



Phenotypic plasticity and specialization in clonal versus non-clonal plants: A data synthesis



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ABSTRACT

Reproductive strategies can be associated with ecological specialization and generalization. Clonal plants produce lineages adapted to the maternal habitat that can lead to specialization. However, clonal plants frequently display high phenotypic plasticity (e.g. clonal foraging for resources), factors linked to ecological generalization. Alternately, sexual reproduction can be associated with generalization via increasing genetic variation or specialization through rapid adaptive evolution. Moreover, specializing to high or low quality habitats can determine how phenotypic plasticity is expressed in plants. The specialization hypothesis predicts that specialization to good environments results in high performance trait plasticity and specialization to bad environments results in low performance trait plasticity. The interplay between reproductive strategies, phenotypic plasticity, and ecological specialization is important for understanding how plants adapt to variable environments. However, we currently have a poor understanding of these relationships. In this study, we addressed following questions: 1) Is there a relationship between phenotypic plasticity, specialization, and reproductive strategies in plants? 2) Do good habitat specialists express greater performance trait plasticity than bad habitat specialists? We searched the literature for studies examining plasticity for performance traits and functional traits in clonal and non-clonal plant species from different habitat types. We found that non-clonal (obligate sexual) plants expressed greater performance trait plasticity and functional trait plasticity than clonal plants. That is, non-clonal plants exhibited a specialist strategy where they perform well only in a limited range of habitats. Clonal plants expressed less performance loss across habitats and a more generalist strategy. In addition, specialization to good habitats did not result in greater performance trait plasticity. This result was contrary to the predictions of the specialization hypothesis. Overall, reproductive strategies are associated with ecological specialization or generalization through phenotypic plasticity. While specialization is common in plant populations, the evolution of specialization does not control the nature of phenotypic plasticity as predicted under the specialization hypothesis.

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1. Introduction

The evolution of clonal versus sexual reproductive strategies is a major aspect of plant life history (Lovett Doust, 1989; Hadany and Otto, 2009; Barrett, 2010). The expression of reproductive strategies should be a response to selection within an environment, and clonal and non-clonal reproductive strategies can be linked to different environments. For example, clonal reproduction can be associated with stressful or marginal habitats such as high altitudes (e.g. Pluess and Stöcklin, 2005; Stöcklin et al., 2009). In contrast,

sexual reproduction can be associated with new environmental stresses experienced during colonization (Pluess and Stöcklin, 2005; Agrawal, 2006). Reproductive strategies may also have important implications on how plants perform across environments. For example, reproductive strategies can be related to ecological specialization (genetically determined local adaptation to increase performance in a given habitat, possibly at a cost of reduced performance in other habitats) or generalization if clonal or non-clonal life histories determine the expression of phenotypic plasticity.

Phenotypic plasticity is predicted to be important in an individual's capacity to adapt to heterogeneous environments (Sultan, 2001; Richards et al., 2006; Griffith and Sultan, 2011). Functional trait (traits associated with resource acquisition and

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growth) plasticity underlies adaptive responses to variable environments (Pigliucci, 2001; McGill et al., 2006; Violle et al., 2007). High functional trait plasticity can underlie the maintenance of performance (i.e. low performance trait plasticity across environments – e.g. Richards et al., 2006). Thus, ecological generalization may emerge from high functional trait plasticity and low performance trait plasticity. In contrast, specialization to a given environment should result in loss of functional trait plasticity (Griffith and Sultan, 2005) since functional traits would express similar values across habitats due to optimization for a given environment. Any change in phenotypic plasticity associated with the expression of reproductive strategies could have important implications on the ecology of a species. However, the nature of the relationship between the evolution of reproductive strategies and phenotypic plasticity remains poorly understood.

Clonal reproduction could be associated with ecological specialization. Clonal growth is thought to be an adaptation in stressful or marginal areas such as cold habitats (e.g. Pluess and Stöcklin, 2005; Stöcklin et al., 2009). Some environmental stresses are static (e.g. altitude) and once populations are adapted to these stresses, phenotypic plasticity is unlikely to be an advantage. In these instances, clonality can be advantageous as it allows daughter ramets to carry the same adaptations as parents. Clonal lineages would then be likely to be adapted to the maternal environment, but perhaps not to other environments. These differences in adaptation should result in ecological specialization. In addition, clonality can augment possibility of local adaptation due to low dispersal ability in clonal propagules and limited gene flow (Fischer and van Kleunen, 2002; Leimu and Fischer, 2008). Alternately, clonal reproduction could also be associated with ecological generalization. For example, clonal plants can actively place their ramets in favorable microhabitats (high light or nutrient patches in heterogeneous environments) through the expression of high phenotypic plasticity (Slade and Hutchings, 1987; de Kroon and Knops, 1990; de Kroon et al., 1994; Huber, 1996; Stoll et al., 1998). Foraging behaviors are generally interpreted as adaptive since more plastic genotypes tend to express higher fitness across environments (e.g. van Kleunen and Fischer, 2005). Although the conditions underlying clonal foraging are small scale variation, the evolution of phenotypic plasticity to small scale environmental heterogeneity should favor the evolution of adaptive plasticity (a type of phenotypic plasticity that increases fitness and is favored by selection). Therefore, adaptive plasticity can help clonal plants to deal with environmental variability, adapt to different habitats and promote the evolution of generalization in clonal plants.

Similarly, species employing an obligate sexual reproductive strategy (non-clonal plants) can be associated with either ecological specialization or generalization. Sexual reproduction can facilitate ecological specialization through high rates of genetic recombination and increased rates of adaptation (Agrawal, 2006; Becks and Agrawal, 2010), and this effect is likely to be greater in non-clonal species. Thus, sex may be beneficial in unfavorable environmental conditions, under stress, and during colonization (Pluess and Stöcklin, 2005; Agrawal, 2006). Alternatively, genetic variation for traits associated with phenotypic plasticity maintained by sexual reproduction and reinforced by selection can lead to the evolution of adaptive plasticity (van Kleunen and Fischer, 2005) by buffering performance across environments, which is associated with ecological generalization.

Specialization to high or low quality environments can shape the expression of phenotypic plasticity. The specialization hypothesis (Taylor and Aarssen, 1988; Lortie and Aarssen, 1996) predicts that individuals specialized to good environments express high performance trait plasticity and bad environment specialists express low performance trait plasticity when compared to

ancestral (less specialized) states. That is, specialization incurs a cost – individuals specialized to a good environment perform poorly in bad environments relative to bad environment specialists resulting in high performance trait plasticity. Similarly, individuals specialized to a bad environment perform poorly in good environments relative to good environment specialist resulting in a low performance trait plasticity. The specialization hypothesis does not make predictions on the expression of functional traits. However, specialization to good or bad environments should be associated with the loss of functional trait plasticity because high functional trait plasticity can limit the loss in performance across environments in generalist (ancestral) non-specialized genotypes. A number of studies support the specialization hypothesis by demonstrating low performance trait plasticity in populations from bad environments (Dong et al., 1996; Valladares et al., 2000, 2002; Lehmann and Rebele, 2005; Eränen and Kozlov, 2008; Grassein et al., 2010; Lemke et al., 2012). However, there are some studies inconsistent with the specialization hypothesis (Stöcklin et al., 2009; Griffith and Sultan, 2011; Molina-Montenegro et al., 2011).

The interplay between reproductive strategies, phenotypic plasticity, and ecological specialization/generalization is important for understanding how plants adapt to variable environments. We have outlined distinct and contrary predictions on how reproductive strategies are related to specialization and generalization and our study addresses this knowledge gap. We tested for differences in phenotypic plasticity and specialization between clonal and non-clonal (obligate sexual) species by surveying literature for studies reporting performance trait plasticity and functional trait plasticity. We addressed the following research questions: 1) Is there a relationship between reproductive strategies (clonal versus non-clonal), phenotypic plasticity, and ecological specialization? 2) Do species specialized in good (productive) habitats express greater performance trait plasticity than those specialized in bad (unproductive) habitats (i.e. is the evolution of specialization consistent with the predictions of the specialization hypothesis)?

2. Materials and methods

2.1. Data collection

Studies were assembled from databases such as ISI Web of Knowledge and Scopus in 2012, by using keywords such as: 'phenotypic plasticity, specialization, clonal, non-clonal, sexual plants'. We used different binary (and ternary) combinations of these five keywords to find the most related studies. For example, after entering 'phenotypic plasticity' keyword, we further restricted our search by entering another keyword such as 'clonal'. By checking reference sections of the selected studies, we found more studies related to our research questions. Moreover, we limited the number of available studies by selecting only terrestrial herbaceous plants and shrubs. We acquired data from experiments with different growing conditions including a control (a benign or high resource treatment) and at least a type of treatment where resource availability was decreased (i.e. treatments such as low light or low nutrients). We acknowledge that our keywords may have been more effective at detecting studies with clonal plants than non-clonal plants. However, we believe that our search was effective at finding clonal plant studies, and an unbiased sample of studies involving obligate sexual species. We used – the term – clonal to mean a plant producing clonal ramets (the production of daughter plants genetically identical to the mother plant on structures such as stolons or rhizomes) rather than clonal lineages. The studies included in this data-synthesis did not specifically manipulate clonal integration or clonal replicates to control for genetics and epigenetics.

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