Apomixis in flowering plants: an overview

A. J. Richards

School of Biology, University of Newcastle upon Tyne, Newcastle upon Tyne NE1 7RU, UK (a.j.richards@ncl.ac.uk)

Apomixis is a common feature of perennial plants, which occurs in *ca.* 60% of the British flora, but has been largely ignored by reproductive theoreticians. Successful individuals may cover huge areas, and live to great ages, favoured by 'symmetrical' selection. Apomixis is favoured by colonizing modes, for instance post-glacially. Despite its theoretical advantages, apomixis usually coexists with sexuality, suggesting 'hidden' disadvantages. Agamospermy (apomixis by seed) is relatively uncommon, but gains from the attributes of the seed. It pays agamospermy genes, which discourage recombination, to form co-adapted linkage groups, so that they become targets for disadvantageous recessive mutant accumulation. Consequently, agamospermy genes cannot succeed in diploids and agamosperms are hybrid and highly heterotic. Agamospermous endosperm may suffer from genomic imbalance, so that nutritious ovules, which can support embryos without endosperm, may be preadapted for agamospermy. When primary endosperm nucleus fertilization ('pseudogamy') continues as a requirement for many aposporous agamosperms, selfing sex becomes preadaptive and archesporial sex remains an option. Apomictic populations can be quite variable although apomictic families are much less variable than sexuals. Only in some diplosporous species does sex disappear completely, and in those species some release of variability may persist through somatic recombination. The search for an agamospermy gene suitable for genetic modification should target fertile sexuals with a single localized agamospermy (*A*) gene, which therefore lack a genetic load. The *A* gene should coexist alongside sexuality, so that it would be easy to select seedlings of sexual and asexual origins. Plants with sporophytic agamospermy provide all these attributes.

Keywords: asexuality; apospory; diplospory; genetic modification; endosperm;
sporophytic agamospermy

1. THE THEORETICAL IMPORTANCE OF APOMIXIS

Higher (vertebrate) animals only reproduce by outcrossing sex and have no choice in the matter. By contrast, many flowering plants can choose between no less than three fundamentally different modes of reproduction: (i) outcrossing sex; (ii) selfing sex; and (iii) asexuality. These influence population structure and evolutionary potential in profoundly different ways. Perennial plants commonly use a combination of all three modes to fine-tune their reproductive strategy to changing ecological circumstances (Richards 1990*a*, 1996, 1997*b*). Consequently, a propensity for asexual reproduction, apomixis, is a major feature of many flowering plant lifestyles.

Nevertheless, remarkably, asexuality has been largely ignored by plant reproductive ecologists, so that major reviews about reproductive strategy or function (Lovett Doust & Lovett Doust 1988; Holsinger 1992; Lloyd 1992; Owens & Rudall 1998; O'Neill & Roberts 2002) fail to discuss apomixis at all. Theoretical structures have suffered accordingly, because vegetative reproduction and unequal genet survival have rarely been featured in model reproductive systems.

Recognition of the importance of asexuality and clonality brings many insights to evolutionary theory and the modelling of mating systems. Considering one of many examples, it has become axiomatic (e.g. Lloyd 1975; Charlesworth & Charlesworth 1978) that stable gynodioecy depends on

(i) cytoplasmic–nuclear transmission;
(ii) females that are much fitter than hermaphrodites; and
(iii) male-sterility polymorphisms that are frequency dependent.

These models make the tacit assumption that asexuality is absent, or without bias. However, Stevens & van Damme (1988) show that if females, or the offspring of females, have a greater vegetative vigour in comparison with hermaphrodites (hybrid vigour and freedom from male load render these very plausible assumptions), such models become untenable. In these circumstances, although females may be severely disadvantaged by low fertility or by automatic-transmission disadvantage when male sterility is under nuclear control, they can nevertheless reach high frequencies, or even fix, so that populations become completely female.

Androdioecy forms a separate, equally compelling case. According to Lloyd (1975), this rare condition should only persist in the unusual circumstances of acute pollen shortage (poor reproductive assurance) in usually SI hermaphrodites. A few cases of androdioecy are now known, but in two of these, *Saxifraga cernua* (Molau & Prentice 1992) and *Lloydia serotina* (B. Jones, personal

Phil. Trans. R. Soc. Lond. B (2003) **358**, 1085–1093
DOI 10.1098/rstb.2003.1294

1085

communication) seed rarely sets in the difficult arctic–alpine conditions they inhabit. Consequently, male mutants, whose flower development presumably uses less resource than in hermaphrodites, persist well by vegetative apomixis.

Many truisms of gender resource allocation, gender fitness, gender ratio, transmission of gender, sexual competition, reproductive fitness, outcrossing theory, pollen discounting, diclinous polymorphism and frequency-dependent selection on mating systems fail as soon as mating-system genotypes reproduce unequally, asexually. A thorough reappraisal of the role played by asexual reproduction in plant reproductive and evolutionary systems is long overdue.

2. THE CONSEQUENCES OF APOMIXIS

(a) *Persistence of sexuality*

It is reasonable to define asexual reproduction as the ability to produce a new ramet (= plant module) by mitotic division, without meiosis or sexual fusion. This is almost synonymous with apomixis ('reproduction without fertilization'; Lincoln *et al.* 1982), although the latter can also imply a suppression of sexual function. Apomixis is often used loosely to mean agamospermy ('seeds without sex'), as in Nogler (1984), but most of the genetic and evolutionary consequences of asexuality do not differ whatever its medium. Agamospermy does have some advantages over vegetative apomixis, but these result from the properties of the seed itself (protection, dormancy, dispersal and freedom from disease), and only the sometimes greater dispersal of seeds might differentiate between the population genetics of vegetative or agamospermous asexual populations.

Asexuality is usually accompanied by sexual reproduction ('facultative apomixis'), but in some apomicts only a few elements of the sexual process remain. Female sexual function may become rare because regular recombination fails in apomicts, so that polyploidy, hybridity, partial sterility or even unisexual populations are promoted. The success of sex in competition with asexual alternatives depends on the generation of sexual variability. When sex becomes rare, so that few new recombinants occur, there should be a 'runaway' tendency for sex to be lost completely (Peck & Waxman 2000).

Male sexual function may survive solely to promote endosperm growth after PEN fertilization ('pseudogamy'). Nevertheless, both pseudogamy and cohabitation with sexuals should maintain sexual male fertility in totally asexual females, so that many plants that are obligate apomicts in female function still produce reductional, functional pollen (e.g. *Taraxacum*; Mogie 1992).

(b) *Agamospermy and polyploidy*

Recombination and segregation, the independent sorting of linked and unlinked genes are essential concomitants of reductional meiosis, and so are closely integrated into the sexual process. The corollary also applies, so that meiotic recombination and segregation only occur as part of the sexual cycle. Lacking recombination, the genomes of obligate asexuals act as giant linkage groups, which form targets for disadvantageous recessive mutant accumulation ('Muller's Ratchet') to challenge their

immortality. This may explain why agamosperms are rarely diploid (Nogler 1984). In diploid asexual mother–daughter lines, accumulated mutants would be expressed in haploid products of reductional meioses, whereas in polyploids these mutants would not often be expressed. Analysis of meioses in diploid apomictic *Arabis holboelii* tends to confirm this hypothesis (Naumova *et al.* 2001).

In this context it is interesting to note that most of the newly formed triploid agamospermous genotypes observed by de Kovel & de Jong (2000) were less vigorous and less fecund than well-established agamospermous genotypes, suggesting that a resorting of accumulated asexual genetic load may also be disadvantageous in novel asexual polyploid genotypes.

(c) *The advantages and disadvantages of sexuality and asexuality*

Sexuality and asexuality are alternative modes of reproduction, with starkly contrasting outcomes. In fact, for many plants, perhaps most, both modes coexist, and the sexual option has been completely lost in only very few. Yet, theoretically, there are many unattractive features of sexual reproduction.

(i) Male sexual selection for display is expensive.
(ii) The reproductive assurance (efficiency) of outcrossing sex is often poor.
(iii) Sex is wasteful of unfit, non-maternal, genotypes ('cost of sex') (Maynard Smith 1978; Richards 1997b).
(iv) Most strikingly of all, males, or in hermaphrodites, male function becomes redundant and this can cause a doubling of reproductive efficiency for female-only asexual populations.

Consequently, a clonally reproducing plant with efficient dispersal should increase its reproductive efficiency by losing the power of sexual reproduction completely (Peck & Waxman 2000). Agamospermy is usually dominant to sexuality, so that Van Dijk & Van Damme (2000) have suggested that if an agamospermy (*A*) gene was successfully cloned and released into the environment, it should succeed at the expense of sexual genes, so that it might constitute a serious environmental hazard.

In practice, such a 'Doomsday' scenario may not be inevitable or even likely. Observations of populations that contain both pollen-bearing asexuals and sexuals with which they are interfertile, for instance in *Taraxacum*, suggest that the reproductive systems typically coexist in stable equilibrium (Menken *et al.* 1995; Meirmans *et al.* 1999). Nevertheless, Bengtsson & Ceplitis (2000) suggest that mixed reproduction will only persist in an evolutionarily stable strategy when the relative fitness of sexuality and asexuality fluctuates between years.

If obligate asexuality were of long-term advantage, it would be expected to predominate over major systematic groupings. This rarely happens, and if we accept the likelihood that variable populations will have been more likely to withstand major environmental changes and catastrophes, we do not find this surprising. What is perhaps more intuitively unlikely is the finding that *de novo* obligate asexuality with a scattered distribution also remains uncommon. Consequently, we must suppose, in most cases, that there is a short-term cost as well as a long-term

penalty to obligate asexuality. This suggests that there are less-than-obvious ongoing advantages to sex, and corresponding disadvantages to asexuality. These may depend on the much greater variability of sexual offspring, as reviewed in the next section.

These advantages of sex have been reviewed by Maynard Smith (1978), Felsenstein (1988) and Richards (1997*a*) among many others, and concern the capability of the environment to provide multiple niches that allow variable siblings to escape competition from each other (so-called 'Tangled Bank'), which is a function of the productivity of the habitat. This is perhaps most strikingly displayed by the so-called 'Red Queen', where hosts and prey should vary so that some will escape the attentions of variable pathogens and predators.

3. THE POPULATION STRUCTURE OF APOMICTS

(a) *Release of variability in asexual populations*

A theoretical consequence of asexuality is a profound lack of variability. An asexual mother should give birth to offspring that are identical to her and to each other, so that if agamospermous, the invariable mother–daughter lines could be regarded as 'seed-clones'. Janzen (1977) described a population of agamospermous dandelions (*Taraxacum*) by the vivid if unrealistic simile of a buried tree, in which the branch tips lie at the soil surface, forming the individual plants. In general, this model is mostly realistic, insofar as an asexual mother does usually give birth to offspring that are identical to her (e.g. Hughes & Richards 1988). Nevertheless, there are various ways by which agamosperms can give rise to heritable variants (reviewed in Richards 1996), but the release of variation is usually several orders of magnitude less than for outcrossing sexual mothers (although it may more closely resemble that for selfing mothers; Hughes & Richards 1989).

(b) *Heterozygote vigour*

Another feature of agamospermy that requires emphasis is the unexpectedly high proportion of loci that are fixed in the heterozygous state. In agamospermous *Taraxacum* populations, approximately half the loci are typically invariably heterozygous, a much higher overall level of heterozygosis than was found in related outcrossing sexuals (Hughes & Richards 1988). This heterozygosis presumably relates to the hybrid origin of most obligate apomicts, and has considerable implications for heterosis. We must expect fixed hybrid apomicts to be vigorous, however invariable they may be. Interestingly, in the mostly sexual canyon live oak, *Quercus chrysolepis*, Montalvo *et al.* (1997) show a significant association between asexuality measured as clonal vigour (number of stems per clone) and the level of heterozygosity.

(c) *How variable are apomictic populations?*

The release of variability within families is often confused with genetic variation in populations. In fact, apomixis raises difficult hierarchical questions about the nature of populations that lack the defining attribute of gene exchange. Semantically, a population could:

(i) be restricted to plants in recent genetic contact, i.e. members of a seed-clone (but how recent?);

(ii) concern all coexisting members of a genus (but how close is 'coexisting', and why choose the genus, when the criterion of gene exchange is missing?);

(iii) compromise a solution, which has often been adopted, would be to take members of the same 'agamospecies' from the same locality (Battjes *et al.* 1992; Kirschner & Stepanek 1994).

In this case, it has often been found in asexual *Taraxacum* that some agamospecies 'populations' of agamospermous *Taraxacum* are virtually invariable, even between localities, whereas others comprise several genotypes even within populations. The agamospecies approach has been criticized by those who do not find the concept of low-amplitude taxa helpful, or think that the agamospecies should be defined by a near-absence of molecular variation (as the 'agamospecies' rank has never been formally recognized, this is in fact a redundant argument).

Whatever taxonomic philosophy or population definition we adopt for habitual apomicts, we can now mostly dismiss earlier models as unrealistic, which suppose that invariable asexual populations are restricted to narrow or undemanding niches (Darlington's 'escape from sterility' (1939), or Janzen's 'lump of mud' (1977)). Coexisting asexual races can potentially fill many diverse niches, particularly if they also have a capability for phenotypic plasticity (Dudman & Richards 1997). Nevertheless, cases are known where a single asexual genotype forms the only representative of the species, and genus, in a locality (e.g. *Sorbus*, Proctor *et al.* 1989).

Much of the preceding argument has been restricted to obligate agamospermy. Where sex and asexuality coexist, we can suppose that the release of variability, and the amount of variability within populations, should be largely dependent on the proportion of births that are of sexual origin. This is strikingly demonstrated by the genus *Garcinia* in which facultative agamospermy is found in a dioecious genus of small tropical trees (Richards 1990*b*). If it is assumed (probably falsely) that the ratio of males and females born after a sexual union should be unity, but that after an asexual birth only female offspring identical to the mother can occur, then the percentage of males at birth, between 0 and 50%, should be proportionate to the frequency of births that are sexual. Because gender longevity may be unequal, the proportion of males at maturity may not be such a good guide (Lloyd 1974).

(d) *Asymmetry of genet distribution*

An interesting insight into the interplay between ramets of sexual and asexual origin has been provided by de Kroon *et al.* (1992). Clonal ramets compete with one another asymmetrically, so that the weaker perish, but ramets from different clones compete symmetrically, so that genetic diversity tends to persist at the expense of identical ramets. The authors highlight two consequences of this structure:

(i) when sexuality and asexuality coexist, estimates of genetic diversity may be unrealistically high;

(ii) because genetic diversity among established clones is favoured by selection, some clones may survive to a great age.

Apomixis does indeed promote immortality, so that it has a profound influence on the structure and evolution

Table 1. *Proportion of native and naturalized members of the flora of the British Isles with and without various forms of asexual reproduction.*

| | asexual reproduction | | | | | |
	absent	without dispersal	dispersal vegetative	floral proliferation	agamospermy	total
number	727	621	380	16	69	1813
percentage of total	40.1	34.2	21	0.9	3.8	100

of populations. If a few successful genotypes live forever, they may come to predominate in populations, so that genotype frequencies become highly skewed, and their abundance and distribution will depend on their age and comparative fitness (as in the clonal ground palm *Geonoma congesta*; Chazdon (1992), where 15% of the largest clones provide 35% of the ramets in the population). In practice, clones may eventually succumb to disease or exhaust their resource, but in species with some capacity for vegetative spread and persistence such as *Rhododendron ferrugineum*, many individuals may prove to be ancient, and limitations on vegetative spread may mean that their age is considerably underestimated (Escaravage *et al.* 1998). Nevertheless, vegetative dispersal can be quite effective, although in the absence of efficient seed dispersal, clonal distribution tends to show a marked spatial pattern, as in the dwarf Japanese bamboo *Sasa senanensis* (Suyama *et al.* 2000). In this study, it is noteworthy that some clones occur over more than 400 m, and may consist of many thousands of shoots.

4. THE DISTRIBUTION OF APOMIXIS

In some biomes, most plant species are facultatively apomictic, so that 60% of a sample of the British flora can reproduce asexually, whereas 25% of species in the same sample combine asexual reproduction with specialized dispersal, so that the disseminule escapes parental competition after birth (table 1).

Most vegetative apomicts remain facultative, so that they can also set sexual seed, although where only one sex is present (*Elodea canadensis*, *Petasites hybridus*), where only one compatibility genotype occurs (*Menyanthes trifoliata*, *Hottonia palustris*), or where sexuality cannot function because of hybridity (*Mentha*, *Mimulus*) or uneven polyploidy (*Potentilla anserina*, *Holcus mollis*), the apomixis may become essentially obligate (references in Richards 1997*a*).

Obligate apomixis is more often associated with specialized organs of vegetative reproduction, which frequently displace the inflorescence ('floral proliferation'), or with the production of seeds (agamospermy) (table 1). Cases of floral proliferation are uncommon, being most common in subarctic Poaceae and Cyperaceae.

Agamospermy has been reported in approximately 330 genera, although gametophytic agamospermy only occurs in about one-third (126) of these (Carman 1997). The proportion of species that show agamospermy is notoriously difficult to estimate, as this reproductive system has encouraged taxonomists to proliferate taxa. Measures of biodiversity, which are normally dependent on species richness, are strongly biased by the inclusion of agamos-

permous agamospecies. Nevertheless, when agamospecies are excluded from such estimates, as is usually the case, important information is lost. As highly focused taxa of narrow rank, agamospecies tend to be particularly effective bioindicators of habitat, distributional history or climate change. If the British and Irish species of *Hieracium*, *Taraxacum* and *Rubus* were included in these statistics, approximately half of all British species of flowering plants would be obligate agamosperms. However, with only sectional taxa included for these genera, it is reasonable to suggest that less than 5% of British and Irish species never reproduce sexually.

(a) *Apomixis and 'Baker's Law'*

Apomixis is particularly associated with Arctic and boreal conditions. Traditionally (e.g. Stebbins 1950), it has been supposed that autonomous reproductive systems are favoured by unfavourable climates and unreliable pollinator service, whereas more modern interpretations note that the low carrying capacity of Arctic environments is suited to reproductive systems such as apomixis which generate few, very fit genotypes (Richards 1997*a*).

Mogie & Ford (1988) point out that apomicts which, like selfers, should be able to establish from single disseminules ('Baker's Law'), were better suited than outcrossing sexuals to colonize remote parts of the post-glacial landscape recently freed from ice and, unlike selfers, they were not hampered on arrival by homozygosity and inbreeding depression. Once 'in possession', early-arriving apomicts may have been able to repel some later advances made by sexuals.

Certainly, there is a marked tendency for remote, isolated and colonizing populations of *Hieracium* section *Pilosella* to be agamospermous (Gadella 1991). A particularly striking example is to be found in the tropical *Rubus alceifolius*, which reproduces sexually in its native southeast Asian range, but old human introductions to Madagascar, and recent occurrences on Reunion which was colonized from Madagascar, are asexual and lacking in variability (Amsellem *et al.* 2001). It seems that sexual colonizers in Madagascar may have given rise to apomictic hybrids with the asexual native *R. roridus*.

5. THE ORIGINS OF AGAMOSPERMY

Agamospermy is not distributed at random, but prevails in certain families (Poaceae, Rosaceae, Asteraceae) at high latitudes, suggesting that certain taxa in these habitats are preadapted to agamospermy. Nevertheless, gametophytic agamospermy has evolved many times even within these families and has adopted varied mechanisms. The essential elements of agamospermy ((i) avoidance of

reductional meiosis, (ii) development of the unfertilized egg, and (iii) independent development of the endosperm) do not function successfully in isolation, and may only recombine rarely in long-lived hybrids, which thus 'escape sterility'.

Gametophytic agamospermy is frequently classified as aposporous or diplosporous, depending on whether the asexually functioning embryo sac is adventitious, or archesporial in origin. The apomixis literature is overladen with terminological niceties of little consequence, but here we have a distinction of real importance.

(i) In apospory, the archesporium remains free, so that sex is also possible (often resulting in polyembryony, where sexual and asexual embryos lie together in the seed).

(ii) In diplospory, where the sole embryo sac is archesporial in origin, only one asexual embryo can be produced.

Occasionally, diplosporous (apomeiotic) and aposporous embryo sacs coexist even in the same ovule, as in the grass *Paspalum minus* (Bonilla & Quarin 1997), although it is unclear whether these apparently unrelated phenomena have converged as the result of a common sexual stimulus, or have resulted from hybridization between facultatively aposporous and diplosporous entities.

Only in some diplosporous species does sex disappear completely and in these species, some release of variability may persist through such meiotic, or by somatic, recombination (Richards 1989). When diplospory is preceded by a restitutional meiosis ('apomeiosis'), some recombination can theoretically occur (and in fact seems to do so, at least in some *Taraxacum*; Malecka 1973; Van Baarlen *et al.* 1999, 2000).

(a) *The requirement for an endosperm*

Typical endosperm of sexual origin is triploid with two genomes of maternal origin and one of paternal origin. Haig & Westoby (1991) view endosperm function as the balanced product of a conflict between endosperm-specific genes of maternal and paternal origin, where genes of maternal origin tend to suppress and genes of paternal origin tend to promote endosperm development (in this way, sexual theory suggests, males are enabled to gestate 'their' own embryos). Consequently, endosperms with genomes departing from this 2 : 1 ratio will normally be non-viable. Because of disturbed or non-reductional meioses, or the absence of double fertilization, most agamospermous endosperms will be unbalanced in this way (Vinkenoog & Scott 2001), so that newly arising agamosperms may have to overcome the problem of endosperm non-viability. Certainly, the requirement for accurate maternal/paternal genome balance has been lost at times in agamosperms, for instance in *Paspalum* where the female : male genome ratio in successful endosperm varies from 2 : 1 to 8 : 1 (Quarin 1999).

It has recently been suggested that resource-rich seeds, typical of Asteraceae such as *Taraxacum* and *Hieracium*, may be able to nurture embryos in the absence of endosperm, thus predapting plants to a pseudogamy-free obligate agamospermy (Van Baarlen *et al.* 1999).

Nevertheless, in most cases, embryogenesis requires endospermal nurture, so PEN fertilization ('pseudogamy') often continues as a requirement for many agamosperms, mostly aposporous, for which archesporial sex therefore remains an option. It has recently been pointed out that pseudogamy selects for self-fertility, so that self-fertility may also have been a preadaptive for the evolution of agamospermy (Noirot *et al.* 1997).

(b) *The control of agamospermy*

An increasing body of opinion, led by Koltunow (1993) and Carman (1997), views the control of agamospermy as essentially a matter of timing. Instead, Spillane *et al.* (2001) use the phrases 'short-circuiting' and 'deregulation' in this context, so that factors that contribute to agamospermy are considered to result from mutations that inhibit the full realization of the sexual process. This is perhaps the more helpful model, so that parthenogenesis is not only seen as the egg cell that undergoes embryony too early, but also as the egg cell that has lost the requirement for a chemical message of male origin as a stimulus to cell division. We must also suppose that the concept of apospory as the later and secondary production of supernumerary embryo sacs is oversimplistic. Rather, the elements that control the location for the transcription of some embryo-sac coding genes may have been deregulated.

6. WHAT IS THE PROBLEM WITH THE AGAMOSPERMY GENE?

Recent reviews have attempted to publicize the agronomic potential of an 'apomixis (agamospermy) gene', which could be added to a crop plant at will, thereby preserving a particularly vigorous, disease- or stress-resistant, or nutritious genotype through subsequent generations (Grossniklaus *et al.* 1998; Van Baarlen *et al.* 1999; Van Dijk & Van Damme 2000; Spillane *et al.* 2001). This would revolutionize plant breeding, so that, for instance, the huge industry that generates F_1 hybrid seed might disappear almost overnight. The benefits would be huge, such that McMeniman & Lubulwa (1997) calculated that the annual benefit of a cloned apomixis gene to the rice industry alone might be worth US$ 2.5 billion.

These potential benefits were already recognized by an earlier generation of plant scientists (Gustafsson 1946–7; Stebbins 1950) to whom modern techniques of GM were unavailable. Despite intensive research for more than a decade (Hanna & Bashaw 1987; Savidan 1992), modern reviews suggest that we are still some distance from the goal of an all-purpose agamospermy gene clone (Dresselhaus & Colombo 2001). In this context, it is perhaps ironic that we have been able to 'fix' a new agamospermous genotype through agamospermous male × sexual female hybridization for more than half a century (e.g. Muntzing 1945; Richards 1970), whereas close-relative cloning of an agamospermous gene was achieved more than a decade ago (Dujardin & Hanna 1989). It is the transfer of agamospermy-controlling material between distantly related taxa that has so far been problematic, and we need to ask why this should have been so.

(a) *One coadapted linkage group or two?*

Early opinion, summarized in Richards (1997*a*), considered that the essential elements of agamospermy, avoidance of reductional meiosis, development of the unfertilized egg, and independent development of the endosperm, do not function successfully in isolation, so that it is reasonable to suppose that at least two completely independent genetic elements are involved in its control. This view may have suffered a diplosporous bias. Since then, work has focused on aposporous grasses (see, for example, Pessino *et al.* 1997; Ozias-Akins *et al.* 1998) and *Hieracium* (e.g. Bicknell *et al.* 2000) and has tended to support Mogie's (1992) contention that only one gene need be involved because the various agamospermy functions are, in his view, developmentally interrelated.

However, by examining the evolution of coadapted linkage groups in other types of reproductive system, we have gained important new insights into this genetic control of agamospermy. Our understanding of how dioecy and heterostyly developed has demonstrated the power of translocation in the creation of coadapted linkage groups such as sex chromosomes or S/s chromosomes (Richards 1997*a*). Such systems depend on homogametic–heterogametic polymorphisms, which only maintain equilibrium ratios because of recessive lethal linkage on the heterogametic (Y or S) chromosome (Richards 1998).

Equally, just because agamospermy can be inherited as a single entity, it does not follow that agamospermy is controlled by a single, localized, clonable DNA sequence. Rather, it seems that 'apomixis may be controlled by large sectors of DNA in which recombination is suppressed' (Bicknell *et al.* 2001), although detailed studies in several genera have suggested that recombination within this 'apomixis supergene' does in fact occur regularly. The visionary concept of Nogler (1984) that agamospermy in *Ranunculus auricomus* was controlled by a recombinable recessive lethal linked to a coadapted linkage group may apply to many other genera and has come of age.

(b) *Agamospermy, the coadapted linkage group and 'genetic load'; effect not cause*

We can now see that the efficient transmission of agamospermy has been enhanced by translocation of the relevant genes onto a single chromosome as a coadapted linkage group, termed here *A*. As for dioecy and heterostyly, recessive lethal linkage may also have assumed vital importance, but as an effect rather than a cause of the supergene.

Because successful agamospermy must avoid reductional meiosis, it bypasses chiasmatic recombination and chromosomal segregation, and so becomes an unavoidable target to mutant accumulation. Consequently, in a mixed population in which agamosperms and sexuals interbreed:

(i) chromosomes that carry the *A* linkage group follow a non-recombinational maternal inheritance, so that they accumulate harmful recessive mutations (a 'genetic load');

(ii) conversely, those chromosomes that code for recombinational, segregational meiosis are 'cleansed' of their mutational load (Nogler 1984; Richards 1997*a,b*).

This model, which proposes that all the genetic elements which control agamospermy (*A*) may come together in linkage to recessive lethals, has several major implications characteristic of agamospermy already discussed:

(i) the strong association of agamospermy with polyploidy;

(ii) the strong association of agamospermy with hybridity and heterozygosis;

(iii) constitutes the short-term cost as well as the long-term penalty to obligate asexuality that theoretical considerations require.

It has recently received strong experimental support from recent studies of Pessino *et al.* (1997) in *Brachiaria*, Ozias-Akins *et al.* (1998) in *Pennisetum*, and those of Noyes & Reiseberg (2000), working with *Erigeron annuus*.

(c) *The genetic load and genetic modification*

The genetic load also has major implications to the cloning of *A*, and the use of such clones in GM crops. *A*-gene linked recessive lethals would have no dominant heterologues when introduced into a novel unrelated genome, so that *A* transgenics would inevitably fail.

Detailed analyses of the inheritance of breakdown products among relatively wide agamospermous × sexual crosses provide rather depressing confirmations of this model. In *Hieracium* section *Pilosella* in which the control of apospory is essentially monogenic (Bicknell *et al.* 2000, 2001), Koltunow *et al.* (2000) show that modifier genes are sufficiently important to its successful function that agamospermy cannot proceed in their absence. In these cases, certain crosses fail, or against expectations are not agamospermous, perhaps because the genetic load associated with the *A* gene complex cannot function in foreign genomes.

Other results can resemble those of Albertini *et al.* (2001) for *Poa pratensis* where presumptive recombinants in an apparently monogenic aposporous system resulted in aposporous plants lacking parthenogenesis, and parthenogenetic plants in which aposporous embryo sacs are absent. Noyes (2000) also uncoupled diplospory and parthenogenesis in *E. annuus*, although he suspected in this case that parthenogenesis was dependent upon resistutional diplospory, as happens in *Taraxacum* (Richards 1970).

In simple terms, it seems that no agamospermy gene has yet been analysed that is sufficiently localized and independent, or free of a genetic load, to function successfully in an isolated clonal state in a foreign genome that lacks dominant heterologues.

7. HOW CAN WE DEVELOP NEW AGAMOSPERMOUS CROPS?

Before research groups undertake the laborious task of localizing and cloning the *A* gene, it is vital that careful planning goes into the choice of the most appropriate gene donor. Most apomicts, including all those currently the subject of major research programmes, possess certain disqualifying attributes. Target species should not

(i) have agamospermy controlled by multiple-factor systems, even if factors are linked but recombinable;

(ii) be sexually sterile or disturbed, and should have a regular male meiosis, so that the chances of introducing destabilizing elements such as transposons to the transgenic product would be minimized.

(a) *The case for sporophytic agamospermy*

Such apomicts do in fact occur, although they are mostly little known and poorly studied. The system they employ is called 'sporophytic agamospermy' or 'adventitious embryony', in which embryos are budded directly from the integuments or nucellus of the ovule. Remarkably, this, by far the most widespread form of agamospermy, has been recorded in no less than 57 families (Carman 1997). Some are cacti, or even orchids, but the long life cycle and tropical habitat of most sporophytic agamosperms has discriminated against their study. They are mostly tropical trees, often fruit trees with expensive fruits and devolved gender function, which have developed apomixis as a reproductive 'back-up'. In a recent major review of the breeding potential of apomixis (Savidan 2000), sporophytic agamospermy rated just six, somewhat dismissive, lines. Nevertheless, a good recent example has been provided by the Indian fruit tree *Commiphora wightii* ('Guggul'), which not only produces sexual and apomictic embryos, but can develop the endosperm autonomously (Gupta *et al.* 1996).

There is probably some preadaptation involved in this system. Typically, the embryo originates from a disorganized, proliferous tumour, which then responds to developmental controlling agents and becomes organized into a tuberous 'proembryo' greatly resembling those that are produced sexually. Consequently, it seems likely that the relatively undifferentiated tuberous sexual embryos that are typical of many large-seeded tropical trees form a syndrome that can be most readily adopted by proliferating ovular tissue (Richards 1990*b*).

Sporophytic agamosperms are mostly diploid and sexually fertile. Frequently, they are polyembryonous, and sexual and apomictic embryos often coexist. It is often easy to differentiate embryos from the position in the large seed from which each embryo emerges.

Many sporophytic agamosperms are pseudogamous, the endosperm requiring PEN fertilization, which has often been achieved as part of the coexisting sexual function. However, in *Garcinia*, it seems that pseudogamy, autonomous embryony and successful embryony in the absence of an endosperm can all occur (Richards 1990*b*). In the large nutritious ovules of *Garcinia*, it is possible that embryony can proceed successfully in the absence of an endosperm (Van Baarlen *et al.* 1999).

The genetic control of sporophytic agamospermy has scarcely been studied, but as only one function (autonomous development of embryos) is involved rather than two or three as is the case for apospory and diplospory, the hope is that the genetic control might be relatively simple and localized. Early work with *Citrus* (Parleviet & Cameron 1959) agreed with this expectation. More recently, Garcia *et al.* (1999) identified no less than six segregating QTL associated with autonomous embryony in *Citrus*. I am not totally convinced that the QTL approach is particularly helpful in the analysis of apomixis genes. Just because markers such as mRNA

moieties are associated with the apomixis syndrome does not mean that all are necessary to its successful function.

Spillane *et al.* (2001) listed several characterized *Arabidopsis* genes that may be involved in embryo initiation, and the most promising of these increase the embryogenic potential of cells in culture (analogous to the disorganized, proliferous tumour that initiates embryony in *Garcinia*). Some of these may prove to be similar to the adventitious embryony moiety. Interestingly, several *Arabidopsis* mutants have now been identified that rather unexpectedly promote endosperm development in the absence of either PEN or egg cell fertilization, or embryony (Spillane *et al.* 2001). If goals are accurately targeted, we may not be too far from the goal of being able to introduce genes for both adventitious embryony and autonomous endosperm into a crop plant.

8. WHAT ARE WE LOOKING FOR? CONCLUSION

Above all, it is important to recognize that the transgenic agamospermous end-product should not be a typical apomict, i.e. a sexually disabled clone that will accumulate genetic accidents, and will act as an invariable target to pests and diseases ('Red Queen'). Historically, mostly asexual crops such as yams and potatoes have mostly proved unsatisfactory if not properly managed, and have often resulted in catastrophic failure and widespread famine.

Rather, the transgenic product should produce both sexual and adventitious asexual embryos, perhaps polyembryonically. In some crops, these embryos and seedlings are readily identified from their position in the fruit/seed. In others, they could be identified by use of a simple marker gene.

When offspring identical to the mother are required, only the asexual offspring would be propagated. When the breeder wishes to develop new genotypes, sexual embryos would be harvested after controlled crosses. In this way, because it is inherited by both sexual and apomictic offspring, the *A* gene should be enabled to escape the clutches of corporate power and would soon become the property of the most impoverished farmer who will be able to apply it to his own requirements within the transgenic crop species.

It is important to remember that should it become possible to transfer an apomixis gene between distant taxa in this way, such techniques will involve not only GM, but also cloning, and so may prove unwelcome to certain shades of public opinion. We should also be aware that Van Dijk & Van Damme (2000) have suggested that if apomixis genes were successfully cloned and released into the environment, they should succeed at the expense of sexual genes, so that they might constitute a serious environmental hazard. However unlikely, this possibility would need to be rigorously investigated before a GM apomixis gene was released.

REFERENCES

Albertini, E., Proceddu, A., Ferranti, F., Reale, L., Barcaccia, G., Romano, B. & Falcinelli, M. 2001 Apospory and parthenogenesis may be uncoupled in *Poa pratensis*: a cytological investigation. *Sex. Pl. Reprod.* **14**, 213–217.

Amsellem, L., Noyer, J.-L. & Hossaert-McKey, M. 2001 Evidence for a switch in the reproductive biology of *Rubus alceifolius* (Rosaceae) between its native range and its area of introduction. *Am. J. Bot.* **88**, 2243–2251.

Battjes, J., Menken, S. B. J. & den Nijs, J. C. N. 1992 Clonal diversity in some microspecies of *Taraxacum* section *Palustria* (Lindb.f.) Dahlst. from Czechoslovakia. *Bot. Jahr. Syst.* **114**, 315–328.

Bengtsson, B. O. & Ceplitis, A. 2000 The balance between sexual and asexual reproduction in plants living in variable environments. *J. Evol. Biol.* **13**, 415–422.

Bicknell, R. A., Borst, N. K. & Koltunow, A. M. 2000 Monogenic inheritance of apomixis in two *Hieracium* species with distinct developmental mechanisms. *Heredity* **84**, 228–237.

Bicknell, R., Podivinski, E., Catanach, A., Erasmuson, S. & Lambie, S. 2001 Strategies for isolating mutants in *Hieracium* with dysfunctional apomixis. *Sex. Pl. Reprod.* **14**, 227–232.

Bonilla, J. R. & Quarin, C. L. 1997 Diplosporous and aposporous apomixis in a pentaploid race of *Paspalum minus*. *Pl. Sci.* **127**, 97–104.

Carman, J. G. 1997 Asynchronous expression of duplicate genes in angiosperms may cause apomixis, bispory, tetraspory and polyembryony among their relatives. *Biol. J. Linn. Soc.* **61**, 51–94.

Charlesworth, B. & Charlesworth, D. 1978 A model for the evolution of dioecy and gynodioecy. *Am. Nat.* **112**, 975–997.

Chazdon, R. L. 1992 Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. *Biotropica* **24**, 43–51.

Darlington, C. D. 1939 *The evolution of genetic systems*. Cambridge University Press.

de Kovel, C. G. F. & de Jong, G. 2000 Selection on apomictic lineages of *Taraxacum* at establishment in a mixed sexual-apomictic population. *J. Evol. Biol.* **13**, 561–568.

de Kroon, H., Hara, T. & Kwant, R. 1992 Size hierarchies of shoots and clones in clonal herb monocultures: do clonal and non-clonal plants compete differently? *Oikos* **63**, 410–419.

Dresselhaus, T. & Colombo, L. 2001 2nd Int. Apomixis Conf. (AO2001) Como, Italy, 24–28 April 2001. *Sex. Pl. Reprod.* **14**, 245–251.

Dudman, A. A. & Richards, A. J. 1997 *Dandelions of Great Britain and Ireland, Handbook 9*. London: Botanical Society of the British Isles.

Dujardin, M. & Hanna, W. W. 1989 Developing apomictic pearl millet: characterisation of a BC3 plant. *J. Genet. Breeding* **43**, 145–151.

Escaravage, N., Questiau, S., Pronon, A., Doche, B. & Taberlet, P. 1998 Clonal diversity in a *Rhododendron ferrugineum* L. (Ericaceae) population inferred from AFLP markers. *Mol. Ecol.* **7**, 975–982.

Felsenstein, J. 1988 Sex and the evolution of recombination. In *The evolution of sex* (ed. R. E. Michod & B. R. Levin), pp. 74–86. Sunderland, MA: Sinauer.

Gadella, T. W. J. 1991 Variation, hybridisation and reproductive biology of *Hieracium pilosella* L. *Proc. K. Ned. Akad. Wet.* **94**, 455–488.

Garcia, R., Asins, M. J., Forner, J. & Carbonell, E. A. 1999 Genetic analysis of apomixis in *Citrus* and *Poncirus* by molecular markers. *Theor. Appl. Genet.* **99**, 511–518.

Grossniklaus, U., Koltunow, A. M. & van Lookeren, M. 1998 A bright future for apomixis. *Trends Pl. Sci.* **3**, 415–416.

Gupta, P., Shivanna, K. R. & Mohan Ram, H. Y. 1996 Apomixis and polyembryony in the guggul plant, *Commiphora wightii*. *Ann. Bot.* **78**, 67–72.

Gustafsson, A. 1946–7 Apomixis in higher plants. I–III. *Lunds Univ. Arsskr.* **42**, 1–67; **43**, 69–179, 181–371.

Haig, D. & Westoby, M. 1991 Genomic imprinting in endosperm: its effect on seed development in crosses between different ploidies of the same species, and its implications for the evolution of apomixis. *Phil. Trans R. Soc. Lond.* B **333**, 1–13.

Hanna, W. W. & Bashaw, E. C. 1987 Apomixis: its identification and use in plant breeding. *Crop Sci.* **27**, 1136–1139.

Holsinger, K. 1992 Ecological models of plant mating systems and the evolutionary stability of mixed mating systems. In *Ecology and evolution of plant reproduction* (ed. R. Wyatt), pp. 169–191. New York: Chapman & Hall.

Hughes, J. & Richards, A. J. 1988 The genetic structure of populations of sexual and asexual *Taraxacum* (dandelions). *Heredity* **60**, 161–171.

Hughes, J. & Richards, A. J. 1989 Isozymes and the status of *Taraxacum* agamospecies. *Bot. J. Linn. Soc.* **99**, 365–376.

Janzen, D. 1977 What are dandelions and aphids? *Am. Nat.* **111**, 586–589.

Kirschner, J. & Stepanek, J. 1994 Clonality as part of the evolutionary process in *Taraxacum*. *Folia Geobot. Phytotax.* **29**, 265–275.

Koltunow, A. M. 1993 Apomixis: embryo sacs and embryos formed without meiosis or fertilisation in ovules. *Pl. Cell* **5**, 1425–1437.

Koltunow, A. M., Johnson, S. D. & Bicknell, R. A. 2000 Apomixis is not developmentally conserved in related, genetically characterised *Hieracium* plants of varying ploidy. *Sex. Pl. Reprod.* **12**, 254–266.

Lincoln, R. J., Boxshall, G. A. & Clark, P. F. 1982 *A dictionary of ecology, evolution and systematics*. Cambridge University Press.

Lloyd, D. G. 1974 Theoretical sex ratios of dioecious and gynodioecious angiosperms. *Heredity* **32**, 11–34.

Lloyd, D. G. 1975 The maintenance of dioecy and gynodioecy in angiosperms. *Genetica* **45**, 325–339.

Lloyd, D. G. 1992 Evolutionarily stable strategies of reproduction in plants: who benefits and how? In *Ecology and evolution of plant reproduction* (ed. R. Wyatt), pp. 137–168. New York: Chapman & Hall.

Lovett Doust, J. & Lovett Doust, L. 1988 *Plant reproductive ecology: patterns and strategies*. Oxford University Press.

McMeniman, S. & Lubulwa, G. 1997 *Development assessment: evaluation of the potential benefits of integrating apomixis in hybrid rice*. Canberra: Australian Centre for International Agricultural Research.

Malecka, J. 1973 Problems in the mode of reproduction in microspecies of *Taraxacum* sect. *Palustria* Dahlst. *Act. Biol. Cracow. ser. Bot.* **16**, 37–84.

Maynard Smith, J. 1978 *The evolution of sex*. Cambridge University Press.

Meirmans, P. G., Calame, F. G. & Bretagnolle, F. 1999 Anthropogenic disturbance and habitat differentiation between diploid sexual and apomictic triploid *Taraxacum* section *Ruderalia*. *Folia Geobot.* **34**, 451–469.

Menken, S. B., Smit, E. & den Nijs, J. C. M. 1995 Genetical population structure in plants: gene flow between diploid sexual and triploid asexual dandelions (*Taraxacum* section *Ruderalia*). *Evolution* **49**, 1108–1118.

Mogie, M. 1992 *The evolution of asexual reproduction in plants*. London: Chapman & Hall.

Mogie, M. & Ford, H. 1988 Sexual and asexual *Taraxacum* species. *Biol. J. Linn. Soc.* **35**, 155–168.

Molau, U. & Prentice, H. C. 1992 Reproductive system and population structure in three arctic *Saxifraga* species. *J. Ecol.* **80**, 149–161.

Montalvo, A. M., Conard, S. G., Thompson Conkle, M. & Hodgskiss, P. D. 1997 Population structure, genetic diversity and clone formation in *Quercus chrysolepis* (Fragaceae). *Am. J. Bot.* **84**, 1553–1564.

Muntzing, A. 1945 The mode of reproduction of hybrids between sexual and apomictic *Potentilla argentea*. *Bot. Notiser.* **107**, 49–71.

Naumova, T. N., van der Laak, J., Osadtchiy, J., Matzk, F., Kravtchenko, A., Bergervoet, J., Ramulu, K. J. & Boutilier, K. 2001 Reproductive development in apomictic populations of *Arabis holboellii* (Brassicaceae). *Sex. Pl. Reprod.* **14**, 195–200.

Nogler, G. A. 1984 Genetics of apospory in apomictic *Ranunculus auricomus* V. Conclusion. *Bot. Helv.* **94**, 411–422.

Noirot, M., Couvet, D. & Harron, S. 1997 Main role of self-pollination rate on reproductive allocation in pseudogamous apomixis. *Theor. Appl. Genet.* **95**, 479–483.

Noyes, R. D. 2000 Diplospory and parthenogenesis in sexual x agamospermous (apomictic) *Erigeron* (Asteraceae) hybrids. *Int. J. Pl. Sci.* **161**, 1–12.

Noyes, R. D. & Reiseberg, L. H. 2000 Two independent loci control agamospermy (apomixis) in the triploid flowering plant *Erigeron annuus*. *Genetics* **155**, 379–390.

O'Neill, S. D. & Roberts, J. A. (eds) 2002 Plant reproduction. In *Annual plant reviews*, vol. 6. Sheffield: CRC Press.

Owens, S. J. & Rudall, P. J. 1998 *Reproductive biology in systematics, conservation and economic botany*. London: Botanic Gardens.

Ozias-Akins, P., Roche, D. & Hanna, W. W. 1998 Tight clustering and hemizygosity of apomixis-linked genetic markers in *Pennisetum squamulatum* implies genetic control of apospory by a divergent locus which may have no allelic form in sexual genotypes. *Proc. Natl Acad. Sci. USA* **95**, 5127–5132.

Parleviet, J. E. & Cameron, J. W. 1959 Evidence on the inheritance of nucellar embryony in *Citrus*. *Proc. Am. Soc. Hort. Sci.* **74**, 252–260.

Peck, J. R. & Waxman, D. 2000 What's wrong with a little sex? *J. Evol. Biol.* **13**, 63–69.

Pessino, S. C., Oretiz, S. P. A., Leblanc, O., do Valle, C. B., Evan, C. & Hayward, M. D. 1997 Identification of a maize linkage group related to apomixis in *Brachiaria*. *Theor. Appl. Genet.* **94**, 439–444.

Proctor, M. C. F., Proctor, M. E. & Groenhof, A. C. 1989 Evidence from peroxidase polymorphism on the taxonomy and reproduction of some *Sorbus* populations in south-west England. *New Phytol.* **112**, 569–575.

Quarin, C. L. 1999 Effect of pollen source and pollen ploidy on endosperm formation and seed set in pseudogamous apomictic *Paspalum notatum*. *Sex. Pl. Reprod.* **11**, 331–335.

Richards, A. J. 1970 Eutriploid facultative agamospermy in *Taraxacum*. *New Phytol.* **69**, 761–774.

Richards, A. J. 1989 A comparison of within-plant karyological heterogeneity between agamospermous and sexual *Taraxacum*, as assessed by the nuceolar organizer chromosome. *Pl. Syst. Evol.* **163**, 177–185.

Richards, A. J. 1990*a* The implications of reproductive versatility for the structure of grass populations. In *Reproductive versatility in the grasses* (ed. G. P. Chapman), pp. 131–153. Cambridge University Press.

Richards, A. J. 1990*b* Studies in *Garcinia*: tropical dioecious fruit trees: agamospermy. *Bot. J. Linn. Soc.* **103**, 233–250.

Richards, A. J. 1996 Genetic variability in obligate apomicts of the genus *Taraxacum*. In *Apomixis and taxonomy* (ed. A. J. Richards, J. Kirschner, J. Stepanek & K. Marhold), pp. 131–140. Uppsala: Opulus Press.

Richards, A. J. 1997*a* *Plant breeding systems*, 2nd edn. London: Chapman & Hall.

Richards, A. J. 1997*b* Why is gametophytic apomixis almost restricted to polyploids? The gametophyte-expressed model *Apomixis News* **9**, 3–4.

Richards, A. J. 1998 Lethal linkage and its role in the evolution of plant breeding systems. In *Reproductive biology in systematics, conservation and economic botany* (ed. S. J. Owens & P. J. Rudall), pp. 71–83. London: Royal Botanic Gardens.

Savidan, Y. H. 1992 Progress in research on apomixis and its transfer to major grain crops. In *Reproductive biology and plant breeding* (ed. Y. Dattee, C. Dumas & A. Gallais), pp. 269–270. Berlin: Springer.

Savidan, Y. H. 2000 Apomixis: genetics and breeding. *Pl. Breeding Rev.* **18**, 13–86.

Spillane, C., Steimer, A. & Grossnicklaus, U. 2001 Apomixis in agriculture: the quest for cloned seed. *Sex. Pl. Reprod.* **14**, 179–187.

Stebbins, G. L. 1950 *Variation and evolution in plants*. New York: Columbia University Press.

Stevens, D. P. & van Damme, J. P. P. 1988 The evolution and maintenance of gynodioecy in sexually and vegetatively reproducing plants. *Heredity* **61**, 329–337.

Suyama, Y., Obauashi, K. & Hayashi, I. 2000 Clonal structure in a dwarf bamboo (*Sasa senanensis*) population inferred from amplified fragment length polymorphism (AFLP) fingerprints. *Mol. Ecol.* **9**, 901–906.

Van Baarlen, P., Verduijn, M. & Van Dijk, P. J. 1999 What can we learn from natural apomicts? *Trends Pl. Sci.* **4**, 43–44.

Van Baarlen, P., Van Dijk, P. J., Hoekstra, R. F. & de Jong, J. H. 2000 Meiotic recombination in sexual diploid and apomictic triploid dandelions (*Taraxacum officinale* L.). *Genome* **43**, 827–835.

Van Dijk, P. & Van Damme, J. 2000 Apomixis technology and the paradox of sex. *Trends Pl. Sci.* **5**, 81–84.

Vinkenoog, R. & Scott, R. J. 2001 Autonomous endosperm development in flowering plants: how to overcome the imprinting problem? *Sex. Pl. Reprod.* **14**, 189–194.

Discussion

R. A. S. Smith (*Department of Biology, Duke University, Durham, NC, USA*). To what extent has the plant kingdom contributed to our understanding of the various reasons proposed for the evolution of sex? To what extent has the plant kingdom provided *empirical* examples of Muller's ratchet, host–parasite, Red Queen or tangled bank models for the evolution of sexual reproduction?

J. Richards. Tremendously. In particular, the work of Antonovics and Ellstrand. Not enough work has been done to examine *why* asexual *Taraxacum* has been as successful and is as geographically widespread as it is. More work should be done on the north–south transition from asexuality to sexuality in this genus.

M. W. Bayliss (*Biotechnology Consultant, Wokingham, UK*). In natural plant populations, apomixis is normally associated with polyploidy, which will help prevent the problems associated with disadvantageous recessive mutations. However, in plant breeding programmes for diploid agricultural plants, homozygous inbred parental lines will have been selected on their performance and this should have effectively removed recessive lethal mutations. As a consequence, it might be possible to isolate agamospermy genes from diploid crop species.

GLOSSARY

GM: genetic modification
PEN: primary endosperm nucleus
QTL: quantitative trait loci
SI: self-incompatibility