On the evolution of clonal plant life histories

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Abstract. Clonal plant life histories are special in at least four respects: (1) Clonal plants can also reproduce vegetatively, (2) vegetative reproduction can be realised with short or long spacers, (3) and it may allow to plastically place vegetative offspring in benign patches. (4) Moreover, ramets of clonal plants may remain physically and physiologically integrated. Because of the apparent utility of such traits and because ecological patterns of distribution of clonal and non clonal plants differ, adaptation is a tempting explanation of observed clonal life history variation. However, adaptive evolution requires (1) heritable genetic variation and (2) a trait effect on fitness, and (3) it may be constrained if other evolutionary forces are overriding selection or by constraints, costs and trade offs. (1) The few studies undertaken so far reported broad sense heritability for clonal traits. Variation in selectively neutral genetic markers appears as pronounced in populations of clonal as non clonal plants. However, neutral markers may not reflect heritable variation of life history traits. Moreover, clonal plants may have been sampled at larger spatial scales. Empirical information on the contribution of somatic mutations to heritable variation is lacking. (2) Clonal life history traits were found to affect fitness. However, much of this evidence stems from artificial rather than natural environments. (3) The relative importance of gene flow, inbreeding, and genetic drift, compared with selection, in the evolution of clonal life histories is hardly explored. Benefits of clonal life history traits were frequently studied and found. However, there is also evidence for constraints, trade offs, and costs. In conclusion, though it is very likely, that clonal life history traits are adaptive, it is neither clear to which degree this is the case, nor which clonal life history traits constitute adaptations to which environmental factors. Moreover, evolutionary interactions among clonal life history traits and between clonal and non clonal ones, such as the mating system, are not well explored. There remains much interesting work to be done in this field which will be particularly interesting if it is done in the field.

Key words: adaptive evolution, clonal integration, constraint, environmental heterogeneity, foraging, genetic variation, guerilla and phalanx strategy, natural selection, phenotypic plasticity, sexual and vegetative reproduction, trade off

'It is a pleasure to see that you are still interested in the same questions that we used to ask some 30 years ago'. John L. Harper on the 5th Clonal Plant Workshop in Bangor, 1997.

'You can get it if you really want, but you must try.' Jimmy Cliff, 1970.

Introduction

Among the modular organisms, clonal plants with potentially independent vegetative offspring (ramets) have particular life histories. Basically, clonal plants can do everything what non-clonal plants can do – and more. Their unifying main life-history characteristic is that they can reproduce not only sexually but also vegetatively. Because vegetative reproduction can be realised in many different ways (and as a consequence may result in different growth forms) and because it allows for selective placement of ramets and for integration between ramets, there is a large variation in clonal life histories. Moreover, clonal plants may express different life histories in different environments.

How did clonal life-history traits come about and how are they maintained? Evolution is driven by selection, genetic drift, inbreeding, gene flow, and mutation. Among these evolutionary forces, only natural selection may lead to adaptation which further requires heritable genetic variation and sufficient time. However, these prerequisites for adaptive evolution need not to be met. Moreover, even if they are, adaptive evolution may be prevented by physiological or physical constraints, trade-offs, or costs, or overriding importance of evolutionary forces other than selection (Stearns, 1992). Therefore, adaptive evolution constitutes one, but not the only evolutionary pathway.

Here we shortly introduce clonal life-history traits, and summarize information on their evolution. We emphasize the question in how far this evolution was and is adaptive, and discuss the role of constraints, trade-offs, costs, and of evolutionary forces other than selection in this context. Our goal is to identify open research questions which we hope will stimulate future work.

Clonal plant life histories

Clonal plants can reproduce sexually and vegetatively. In vegetative reproduction by clonal growth clonal plants may grow short or long spacers or both. The growth form associated with short spacers, termed phalanx strategy, and the one with long spacers, termed guerilla (Lovett Doust, 1981), constitute the ends of a continuum. Clonal growth does not necessarily follow a fixed growth pattern, but may actively serve to place ramets in more benign habitat patches (Harper, 1981; Bell, 1984; Schmid, 1990; Hutchings and de Kroon, 1994). This phenotypic plasticity may be termed foraging behaviour (Bell, 1984). Finally, ramets may remain physically connected and physiologically integrated (Pitelka and Ashmun, 1985). Clonal integration potentially allows for division of labour between ramets, which may specialise for certain tasks, such as sexual reproduction, nutrient uptake, or storage (Alpert and Stuefer, 1997).

Based on these considerations, we can define clonal life histories in the space spanned by the four dimensions of (1) vegetative vs. sexual reproduction and

recruitment, (2) growth form, (3) the tendency for plastic foraging by selective ramet placement, and (4) the degree of clonal integration between ramets. Of these clonal traits, foraging per definition constitutes phenotypic plasticity, and the other traits may also respond plastically to different environments. It is interesting to note that all four dimensions are genet characteristics, which are more than the sum of ramet characteristics. (Throughout this paper, we deal with plants that reproduce vegetatively by means of clonal growth. For plants that produce vegetative offspring lacking the potential to remain connected to the parent plant, such as bulbils or agamic seed, only our considerations regarding vegetative vs. sexual reproduction apply.)

Clonal life-history traits do not evolve independently from each other. For example, plants with short spacers generally also have a higher rate of vegetative reproduction and a higher degree of physical (and possibly) physiological integration among modules (Lovett Doust and Lovett Doust, 1982; Schmid and Bazzaz, 1991; Stöcklin, 1992). However, high degrees of physical disintegration were found in a study of 24 perennial tussock-forming, i.e. phalanx-type, grasses (Wilhelm, 1995). Moreover, larger distances between ramets of guerilla plants suggest, that they experience steeper environmental gradients, which may lead to higher degrees of integration because they promote the transport of water and resources between ramets, and that selection for integration may have been stronger.

Moreover, clonal life-history traits are also not independent of non-clonal ones. For example, high degrees of phalanxness may result in mono-clonal patches where the availability of outcrossing pollen may be low (Charpentier *et al.*, 2000) and the selfing rate high as a consequence of geitonogamous pollination between flowers of the same clone (Eckert, 2000). This in turn, can affect inbreeding depression and the evolution of the mating system. A high selfing rate may select for self-incompatibility, whereas low availability of outcrossing pollen may select for self-compatibility. The latter seems to be more important for clonal grasses, where phalanx species tend to be self-compatible and guerilla species to be self-incompatible (Silander, 1985).

Clonality may also interact with seed dispersal and seed provisioning. In clonal plant populations with only initial seedling recruitment, small and easily dispersed seeds may be of advantage, while larger seeds may offer an advantage in populations with repeated seedling recruitment (Eriksson, 1989, 1997; Stöcklin and Favre, 1999).

Macroevolution and comparative studies among species

Clonality existed before sexual reproduction evolved, e.g. in microorganisms (Andrews, 1998). Nevertheless, clonal angiosperms were (most likely) derived

from a non-clonal form (Takhtajan, 1980). Within the angiosperms the evolution of clonal plants from non-clonal ancestors has taken place many times and in many different taxa (Klimes *et al.*, 1997).

Clonal angiosperms are more common in wet, nutrient-poor, cold, shaded (Tiffney and Niklas, 1985; Callaghan, 1988), and undisturbed habitats (Klimes *et al.*, 1997). However, in many cases they are able to successfully colonise extremely disturbed areas such as road sides, wastelands, river and sea shores, where non-clonal plants are relatively rare (Fahrig *et al.*, 1994). An obvious explanation for such ecological patterns of distribution is that clonal life histories constitute adaptations.

However, this explanation constitutes a hypothesis which needs to be tested. A classification according to the four clonal dimensions described above could allow the test of more precise hypotheses than just comparing between non-clonal and clonal plants. E.g., instead of asking whether clonal plants rather occur in undisturbed habitats than non-clonal plants do, we could more precisely ask whether a higher degree of vegetative recruitment among species is associated with a higher degree of disturbance of their habitats. Moreover, it may be hypothesized that more plastically foraging plants favour spatially more heterogeneous habitats. Stöcklin (1992) found that guerilla species were more successful in open alpine habitats and phalanx in closed grasslands. Jonsdottir and Watson (1997) found that nutrient-poor habitats favoured clonally integrated species. Clonal plants with pronounced vegetative reproduction had lower rates of local extinction from nutrient-poor calcareous grasslands than plants without pronounced vegetative reproduction (Fischer and Stöcklin, 1997). This could be extended to a multivariate approach to elucidate which characteristics of clonal life histories are associated with, and possibly responsible for, the occurrence of a clonal plant in a particular habitat. To this end, a morphological classification such as the one of clonal plants in the flora of central Europe (Klimes *et al.*, 1997) could be complemented with a more functional classification according to the four clonal dimensions, and with information on sexual life-history traits such as mating system, and the number and size of seeds. Criteria for the classification of the degree of integration have been developed by Jonsdottir and Watson (1997).

Growth form (phalanx vs. guerilla), plastic foraging, and clonal integration all have to do with the spatial arrangement of ramets of clonal plants. An optimal scale of spatial heterogeneity has been predicted for foraging responses (Sutherland and Stillman, 1988), and the scale of spatial heterogeneity plays a role in determining fitness in experiments in greenhouse and garden (Hutchings and Wijesinghe, 1997). Moreover, natural habitats are spatially heterogeneous at small scales (Lechowicz and Bell, 1991; Skalova *et al.*, 1999). Given the recent emphasis on clonal integration, and especially on its benefits in spatially

heterogeneous habitats, it is striking, that it is not known whether the spatial scale of heterogeneity in habitat characteristics matches the one of clonal growth and clonal integration. To date it has not even been shown, that clonal plants rather occur in heterogeneous habitats in nature.

Microevolution

The process of adaptation of a trait requires that the trait affects fitness and heritable genetic variation for the trait. If this process is going on for sufficient time, a state of adaptation may be reached, where different trait values optimise fitness in different environments. Such a state can be recognized by transplanting experiments, where fitness benefits and genetic variation should meet 'home-away' expectations for local adaptation (Schmid, 1985). This may be indicated by genotype–environment interactions with correspondingly crossing reaction norms for fitness (van Tienderen, 1992).

If the genotypes in heterogeneous environments encounter both environments, adaptive plasticity may evolve (Bradshaw, 1965; Scheiner and Lyman, 1991). This may lead to genotype–environment interactions in adaptive traits, when plants from heterogeneous and homogeneous environments are compared. The inspection of genotype–environment interactions in fitness and in life-history traits, therefore, provides an important tool in the study of adaptation of both plant traits and their plasticity.

Fitness benefits of clonal traits and of their plasticity

In clonal plants, there are several levels of selection, including the cell, the module, the ramet, groups of ramets, and whole genets (Sackville Hamilton *et al.*, 1987; Tuomi and Vuarisalo, 1989; Keller, 1999). This makes the measurement and prediction of clonal plant fitness notoriously difficult (Winkler and Fischer, 1999). For practical purposes, fitness is frequently measured as biomass in experiments and as abundance in mathematical models.

All four clonal life-history traits appear to affect fitness. Mathematical models showed fitness effects of sexual vs. vegetative recruitment, which depended on the scale of disturbances (Winkler and Fischer, 1999) and on growth form, where phalanx species had an advantage at small disturbances and guerrilla at large ones (Winkler and Schmid, 1995; Winkler *et al.*, 1999). In further models, fitness effects were found for foraging (Sutherland and Stillman, 1988; Cain, 1994; Oborny, 1994; Cain *et al.*, 1996), and for integration (Oborny *et al.*, 2000), which also depended on the scale of spatial heterogeneity. Experiments showed fitness effects of growth form which depended on ramet density (Schmid and Harper, 1985; Humphrey and Pyke, 1998), and fitness benefits of foraging

in a spatially heterogeneous competitive environment (van Kleunen and Fischer, 2001). Clonal integration was beneficial in spatially heterogeneous environments (Hutchings and Wijesinghe, 1997, and references therein), especially for steep environmental gradients (e.g. in nutrient availability for the stoloniferous *Fragaria chiloensis*; Friedman and Alpert, 1991).

Fitness as a phenotypic trait depends on both the genetic composition of an individual and on its natural environment. However, most life-history work has been done in artificial environments. While benefits of integration have been demonstrated in artificial heterogeneous environments (and integration even allowed for beneficial division of labour in reciprocally complementary environments; Stuefer *et al.*, 1994), in the field integration mainly seems to serve for parental care (Alpert, 1995), and to enable invasion into unfavourable patches, such as salt pans (Pennings and Callaway, 2000). Among the artificial environments used to study clonal life-history traits, abiotic stress and competition have been emphasized, whereas other biotic interactions such as intraspecific density (Holler and Abrahamson, 1977; Schmid and Harper, 1985; Humphrey and Pyke, 1998), disease, herbivory (Schmid *et al.*, 1988; Bach, 2000), and pollination (Saikkonen *et al.*, 1998) received less attention. In the presence of disease clonal growth may be favourable because it may allow plants to escape (D'Hertefeldt and van der Putten, 1998). On the other hand, clonal integration may allow disease transmission between connected ramets. However, the likelihood of disease transmission decreases with internode length (Wenström and Ericson, 1992; Piqueras, 1999), which may result in a selection pressure for guerillaness in the presence of disease. Plants affected by disease and herbivory have been found to exchange signals via volatiles (Seskar *et al.*, 1998; Dolch and Tschardt, 2000). In clonal plants, internal signalling between ramets may facilitate induced plant defence and thus be important for the response to disease and herbivory. An alternative strategy for a clonal plant in the presence of parasites is to split into independent ramets, or at least to detach affected ramets (McCrea and Abrahamson, 1985).

A plastically reduced ratio of sexual relative to vegetative reproduction was found at higher intraspecific density (in Schmid and Harper, 1985 (*Bellis perennis*); Humphrey and Pyke, 1998), and an increased ratio also at higher density (Holler and Abrahamson, 1977; Schmid and Harper, 1985 (*Prunella vulgaris*) and in response to nutrient and light availability (van Baalen *et al.*, 1990). Higher soil compactness caused a more compact growth form (Schmid and Bazzaz, 1990). While there is evidence that plasticity serves to actively place ramets in more benign habitat patches, this has not emerged as a general phenomenon (de Kroon and Hutchings, 1995). Plasticity in clonal integration has not been studied so far. However, e.g. resource sharing between ramets could be affected by the presence of herbivores, or be different in environments with different heterogeneous distributions of nutrients.

Plastic responses may be passive and non-adaptive, or they may constitute adaptive plasticity with associated fitness benefits of the response. Passive plasticity may mask active plasticity if both are directed in different directions. E.g., under shading by competing plants the adaptive response would be internode elongation, but internodes may still grow shorter because of the competitive effect on nutrients. Therefore, the appropriate null model for active plasticity in internode length would be shorter internodes under unfavourable than under benign conditions (van Kleunen and Fischer, 2001). Benefits of plasticity in clonal traits have been shown in mathematical models, where plastically increased sexual reproduction was of advantage under poor conditions, because seed dispersal can act as an escape mechanism (Williams, 1975; Gardner and Mangel, 1999), and where growth form plasticity was of advantage, which enabled vegetative offspring to avoid occupied recruitment sites (Winkler and Schmid, 1995; see above for benefits of plastic foraging). Fitness benefits of plastic foraging have been experimentally confirmed in a heterogeneous competitive environment for a stoloniferous herb (van Kleunen and Fischer, 2001) but not for a grass with heterogeneously distributed soil nutrients (Humphrey and Pyke, 1997). However, field evidence for benefits of plasticity in clonal life-history traits is lacking.

Genetic variation

Although populations of clonal plants may consist of only a few large genets (Mitton and Grant, 1996), neutral genetic variation generally appears to be similar in populations of clonal and non-clonal plants (Widén *et al.*, 1994; Ellstrand and Roose, 1987; McLellan *et al.*, 1997). However, in comparative analyses of genetic variation between clonal and non-clonal plants potentially confounded phylogenetic effects were not taken into account (see Mazer, 1998 for a discussion of phylogenetic corrections in comparative analyses). Moreover, the reviews cited above compared studies without consideration of the spatial scale of sampling. Therefore, it can not be excluded that per-area measures of genetic variability are lower in clonal plants than in non-clonal plants, while they may not be on a per-population scale.

Genetic variation in plant populations is not only affected by the degree of clonality, but may also differ between clonal plants with different growth forms. Therefore, a classification of plant species only not just coarsely into clonal and non-clonal but plants into the classes of the four dimensions mentioned above could help to clarify the role of clonality for genetic variation in a population. Moreover, genetic variation may also be determined by the mating system, gene flow, population size, and environmental heterogeneity (Hartl and Clark, 1994). Moreover, clonal life-history traits may covary with environmental characteristics. For example, the effect of environmental het-

erogeneity on genetic variation might be reduced in plants with high degrees of clonal integration. A classification of species according both to the clonal dimensions and to other factors affecting genetic variation could reveal the relative importance of clonal life histories for genetic variation.

With the increased availability of genetic markers the number of studies on neutral genetic variation in clonal plants has increased in recent years. However, what finally counts for the evolution of life-history traits is additive genetic (i.e. heritable) variation, which may not be revealed by neutral markers (Butlin and Tregenza, 1998; Prati, 1998). Past selection may have depleted additive genetic variation in life-history traits, and especially so because they are under stronger selection than other traits (Mousseau and Roff, 1987). However, this need not be the case because additive genetic variation in life-history traits may be maintained by several mechanisms, namely spatial or temporal variation in selection pressures (environmental heterogeneity), mutation-selection balance, genotype-by-environment interactions, flat fitness profiles, and negative genetic correlations due to antagonistic pleiotropy or linkage (Stearns, 1992; Falconer and Mackay, 1996; McLellan *et al.*, 1997).

Unfortunately, studies on quantitative genetic variation in clonal life-history traits are scarce. Significant variation among genotypes of clonal plants has been reported for the allocation to sexual and vegetative reproduction (Schmid and Weiner, 1993; Prati and Schmid, 2000), for growth form and foraging, respectively (Cheplick, 1995, 1997; Humphrey and Pyke, 1997; Skalova *et al.*, 1997; Cheplick and Gutierrez, 2000; van Kleunen *et al.*, 2000a; van Kleunen and Fischer, 2001), and for clonal integration (Alpert, 1999; van Kleunen *et al.*, 2000b). These studies underline the importance of using several genotypes in studies on clonal life histories (de Kroon *et al.*, 1994). Moreover, the broad-sense heritability demonstrated by variation among genotypes suggests that there is heritable variation in clonal life-history traits. However, in order to estimate narrow-sense heritabilities, which would demonstrate additive genetic variation, more sophisticated quantitative genetic studies are required, which use half-sib designs, parent-offspring regressions, or crossing designs (Falconer and Mackay, 1996).

There is quite some theoretical, but no empirical, information on the fate of mutations in clonal plants and on their importance for quantitative genetic variation. If there is no selection against mutations, somatic mutations were predicted to contribute as much or even more to genetic change than meiotic mutations (Orive, 2001). However, selection among cells will decrease the likelihood of fixation of deleterious mutations, and, compared with sexual offspring, especially so in multicellular vegetative offspring (Otto and Orive, 1995). The likelihood of fixation of mutations in apical meristems is larger in plants with unstratified meristems than in plants with stratified meristems, which are found in most higher plants (Pineda-Krch, 2001). According to the

somatic mutation theory of clonality (Klekowski, 1997), with increasing plant age meristems accumulate mutations, which reduce the likelihood of sexual reproduction. Therefore, evolutionary change becomes entirely dependent on very rare somatic mutations with advantageous phenotypic effects (Klekowski, 1997).

Genotype–environment interactions

In addition to the studies on genetic variation in plastic foraging mentioned in the previous section, there are only few other studies on genotype–environment interaction in clonal life-history traits. As a consequence of local adaptation reaction norms of genotypes originating from different habitat types may cross when they are reciprocally transplanted between home and away environments. Genotype-by-environment interactions which were in line with the local adaptation hypothesis have been found in *Ranunculus reptans* for the allocation to sexual and vegetative reproduction in response to interspecific competition (Prati and Schmid, 2000), and for foraging characteristics (van Kleunen *et al.*, 2000b; van Kleunen and Fischer, 2001). These studies can be interpreted as evidence for broad-sense heritability of observed plasticity, and therefore suggest that plasticity in clonal life-history traits may evolve as an adaptation. However, it is not clear whether selection acts directly on plasticity itself or only indirectly, as a correlated response due to selection on mean values in single environments (Via, 1993; Scheiner, 1993; Schlichting and Pigliucci, 1998). Moreover, until now there is no information on narrow-sense heritability in plasticity of clonal life-history traits.

Constraints on adaptive evolution

Phylogenetic constraints may have prevented the adaptive evolution of clonal life-history traits in some taxa (van Groenendael *et al.*, 1996). Moreover, even if there are fitness effects of and additive genetic variation in clonal life-history traits, their adaptive evolution may still be constrained for other reasons. Physical constraints could limit the evolution of clonal life-history traits, in a similar way as the length of internodes of non-clonal plants is limited by a critical buckling height (Niklas, 1988). Moreover, physiological or genetic trade-offs, i.e. negative genetic correlations, between life-history traits can constrain their evolution. For sexual vs. vegetative reproduction both kinds of trade-off have been reported (physiological: Watson and Caspar, 1984; Piquot *et al.*, 1998; Prati, 1998; genetic: Geber *et al.*, 1992; Prati and Schmid, 2000). The hierarchical organisation of clonal plants into ramets and genets may also lead to trade-offs between these levels, which, however, are hardly explored. A trade-off between ramet and genet size was reported in *Trifolium fragiferum*,

where clones produced fewer but larger ramets if they were grown in higher vegetation (Huber and Wiggerman, 1997). Severing clones, i.e. disrupting clonal integration, led to the formation of more but smaller ramets in *Scirpus maritimus* (Charpentier *et al.*, 1998). Another potential trade-off could be the one between foraging at the genet level (via plasticity in internode length to position ramets) and foraging at the ramet level (via plasticity in leaf length).

The evolution of clonal life-history traits may also be constrained by costs. Plants of *Potentilla anserina* with a high allocation to sexual reproduction in one season had to compensate this by a reduction in sexual reproduction in the following season (Saikkonen *et al.*, 1998). Vegetative reproduction, on the other hand, may result in less developmentally stable offspring than sexual reproduction (Schmid and Bazzaz, 1990). There are several potential costs of clonal integration, such as costs of maintenance of the connecting tissues between ramets (Pitelka and Ashmun, 1985), the energy required for translocation between ramets (Epstein, 1972), the spread of pathogens through the connecting tissues (Cook, 1985; Wennström and Ericson, 1992; Piqueras, 1999), and the costs of translocation incurred by the source ramets (Caraco and Kelly, 1991). However, with the exception of the last one (Salzman and Parker, 1985; Stuefer *et al.*, 1994; van Kleunen and Stuefer, 1999; van Kleunen *et al.*, 2000b), these potential costs of integration have hardly been studied empirically.

Furthermore, phenotypic plasticity in clonal life-history traits may not only be beneficial, but may also incur costs. Several potential costs of plasticity have been identified, including costs for the maintenance of the physiological and genetic machinery for a plastic response (DeWitt *et al.*, 1998). The only study on costs of plasticity in a clonal trait detected costs of horizontal foraging in *R. reptans* (van Kleunen *et al.*, 2000a).

Evolutionary forces other than selection

In addition to the constraints on adaptive evolution mentioned in the previous section, adaptive evolution may be prevented if selection is overruled by other evolutionary forces such as inbreeding, genetic drift and gene flow (Hartl and Clark, 1994; Falconer and Mackay, 1996). However, studies on these other forces, which explicitly address the clonality of plants, are scarce.

Effective population size has been theoretically predicted to be smaller in clonal than in non-clonal plants which suggests a higher importance of genetic drift in clonal plants (Orive, 1993). However, empirical evidence of differentiation in neutral genetic variation among populations appears as large for clonal as for non-clonal plants, which suggests that genetic drift is as pronounced in clonal as in non-clonal plants (Fischer *et al.*, 2000; Stehlik and Holderegger, 2000; Wolf *et al.*, 2000).

In clonal plants, geitonogamy may largely contribute to selfing (Eckert, 2000), and as a clone grows and produces more flowers, selfing is likely to increase (Handel, 1985). This might imply that selfing is stronger in clonal plants than in non-clonal plants. However, while this pattern was confirmed in a comparative study among species, it disappeared when a phylogenetic correction was applied (Klimes *et al.*, 1997).

The degree of selfing and the relative importance of vegetative reproduction may affect the evolution of inbreeding depression. High levels of inbreeding may result in purging of genetic load, and if rates of selfing are higher in clonal than in non-clonal plants, this may result in lower inbreeding depression in clonal plants than in non-clonal plants. Moreover, increased selfing was predicted to increase the rate of fixation of favorable recessive mutations (Charlesworth, 1992). However, in a modeling study, the degree of asexual reproduction increased generation time and therefore generally increased inbreeding depression because it decreased the relative number of opportunities to purge genetic load (Muirhead and Lande, 1997). Moreover, purging of genetic load appears not to be a consistent force in evolution (Byers and Waller, 1999). Despite these theoretical considerations it is not known whether inbreeding depression is more or less severe in clonal than in non-clonal plants.

Little is known about differences in gene flow between clonal and non-clonal plants. Generally, clonal propagules are larger, more vulnerable to desiccation than seeds, and lack dormancy and any mechanisms to promote dispersal (Silander, 1985). Therefore, they may be expected to exhibit relatively limited dispersal compared to seed, and thus not to contribute much to gene flow. Nevertheless, even a small contribution of clonal growth will lead to overestimates of genetic neighborhood size if clonal growth is not considered (Gliddon *et al.*, 1987). Clonal growth was even estimated to be the major source of gene flow for plants of *T. repens* older than 5 years (Gliddon and Saleem, 1985). There may be further examples for large contributions of clonality to gene flow, such as long-distance dispersal of floating clonal propagules of woody plants of lake or river shores.

New methods for the study of microevolution of clonal plants

There are several useful methods in microevolution which have hardly been applied to study clonal life histories. To see if trait variation affects fitness, phenotypic variation can be subjected to selection gradient analysis, where individual fitness measures are regressed on trait values (Lande and Arnold, 1983), or, to avoid biases due to environmental covariances between fitness and trait, genotypic fitness measures are regressed on genotype trait means (Rausher, 1992). Lacking phenotypic or genetic variation can be created by experimental manipulations. Phenotypic variation can be created using phy-

tohormones, different light qualities for seedling growth (Schmitt *et al.*, 1999), or by cutting plant parts, e.g. severing stolon internodes (Pitelka and Ashmun, 1985). Genetic variation can be created by crossing distinct ecotypes, which yields variable F2 progeny for further experimentation (Jordan, 1991). Enhanced genetic variation can also be studied in mutants and transgenic plants (Schmitt *et al.*, 1999).

Heritability of and genetic correlations among traits may differ between environments (Falconer and Mackay, 1996), and therefore also between artificial and natural environments. Moreover, heritabilities may be overestimated in artificial environments of low variability (Roff and Simon, 1997). Heritable genetic variation in and genetic correlations between clonal life-history traits can be assessed in natural situations, when the relatedness among measured individuals is known from molecular markers (Lynch, 1999, Ritland, 2000). Moreover, Lynch (1999) recently developed a method to estimate genetic correlations in the field without knowledge of the relatedness among the measured individuals. The accuracy of this method increases with the number of and relatedness among individuals and higher heritability of the correlated traits.

Information from molecular genetic markers can be combined with quantitative genetic variation to identify so-called quantitative trait loci (QTL), i.e. loci that are responsible for quantitative genetic variation (Lynch and Walsh, 1998). This may allow to identify loci which affect clonal life-history traits. The relative effects of such loci on quantitative traits can be estimated with correlation analyses (Falconer and Mackay, 1996). To date, QTL analyses have not been applied to clonal life-history traits.

The recently developed cDNA microarray technology allows to directly study gene expression (Schaffer *et al.*, 2000). It takes advantage of cDNA, i.e. DNA which is complementary to messenger RNA. cDNA from sampled plants can be hybridized with DNA sequences of known genes, which allows to detect gene expression. The use of chips with many genes and of robots allows to screen the expression of more than 1000 genes simultaneously (Schena *et al.*, 1995). Among the current uses of the method is the study of induced plant defense (Schenk *et al.*, 2000). Similarly, it could be applied to study the change in gene expression in plastic foraging responses to different environments. However, because this technique requires the knowledge of the function and sequence of genes, it is restricted to very few well-investigated model species, such as *Arabidopsis thaliana* and wheat. It will be interesting to see, in how far microarray chips designed for these species will also work in closely related clonal species.

Molecular genetic methods have already proven to be useful in distinguishing different genets of clonal plants. When molecular data are combined with spatial data on the location of ramets and on the distance between vegetative parent and offspring, they allow the estimation of the ratio of sexual vs. vegetative recruitment (Harada *et al.*, 1997; Schlöpfer and Fischer, 1998). Moreover, because

molecular genetic markers are assumed to be selectively neutral, they provide useful tools in the study of non-adaptive evolutionary forces such as genetic drift, inbreeding and gene flow (Hartl and Clark, 1994; Ouborg *et al.*, 1999).

Conclusions

It appears very likely that clonal life-history traits are adaptive. However, it is neither clear to which degree this is the case, nor which clonal life-history traits constitute adaptations to which environmental factors. Moreover, despite the considerable progress in the understanding of the ecology and evolution of clonal plants achieved in the last decades, our knowledge is still based on relatively few case studies, which almost exclusively deal with herbaceous, stoloniferous or rhizomatous, plants.

The most urgent open questions concern (1) fitness effects of clonal life-history variation in the field, (2) heritable variation in clonal life-history traits, (3) the contribution of somatic mutations to this variation, (4) the evolutionary interaction between different clonal traits and between clonal and non-clonal traits, (5) the evolutionary interaction of clonal traits with biotic interactions, (6) the role of phenotypic plasticity in clonal life histories, and (7) constraints, costs, and trade-offs. In addition to studies addressing single of these questions, comprehensive studies would be especially valuable.

There remains much interesting work to be done in this field – which will be particularly interesting if it is done in the field.

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