al.*, 2005b	Europe	85 maizes, 1950–2001	55 SSRs	R by GD*	20%*	GS
Le Clerc *et al.*, 2005	France	133 maizes, 1930–2001	57 SSRs	R by AMOVA*	18% after 1996	GS
Russell *et al.*, 2000	Northern Europe	101 barleys, 1884–1998	28 SSRs	–	28%	–
Koebner *et al.*, 2003	UK	134 barleys, 1925–1995	144 AFLPs/22 SSRs	M by AMOVA*	–	GS
Fu *et al.*, 2003a	Canada	96 oats, 1886–2001	30 SSRs	M by similarity*	After 1970s*	–
Fu *et al.*, 2004	Canada	96 oats, 1886–2001	442 AFLPs	M by PFL*	–	–
Fu *et al.*, 2003b	North America	54 flaxes, 1910–1998	84 RAPDs	M by PFL*	–	–

CIMMYT, International Maize and Wheat Improvement Center.

[a] Number of cultivars assayed, with the period of cultivar release.

[b] I, increase in diversity; R, reduction; M, maintained; AMOVA, analysis of molecular variance; GD, genetic distance; PFL, proportion of fixed loci; PIC, polymorphic information content; PCO, principal coordinate analysis.

[c] Other impact: GS, genetic shift; NGS, no genetic shift.

* Results with statistical tests of significance; –, results not available.

findings for wheat are with respect to other major agricultural crops. As discussed below, these assessments are known to be full of biases from different sources and interpretations of the summarized research findings must be made cautiously, particularly for those studies showing genetically stable genepools. For example, the overall genetic diversity measured by three different similarity methods did not change significantly between older and recently released cultivars of Canadian wheat, even with a significant allelic reduction (19%) from pre-1910 wheat cultivars to those released after 1990 (Fu *et al.*, 2005). Similarly, current and older maize inbreds did not differ in overall genetic diversity, even showing a significant reduction (35%) in the average number of alleles per locus (Lu and Bernardo, 2001).

Allelic diversity

It is possible that plant breeding affects only certain regions of the plant genome, as genetic improvement normally targets specific traits or related genes located on specific chromosomal segments. Thus, assessments of allelic diversity changes should be more informative for understanding the impact of plant breeding. Ten studies assessing allelic diversity changes were part of this survey (Table 1). All showed the introduction (or addition) of new alleles by breeding into the improved genepools of wheat, maize, barley and oat over time, but more SSR alleles disappeared than were introduced, particularly in the last two to three decades. Only five of the 10 studies tested the significance of the allelic reductions, and all of these were statistically significant. The levels of allelic reduction from older cultivars to those developed in the last two decades ranged from 12 to 35%. Thus, the impact of plant breeding on allelic diversity is evident and substantial, not only in multiple crop species, but also in improved genepools established in different countries or regions (Table 1). The most convincing allelic reductions were those observed in the Canadian oat and wheat cultivars developed over the 20th century (Fu *et al.*, 2003a, 2005), in French bread wheat cultivars released between 1800 and 2000 (Roussel *et al.*, 2004) and in the commercial hybrid maize breeding programme since the 1930s in the American private sector (Duvick *et al.*, 2004). Plausible explanations proposed for these allelic reductions are the extensive use of a few elite breeding lines with strong recurrent selection after backcrossing or selfing, and the inadequate introgression of genetically diverse germplasm into breeding programmes.

Clear-cut evidence was found for allelic reduction at individual loci in the improved genepool of Canadian oat, as shown in figure 2D of Fu *et al.* (2003a) for locus AM31. Seven alleles were detected in cultivars released before 1950, but only two alleles remained in cultivars released after 1980. In the same study, five of 11 (45%) genomic SSR (gSSR) loci showed allelic reduction and two showed allelic increase. Using mapped gSSR and expressed sequence tag (EST) SSR markers, it was possible to characterize in detail the allelic reductions in non-coding and coding regions of 75 Canadian hard red spring wheat cultivars released between 1845 and 2004 (Fu *et al.*, 2005, 2006). In these assessments, 267 alleles were detected at 31 gSSR loci and 138 alleles at 37 EST-SSR loci. A significant allelic reduction was observed at three (8%) EST-SSR loci for cultivars released after 1990 and at four (13%) gSSR loci for cultivars released after 1970. Sixteen (12%) EST-SSR alleles present in the pre-1910 cultivars were undetected in cultivars released after 1990 and were distributed over 14 (38%) EST-SSR loci, while 51 (19%) gSSR alleles that had disappeared were spread over 27 (87%) gSSR loci. Thus, the disappearance of gSSR alleles was more widespread in the wheat genome than that of EST-SSR alleles. The undetected EST-SSR alleles occurred at frequencies ranging from 0.03 to 0.17 and averaged 0.07, while the frequencies of the undetected gSSR alleles ranged from 0.01 to 0.37 and averaged 0.07. Clearly, most of the EST-SSR and gSSR alleles that had disappeared were rare, but some frequent alleles also were lost. These contrasting findings demonstrate that the century-long wheat breeding effort in Canada has had considerable impact on both non-coding and coding segments of the wheat genome, although more impact was observed on non-coding chromosomal regions.

Genetic shift

Donini *et al.* (2000) were the first to report genetic shift from older to recently developed cultivars in an improved genepool; how commonly this genetic shift occurs in improved genepools of agricultural crops remains less clear. This survey identified eight studies assessing genetic shifts in improved genepools (Table 1). Genetic shift was evident in seven genepools of wheat, barley and maize established in the UK, France, Italy and Canada. The most convincing genetic shifts were those found in spring barley cultivars released from the 1920s to 1990s in the UK (Koebner *et al.*, 2003, figure 2B) and in hard red spring wheat cultivars released from 1845 to 2004 in Canada (Fu *et al.*, 2005, figure 3A). For example, the hard red spring wheat cultivars released in Canada before 1930 were genetically distinct from those developed after 1970, and cultivars of both periods did not overlap on PCA plots. These studies indicate that plant breeding can effectively change the genetic background of an improved genepool.

Challenge and opportunity

Results from this survey suggest that crop genetic diversity generally has not been significantly reduced by modern plant breeding, but that it has begun to decline. Increasing crop genetic diversity is possible provided appropriate plant breeding procedures are applied. Thus, the molecular evidence collected here does not fully support the public concern expressed on reduced crop genetic diversity. Plant breeding has generated multiple selective impacts on the plant genome; thus, the role of plant breeding in widening crop genetic diversity has not been fairly evaluated. Given that the majority of improved genepools assessed remained largely unchanged, the public concern may be somewhat over-stated especially if allelic reduction is only associated with undesirable traits for which elimination is a goal of modern plant breeding.

Because molecular studies on diversity changes in improved genepools of major agricultural crops have been insufficient, questions can be easily raised about the generality of the molecular data reported. The informativeness of the molecular assessments cited, particularly those assessing changes in overall genetic diversity, can also be questioned given that certain limitations were observed in these molecular assessments. To make future molecular assessments more informative, these issues are discussed separately in some detail and several suggestions are made below to guide further studies.

Problems

Six major issues were identified from these 23 studies, which may have compromised some diversity of the reported assessments. If not properly addressed, these problems can introduce bias in the assessment of diversity change and reduce the precision of diversity estimates, all of which affect statistical tests of significance. More effects are expected in the assessments of overall genetic diversity than allelic diversity. Thus, caution is warranted in conducting molecular diversity assessments.

First, bias may have existed in sampling cultivars from a specific breeding programme. The ideal scenario would be to assess all the cultivars released from all programmes over the breeding periods. However, some older, important cultivars may have been lost and some newly developed cultivars may not be accessible, particularly those developed in the private sector. Thus, the current practice is to select cultivars with the most production in a country or region within a breeding period and those that had a great impact on breeding programmes (Koebner *et al.*, 2003; Le Clerc *et al.*, 2005). However, such selection may favour dominant, but genetically related, cultivars.

Second, grouping the cultivars to represent specific breeding periods has been largely arbitrary and such grouping could bias the assessment of diversity change over time. Attention has not been adequately given to the separation of the change from landraces to modern plant breeding (Reif *et al.*, 2005a), which may have biased upward the negative impacts reported on the plant genome.

Third, assessments of regionally developed cultivars may not be informative since the breeding practices in specific programmes may differ for regions with cultivars having different selection pressures (Reif *et al.*, 2005b; Roussel *et al.*, 2005). Also, bias may have existed in the selection of cultivars from different regions. Thus, these problems may have diluted the resolution of the selective impacts of plant breeding (Christiansen *et al.*, 2002; Roussel *et al.*, 2005).

Fourth, not all of the molecular markers applied were equally informative for diversity assessments (Nybom, 2004). RAPD and AFLP markers are largely di-allelic, offering limited resolution to assess allelic diversity and effectively provide only a measure of genetic distance, calculated from various similarity measures (Fu *et al.*, 2003b, 2004; Khan *et al.*, 2005). SSR markers are multi-allelic, offering better resolution to assess allelic diversity changes, but not all of the SSR studies have assessed the changes of both allelic diversity and overall genetic diversity (Fu *et al.*, 2003a, 2005), thus yielding little confirmation on the overall impact of plant breeding.

Fifth, not all of the genetic diversity measures applied were equally sensitive to plant breeding practices, and different diversity measures may have different levels of accuracy and precision (Mohammadi and Prasanna, 2003; Fu *et al.*, 2005). For example, the average pairwise difference of molecular markers obtained by AMOVA may be more sensitive to the selective pressures of plant breeding than similarity measures of large standard errors, but missing data could add more bias to the former measure. Some diversity measures assumed that all the cultivars assayed were inbred, but this assumption may not always hold since within-cultivar variation in older cultivars may be substantial (Soleimani *et al.*, 2002; Maccaferri *et al.*, 2003). The amount of bias from bulking individual seedlings for each cultivar, applied in some studies, remains unclear (Fu, 2003).

Last, not all comparisons of genetic and allelic diversity were subject to statistical tests of significance (Table 1), which adds little confidence to the interpretion of the diversity changes and complicates any generalization of published findings. Allelic counts were sensitive to the number of cultivars assayed, but some SSR studies did not correct the bias of unbalanced group sizes (Russell *et al.*, 2000; Duvick *et al.*, 2004), thus weakening the argument of the allelic reductions found (Lu and Bernardo, 2001; Fu *et al.*, 2003a).

Possible solutions

For a better understanding of the selective impacts of plant breeding on crop genetic diversity, an informative assessment of diversity changes should help to answer the following questions: (i) Does overall genetic diversity or allelic diversity in an improved genepool change over breeding periods and if so, by how much? (ii) If allelic loss is found, where are the lost alleles located on the plant genome? (iii) What are the characteristics of the lost alleles? (iv) Are all the lost alleles associated with undesirable traits? These questions can be addressed using mapped multi-allelic markers such as SSRs (including EST-SSRs), although these are not currently available for all agricultural crops.

Each assessment should consider all the issues discussed above, minimize possible biases at every level, and focus on specific long-term breeding programmes. A well-defined genepool should be similar to the commercial hybrid maize genepool described by Duvick *et al.* (2004). The analysis should focus more on allelic diversity and less on overall genetic diversity, as allelic diversity is more sensitive to plant breeding practices. For allelic diversity assessments, unbalanced group sizes of cultivars should be weighted using appropriate methods such as the permutation procedures applied in Fu *et al.* (2003a, 2005). Applications of well-mapped SSR markers, particularly EST-SSRs, should help determine the distribution of lost alleles on the plant genome, the characteristics of the lost alleles and the proportion of the lost alleles that is associated with undesirable traits. If all the cultivars developed over time can be assessed, the contribution of genetic drift and breeding selection to allelic reductions could also be inferred (Helms *et al.*, 1989). Having this complete information in an improved genepool should not only provide insight into the impact of plant breeding on the plant genome, but also enhance future plant breeding efforts.

Concluding remarks

The literature survey presented here identified a relatively small number of molecular studies that have been published on diversity change. These studies suggest that the genome-wide reduction of crop genetic diversity accompanying genetic improvement over time is relatively minor, but that allelic reduction at individual loci is substantial. Furthermore, genetic shift was evident in some crop genepools. Based on these limited research findings, we concluded that plant breeding not only can narrow or widen the genetic base, but also can shift the genetic background of an improved genepool.

The research findings summarized here offer some support for public concerns regarding the reduced genetic diversity of cultivated plants and justify, at least partly, the need for continuous efforts to conserve improved plant germplasm, particularly that of older cultivars. Improper conservation of genetically improved germplasm will worsen the genetic narrowing reported here and may eventually result in genetic erosion in these crops. More efforts are needed to assess genetic diversity changes in major agricultural crops. More emphasis should be placed on specific long-term breeding programmes, the use of well-mapped multi-allelic markers such as SSRs and the association assessments of allelic reduction with undesirable traits. These assessments should help monitor the genetic risks of releasing newly developed plant germplasm, create effective strategies for conserving crop germplasm and develop more sustainable breeding programmes for the future.

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