

INVITED REVIEW

Contributions of Domesticated Plant Studies to our Understanding of Plant Evolution

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Received: 1 March 2005 Returned for revision: 8 June 2005 Accepted: 29 July 2005 Published electronically: 13 September 2005

- **Background** Plant evolutionary theory has been greatly enriched by studies on crop species. Over the last century, important information has been generated on many aspects of population biology, speciation and polyploid genetics.
- **Scope** Searches for quantitative trait loci (QTL) in crop species have uncovered numerous blocks of genes that have dramatic effects on adaptation, particularly during the domestication process. Many of these QTL have epistatic and pleiotropic effects making rapid evolutionary change possible. Most of the pioneering work on the molecular basis of self-incompatibility has been conducted on crop species, along with the sequencing of the phytopathogenic resistance genes (R genes) responsible for the 'gene-to-gene' relations of coevolution observed in host–pathogen relationships. Some of the better examples of co-adaptation and early acting inbreeding depression have also been elucidated in crops. Crop–wild progenitor interactions have provided rich opportunities to study the evolution of novel adaptations subsequent to hybridization. Most crop/wild F₁ hybrids have reduced fitness, but in some instances the crop relatives have acquired genes that make them more efficient weeds through crop mimicry. Studies on autopolyploid alfalfa and potato have uncovered the means by which polyploid gametes are formed and have led to hypotheses about how multi-allelic interactions are associated with fitness and self-fertility. Research on the cole crops and wheat has discovered that newly formed polyploids can undergo dramatic genome rearrangements that could lead to rapid evolutionary change.
- **Conclusions** Many more important evolutionary discoveries are on the horizon, now that the whole genome sequence is available of the two major subspecies of rice *Oryza sativa* ssp. *japonica* and *O. sativa* ssp. *indica*. The rice sequence data can be used to study the origin of genes and gene families, track rates of sequence divergence over time, and provide hints about how genes evolve and generate products with novel biological properties. The rice sequence data has already been mined to show that transposable elements often carry fragments of cellular genes. This type of genome shuffling could play a role in creating novel, reorganized genes with new adaptive properties.

Key words: Crop domestication, self-incompatibility, R genes, hybridization, genome evolution, polyploidy.

INTRODUCTION

The purpose of this paper is to describe the contributions of crop research to evolutionary biology, particularly in the areas of population genetics, speciation and polyploidy. Population genetic studies are reviewed that deal with the underlying mechanisms regulating quantitative variation in populations, the cohesiveness of the genome (co-adaptation), sexual incompatibility systems and host–pathogen evolution. Studies of speciation are described that concern what constitutes a species, the role of hybridization and introgression in evolutionary change, and the degree of genome evolution after speciation. Polyploid studies are outlined that provide information on the adaptive benefit of polyploidy, the nature of self-infertility in autopolyploids, and the capacity of polyploids to evolve. The recent sequencing of two subspecies of rice is also discussed in the context of evolutionary biology.

POPULATION GENETICS

Quantitative genetics

Knowledge about the underlying genetics is critical to understanding how quantitative traits evolve over time.

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In the early 1900s, crop geneticists first began to wonder whether more continuous traits such as plant height and seed weight were inherited according to Mendelian laws. Johannsen (1903) showed that such variation was indeed influenced by genes, but that the environment also played a role—he was the first to distinguish between genotype and phenotype. Yule (1906) hypothesized that quantitative variation could be caused by several genes having small effects, and Nilesen-Ehle (1909) and East (1916) confirmed this suspicion using wheat and tobacco. Several statistical techniques were then developed to partition the total variability within a population into its various genetic, environmental and interaction components (for reviews, see Mather and Jenks, 1977; Fehr, 1987; Falconer and Mackay, 1996).

Most recently, molecular markers have provided a means to dissect the genetic basis of the complex traits that are regulated by many individual quantitative trait loci (QTL) (Tanksley, 1993; Patterson *et al.*, 1998). Plant breeders now regularly employ QTL analyses to tag the key genes regulating agronomic traits, and evolutionary biologists have found the technique to be valuable in identifying the genetics of important adaptive traits and reconstructing the speciation process (Rieseberg, 2000).

A considerable amount of work has been conducted to identify those QTL associated with the process of crop domestication (Hancock, 2004). One of the most striking

with four yield traits, and found that almost all of them significantly interact with at least one other QTL. Mei *et al.* (2003) even found that a greater proportion of the total phenotypic variation found in rice was due to epistatic interactions than additive ones.

Doebly's group has discovered a significant epistatic interaction in maize between a QTL on chromosome arm 1L (QTL-1L) and another on chromosome arm 3L (QTL-3L) that both influence the number and length of the internodes in both the primary lateral branch and inflorescence (Doebly *et al.*, 1995; Lukens and Doebly, 1999). Alleles at these loci derived from either maize or teosinte had the strongest phenotypic effect in their own species background, further signalling the complexity of genomic interactions in *Zea mays*. Numerous QTL studies of crop species have uncovered genes with pleiotropic effects, where they affect a number of traits simultaneously. As a result, their selection would make large-scale phenotypic change much more rapid than if the traits were evolving separately.

The *fin* gene in dry beans conditions the earliness of flowering, and has significant effects on node number on stems, pod number, and the number of days from flowering to fruiting (Koinange *et al.*, 1996). Several pleiotropic QTL have been identified in *Zea* including: *teosinte glume architecture 1 (tb1)*, which effects internode lengths, inflorescence sex and structure, *teosinte branched 1 (te1)*, which also effects internode lengths, numbers and inflorescence sex, and *suppressor of sessile spikelets1 (sos1)*, which effects branching in the inflorescence and the presence of single vs. paired spikelets in the ear (Doebly *et al.*, 1995). Allard (1988) identified a number of marker loci for quantitative traits in barley that had significant additive effects on several to many quantitative traits. In one case, a QTL analysis proved that a suspected pleiotropic effect did not exist. Frary *et al.* (2004) found little overlap in the QTL determining the size and shape of leaflets, sepals and petals of tomato, even though leaves have long been considered antecedent to flowers.

Many of the QTL associated with the domestication syndromes are clustered close together on the same chromosome. Such close associations of genes would reduce the amount of segregation between these adaptively important genes and in a sense 'fix' the crop type, again allowing for rapid change. These genic assemblages are very similar to the 'supergenes' that have been described in native species (Ford, 1975). Koinange *et al.* (1996) found the distribution of domestication syndrome genes to be concentrated in three genomic regions, one of which greatly effected growth habit and phenology, the other seed dispersal and dormancy, and a third the size fruit and seed. Doebly *et al.* (1990) found five of the QTLs that distinguish maize and teosinte in a tight cluster on chromosome 8. These genes regulated: (a) the tendency of the ear to shatter, (b) the percentage of male spikelets in the primary inflorescence; (c) average length of internodes on the primary lateral branch; (d) percentage of cupules lacking the pedicellate spikelet; and (e) the number of cupules in a single rank. Wright *et al.* (2005) found a number of candidate genes on this chromosome and others that had putative functions in plant growth. Many of

the genetic factors controlling domestication-related traits were also concentrated on a few chromosomal blocks in pearl millet (Poncet *et al.*, 1998), tomato (Grandillo and Tanksley, 1996) and rice (Xiang *et al.*, 1999). The linkage relationships of the QTL associated with domestication-related traits have been found to be conserved in eggplant, tomato, pepper and potato (Doganler *et al.*, 2002; Frary *et al.*, 2003). Considerable synteny has also been found between the chromosomal region carrying the major heading-date QTL in perennial ryegrass and the rice region with the Hd3 heading-date locus (Armstead *et al.*, 2004).

Co-adaptation

Most evolutionary biologists consider the genome to be cohesive, with selection operating on the whole phenotype of an individual and not only on the product of single genes. The evolutionary ramification of this genomic complexity is that alleles are selected at two levels: (1) how well they function in the environment, and (2) how well they function together. Hybrids between different populations of the same species are sometimes weak or inviable (Wallace, 1968). Such 'hybrid breakdowns' are thought to arise because the gene pools within populations have been selected over time for their harmonious interaction. When individuals are crossed from variant populations, their genes may not be well integrated and therefore produce poorly adapted offspring.

Most of the most graphic examples of hybrid breakdowns have been demonstrated in animals, although a particularly good example of hybrid breakdown has been documented in the bean, *Phaseolus vulgaris* (Gepts, 1988, 1998). There are large- and small-seeded races from South America and Mexico which when crossed produce high percentages of weak, semi-dwarf progeny. This reduction in hybrid fertility and vigour is associated primarily with two independent loci DL₁ and DL₂, although many other differences exist in the gene pools of the geographic races, including distinct phaseolin seed proteins, electrophoretic alleles, chloroplast DNA, flowering times and floral structures (Shii *et al.*, 1981; Gepts and Bliss, 1985; Chacón *et al.*, 2005).

Hogenboom (1973, 1975) coined the term 'incongruity' to describe the pre-fertilization barriers that sometimes arise between divergent taxa of crop species. He felt that inter-species crosses often fail because one species lacks the genetic information necessary to properly co-ordinate the critical functions of the other through disrupted gene regulation, the absence of a gene, or poor genomic-cytoplasmic interactions. Haghghi and Ascher (1988) provided circumstantial evidence of this phenomenon by showing that the vigour of inter-specific crosses of *Phaseolis vulgaris* and *P. acutifolius* can be improved through several rounds of crosses, presumably through selection for the most co-ordinated genes.

Genetic systems influencing outcrossing rates

The breeding system of plants has a strong influence on variation patterns, with largely outcrossed species being

much more heterozygous than highly inbred ones. One of the plant systems forcing outcrossing is dioecy where there are separate male (pistillate) and female (staminate) sexes. In most plant species, there are not separate chromosomes that regulate sex as in animals, although there are exceptions. Mapping studies have led to the conclusion that papaya (*Carica papaya*) has an incipient sex chromosome that is still in the process of evolving. It contains a primitive Y chromosome with a male-specific region that accounts for 10% of the chromosome (Liu *et al.*, 2004; Ma *et al.*, 2004). Recombination is severely repressed in this region leading to permanent heterozygosity in females.

Outcrossing is also encouraged by the self-incompatibility systems (SI), gametophytic and sporophytic. In gametophytic systems, pollen germination and tube growth is dependent on the genotype of the parent; while in sporophytic systems, pollen performance is based on the genotype of the male parent (Lewis, 1979; de Nettancourt, 2001).

The bulk of the work that has been done on the molecular basis of self-incompatibility has been conducted on crop plants (McCubbin and Kao, 2000; Silva and Goring, 2001; Nasrallah, 2002). There appear to be three major types of SI mechanisms (Kao and Tsukamoto, 2004). In the Brassicaceae (cole crops) with sporophytic incompatibility, self-pollen germination is inhibited through the interaction of a pollen protein (SP11/SCR), a stylar receptor kinase (SKR), a glycoprotein (SLG) and several other proteins. The mechanism of rejection is due to the prevention of pollen grain hydration and germination (Kemp and Doughty, 2003). In the Papaveraceae (poppy) with gametophytic self-incompatibility, self-pollen tube growth is rejected at the stigmatic surface by the interaction of a stigmatic S protein, a pollen S receptor (SBP), a calcium-dependent protein kinase (CDPK) and a glycoprotein. Pollen tube growth is arrested by a cascade of events associated with an increase in cytosolic calcium and a disruption of the cytoskeleton. In the gametophytic Solanaceae (tobacco, tomato, petunia and potato) and Rosaceae (apple, cherry and pear), self-pollen tube growth is inhibited within styles by a pistil-released RNase (S-RNase) that selectively destroys the RNA of self-pollen tubes. Pollen S proteins determine S-RNase stability in self- vs. non-self styles (Sijacic *et al.*, 2004; Ushijima *et al.*, 2004). Gametophytic SI in the Solanaceae, Scrophulariaceae and Rosaceae appear to have a common origin (Igc and Kohn, 2001).

A phenomena called ‘early acting inbreeding depression’ can mimic SI, when selfed embryos abort as deleterious alleles are expressed during seed development or the outcrossed progeny display a hybrid vigour that enables them to out-compete the selfed ones (Weins *et al.*, 1987; Weller and Ornduff, 1989; Seavey and Carter, 1994). This mode of self-infertility has been clearly elucidated in the crop plants alfalfa, blueberries and coffee, which were historically misclassified as self-incompatible due to poor selfed seed set (Busbice, 1968; Crowe, 1971; Krebs and Hancock, 1991). Early acting inbreeding depression differs from SI, in that different genotypes display a range in self-fertility. Significant positive correlations are also found in species with early acting inbreeding depression between self- and out-cross

fertility and the percentage of aborted ovules and inbreeding coefficients (Hokanson and Hancock, 2000).

Co-evolution

Several types of co-evolution have been described in the literature about evolution, including mutualism, character displacement and host-pathogen evolution. Some of the best examples of host-pathogen evolution are found in the crop literature, where constant battles are fought to find new sources of resistance to rapidly evolving pest populations (Allard, 1990). For example, dominant alleles have been identified at more than five loci in wheat that confer resistance to the Hessian fly, but alleles exist for each locus in the fly that confer counter resistance (Hatchett and Gallum, 1970). Dozens of examples of ‘gene-for-gene’ relations have been described in pathogen/host systems where there is a gene for susceptibility or resistance in the crop to match each gene for virulence or avirulence in the pathogen (Martin and Ellingboe, 1976; Leath and Pederson, 1986; Hautea *et al.*, 1987; Pederson and Leath, 1988).

Specific genes have been identified in plants that are associated with these ‘gene-for-gene’ relationships. These phytopathogenic resistance genes (R genes) encode proteins that recognize specific pathogen-derived proteins and trigger a cascade of resistance responses leading to cell death (Martin *et al.*, 2003; Nimchuk *et al.*, 2003). A number of R genes have been cloned and sequenced from mainly crop species and arabidopsis. They are found in tandem arrays of multiple copies and display considerable variability due to both point mutations and unequal meiotic recombination (Shamray, 2003; Kruijt *et al.*, 2004; Xiao *et al.*, 2004). Balancing selection is thought to be the main force maintaining high levels of R gene diversity in populations, although frequency-dependent selection and drift also play important roles (Bergelson *et al.*, 2001; Caicedo and Schaal, 2004).

SPECIATION

Nature of species

A topic of continual discussion among evolutionary biologists is how to define a species. Probably the most popular concept is the ‘biological species’ as ‘groups of actually or potentially interbreeding natural populations, which are reproductively isolated from each other’ (Mayr, 1942; Schemske, 2000). While the biological species concept allows for the unambiguous delineation of species, it is still not without problems (Hancock, 2004). Strongly divergent groups of plants often maintain some degree of inter-fertility even though they differ at numerous loci and are effectively evolving on their own. Plants also show great ranges in self-fertility from obligate outcrossing to complete selfing to apomixis (uniparental). In a highly inbred or apomictic group, every individual would be a species according to the biological species concept.

Numerous concepts have been developed which include ecological with reproductive criteria to better define species; however, no single model solves all of the potential

problems in trying to define separate evolutionary units. Levin (2000) even suggests that ‘the choice of a species concept has to do, in part, with the perspective that gives one satisfaction’. Harlan and deWet (1972) developed what they called the ‘gene pool system’ to deal with varying levels of inter-fertility between related taxa of crop species and their relatives. They recognized three types of genic assemblages:

- (1) primary gene pool (GP-1)—hybridization easy, hybrids generally fertile;
- (2) secondary gene pool (GP-2)—hybridization possible, but difficult; hybrids weak with low fertility;
- (3) tertiary gene pool (GP-3)—hybrids lethal or completely sterile.

The primary gene pool is directly equivalent to the biological species. The recognition of GP-2 and GP-3 allows other levels of inter-fertility to be incorporated into the overall concept of species. These are related taxa which share a considerable amount of genetic homology with GP-1, but are divergent enough to have greatly reduced inter-fertility. Several agronomically important groups have been described using this system including legumes, wheat and most of the other cereals (Harlan and deWet, 1975; Smartt, 1984).

Hybridization and introgression

Thoughts about the relative importance of hybridization and introgression in plant evolution have switched back and forth over time, but with the advent of molecular markers in the 1980s support has been greatly bolstered (Rieseberg, 1995; Rieseberg *et al.*, 2000). Some of the best examples of introgression have been observed between crop species and their native relatives. Evidence for crop introgression into wild populations of congeners has been provided for 31 species, including alfalfa, barley, beets, cabbages, canola, cotton, carrots, cassava, chili, cocona, common bean, cowpea, finger millet, foxtail millet, hemp, hops, lettuce, maize, oats, pearl millet, pigeon pea, potato, quinoa, radish, raspberry, rice, rye, sorghum, soybean, squash, sunflower, tomato, watermelon and wheat (Ellstrand *et al.*, 1999; Jarvis and Hodgkin, 1999).

Most F₁ hybrids of cultivated and wild congeners have reduced fitness in nature and the genes of domesticated plants rarely travel far from narrow hybrid zones. However, some wild plants have acquired crop genes that make them more effective agronomic weeds. In some instances, genes have introgressed into wild plants that allow them to ‘mimic’ the habit of domesticated ones, and thus escape removal in agronomic sites by farmers. The weed may look identical to the crop until seed dispersal, or the weed seeds may be impossible to separate from the agronomic source.

Crop mimicry has been particularly prevalent among the grains (Harlan *et al.*, 1973; Harlan, 1992). A classic example of crop mimicry can be found in sugar beet fields in Europe, where weed introgressants bolt and scatter seeds before crop harvest (Viard *et al.*, 2002). There are weedy bolters which probably resulted from the contamination of

seed producers by pollen from wild individuals, and bolters that emerge from the seed bank containing wild/crop introgressants. The bolters carry the dominant B allele which cancels any cold requirement.

Wild/crop hybridizations have also resulted in alterations of the crop itself, when farmers have exploited new, useful genetic combinations (Hancock, 2004). Farmer selection of crop/weed introgressants may have played a particularly important role in the early development of crops, as agriculture spread out of the centres of origin. It is difficult to document the historic introgression of native genes into crops, but Jarvis and Hodgkin (1999) have identified nine examples where today’s farmers are selecting crop/wild introgressants.

Hybridization can lead to new adaptations appearing in recipient species, but high amounts of gene flow and hybridization can also lead to extinction (Levin *et al.*, 1996; Buerkle *et al.*, 2000). There can be ‘genetic assimilation’, where the hybrids are fertile, and they replace pure conspecifics of either or both hybridizing taxa, and there can be ‘demographic swamping’, where population growth in a numerically inferior taxa is retarded by the formation of hybrid seed, and population growth falls below the replacement level.

Some of the clearest examples of genetic assimilation and demographic swamping have been observed in interactions between crops and wild relatives. Genetic assimilation is likely occurring on the Galapagos Islands between the native species *Gossypium darwinii* and the crop, *G. hirsutum* (Wendel and Percy, 1990). In California, the cultivated radish, *Raphanus sativus*, and the jointed charlock, *R. raphanistrum*, have completely merged (Panetsos and Baker, 1967). Hybridization with cultivated rice is thought to have led to the near extinction of the endemic Taiwanese taxon, *Oryza rufipogon* spp. *formosana* through genetic assimilation (Kiang *et al.*, 1979). In fact, most populations of native Asian subspecies of *O. rufipogon* may be endangered through hybridization with the crop (Chang, 1995; Ellstrand *et al.*, 1999).

Genome evolution

Of interest to many evolutionary biologists, is the degree of genetic change associated with speciation. As previously mentioned, molecular markers are increasingly being used to construct genetic maps of species, and these maps have expanded our knowledge of genome structure and evolution. By comparing maps of related species, it is possible to evaluate the kinds of genomic changes that accompany speciation (Reiseberg *et al.*, 1995, 1996).

A large amount of work has been devoted to studying the degree of linkage conservation or ‘genome evolution’ that exists across a number of crop species (Bennetzen, 2000; Paterson *et al.*, 2000), with variable results. In the initial comparative mapping studies conducted with limited genetic markers and progeny populations, gene order appeared highly conserved in several families including the Fabaceae (lentil and pea: Weeden *et al.*, 1992; mung bean and cowpea: Menancio-Hautea *et al.*, 1993), the Solanaceae (potato and tomato: Tanksley *et al.*, 1992) and the Poaceae (maize,

rice and sorghum: Devos and Gale, 2000). However, the gene order appeared quite divergent in the Poaceae (rye and wheat: Devos *et al.*, 1992*a, b*), the Solanaceae (pepper and tomato: Livingstone *et al.*, 1999) and the diploid and amphiploid *Brassica* species (Paterson *et al.*, 2000). Very limited conservation has also been found in the most recent fine scale comparisons of maize, rice and sorghum, when mapped bacterial artificial chromosome (BAC) sequences have been used to measure collinearity (Lai *et al.*, 2004).

POLYPLOIDY

Adaptive benefit of polyploidy

One of the most intriguing questions facing plant evolutionists is why there are so many polyploid species. The majority of plant species have high chromosome numbers and it has been estimated that 2–4% of all speciation events represent polyploidy (Ramsey and Schemske, 1998; Otto and Whitten, 2000). Ancient cycles of genome duplication have been documented in a number of crop species including the cole crops, corn, cotton, soybean and many of the important cereals (Blanc *et al.*, 2000; Wendel, 2000; Lukens *et al.*, 2004). The complete sequence data recently completed for Arabidopsis and rice support this notion (Bennetzen, 2002). The most commonly implicated advantage of polyploidy over diploidy is increased heterozygosity (Barber, 1970; Manwell and Baker, 1970), and nearly all polyploids that have been examined with molecular markers have been found to have high levels of heterozygosity (Gottlieb, 1982; Soltis and Soltis, 1993, 1999).

Most polyploids are thought to have arisen through the unification of unreduced gametes (Harlan and deWet, 1975; Bretagnolle and Thompson, 1995). The initial level of heterozygosity transmitted via these unreduced gametes has been shown in crop plants to be dependent on the process of $2n$ -gamete formation. There are a number of events that can result in unreduced gametes, but the most common are first division restitution (FDR) and second division restitution (SDR). In FDR, homologous chromosomes do not separate during meiosis I, while in SDR sister chromatids do not separate during meiosis II. Assuming one crossover per chromosome, it has been calculated that FDR transmits 80.2% of the parental heterozygosity to the gametes and SDR transmits 39.6% (Hermson, 1984). Cytogenetic studies of FDR and SDR have been undertaken in potato (Mok and Peloquin, 1975; Mendiburu and Peloquin, 1977; Douches and Quiros, 1988), alfalfa (Vorsa and Bingham, 1979) and maize (Rhodes and Dempsey, 1966).

Self-fertility in polyploids

It has long been assumed that polyploid species should have higher rates of self-fertilization than their diploid progenitors (Stebbins, 1950), because selfing would facilitate the likelihood of finding mates after the initial polyploidization event and having multiple genes would shield the raw polyploids from the deleterious effects of inbreeding (Marple, 2004).

Numerous studies of natural species have shown that polyploidy can in some instances increase levels of self-fertility through the breakdown of self-incompatibility systems (Mable, 2004). This probably occurs because of competition among alleles in diploid pollen (Stone, 2004). However, there is not a strong association between polyploidy and self-compatibility at the level of species or family, and it is more likely that polyploids carrying multiple alleles will show varying levels of self-compatibility (SC) rather than a complete breakdown of SI. Several recent studies on sour cherries have shown that levels of SC are associated with the segregation of functional and nonfunctional alleles at the *pollen-S* locus (Hauck *et al.*, 2002; Ushijima *et al.*, 2004; Yamane *et al.*, 2005).

There is some direct evidence that tetraploid species can tolerate more inbreeding than their diploid progenitors (Husband and Schemske, 1997; Cook and Soltis, 2000), but this has not been found to be the case in the autopolyploid crop species, alfalfa and potato. In fact, both these species are highly outcrossed and very subject to inbreeding depression (Bingham, 1980). It has been proposed that self-infertility in these autopolyploid species might be tied to the loss of higher-order allelic interactions in what is known as the overdominance model of inbreeding depression (Bever and Felber, 1992). Evidence for this possibility has come from the observation that inbreeding depression in alfalfa and potato is much greater than would be predicted by the coefficient of inbreeding in a two-allele model (Busbice and Wilsie, 1966; Mendoza and Haynes, 1974; Mendiburu and Peloquin, 1977).

Supportive data for the importance of higher-order allelic interactions in autopolyploids has come from comparisons of the self-fertility of autotetraploids of alfalfa with different genetic structures. Bingham and his group (Dunbier and Bingham, 1975; Bingham, 1980) produced diploids from natural tetraploids by haploidy, generated diploid hybrids, and then doubled the diploid hybrids using colchicine treatments to obtain defined two-allele duplexes (di-allele loci). These were then crossed to produce double hybrids with presumed tetra-allelic interactions. When the performance of these different structured populations was compared, 'progressive heterosis' was observed as the diploid hybrids had higher above-ground biomass than their diploid parents, and the double hybrids had the highest productivity of all.

Genetic differentiation in polyploids

In spite of the advantages thought to be associated with increased heterozygosity, polyploidy has long been considered to be a conservative rather than a progressive force in evolution (Stebbins, 1950, 1971; Grant, 1981). It was thought that the presence of multiple alleles reduced the effect of single alleles and genetic differentiation was further restricted by the lack of segregation due to fixed heterozygosities in allopolyploids and the reduced rate of segregation due to tetrasomic inheritance in autopolyploids.

This conservative opinion about the evolutionary potential of polyploids has dramatically changed in recent years. Polyploids may indeed evolve slower than diploids due to

the buffering effect of multiple alleles, but they may actually have a broader adaptive potential. There is a greater potential dose span between additive alleles in polyploids, allowing for a greater range in phenotype, and the higher levels of genetic variability generally found in polyploids allows for more possible assortments of genes (Hancock, 2004). This possibility has been most dramatically demonstrated in the breeding of polyploid crop species. Over two-thirds of crop species are polyploids, and breeders have substantially improved most of them for numerous traits. A particularly dramatic example can be seen for the autoallo-octoploid strawberry where Bringham and Voth (1984) have been able to increase its yields by 500% over 25 years of artificial selection.

There is growing evidence that there is genome downsizing in polyploidy plants after formation (Lai *et al.*, 2004; Leitch and Bennett, 2004) and synteny among homeologues can decay rapidly after polyploidy (Ilic *et al.*, 2003; Langham *et al.*, 2004). Exciting studies on the cole crops and wheat have also indicated that newly formed polyploids can undergo dramatic genome rearrangements that could result in rapid evolution. Song *et al.* (1995) produced reciprocal hybrids between the diploids *Brassica rapa* and *B. nigra*, and *B. rapa* and *B. oleraceae*. The F₁ individuals were colchicine doubled and progenies were generated to the F₅ generation by selfing. They then conducted an RFLP analysis of F₂ and F₅ individuals of each line, using 89 nuclear DNA probes, and found substantial genomic alterations in the F₅ generation, including losses of parental fragments and gains of novel fragments (Fig. 2). Almost twice as much change was observed in the combinations involving the two most distant relatives, *B. rapa* and *B. nigra*, and they observed more change in some nuclear/cytoplasmic combinations than others.

In the work on wheat, Feldman *et al.* (1997) began by examining RFLP patterns in natural diploid and allopolyploid species. They used 16 probes that were from low-copy, non-coded DNA. Nine of these probes were found in all the diploid species, indicating they were conserved, but when they examined aneuploid and nullisomic lines, they found that each sequence was only retained in one of the allopolyploid genomes. In follow-up work, Liu *et al.* (1998a, b) examined RFLP fragment profiles of both coding and non-coding sequences in synthetic tetraploid, hexaploid and octoploids of *Triticum* and *Aegilops* that had been selfed for three to five generations. They obtained similar results to Feldman *et al.* (1997), observing non-random sequence elimination in all the allopolyploids studied, along with the occasional appearance of unique fragments. They also found that some of the changes were brought about by DNA methylation. By comparing crosses with and without the *PHI* gene that regulates bivalent pairing, they were able to deduce that intergenomic recombination did not play a role in the sequence change, as both types of crosses yielded about the same amount of change.

In two further studies, the Feldman group found that the direction of sequence change in wheat followed a different pattern to that observed by Song's group in *Brassica*, and confirmed that some sequences were silenced by

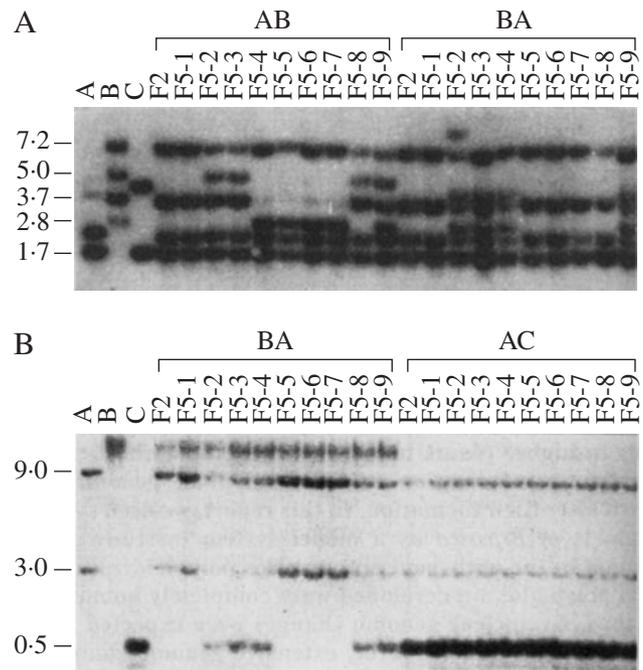


FIG. 2. Nuclear RFLP patterns of *Brassica rapa*, *B. nigra*, *B. oleraceae*, F₂ hybrids between them and F₅ populations. (A) *Hind*III-digested DNAs probed with EZ3, which show a loss of fragments and a gain of fragments in some F₅ plants (5.0 kb and 2.8 kb). (B) *Hpa*II-digested DNAs probed with EC3C8 showing a gain of a 0.5-kb fragment in five BA F₅ plants, which does not exist in either the A or B parental genome, but which is present in the C genome parent and all AC F₅ plants (Song *et al.*, 1995).

elimination, while others were silenced through methylation. Ozkan *et al.* (2001) analysed diploid parental generations, F₁ progeny and the first three generations of (S₁, S₂ and S₃) of synthetic hybrids of several species of *Aegilops* and *Triticum*. When they followed the rate of elimination of eight low-copy DNA sequences, they found that sequence elimination began earlier in the synthetic allopolyploids that most closely represented naturally occurring ones, and sequence elimination was not associated with cytoplasm. Shaked *et al.* (2001) used AFLP and methylation-sensitive amplification polymorphism fingerprinting (MSAP) to evaluate another set of diploid and tetraploid hybrids within and between genera. They also found considerable sequence elimination after polyploidy that occurred most rapidly in allopolyploids of the same species rather than different species. Further analysis indicated that some of the sequences were eliminated, while others were altered by cytosine methylation.

The Feldman group has suggested that the observed sequence alterations may play a physical role in how chromosomes pair, resulting in the bivalent meiotic behaviour of newly formed allopolyploids. However, sequence losses do not appear to be necessary for bivalent pairing behaviour, as Liu *et al.* (2001) found little evidence of change in 22 000 AFLP loci in artificial hybrids of cotton, even though pairing in cotton tetraploids is strictly bivalent. It is also unknown why the most divergent genomes were altered the most in *Brassica*, while the opposite was true in wheat. Perhaps transposons play a role, with the direction

and degree of perturbations being associated with the unification of genomes with or without unique mobile elements.

Emerging research

The almost completed sequencing of the two major subspecies of cultivated rice, *Oryza sativa* ssp. *japonica* (Goff *et al.*, 2002) and *O. sativa* ssp. *indica* (Yu *et al.*, 2002) offers plant evolutionary biologists with a number of exciting research possibilities. Opportunities abound for studying the nature of adaptation at the molecular level, as these two species have very distinct ecological ranges. The *indica* subspecies is most widely cultivated in China and most of Asia, while the *japonica* rice is grown in Japan and other temperate regions. The rice sequence data can be compared with other species sequences to examine rates of evolution in a wide range of selectively significant and neutral traits.

Broad comparisons of molecular evolution across species boundaries are likely to be possible, as the relative numbers and types of genes found in rice are very similar to those found in arabidopsis, and at least 80 % of the genes that have been found in arabidopsis are in rice. The plant genome appears to quite distinct from the fungal and animal ones, as about one-third of the genes found in plants are missing in the fungi and animals, and the genomes of both rice and arabidopsis have many more copies of genes than the other two kingdoms (Bennetzen, 2002). The sequence data now available will afford evolutionary biologists with the opportunity to study the origin of gene families, track their subsequent divergence and should provide hints about how genes diverge and produce proteins with novel biological properties.

Evolutionary biologists have already begun to mine the rice sequence data and have made some very interesting observations. Paterson *et al.* (2004) compared genomic data from rice with other taxa, and came to the conclusion that an ancient polyploidization occurred before the divergence of the cereals. Vandepoele *et al.* (2003) used the rice genome data to conclude that aneuploidy, and the duplication of one chromosome, played an important role in cereal evolution. Most recently, Jiang *et al.* (2004) used rice sequence data to discover that common transposable elements, MULEs, often carry fragments of genes. This likely represents an important mechanism for the evolution of genes in higher plants, where genomic sequences are shuffled and reorganized to create novel, adaptively significant genes. Without complete sequence data, the prevalence of this phenomenon would not have been recognized.

ACKNOWLEDGEMENTS

I would like to acknowledge the rich environment in the plant sciences at Michigan State University. In few other places in the world is there such a well-stocked pool of evolutionary biologists, molecular biologists and plant breeders. Vigorous, inter-departmental programmes exist in ecology, evolutionary biology and behaviour; genetics; plant breeding and genetics; and molecular and cellular biology.

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