Plant Ecol (2015) 216:227–233
DOI 10.1007/s11258-014-0430-z

Epigenetics: a potential mechanism for clonal plant success

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Received: 11 July 2014 / Accepted: 10 November 2014 / Published online: 24 December 2014

Abstract Clonality in plants is widespread and includes species that span temporally and spatially heterogeneous environments. Yet, theory predicts that clonally reproducing plants evolve at slower rates, risk accumulating more mutations than sexuals, and potentially lack the benefits of DNA repair mechanisms afforded by meiosis. Does the apparent success of clonal plants contradict the severe costs of clonal reproduction suggested by theory? We examine how epigenetics may confer ecological advantages to clonal plants that could outweigh these evolutionary costs. Relying to various degrees on vegetative reproduction, the capacity to conserve or reverse gene regulation changes over cell divisions has clear potential for optimization of plasticity and acclimation in response to environmental variation encountered. Clonal plants may be one of the best examples of organisms taking advantage of epigenetic acclimation as an alternative to the slower mechanisms of adaptation through natural selection. If epigenetic processes are important in matching organismal response to the environment, this may prove to be a mechanism that will buffer plants against the challenges of current and future rapid environmental changes.

Keywords Epigenetic change · Clonal plant · Plasticity · Environmental response · Diversity

Theory predicts that clonally reproducing plants evolve at slower rates, risk accumulating more mutations than sexuals, and potentially lack the benefits of DNA repair mechanisms afforded by meiosis (Gabriel et al. 1993; mutational meltdown, Lynch et al. 1993; Muller's ratchet, Muller 1964). This suggests they are successful for evolutionarily short periods of time and under stable environments (Silvertown 2008). Yet, clonality in plants is widespread and includes species that span heterogeneous environments, are long-lived and face a range of environmental changes during their lifetime, and have survived major climatic changes such as those of the Pleistocene. Today, clonal plants make up perhaps 40 % of our planet's flora (Tiffney and Niklas 1985) dominate grasslands, deserts, wetlands, and tundras as major primary producers, comprise some of our most important crops, including almost all bioenergy crops, and feature many of the most invasive plants. Some of earth's largest, tallest, oldest, most extensive, and rarest plants are clonal. Being extremely modular organisms, clonal plants, whether large integrated clones, or fragmented into

Communicated by C. Holzapfel.

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countless pieces, challenge our notions of individuality. Does the apparent success of clonal plants contradict the severe costs of clonal reproduction suggested by theory? Here, we address this question from an ecological perspective in light of recent advances in our knowledge of epigenetic processes and their potential role in organismal evolution (Verhoeven and Priete 2013). First, we outline the characteristics of clonality in plants. We then discuss the growing understanding of epigenetics and its potential for both dynamic and stable responses to environmental heterogeneity. Finally, we examine how epigenetic processes may confer advantages to clonal plants under a range of ecological conditions and predict the success of clonal plants under current environmental change.

In higher plants, clonal reproduction can be achieved through agamospermy (seed apomixis) or vegetative spread. Agamospermous plants produce seed without sexual fusion, thereby affording advantages of seed dispersal without pollination risks. Vegetative spread, commonly referred to as clonal spread, includes vegetative apomixis, where sexual reproduction is absent, or rare (Stebbins 1950) and facultative vegetative reproduction from sprouts, rhizomes, stolons, etc., that may result in independent vegetative ramets. In either case, the seed or the ramet are genetic copies of the parent plant and have not undergone sexual recombination. Savidan (2010) argues that few, if any, plants are likely to be obligately clonal in nature. Furthermore, episodes of sexual reproduction may partly explain the maintenance of genetic diversity and the persistence of many clonal species. Vallejo-Marin et al. (Vallejo-Marín and Dorken 2010) explain that sexual investments can have diminishing fitness returns. As potential benefits of clonal growth increase, a point of diminishing returns from sexual reproduction is reached where resources are more optimally used for clonal growth (Fig. 1). The extent of asexual reproduction depends upon the interaction of species' genomes and environmental forces. Interestingly, among higher plant groups, asexual reproduction is rare in conifers (Redwood, Douhovnikoff et al. 2004); yet, it is extensive in angiosperms and is a trait of many successful introductions and invasions (Phragmites, Douhovnikoff and Hazelton 2014, reviewed in Pyšek 1997).

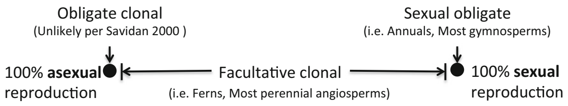

Fig. 1 Spectrum of asexual and sexual life history strategies. Clonal plants take advantage of a combination that runs from very rare sexual reproduction to very rare clonal reproduction

What can explain the success of clonality in apparently dynamic contemporary environments that should call for genetically diverse populations on which local selection can act? Plasticity, the ability of a genotype to produce a range of phenotypes in response to environmental variation, commonly expressed experimentally by reaction norms (Pigliucci 2001), can offer a rapid response not possible through genetic adaptation. Recent evidence suggests, that in part, plastic responses may be mediated by gene regulation to produce variable epigenomes that afford epigenetic acclimation that can be reversible in the short term or passed from one generation to the next in the long term (Rapp and Wendel 2005). There are clear adaptive advantages to these intermediate and reversible responses to environmental conditions. Adaptive plasticity has been shown to evolve rapidly (Sultan et al. 2013) and epigenetic-based plasticity is predicted to evolve rapidly as well (Zhang et al. 2013). Clonal plants may be one of the best examples of organisms taking advantage of epigenetically derived acclimation (epigenetic acclimation) as an alternative to the slower mechanisms of adaptation through natural selection. If epigenetic processes are important in matching organismal response to the environment, this may prove to be a mechanism that will buffer plants against the challenges of current and future rapid environmental changes.

What is epigenetics?

The last decade has seen great progress in our understanding of epigenetics, allowing us to move beyond the constraints of traditional evolutionary genetics by incorporating lasting acclimation into existing models of plant ecology (Bossdorf et al. 2008). Broadly speaking, epigenetics is a form of plasticity. Epigenetics is that portion of phenotypic plasticity represented by "mitotically and/or meiotically heritable changes in gene function that cannot be explained by changes in DNA sequence" (Bock and Lengauer 2008). Non-epigenetic plasticity would include acclimation due to physiological or behavioral responses not involving heritable changes in gene regulation and possibly not involving gene regulation at all, such as feedback inhibition. Epigenetic alterations occur during cell development and proliferation, in response to environmental conditions. These alterations can be swift, or can build over time and are flexible, or ontogenetically irreversible (Geng et al. 2013). These can range from short-term reversible down- and up-regulation (flexible alterations) to changes in regulation fixed for the lifetime of the genotype (stable alterations) and even, in some cases, through multiple generations (heritable alterations) (Verhoeven et al. 2010). For clonal plants that rely to various degrees on vegetative reproduction, the capacity to conserve or reverse gene regulation changes over cell divisions has clear potential for optimization of plasticity and acclimation in response to environmental variation encountered. The mechanism of DNA regulation can include DNA methylation, histone hypo-acetylation, chromatin modifications, small non-coding RNA's, and chromosome inactivation while not changing the primary gene sequences (Rapp and Wendel 2005). We will refer to those alterations that are maintained and transferred to subsequent meiotic generations as heritable epigenetics.

Epigenetics in clonal plant ecology

Modularity is an important factor in the success of plants and clonality is the extreme example of modularity (Pedersen et al. 1995). The capacity for plant modules or ramets to adjust to spatial and temporal heterogeneities can optimize genet performance. Circumstances exist where midterm acclimation, the dosage regulation of genes in addition to simple activation and silencing, and the potential for reversal at different rates allow for a broad range of fine-tuned modifications (Bräutigam et al. 2013). Here, we describe four types of mitotically conserved acclimations that are reflective of epigenetic alterations that can have important ecological implications within clonal plants, especially when considered in tandem with the well-reviewed ecological advantages and disadvantages inherent in the clonal growth form. Epigenetics, with the potential to last longer than other forms of plasticity, respond more quickly than natural selection, and make available an expansive range of possible genetic responses, may be a mechanism for countering the disadvantages of clonality described above and in some cases may even complement the advantages to clonality.

Spatial heterogeneity acclimation

The flexibility and rapidity of epigenetic responses can permit differential responses in a heterogeneous environment faster than local genetic adaptation, but potentially more lasting than other forms of plasticity. For modular clonal plants, ramets may develop to best match the microenvironments encountered (van Kleunen and Fischer 2001). For example, a genotype might forage across the landscape and develop modules that differentially specialize in the uptake of resources (reviewed in Hutchings and de Kroon 1994). As Wang et al. (2011) point out, this has been experimentally shown for *Trifolium repens* (Stuefer et al. 1996), *Fragaria chiloensis* (Roiloa et al. 2007), *Potentilla anserina* (van Kleunen and Stuefer 1999), *Potentilla reptans* (Stuefer et al. 1994), *Glechoma hederacea* (Birch and Hutchings 1994), *Glechoma longituba* (Chu et al. 2006), and *Schoenoplectus americanus* (Ikegami et al. 2008).

Temporal heterogeneity acclimation

With environmental fluctuations through time, epigenetic responses adjust to the most current conditions. A well-studied example of developmental epigenetic response to environmental cues is vernalization, "any effect of chilling that has a forcing effect" (reviewed in Chouard 1960, reviewed in Bräutigam et al. 2013). In addition to temperature variation, epigenome responses have been observed in response to pathogen, herbivore, low salt, and low nutrient stimulus (Verhoeven et al. 2010). This flexibility permits a clonal plant to match the character of new ramet production with current conditions, a useful trait for long-lived organisms.

Progressive acclimation

Epigenetic responses can build through time (Bräutigam et al. 2013). This response suggests that if an organism lives long enough and has the capacity to generate new modules, it can increase in fitness over time. For example, the first individuals of an introduced species may not be optimally acclimated to local conditions, but over a number of ramet generations, new stems could progressively acclimate as more epigenetic responses develop. This may be an additional explanation (to propagule pressure) for observed lag times between the introduction of exotic species and development of an invasive character (Pérez et al. 2006) in species such as *Ranunculus reptans* (Fischer et al. 2000) and *Rhamnus frangula* (Frappier et al. 2003).

Hormesis

"Hormesis represents a state in which an organism's response to an environmental stressor varies with its level of exposure" (Costantini 2014). This has been observed in plants such as *Cakile maritime* where previous exposure to drought stress increased salinity tolerance (Ellouzi et al. 2013). It is likely that epigenetics plays an important role in this form of plasticity that primes an organism for resistance to future stressors and is another example of how modules of a clonal plant could acclimate and even adapt to variation and change.

Even though sexual reproduction may be rare in clonal plants, meiotically inherited epigenetics can amplify the diversity that results and lower the threshold of diminishing returns for sexual reproduction described by Vallejo-Marín and Dorken (2010) and thus allow a greater reliance on clonal growth. Heritable epigenetics includes more persistent alterations that can be transferred across generations. Such responses are adaptive to the extent that individuals that are fittest will most likely contribute successful epigenomes to the next generation. Boyko and Kovalchuk (2011) refer to this as "soft inheritance" in contrast to Mendelian "hard inheritance" and describe it as a "fast and flexible system" that may enable rapid tuning of the next generation of plants to a new growth environment. Here, we describe two types of adaptation that are reflective of heritable epigenetic alterations that may play an important role in clonal plant success despite low rates of sexual recombination.

Pre-acclimation of next generation

In cases of heritable epigenetics, offspring have the advantage of early optimal acclimation (Harper 2005, Verhoeven et al.2010). Each time a parent passes on information to the next generation about local conditions, development of the next generation can occur more efficiently and with more specificity. For example, nutrient-stressed mother plants were significantly more likely to produce seedlings with increased root:shoot ratios, and this effect was found to persist for multiple generations (Verhoeven et al. 2010). Pre-acclimation is particularly advantageous in traits that are costly and non-reversible and in response to stochastic environmental conditions (Jablonka et al. 1995). For example, in a high herbivory setting, the early onset of a defensive response could improve success of seedlings. In some cases, epigenetic changes may persist as a "Phenotypic memory" (Jablonka et al. 1995) even after the environmental stimulus is gone. For example, epigenetic response to herbivory might result in low N leaves. If this change is conserved, stochastic herbivore attacks might be less problematic. (Spruce, Yakovlev et al. 2012, vernalization, Bräutigam et al. 2013).

Rapid adaptation

Each generation can further optimize its epigenetic response to local conditions independent of genetic natural selection. In a few generations, a small population can become better adapted (Jablonka et al. 1995, Lira-Medeiros et al. 2010). Similar to the mitotic progressive acclimation described above, this meiotic adaptation is consistent with observed lag times in the transition of introduced species to invasiveness (Pérez et al. 2006).

Epigenetic diversity

Like genetic diversity, heritable epigenetic diversity can have adaptive effects on populations (Latzel et al. 2013). For example, in the presence of pathogens and competitors, Latzel et al. (2013) measured 44 % greater productivity in epigenetically diverse *Arabidopsis* populations than in uniform populations. Evidence is growing that shortfalls in genetic diversity can be balanced by epigenetic diversity and facilitate plant population success (Rollins et al. 2013). This dynamic could mitigate lack of genetic diversity that is a major perceived shortcoming of clonal reproduction, and explain the invasiveness, persistence, age, and productivity of many clonal plant populations.

Polyploidy is perhaps the extreme example of genome diversity and offers considerable opportunity for epigenomic regulation. Many clonal species are polyploid (Mock et al. 2008, Beck et al. 2011). Comparing the incidence of polyploidy among annuals, biennials, and clonal perennials, Gustafsson (2010) first reported clonal plants were twice as likely to be polyploid than annuals or biennials (Baldwin and Husband 2013). It is unclear if clonality is selected for and facilitated by polyploidy or the other way around; however, epigenetics could be the mechanism by which this larger toolbox can be brought into play. With the capacity to adjust gene regulation, the added chromosomes and associated genes may provide a source of potential effective diversity far greater than found in diploid species. Dynamic monoallelic expression, when only one allele is expressed and which homologous allele expressed can change, has been observed in up to 24 % of mammalian cells (Deng et al. 2014). Its frequency in plants is still unknown; however, this suggests a potential mechanism for the dynamic expression of some alleles on a set of chromosomes and the silencing of others.

Future research directions

Many clonal plant species demonstrate extremes in life history strategies. *Phragmites australis* (Kettenring et al. 2010), *Arundo donax* (Kui et al. 2013), and *Fallopia japonica* (Hollingsworth and Bailey 2008) are just a few examples of extremely competitive and invasive clonal plants (reviewed in Thompson et al. 1995). *Sequoia sempervirens* (Douhovnikoff et al. 2004) and *Populus tremuloides* (Mock et al. 2008) exemplify the potential for great longevity in clonal plants (reviewed in de Witte and Stöcklin 2010). *Salix sp.* (Douhovnikoff et al. 2005, Douhovnikoff et al. 2010) and clonal grasses (reviewed in Fahrig et al. 1994) are good examples of clonal plants that demonstrate great resilience to disturbance and extreme environmental conditions. All of these life history strategies benefit from some form of lasting acclimation across spatially or temporally heterogeneous environments, thus necessitating a high level of responsiveness at time scales shorter than natural selection permits. In each case, epigenetic responses could provide a mechanism for this acclimation.

Clonal plants make ideal in situ epigenetic study species with their natural replication of identical genotypes, which permits the control for genetic makeup and within and between genotype comparisons. To date, most work exploring plant epigenetic responses has been conducted on somaclonal variants produced through plant tissue culture (Neelakandan and Wang 2012, Sun et al. 2014) or ex situ *Arabidopsis* experiments (Latzel et al. 2013). We are only just seeing the first reports of in situ plant ecology studies (*Laguncularia racemosa*, Lira-Medeiros et al. 2010; *Viola cazorlensis*, Herrera and Bazaga 2011; *Betula ermanii*, Wu et al. 2013) and even fewer in situ clonal plant studies (*Fallopia aponica*, Richards et al. 2012; *Helleborus foetidus*, Herrera et al. 2014). Some of the important attributes of clonal plants need to be re-examined in the light of recent advances in our knowledge of phenotypic plasticity and diversity of epigenomes, e.g., (1) does resource sharing among ramets permit a population to exploit environmentally heterogenous sites, such as by division of labor? If so, do ramets respond to the environmental variation through epigenetic change? Is such change heritable through developing lineages of ramets? Are epigenetic changes readily reversible, or does canalization determine future responses? (2) How is the balance between sexual and asexual reproduction mediated in facultatively clonal plants? Do facultatively clonal plants respond to environmental stresses by differential resource allocation to sexual or asexual reproduction? If so, is the response a function of a plastic genome, or a function of epigenetic responses? (3) The paradigm that clonal plants are less genetically diverse than sexual plants is no longer accepted. However, we still know little about what determines the observed variation in genetic diversity among species or populations of clonal plants. How important is the role of epigenetic change in determining levels of variation within and among populations? Does epigenetic change become more important in peripheral populations where genetic diversity is commonly low and immigration may be low?

Climate change is likely to be one of the most important challenges to natural populations of organisms. For plants, the capacity to migrate to suitable environments is limited by dispersal and by landscape fragmentation and adaptation to new environments through natural selection will be too slow. Evidence from alpine and high-latitude vegetation suggests that clonal plant communities have been stable through long periods of time that span important climatic changes (Grabherr and Nagy 2003). Clonal plants, even at climatic extremes, can be intermitently capable of sexual reproduction and may harbor important levels of genetic diversity (de Witte et al. 2012) that provide resilience to climate change. Indeed, de Witte et al. (2012) predict that local extinctions of long-lived clonal plant populations are unlikely under a moderate climate change scenario over the next century. The flexibility that altered epigenomes can provide may prove to be one way in which plants, both clonal and sexual, will be buffered against environmental change, allowing enough time for natural selection to operate.

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