

REVIEW ARTICLE

Wild relatives and crop cultivars: detecting natural introgression and farmer selection of new genetic combinations in agroecosystems

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Abstract

Whether new combinations of genes that result from hybridization and introgression between wild and cultivated taxa are maintained, with the resultant development of populations with new characteristics, depends on natural selection, and in the case of crops, on human selection. While many cases of deliberate introgression of desirable traits into crop cultivars as part of breeding programmes are known, the extent and significance of natural or farmer-assisted introgression is uncertain. A range of techniques have been used to document natural hybridization and introgression of agricultural crops and their wild relatives in many crops including maize, wheat, barley, oats, pearl millet, foxtail millet, quinoa, hops, hemp, potato, cocona, casava, common bean, cowpea, pigeon pea, carrots, squash, tomato, radish, lettuce, chilli, beets, sunflower, cabbage, and raspberries. However, the majority of these studies are based on morphological characters, and few have investigated the frequency with which such new types are produced and retained in natural and agroecosystems for farmer selection. Even more limited is information on the role of farmers in recognizing and selecting new genetic variation from the natural introgression of crops with their wild relatives, and the impact, once selected, of these new genetic combinations on the crop diversity. Molecular evaluation of natural introgression linked to investigations of farmer recognition and use of introgressed types provide ways of evaluating whether farmer selection for introgressed types is a significant process in increasing the genetic diversity of crop plants.

Keywords: agroecosystem, crop cultivars, crop wild relatives, farmer selection, molecular evaluation, natural introgression

Received 11 February 1999; revision received 29 April 1999; accepted 13 July 1999

Introduction

New combinations of genes resulting from hybridization and introgression between wild relatives and their crop cultivars have been important in the evolution of domestic crop species (Stebbins 1959; Harlan 1965; Slatkin 1987; Prescott-Allen & Prescott-Allen 1988; van Raamsdonk & van der Maesen 1996). Others have suggested that natural introgression between wild relatives and their crop cultivars continues to be a factor in increasing the genetic diversity of modern crops today (Anderson 1949, 1961; Bradshaw 1975; Pickersgill 1981; Arnold 1992; Quiros *et al.*

1992; Altieri & Montecinos 1993). Many authors suggest that systems where natural introgression is occurring should be evaluated as a component of risk assessment for the release of transgenic crops (Snow & Moran Palma 1997; Ellstrand & Hoffman 1990; Crawley *et al.* 1993; Raybould & Gray 1993, 1994; Dale 1994; Darmency 1994; Linder & Schmitt 1994; Regal 1994; Scheffler & Dale 1994; Jorgensen & Andersen 1995; Hancock *et al.* 1996).

The importance of introgression in enlarging the useful crop gene pool continues to be the subject of debate (Ehrlich & Raven 1969; Slatkin 1987; Arnold & Hodges 1995; Rieseberg 1995). While many cases of deliberate introgression of desirable traits into crop cultivars as part of breeding programmes are known, the extent and

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significance of natural or farmer-assisted introgression is uncertain (Jarvis & Hodgkin 1998). Few studies have accurate measurements of the extent of introgression within the populations in question. Even more limited than studies on natural introgression, however, are published studies investigating the role of farmers in recognizing and selecting the new genetic variation that has occurred from natural introgression.

In this study we evaluate the literature and methods used to document natural introgression and farmer selection of new genotypes in agroecosystems. We then suggest areas for investigation that link molecular evaluation with agroecological studies in centres of crop diversity to evaluate the extent of farmer selection for introgressed types and its significance in increasing the useful genetic diversity of crop plants.

Detecting introgression and hybridization in plant populations

Hybridization and subsequent introgression require pre-mating and postmating barriers to be overcome (Sano 1993). Prerequisites for hybrid formation include sympatric parents that occupy similar habitats, overlapping flowering times, similar pollinators, and intertaxa compatibility (Darwin 1859; Antonovics 1968; Ottaviano *et al.* 1988; Sarr *et al.* 1988; Langevin *et al.* 1990; Hancock 1992; Freyre *et al.* 1996). The amount and frequency of gene flow between a crop cultivar and its wild relative will be affected by the breeding system of the plants (Hancock *et al.* 1996). Several authors have questioned earlier assumptions of Anderson (1949), Heiser (1973), and Lewontin & Birch (1966) that hybrids were morphologically intermediate, were uniformly less fit than their parents, and had competitive advantage only in unoccupied areas such as disturbed landscapes (Rieseberg & Ellstrand 1993; Arnold & Hodges 1995; Rieseberg 1995, 1997). Others have speculated that the large number of novel characters that hybrids are noted to contain could be due to increased mutation rates, new combinations of alleles, previously unexpressed alleles that may be under a new regime of regulation, or the fixation of recessive alleles from the parents (Barton & Hewitt 1985; Rieseberg 1995). The majority of authors agree, however, that new combinations of genes can arise from hybridization and introgression.

A range of classical morphological and molecular techniques have been used to document natural hybridization and introgression between agricultural crops and their wild relatives in a wide variety of crops (Table 1).

Table 1 suggests that introgression may have occurred (or continue to occur) in a substantial number of crops. However, as several authors have indicated, some caution is needed in interpreting the evidence. Hybridization and introgression are often difficult to detect and are not

necessarily indicated by the occurrence of the characters of one taxon in another (Dobzhansky 1941; Donald & Hamblin 1983). Similar characters in crops and their wild relatives may occur because of a common ancestor, or as a result of convergent evolution (Doebley 1989; Nason *et al.* 1992; Wilson 1992).

The majority of the studies documenting natural introgression reported in Table 1 were based on morphological studies. The number of characters that can be investigated in this way is limited and it is often suggested that biochemical (seed proteins or isozymes) and molecular markers may provide better evidence for introgression. In these cases it may be possible to identify distinct types characteristic of the different species and look for these in populations where introgression is thought to have occurred.

Cytological techniques can also be used to detect introgression as in the case of wheat (Zohary & Feldman 1962), potato (Hawkes 1956; Hawkes & Hjerting 1989), lettuce (Zohary 1991), and chilli (Pickersgill *et al.* 1979; Pickersgill 1981). Kato (1996) examined chromosome knobs in maize to demonstrate introgression from teosinte. Another approach that is used involves analysis of chromosome pairing as in soybean (Singh & Hymowitz 1988), and in potato (Watanabe & Peloquin 1989). Most recently, genomic *in situ* hybridization (e.g. Schmidt *et al.* 1994) has proved to be a particularly powerful way of demonstrating the presence of introgressed sequences in a number of species especially cereal crops and beet (e.g. Schwarzacher *et al.* 1992; Schmidt *et al.* 1994). The method allows location and quantification of alien DNA and is fast, accurate and sensitive and is likely to offer a general method of considerable potential in further studies.

Molecular techniques now provide a considerable range of methods for identifying alien sequences in a particular species and hence of establishing the extent of introgression. Random amplified polymorphic DNA (RAPDs), restriction fragment length polymorphisms (RFLPs) and microsatellite analysis have been used to examine nuclear DNA, chloroplast DNA (cpDNA) and mitochondrial DNA (mtDNA) to provide evidence of introgression occurrence (Hillis 1987; Schmidt & Heslop-Harrison 1993, 1996; Watanabe 1994; Bonhomme *et al.* 1995; Francis *et al.* 1995; Jia *et al.* 1996; Linder *et al.* 1998). While these methods greatly enhance our capacity to determine whether introgression has occurred, certain problems remain. The marker studied needs to be present in the introgressed segment and within-species polymorphism for the marker needs to be ruled out as a possible cause of any observed differences. Molecular markers, particularly amplified fragment length polymorphisms (AFLPs), can now provide many hundreds of markers scattered through the genome. Such marker systems would appear to be ideally suited to the study of introgression and would certainly

Table 1 Documented cases of natural hybridization and introgression of crops and wild relatives. References that mention farmer selection and/or use of new types are marked with an asterisk

Crop	Reference(s)	Technique(s) used to measure introgression
Alfalfa (<i>Medicago sativa</i>)	Small (1984)	Morphology
Barley (<i>Hordeum vulgare</i>)	Hadjichristodoulou (1992a,b) Harlan (1995) Murphy <i>et al.</i> (1982) Sakti & Pietrack (1987) Tovia & Zohary (1962) von Bothmer <i>et al.</i> (1989) von Bothmer <i>et al.</i> (1995)	Morphology Morphology Morphology, isozymes Morphology Morphology Morphology Morphology
Beets (<i>Beta vulgaris</i>)	Boudry <i>et al.</i> (1993) Hammer <i>et al.</i> (1987) Santoni & Berville (1992) Schmidt & Heslop-Harrison (1996) Stace (1975)	RFLPs (mtDNA, cpDNA, cytDNA) Morphology RFLPs Microsatellites, genomic DNA Morphology
Cabbages, mustards, rapes (<i>Brassic</i> spp.)	Eber <i>et al.</i> (1994) Jorgensen & Andersen (1994) Perrino & Hammer (1985) Snogerup <i>et al.</i> (1990)* Stace (1991) Worede (1986)*	Cytology, isozymes Morphology, cytology, isozymes, RAPDs Morphology Morphology Morphology Morphology
Carrots (<i>Daucus carota</i>)	Small (1978) St. Pierre & Bayer (1991) Wijnheijmer <i>et al.</i> (1989)	Morphology, isozymes Isozymes Morphology
Casava (<i>Manihot esculenta</i>)	Schaal (1998)	RFLPs
Chilli (<i>Capsicum annuum</i>)	Doebly (1989) Nahban (1985)* Pickersgill (1981) Pickersgill <i>et al.</i> (1979) Pickersgill (1991) van Raamsdonk & van der Maesen (1996)	Isozymes Morphology Cytology Morphology Cytology Morphology, isozymes
Cocona (<i>Solanum sessiliflorum</i>)	Salick (1992)*	Morphology, isozymes
Common bean (<i>Phaseolus vulgaris</i>)	Beebe <i>et al.</i> (1997) Debouck (1988) Debouck <i>et al.</i> (1993) Freyre <i>et al.</i> (1996) Gepts (1988), (1990), (1993) Gepts & Bliss (1986) Llaca <i>et al.</i> (1994) Salinas <i>et al.</i> (1988) Schmit <i>et al.</i> (1993)	Morphology, seed protein Morphology Morphology Morphology, seed protein, RAPDs Morphology, seed protein Morphology, seed protein RFLPs (cpDNA) Morphology RFLPs (cpDNA)
Cowpea (<i>Vigna unguiculata</i>)	Padulosi (1993) Vaillancourt <i>et al.</i> (1993)	Morphology Isozymes
Foxtail millet (<i>Setaria italica</i>)	de Wet <i>et al.</i> (1979) Till-Bottraud <i>et al.</i> (1992)	Morphology RFLPs (cpDNA)
Hemp (<i>Cannabis sativa</i>)	Small (1984)	Morphology
Hops (<i>Humulus lupulus</i>)	Small (1980); (1984)	Morphology

Table 1 Continued

Crop	Reference(s)	Technique(s) used to measure introgression
Lettuce (<i>Lactuca sativa</i>)	van Raamsdonk (1995) van Raamsdonk & van der Maesen (1996) Zohary (1991)	Morphology Morphology Morphology, cytology
Maize (<i>Zea mays</i>)	Benz <i>et al.</i> (1990)* Castillo-Gonzalez & Goodman (1996) Doebley <i>et al.</i> (1984) Doebley <i>et al.</i> (1987) Doebley (1989), (1990) Kato (1996) Johannessen (1982)* Lumholtz (1902)* Mangelsdorf (1961) Wilkes (1970)* (1977)* (1993)*	Morphology Morphology Isozymes Isozymes, RFLPs, (cpDNA) Morphology, isozymes Cytology Morphology Morphology Morphology, cytology Morphology
Oats (<i>Avena sativa</i>)	Baum (1977)	Morphology
Pearl millet (<i>Pennisetum glaucum</i>)	Brunken <i>et al.</i> (1977) Couturon <i>et al.</i> (1997) Renno <i>et al.</i> (1997) Robert <i>et al.</i> (1991), (1992) Robert & Sarr 1992* Tostain (1992)	Morphology Morphology Morphology, isozymes Morphology, isozymes Morphology Morphology, isozymes
Pigeon pea (<i>Cajanus cajan</i>)	Smartt (1990) van der Maesen (1986)	Morphology, seed protein inhibitor, isozymes Morphology, cytology, isozymes
Potato (<i>Solanum tuberosum</i>)	Grun (1979), (1990) Hawkes (1956) Hawkes & Hjerting (1989) Hosaka (1995) Hosaka <i>et al.</i> (1988) Johns & Keen (1986)* Johns <i>et al.</i> (1987) Quiros <i>et al.</i> (1992)* Rabinowitz <i>et al.</i> (1990) Ugent (1970)* Watanabe & Peloquin (1989) Zimmerer & Douches (1991)	Morphology, cytology, isozymes cpDNA and mtDNA restriction mapping Morphology, cytology Morphology, cytology RFLPs (cpDNA) RFLPs (cpDNA) Morphology Morphology, isozymes Morphology, isozymes Morphology, isozymes Morphology Cytology (chromosome segregation) Morphology, isozymes
Quinoa (<i>Chenopodium</i> spp.)	Wilson (1990b) Wilson & Heiser (1979) Wilson & Manhard (1993)	Morphology, isozymes Morphology, isozymes Morphology, isozymes
Radish (<i>Raphanus sativus</i> L.)	Hammer & Perrino (1995) Klinger <i>et al.</i> (1992) Klinger & Ellstrand (1994)	Morphology Morphology, isozymes Morphology
Raspberries (<i>Rubus</i> sp.)	Jennings (1988) Luby & McNichol (1995)	Morphology Morphology
Rice (<i>Oryza sativa</i> , <i>O. glaberrima</i>)	Chu & Oka (1970) Langevin <i>et al.</i> (1990) Morishima <i>et al.</i> (1961) Oka & Chang (1959), (1961) Oka & Morishima (1971) Richards (1986)* Second (1982)	Morphology, isozymes Morphology, isozymes Morphology Morphology Morphology Morphology Isozymes
Rye (<i>Secale cereale</i>)	Hammer <i>et al.</i> (1987) Vences <i>et al.</i> (1987)	Morphology Morphology, cytology, isozymes

Table 1 Continued

Crop	Reference(s)	Technique(s) used to measure introgression
Sorghum (<i>Sorghum bicolor</i>)	Aldrich & Doebley (1992) Arriola & Ellstrand (1996) Baker (1972), (1974) Barrett (1983) de Wet (1978) Doggett & Majisu (1968)* Harlan (1992) Jones & Sieglinger (1951)	RFLPs (cpDNA) Morphology, isozymes Morphology Morphology Morphology Morphology Morphology Morphology
Soybean (<i>Glycine max</i>)	Doyle (1988) Singh & Hymowitz (1988)	<i>In situ</i> hybridization Chromosome analysis
Squash (<i>Cucurbita</i> spp.)	Bretting (1990) Decker-Walters <i>et al.</i> (1988); (1990) Decker (1988) Kirkpatrick & Wilson (1988) Merrick & Nabhan (1984)* Nabhan (1984), (1985)* Nee (1990) Wilson (1990a)	Morphology Morphology, isozymes Morphology, isozymes Isozymes Morphology Morphology Morphology Morphology, isozymes
Sunflower (<i>Helianthus annuus</i>)	Arias & Rieseberg (1995) Heiser (1965) Linder <i>et al.</i> (1998) Rieseberg (1991), (1995) Rieseberg & Seiler (1990)	RAPDs Morphology RAPDs Isozymes, cpDNA restriction mapping Isozymes, cpDNA restriction mapping
Tomato (<i>Lycopersicon esculentum</i>)	Rick (1958) Rick <i>et al.</i> (1975) Rick & Holle (1990)	Morphology Morphology, isozymes Morphology, isozymes
Watermelon (<i>Citrullus lanatus</i>)	Zamir <i>et al.</i> (1984)	Isozymes
Wheat (<i>Triticum aestivum</i>)	Harlan (1965) Hammer & Perrino (1984) Zohary (1971) Zohary & Feldman 1962	Morphology Morphology Morphology, cytology Morphology, cytology

alleviate some of the problems noted above. However, it will still be necessary to rule out within-species polymorphism for any markers used to establish that introgression has occurred. Thus, the extent of differences between wild and cultivated species will also affect the effectiveness of such methods.

In some situations, it is possible to combine different approaches. Direct observation of characteristics (morphological, biochemical or molecular) that appear to derive from another taxa can be combined with other analytical studies that provide evidence of introgression. Thus, genetic mapping data can be used to identify introgressed sequences. These often recombine poorly, if at all, with the host DNA so that different estimates of genetic linkage between pairs of loci will be obtained, and associated with the characteristics that appear to come from other taxa. Equally, molecular, genetic and agromorpho-

logical studies can be combined with field studies by agronomists, ecologists, anthropologists and other social scientists to provide data supporting the likelihood of introgression.

Selection in natural and agroecosystems

The information used to compile Table 1 reveals suggestive evidence that introgression between crops and their wild relatives provides a broadened genetic base for natural and human selection. However, whether new hybrid or introgressed types survive and reproduce to form populations in the environment they find themselves will depend on the prevailing selective factors and the size and genetic structure of the recipient population, be it a crop cultivar or a wild population (Hancock 1992).

In natural systems, the survival of a population is

affected by the population structure and breeding system, by life-history characteristics of the plant and by natural selection factors, including soil type, climate, toxic elements, pest, diseases, historical, stochastic and disturbance events (Pickett & White 1985; Chesson & Case 1986; Hedrick 1986; Slatkin 1987; Huenneke 1991; Frankel *et al.* 1995). In contrast, in agricultural systems, in addition to the effects of population structure and natural selection, human selection and management also affect the survival of crop populations (de Wet & Harlan 1975; Donald & Hamblin 1983; Nabhan 1985; Salick 1992; Jarvis *et al.* 1998). Over 40% of the world's agricultural area is still under the management of small-scale farmers that continue to utilize traditional crop varieties to meet their production needs (M. Iwanaga, personal communication). This is particularly significant in countries where traditional cultivars of major crops continue to be grown in proximity to their wild relatives. For example, at least 50% of the area under maize production in Mexico, more than 50% of the area under rice production in Nepal, and over 80% of the area under millet production in Burkina Faso are cultivated with traditional varieties (Perales 1998; Upadhyaya 1996; Zangre 1998). Under these traditional agroecosystems, farmers make decisions concerning planting, managing, harvesting and processing their crops. They will select plants with preferred agromorphological characters or influence the survival of certain genotypes by planting a crop in a particular microenvironment or using particular farming management methods (Boster 1985; Johns & Keen 1986; Benz *et al.* 1990; Zimmerer & Douches 1991; Bellon & Taylor 1993; Casas & Caballero 1996; Louette *et al.* 1997; Jarvis *et al.* 1998).

Recently, the role of farmer selection and management of local crop resources has been gaining more attention (Richards 1985, 1986; Altieri & Merrick 1987; Gliessman 1990; Bellon 1991, 1996; Berg *et al.* 1991; Brush 1991; Brush *et al.* 1992, 1995; Sperling & Loevinsohn 1993; Salick 1995; Valdivia *et al.* 1995; Li & Wu 1996; Salick *et al.* 1997; Jarvis & Hodgkin 1999). The literature, however, is limited in its discussion of examples where farmers, in their selection and experimentation of new varieties, may be actively including and maintaining new genetic variation from the introgression of crops with their wild relatives. The few exceptions, mainly single observation or anecdotal statements, are found only for sorghum, rice, maize, pearl millet, common bean, potato, cocona, squash, cabbage and chilli (Table 2).

It is clear from this review that there is a lack of information in the literature on farmer selection of new genetic combinations resulting from introgression. What is also lacking from the literature on farmer selection is systematic discussion on whether new genetic combinations, normally not chosen for food products, are selected and maintained out of necessity during times of war and famine.

The literature also does not evaluate cases where farmers do not have resources or sufficient labour to remove all the 'off types' in the field or who are poorly skilled in distinguishing weeds from local cultivars (Jarvis & Hodgkin 1998).

The above case studies do show us that, for some crops, e.g. sorghum and cocona, strong natural and human selection pressures against some types may have limited new genetic combinations in spite of substantial gene flow. For other crops, as noted by Decker-Walters *et al.* (1990: p. 787) for squash, 'infrequent introgression, differentially affected by human selection, might explain the dominance of some "foreign" alleles in *Cucurbita moschata* (e.g. Skd-Is) and the absence of other alleles (e.g. Idh-2 m).' Gepts (1990) also postulated in his studies of *Phaseolus* that even rare events, if they occur over thousands of years, or the time for domestication of the common bean, could have a substantial impact on the retention of new genotypes. These results are contrary to the idea of Ehrlich & Raven (1969) who believe that substantial gene flow is needed for new genotypes to be retained.

The above studies also indicate that although introgression is more common in outbreeding crops, under particular environments and for certain genotypes, gene flow frequency in inbreeding crops can also be fairly high, as with the cases of common bean and rice (Salinas *et al.* 1988; Gepts 1990; Langevin *et al.* 1990). Thus, of equal importance to whether introgression occurs is knowledge of the frequency by which new types are produced and retained in natural and human-impacted systems for farmer selection.

Linking molecular evaluation with farmer-mediated selection

The evidence of farmer selection and use of introgressed types presented in Table 2 relies predominantly on morphological identification. Caution should therefore be used in interpreting this information, as evidence of introgression based solely on morphological characters does not rule out the possibility of common ancestors or convergent evolution (Donald & Hamblin 1983). Even where biochemical, cytological and molecular evidence for introgression were available (Table 2), the information in the literature was not systematically linked to observations of farmer selection and use of new or novel genotypes.

Therefore, no conclusions can be made from the literature reviewed on the extent and significance of natural or farmer-assisted introgression. To make such conclusions, sites need to be located and studied where gene flow occurs and crop cultivars are managed in association with their wild relatives. Gene flow may occur directly from wild or weedy relatives into the cultivated crop, with the product retained by the farmer. The process may also be

Table 2 Documentation of farmer selection and/or use of introgressed types and biochemical/molecular confirmation

Crop	Documentation of farmer selection and/or use of introgressed types	Confirmation of introgression through cytological, biochemical and molecular techniques
Cabbage (<i>Brassica</i> spp.)	In Ethiopia, Worede (1986) has noted that different species of cultivated and wild types of <i>Brassica</i> are grown together by farmers resulting in genetic diversification from introgression of the different species. These intermediate <i>Brassica</i> types are used for forage as well as vegetables. Snogerup <i>et al.</i> (1990) observed preferential maintenance of hybrid types for animal forage.	Eber <i>et al.</i> (1994) set up an experiment to allow spontaneous interspecific gene flow between male-sterile rapeseed (<i>Brassica napus</i>) and weedy <i>B. adpressa</i> and <i>R. raphanistrum</i> . They confirmed hybridization in offspring by chromosome number, chromosome pairing and isozyme analysis. Jorgensen & Andersen (1994) used cytology, species specific RAPDs and isozyme markers to demonstrate from 9% to 93% hybrids in the seed set of the mixed <i>B. napus</i> and weedy <i>B. campestris</i> stands.
Cocona (<i>Solanum sessiliflorum</i>)	Salick (1992) studied farmers actively selecting against spiny types, i.e. selecting against a wild/weedy characteristic and for a variety of fruit types; selection pressures were higher in pastures and swidden gardens and lower in riverbanks. Concurrently, farmers selected for a variety of fruit types, postulated as a maternally inherited trait.	Electrophoretic analysis to identify mechanisms of maternal influence on cocona were not significant (Salick 1992).
Maize (<i>Zea mays</i>)	First recorded by Lumholtz (1902 cited in Wilkes 1970) and later described in more detail by Wilkes (1970, 1977, 1993) and Benz <i>et al.</i> (1990), Mexican farmers not only allow teosinte to remain in their fields, but also actively exploit its occurrence for crop, improvement by mixing introgressed seeds in their seed stock.	Mangelsdorf (1961) and Kato (1996) have presented evidence for introgression of teosinte and maize based on the distribution and placement of chromosome knobs in both taxa. Doebley (1989, 1990) and colleagues Doebley <i>et al.</i> (1987) have provided isozymes and cpDNA evidence of bidirectional gene flow between teosinte and maize.
Pearl millet (<i>Pennisetum glaucum</i>)	According to Robert & Sarr (1992: p. 208) hybrid plants in west Africa are frequently not eliminated by the farmers due to 'traditional beliefs, difficulty of recognition, or in starvation periods.' Couturon <i>et al.</i> (1997) noted that farmers select and manage hybrid genotypes in Niger.	Tostain (1992) and Robert <i>et al.</i> (1991), Renno <i>et al.</i> (1997) and used isozyme studies to confirm the occurrence of introgression in the Sahel. Robert <i>et al.</i> (1992) and Robert & Sarr (1992) postulate that pollen competition played a large role in keeping cultivated and wild populations separate.
Potato (<i>Solanum</i> spp.)	Andean farmers rarely remove wild or weedy populations of potato species from their fields and in this way wild germplasm is introduced into both diploid and tetraploid cultigens (Ugent 1970). Johns & Keen (1986) noted two cases of deliberate selection of new potato genotypes by farmers in their studies in Bolivia. Surveys by Quiros <i>et al.</i> (1992) revealed that Andean farmers manage botanical seed propagation to eliminate disease, rejuvenate stock and create new cultivars.	Rabinowitz <i>et al.</i> (1990) used isozymes to reveal high levels of spontaneous hybridization between diploid cultivated <i>Solanum stenotomum</i> and weedy <i>S. sparsipilum</i> . Quiros <i>et al.</i> (1992) compared morphological data to isozymes and suggest evidence of natural introgression between different potato types. Watanabe & Peloquin (1989) suggest that the high frequency of parallel spindles found in 2x and 4x taxa were due to continuous introgression from diploid to tetraploids via sexual pollination. Hosaka <i>et al.</i> (1988) used DNA hybridization to reveal differences in cpDNA of <i>Solanum tuberosum</i> ssp. <i>tuberosum</i> and <i>S. chacoense</i> . Hosaka (1995) used cpDNA types to reveal introgression between wild relatives and cultivated <i>S. stenotomum</i> .

Table 2 Continued

Crop	Documentation of farmer selection and/or use of introgressed types	Confirmation of introgression through cytological, biochemical and molecular techniques
Rice (<i>Oryza sativa</i> , <i>O. glaberrima</i>)	Richards (1986) noted that rice farmers in Sierra Leone, who are in debt and must borrow rice farm lenders, receive 'unclean' seeds full of weedy rice which is then incorporated into their fields.	Langevin <i>et al.</i> (1990) and Second (1982) used isozymes to show evidence of introgression between wild and cultivated rice grown in common gardens. They noted different incidences for hybridization for different cultivars.
Sorghum (<i>Sorghum bicolor</i>)	Doggett & Majisu (1968) noted natural crosses in farmer fields of wild and cultivated sorghum. Although hybrid plants were usually uprooted by farmers some persist after harvest. They postulated that these hybrids facilitate introgression between wild species and cultigens. Dogget and Majisu asked women farmers evaluate offspring of hybrid crosses, one third of the offspring were identified by the women as local varieties suitable for planting.	Aldrich & Doebley (1992) compared RFLPs for cpDNA and rDNA to earlier isozyme data to show introgression between wild and cultivated sorghum to be a common occurrence. Arriola & Ellstrand (1996) showed the frequency and rate of spontaneous crop-to-weed gene flow using isozymes; they concluded also that hybridization between <i>S. bicolor</i> and weedy <i>S. halepense</i> does occur at a substantial rate.
Squash (<i>Cucurbita</i> spp.)	Merrick & Nabhan (1984) described farmers in the Sonora, Mexico who recognized that when wild squash grew near the edge of their fields, bitterness would enter into the cultivated squashes making them uneatable.	Decker-Walters <i>et al.</i> (1988, 1990), Kirkpatrick & Wilson (1988) and Wilson (1990) and Decker (1988) used isozyme analysis to confirm introgression between <i>Cucurbita</i> spp. Decker-Walters <i>et al.</i> (1990; p. 787) further noted that 'infrequent introgression, differentially affected by human selection, might explain the dominance of some "foreign" alleles in <i>C. moschata</i> (e.g. Skd-Is) and the absence of other alleles (e.g. Idh-2m)'.
Chilli (<i>Capsicum annuum</i>)	Nabhan (1985) noted that farmers in Mexico insisted that wild chillies were contributing genes to cultivated chillies making the cultivated chillies too spicy to sell to the market.	Pickersgill (1981, 1991) use different numbers of acrocentric chromosome pairs to identify the occurrence of introgression between wild and cultivated <i>C. annuum</i> . She notes that outcrossing in field conditions can vary from 1% to 70%. Doebley (1989) used isozymes to distinguish three parallel domestication sequences from wild to cultivated types.

indirect, with gene flow moving from the cultivated field to wild or weedy types at the field margin and new types being selected and brought into the farming system by the farmer. To locate such areas, information on the distribution, life histories and ecological amplitude of wild relatives and crop cultivars coupled with information on the areas where they occur and how they are being managed is essential (Ingram & Williams 1984; Hodgkin & Arora 1999).

Detection of introgression will be more difficult under certain situations than others. For high frequency outcrossing crops, where few detectable traits separate the crop from its wild relative, detecting the extent of introgression will be difficult. In these situations, the crop and its wild relative may, in reality, be one continuous gene pool separated only by ongoing natural and

human selection and thus introgression adds little new diversity to the crop gene pool. For other crops, rare occurrences may have played an important role for maintaining crop diversity, but these historical events will again be difficult to detect. Detection of introgression may be easiest for crops with moderate gene flow and whose wild relatives contain a number of dissimilar characters. This final group may also be the most important for providing a broadened genetic base for farmer selection.

Because of the complex nature of determining whether novel genotypes have been incorporated into traditional agricultural systems by farmers, a multidisciplinary approach is needed that includes inputs from both the natural and social scientists, including geneticists, anthropologists, ethnobotanists and biogeographers. This review

has focused primarily on methods to determine whether introgression occurs. Methods used to examine farmer modification of the genetic structure of crops in traditional agricultural systems is found elsewhere (Boster 1985; Johns & Keen 1986; Zimmerer & Douches 1991; Casas & Caballero 1996; Sthapit *et al.* 1996; Louette *et al.* 1997; Pham *et al.* 1998; Xu *et al.* 1999).

The information reviewed here has shown that introgression between crop cultivars and their wild relatives is an ongoing process affecting the genetic diversity of crops today. In many parts of the world, farmers depend on a large genetic base in the form of local crop cultivars for their livelihood (Richards 1986; Bellon 1996). For resource-poor farmers, a diversity of locally adapted crop cultivars may be the only option available for adequate production on poor soils in the absence of fertilizers, to insure against rainfall variability, and to cope with different pest and pathogens in the absence of pesticides (Glass & Thurston 1978; Clawson 1985; Bellon & Taylor 1993). The availability of large gene pools becomes even more essential as farmers need to adapt over time to changing conditions that result from new population pressures, land degradation, and environmental change.

There is an increasing recognition of the value of the on-farm maintenance of crop varieties as a component of our conservation efforts (Altieri & Merrick 1987; Brush 1991). The Convention of Biological Diversity (CBD) notes that a key requirement for the conservation of biological diversity is the *in situ* conservation of ecosystems, including, '... the maintenance and recovery of viable populations of species in their natural surroundings and, in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties (UNEP 1994).' Substantial work is now in progress to test the effect of ongoing natural and human selection processes on local crop genetic diversity conserved *in situ* on-farm (Jarvis *et al.* 1998). Within this context, introgression renders an important option for new genes to enter into crop varieties and become part of the domestic gene pool, and, in doing so, provides a key role for the *in situ* conservation of crops and their wild relatives.

With the recent advent of 'terminator genes' that sterilize seeds produced from agricultural crops (Edwards 1998) and other biotechnological proposals that propose to shut off gene flow processes, such as converting non-selfing to apomixis plants, the need to evaluate the importance of natural introgression and farmer selection in the maintenance of crop diversity is even more urgent. Evaluation of the potential of these new technologies to reduce genetic diversity is strongly advised before releasing such products into centres of crop diversity where the farmer's survival is linked to the maintenance of this diversity. Such investigations will require systematic information on farmer-managed systems coupled with molecular

techniques, in particular a mixture of *in situ* hybridization and microsatellites, together with classical cytological analysis, to detect and evaluate the extent of ongoing introgression, selection and maintenance of new genotypes in the agroecosystem.

Acknowledgements

We wish to thank Dr Robert Koebner for his valuable insights on the advantages and disadvantages of the various techniques for detecting introgression. We would also like to thank two anonymous reviewers for their helpful comments and corrections. Finally, we thank Nicky O'Neill for her assistance in editing the bibliography database for this paper.

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This review arose as a preliminary step in the formation of a project by Devra Jarvis and Toby Hodgkin, supported by the International Plant Genetic Resources Institute (IPGRI), to investigate the significance of wild-crop introgression and farmer selection for sorghum in Uganda and for chilli in Mexico for the maintenance of crop genetic diversity for farmer use. Devra Jarvis is a botanist trained in Quaternary palynology and currently responsible for coordinating IPGRI's work in the *in situ* conservation of crops and their wild relatives. Toby Hodgkin works on genetic aspects of conservation. Both are members of the Genetic Resources Science and Technology Group of IPGRI.
