Front. Biol. China 2007, 2(3): 256–262
DOI 10.1007/s11515-007-0036-0

REVIEW

Asexual and sexual reproductive strategies in clonal plants

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Abstract Most plants can reproduce both sexually and asexually (or vegetatively), and the balance between the two reproductive modes may vary widely between and within species. Extensive clonal growth may affect the evolution of life history traits in many ways. First, in some clonal species, sexual reproduction and sex ratio vary largely among populations. Variation in sexual reproduction may strongly affect plant's adaptation to local environments and the evolution of the geographic range. Second, clonal growth can increase floral display, and thus pollinator attraction, while it may impose serious constraints and evolutionary challenges on plants through geitonogamy that may strongly influence pollen dispersal. Geitonogamous pollination can bring a cost to plant fitness through both female and male functions. Some co-evolutionary interactions, therefore, may exist between the spatial structure and the mating behavior of clonal plants. Finally, a trade-off may exist between sexual reproduction and clonal growth. Resource allocation to the two reproductive modes may depend on environmental conditions, competitive dominance, life span, and genetic factors. If different reproductive modes represent adaptive strategies for plants in different environments, we expect that most of the resources should be allocated to sexual reproduction in habitats with fluctuating environmental conditions and strong competition, while clonal growth should be dominant in stable habitats. Yet we know little about the consequence of natural selection on the two reproductive modes and factors which control the balance of the two reproductive modes. Future studies should investigate the reproductive strategies of clonal plants simultaneously from both sexual and asexual perspectives.

Keywords clonal growth, variation of sexual reproduction, clonal architecture, mating system, trade-off

1 Introduction

Many of the herbaceous species are clonal, such as most ferns, mosses and many angiosperms, and they play an important role in many community and ecosystem processes (Oborny and Bartha, 1995; de Kroon and van Groenendael, 1997). Clonal plants can propagate both clonally and sexually, and the fitness of a genet is determined both by traits associated with successful seed production and by traits imparting successful clonal spread (Mclellan et al., 1997). Phenotypically, the two reproductive modes of clonal plants differ in dispersal distance, the phenology of offspring production, and the success of establishment (Winkler and Fischer, 2001). Because both modes of reproduction require resources, a trade-off between them is inevitable and different genotypes may have different allocation patterns (Eriksson, 1997; Prati and Schmid, 2000). The expected trade-off between sexual and clonal growth is complex and often difficult to detect because clonal growth can increase the reproductive output of a genetic individual at the same time as it allows an individual to expand and monopolize resources (Prati and Schmid, 2000; Pan and Price, 2002). Moreover, fitness can be realized through various patterns of allocation to sexual reproduction, vegetative reproduction, or future sexual reproduction through contemporary production of vegetative propagules (Westley, 1993). Because of the complex life-cycle, the relative contribution of either mode of reproduction to population growth is often unknown. It is still unclear to what extent the trade-off between clonal growth and sexual reproduction depends on genetics versus resource.

Clonal growth can also influence spatial patterns of plant mating. For example, localized clonal spread may interfere with sexual reproduction by reducing pollen transfer and mating between genets (Handel, 1985). High levels of geitonogamy may have a major impact on the evolution of mating system, which conversely may impose strong selection on clonal growth forms (Silander, 1985). There might be co-evolutionary interactions between the spatial structure and the mating behavior of clonal plant species (Charpentier, 2002).

Translated from *Acta Phytoecologica Sinica*, 2006, 20(1): 174–183
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Clonality by itself, and the various ways by which it is realized in plants, has a wide array of ecological and evolutionary consequences (Stuefer et al., 2002). In this paper, we summarize some recent developments in the research on interactions between clonal growth and sexual reproduction. Our goal is to identify open research questions which we hope will stimulate future work.

2 Costs and benefits of clonal growth and sexual reproduction

Clonal growth and sexual reproduction both have benefits and costs. Plants with clonality are advantageous in resource acquisition, successful establishment of offspring in new environments, and risk aversion (Cook, 1985). Clonal offspring can easily live through seedling period and establish successfully because of the supply from the mother ramet (Lovett Doust, 1981). Yet, clonal growth can also bring about costs. Physiological connection makes diseases transmission easier between ramets. Decrease of resources available for sexual reproduction will lead to low level of genetic diversity. Compared with seed offspring, clonal ramets can only disperse within a much shorter distance and usually are clumped around the mother ramet, which inevitably leads to geitonogamy, i.e. self-pollination resulting from transfer of pollen between flowers on an individual (Handel, 1985; Vange, 2002). These interactions between ramets reduce the benefits of clonal growth (Loehle, 1987). Contrary to clonal growth, sexual offspring have high rate of mortality and low level of successful establishment. But sexual reproduction can maintain higher level of genetic diversity. In addition, seeds can safely spend unfavorable condition through dormancy and spread much longer than clonal offspring and easily colonize new habitats.

3 Sexual reproduction of clonal plants

The reproductive mode of plant determines the transmission of genes in time and space, hence variation in reproductive mode is widely expected to be a major determinant of population genetic structure. Most perennial plants can regenerate through seed and clonal growth. The production and recruitment of sexual vs. clonal progeny may often vary widely within a species in response to ecological and/or genetic factors that limit one or other reproductive mode (Eckert, 2002; Eckert et al., 2003). The most extreme example is that species have abandoned sexual reproduction for some form of clonal reproduction, at least in some habitats or parts of their geographic range (Philbrick and Les, 1996; Eckert, 2002).

3.1 The variation of sexual reproduction in clonal plant

Sexual reproduction of clonal plants varies to a considerable extent. In some highly clonal plant, clonal propagation is significantly increased such that they hardly produce any seeds (Molau and Prentice, 1992, but see Lopez-Almansa et al., 2003). Sex ratios of many clonal plants deviate significantly from 1:1; for example, Bowker et al. (2000) investigated the sex ratios of a desert moss *Syntrichla caninevis* (Pottiaceae) in10-ha area in southern Nevada Mojave Desert. They found an expressed ramet sex ratio of 14 female:1 male ($N = 890$), with 85% of ramets not expressing sex over their life span, and an expressed population sex ratio of 40 female : 2 male : 1 mixed-sex ($N = 89$), with 52% of populations not expressing sex. Their study indicated that sex expression of *Syntrichla caninevis* was associated with soil moisture content and ramet size. McLetchie et al. (2002) used a modeling approach to investigate the dynamics of sex ratios in a clonal dioecious liverwort (*Marchantia inflexa*). They found that females gradually eliminated males at low to moderate disturbance frequency, whereas males eliminated females at high disturbance frequency. This pattern did not hinge on whether sexual propagules could germinate within the patch, but asexual reproduction played an important role. The study suggested an important role of clonal growth for determining local sex ratios in this species. The skewed sex ratio also existed in hydrophytes, such as *Stratiotes aloides*, in which male and female plants tend to be confined to different parts of the species' European range so that sex is not possible in most populations (Hutchinson, 1975). Hammerli and Reusch (2003a) exposed the flowering shoots of *Zostera marina* L. to self and cross-pollen and to neighborhoods of their own and a mix of foreign vegetative shoots. They found flowering shoots that had been exposed to cross-pollen showed a significantly lower female/male ratio at peak flowering.

Moreover, flower, fruit, seed production and seedling recruitment of clonal plants vary among populations, especially in geographical range boundaries (Dorken and Eckert, 2001). For example, in *Decodon verticillatus* style morph frequencies vary widely among populations and populations with only a single style morph are most common near the northern limit of the species' range (Eckert and Barrett, 1992). On average, each ramet in monomorphic populations produced 15 seeds, while each ramet in tri-morphic populations produced 1139 seeds. Nearly half of the monomorphic populations produced no seed at all (Dorken and Eckert, 2001).

3.2 Factors leading to the variation of sexual reproduction

Much evidence showed that genetic and ecological factors can both affect sexual reproduction of clonal plants (Klekowski, 1997; Dorken and Eckert, 2001). Permanent genetic sterility at the genet level may be caused by a change in ploidy or some other chromosomal irregularity that impairs meiosis (Stebbins, 1971). Somatic mutation may be another factor that leads to sexual extinction in diploid clonal plants due to segregation offspring genotypes that exhibit high genetic loads (Klekowski, 1997). However, there are nearly no quantitative works on sterile genotype frequencies in fertile populations of clonal plants. Dorken and Eckert (2001) found most of *Decodon verticillatus* from north geographical populations can produce more seeds in greenhouse than in field. This indicates that the fertility of *Decodon verticillatus* is not only affected by genetics but also by environment. In clonal plants, ecological and genetic factors may jointly contribute to reduced sexual fertility. Genetic sterility may be fixed through the accumulation of sterility mutations in populations where sexual recruitment is impaired by the environment (Eckert, 2002).

4 Interaction between clonal growth and plant mating system

Most clonal plants are polycarpic perennials. The spatial dispersion of clones within a population may have several significant consequences (Eckert, 1999). Although many clonal plants can prevent geitonogamy within a single inflorescence through dichogamy and sequential flowering (reviewed in Bai and Zhang, 2004), between-ramet geitonogamy may be unavoidable in large clones (Handel, 1985; Vange, 2002), resulting in considerable loss of male and female fitness in plants (Harder and Barrett, 1995).

4.1 Impact of genet size on mating patterns

Clonal growth may produce significant genotypic patchiness within populations that can have a variety of important consequences (Reusch et al., 1999; Eckert, 2000), and genet size may have important impact on mating systems of clonal plants. Generally speaking, the rate of geitonogamy increases with genet size (Handel, 1985; Back et al., 1996). Large genet size presents large floral display which is more attractive to pollinators and thus increases mating opportunities (Thompson, 2001). Because of lack of outcrossing pollen, seed set of self- incompatible clonal plants may be decreased in larger genets (Wilcock and Jennings, 1999), whereas in self-compatible clonal plants, mating system may change from outcrossing to selfing with increasing genet size (Handel, 1985). Although several studies have showed that lager clones had higher levels of geitonogamy and the associated fitness costs (Back et al., 1996; Wilcock and Jennings, 1999; Eckert, 2000), few works have directly tested the impact of genet size on selfing rate and the various components of selfing (within-flower, or between-flower, or between-ramet self-pollination) (Lloyd, 1992; Jarne and Charlesworth, 1993; Eckert, 2000). The development of molecular markers may help answer these questions (Liao, 2004).

4.2 The impact of population size on mating patterns

Population size is another important factor that affects the mating patterns of clonal plant. Small populations are less attractive to pollinators and thus lack of acceptable pollen (Byers, 1995; Charpentier et al., 2000; Charpentier, 2002). However, clonal growth can compensate for the negative effect of small population size on pollinator attraction through large floral display (Charpentier, 2002). Wolf and Harrison (2001) examined the effects of habitat area and patch isolation on reproductive success of a self-incompatible clonal plant *Calystegia collina* (Convolvulaceael) in northern California's coast ranges. Their studies showed that flower and fruit production were significantly higher on large serpentine outcrops than on small outcrops. Successful pollination was positively affected by flower density and the number of other flowering patches within 100 m of a *C. collina* patch. These findings demonstrate that habitat size may have strong effects on the reproductive success by enhancing opportunities for successful sexual reproduction. Ushimaru and Kikuzawa (1999) also found that population structure have strong effect on mating system through their studies on four clonal Japanese *Calystegia* species (Convolvulaceae). Fruit and seed sets in self-incompatible plants *Calystegia hederacea* and *C. japonica* were limited by failure to transfer pollen among clones. Vigorous clonal growth may decrease local sexual reproductive success. However, we note that there is also evidence that seed production has no relation with population size (Aspinwall and Christian, 1992).

4.3 The effect of clonal structure on mating systems

Clonal architecture decides the special distribution of ramets and thus may affect breeding systems and reproductive potential. Whether the ramets are clumped or intermingle in a genet may have a strong impact on geitonogamy. Many "phalanx" species are self-compatible or predominantly selfing, while most "guerilla" species are self-incompatible (Stebbins, 1950; Silander, 1985). This suggests that clonal architecture is associated with mating system strategies and mating system may impose strong selection on clonal structure (Ushimaru and Kikuzawa, 1999). Considering the mating costs of geitonogamy, one could predict that clonal plants with a clumped architecture should present traits or combinations of traits that prevent geitonogamy, and that clonal plants with a guerilla architecture should be considered as a selected trait for plant to increase floral display and avoid geitonogamy at the same time (Charpentier, 2002).

The effectiveness of different traits on reducing male and female geitonogamy cost needs to be considered when analyzing the correlation between clonal growth and geitonogamy cost. However, there has been almost no effort to quantify the effect of different clonal architecture on mating system, or to investigate whether plants with different breeding systems possess different architectures (Eckert, 1999). More experimental studies are needed to compare the effect of clonal growth on mating system between different types of clonal architecture. For example, we may manipulate the spatial structure of genets to examine the effect of spatial distribution of ramets on rates of cross- and self-pollination and to understand whether clumped clonal plants display more traits to prevent geitonogamy than guerilla clonal plants (Charpentier, 2002).

5 Trade-off between clonal growth and sexual reproduction

Life history theory predicts that present reproduction imposes a potential cost on fitness by reducing the opportunity for future reproduction (Williams, 1966). Trade-offs due to finite resources are thought to place a universal constraint on the evolution of life-history traits because genotypes that invest heavily in one trait or activity must reduce their investment in other traits (Roff, 1992; Stearns, 1992). In theory, allocation to reproduction is straightforward and measurable. However, in practice, it's hard to detect because there are many possible allocation patterns and allocations in individual plant are often in a hierarchical manner. The variation in resource allocation to clonal growth versus sexual reproduction may be determined by genetics (Bostock, 1980; Reekie, 1991; Ronsheim and Bever, 2000; Hartemink et al., 2004), plant size (Hartnett, 1990; Mendez and Obeso, 1993; Schmid and Bazzaz, 1995; Sato, 2002), age (Lopez et al., 2001), environmental conditions and population density (Abrahamson, 1975; Holler and Abrahamson, 1977; Nishitami et al., 1999; Ronsheim and Bever, 2000; van Kleunen et al., 2001).

5.1 Effects of population density on resource allocation between clonal growth and sexual reproduction

In a clonal plant population, ramet density plays an important role in life history evolution. Population density will increase due to clonal growth, leading to higher intraspecific competition, which in turn can change the allocation of resources to clonal growth and sexual reproduction and thus affect fitness, genet size, reproductive values, population size and genetic structure (Heywoods, 1986). The response to selection under different densities may depend on special structure of clonal plant. It is advantageous to allocate more resources to sexual reproduction in dense populations for seed dispersal may act as an escape mechanism from the unfavorable site (Abrahamson, 1975; Gardner and Mangel, 1999; van Kleunen et al., 2001). In *Ranunculus reptans*, clones in the low density treatment, on average, had more rosettes and rooted rosettes than clones in the high density treatment in a greenhouse experiment. Yet, the relative allocation of the populations to sexual versus vegetative reproduction was higher in high density treatment. Seeds produced in the high-density treatment were 24% higher than that in low-density treatment. This suggests that with increasing density, allocation to sexual reproduction increases more than allocation to vegetative reproduction in *R. reptans*. Intraspecific competition is an important factor in the life-history evolution of *R. reptans* (Van Kleunen and Fischer, 2001). However, increasing resource allocation to clonal growth may make the genet more competitive in high density population (Loehle, 1987).

In clonal plants, offspring from clonal growth and sexual reproduction differ in dispersal distance and the success of establishment. These differences may lead to spatial heterogeneity in local density of offspring. Clonal offspring tend to grow in local clumps where plant density is higher than the mean density of the whole population. In contrast, seeds may establish at relatively low plant density, therefore, these difference may be important in determining optimal resource allocation (Nishitami et al., 1999). Intraspecific competition may refer to both competitions among genets and among ramets (Sackville Hamilton et al., 1987; Schmid, 1990). When growing different genotypes of *Ranunculus reptans* with and without competition in a plant room, Prati and Schmid (2000) found considerable environmental and genetic variation in life history traits. Lake genotypes invested more into sexual reproduction and performed better without competition, whereas land genotypes invested more into vegetative reproduction and grew better under competition. There was a significant genetic trade-off between sexual and vegetative reproduction in *Ranunculus reptans.* Rautiainen et al. (2004) examined resource allocation to clonal growth and sexual reproduction in *Potentilla anserina* in relation to intraspecific competition between monoclonal and multiclonal ramets. It was shown that competition suppressed both growth and reproduction, but there was no treatment response in relative investment at genet level, although both mother ramets and their daughters showed clear effects when analyzed separately. When experiencing competition, the mother ramet allocated relatively more to flowers, whereas allocation to vegetative growth was more intense when competition was absent. The results imply that *P. anserina* can modify the allocation of resources to different life-history traits according to competitive stress.

5.2 Effect of genet size on resource allocation to clonal growth vs. sexual reproduction

Plant size usually accounts for individual variation of resource allocation within a population under relative constant environmental conditions (Samson and Werk, 1986). A size-dependent pattern of resource allocation may differ among clonal species, because the ecological characteristics of clonal offspring and sexual offspring vary greatly among species. Genet size is correlated with sexual reproduction (Watson and Casper, 1984) and genet mortality rate (Cook, 1979; Eriksson and Jerling, 1990). Generally, larger clones have a higher reproductive output. Size-dependent resource allocation depends on the relative potential probability of seed and ramet establishment (Sakai, 1995). For instance, Schmid and Bazzaz (1995) compared the size dependency of sexual reproduction and clonal growth in two clonal plant *Aster lanceolatus* and *Solidago canadensis*. They found that both species required a threshold for sexual reproduction to occur, and above the threshold sexual reproduction increase with plant size. Resource allocated to clonal growth was also correlated to plant size, but was no evidence of a threshold size for clonal growth. Sato (2002) studied a perennial forest herb *Laportea bulbifera* and had got the same results. Large plants of *L. bulbifera* produced both male and female inflorescences with propagules, while small plants produced only vegetative propagules. Biomass of propagules, male inflorescences, and infructescences with achenes were all positively correlated with plant size. The increase in investment with plant size was more pronounced for propagule production than for sexual reproduction.

5.3 Resource allocation patterns of clonal plants in manipulated experiment

For clonal plants, it is difficult to directly investigate resource allocation between the two reproductive modes in field experiments, because resource allocation to various life history functions may depend on various conditions. Manipulating the effort that a plant makes to a certain vital function can reveal the relative importance of life history functions (Stearns, 1989; Ehrlen, 1999; Garcia and Ehrlen, 2002). For example, *Butomus umbellatus* significantly reduced clonal bulbil production when half of all flowers were pollinated in a greenhouse experiment. Increasing seed production can cause a significant but nonlinear trade-off between sexual reproduction and clonal growth in *B. umbellatus*. Trade-offs were stronger under high nutrient conditions than under low nutrient conditions (Thompson and Eckert, 2004). Westley (1993) found experimentally induced failure of sexual reproduction can increase allocation to asexual reproduction under common garden conditions. Hartemink et al. (2004) investigated the response to continuous removal of either flower buds or rosette buds in three perennial grassland species, *Hypochaeris radicata, Succisa pratensis* and *Centaurea jacea*. In a garden experiment, they distinguished two possible responses: compensation for lost buds by making more buds of the same type, and switching towards development of other life history functions, but bud removal had significantly different effects in each of the three species. The degree of compensation and the expression of trade-offs between life history functions differed markedly between species and seemed to be related to longevity and developmental constraints.

However, not all plants exhibit trade-off in their life history strategies. Whether the trade-off will be apparent depends on the amount of available resource. Strong trade-off can be detected only when available resource is very limited (Reznick, 1985; Biere, 1995). Moreover sexual reproduction and clonal growth may be constrained by different kinds of limiting resources, therefore increasing investment to one reproductive mode may not necessarily lead to reduced allocation to the other reproductive mode (Reekie, 1999).

6 Conclusion and promising directions for future research

Because clonality is such a common phenomenon in nature, clonal plant research has covered a wide variety of topics within the plant science. Although plant ecologists have long realized that most clonal plants both reproduce vegetatively and sexually, the balance between the two reproductive modes may vary widely among species as well as among populations within species. However, clonality as a subject of ecological and evolutionary research was confined to a relatively narrow set of conspicuous consequences of clonality, such as physiological integration, mobility and architectural flexibility (Stuefer et al., 2002). Few studies have investigated the consequence of natural selection on the two reproductive modes and the genetic and ecological factors that affect the balance between the two reproductive modes. There is still much room for further research on these issues. The following questions may attract more attention in future studies.

1. How does the variation of sexual reproduction between and within species impact on the local adaptation and geographical evolution; whether the lost of sex will lead to strong clonal growth and vegetative growth in clonal plant; and what are the key factors that decide the balance between the two reproduction modes (Eckert, 2002);
2. Clonal architecture may have strong impact on plant mating system. Experiment should be designed to test the co-evolution between the clonal structure and mating patterns through comparing plants with different architecture (phalanx or guerilla);
3. If different resource allocation patterns represent adaptive strategies for clonal plants in different environments, we can predict that more resource should be allocated to sexual reproduction in disturbed and competitive environment, while clonal growth should be dominant in stable habitats. More field and manipulating experiments are needed to test these hypotheses.

Acknowledgements This work was financially supported by the National Natural Science Foundation of China (No. 30430160) and the Doctoral Program for Higher Education (No. 20030027021).

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