



Petunia floral trait plasticity in response to soil nitrogen content and subsequent impacts on insect visitation[☆]



Cassie J. Majetic^{a,*}, Andrea M. Fetters^{a,b}, Olivia M. Beck^a, Elizabeth F. Stachnik^a, Katelyn M. Beam^a

^a Department of Biology, Saint Mary's College, Notre Dame, IN, USA

^b Present address: Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA

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ABSTRACT

Plastic changes in floral trait phenotypes in response to biotic factors (i.e., herbivory and pollination) are known to impact pollinator behavior. In contrast, research on abiotic factors suggests substantial plasticity in floral traits, but has rarely explored the implications that such changes have on the behavior of putative pollinators. We explored the possibility of floral trait plasticity in *Petunia hybrida* Vilm. genotypes in response to soil nitrogen concentration, and the potential impact that such plasticity might have on insect visitation. Given the role of nitrogen in plant growth and biochemistry, we predicted increases in floral scent, pigmentation, and floral size with increased nitrogen. We further predicted that insect visitors would respond to this phenotypic plasticity by altering behavior patterns. Our results suggested little plasticity in floral color and floral scent in response to nitrogen. We found no changes in anthocyanin concentration per unit of floral tissue under increased nitrogen conditions. Of nine benzenoid/phenylpropanoid volatile compounds examined, only one (eugenol) increased per unit floral tissue with increasing nitrogen concentration. In contrast, floral size followed the predicted pattern, with clear increases in both corolla size and display size with increasing nitrogen. All traits varied among genotypes, indicating genotype-specific trait expression. Field-based choice experiments using genotypes from control, low, and high nitrogen treatments suggested support for our behavioral hypothesis: insects visited plants with increased soil nitrogen at a significantly higher rate than those without additional nitrogen. This pattern suggests that putative pollinators are likely responding to plastic changes in display size, corolla size, and/or eugenol emission. We also found a significant difference in insect visitation between genotypes, as predicted by floral phenotype differences found for these true-breeding lines, and a strong interaction between genotype and treatment, suggesting that differences in genotype responses to nitrogen treatments result in differential insect behavior patterns.

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1. Introduction

The concept of phenotypic plasticity, the ability of an organism to produce differential phenotypes based upon the conditions of the environment (Pigliucci, 2001), has been extensively explored for a variety of plant species-environmental factor combinations e.g., the pioneering ecotype work of Clausen, Keck, and Hiesey (as reviewed in Núñez-Farfán and Schlichting (2001)), variation in water availability (Caruso et al., 2006), and specific latitudi-

nal gradients (Stinchcombe et al., 2004). Such studies have led researchers to recognize the malleability of plant phenotype in response to environmental conditions and the ability of plants to maximize fitness through changes in gene expression, rather than natural selection over longer periods of time (although see discussions and reviews of adaptive phenotypic plasticity and natural selection for the ability to be plastic, as in Palacio-López et al., 2015; Pigliucci, 2001; Sultan, 1995; van Kleunen and Fischer, 2005).

Many studies of phenotypic plasticity in plants have focused on vegetative traits and resource allocation (Dorken and Barrett, 2004; Mal and Lovett-Doust, 2005; Navas and Garnier, 2002; Pélabon et al., 2013; Poorter and Nagel, 2000; Sultan, 1995). However, researchers have also explored phenotypic plasticity in plant reproductive traits, particularly in response to herbivory (Hoffmeister

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* Corresponding author.

E-mail address: cmajetic@saintmarys.edu (C.J. Majetic).

et al., 2015; Lehtilä and Strauss, 1997, 1999; Schiestl et al., 2014; Theis et al., 2009) or prior pollinator activity (Harder and Johnson, 2005; Ida and Kudo, 2003; Theis and Raguso, 2005; Weiss, 1995; Weiss and Lamont, 1997). By altering phenotypic expression of pollinator-attractive traits in response to these biotic factors, plants may additionally alter pollinator attraction (Hoffmeister et al., 2015; Weiss, 1995) and change fruit and/or seed set (Poveda et al., 2003), although plasticity studies do not always examine these possibilities.

The impact of abiotic factors on plasticity of floral traits has also been explored to some extent, albeit not always in the language traditionally associated with phenotypic plasticity e.g., temperature (Hansted et al., 1994; Jakobsen and Olsen, 1994), air pollution (McFrederick et al., 2008), water and nutrients (El-Mokadem Hoda and Mona, 2014; Gouinguene and Turlings, 2002; Schlichting, 1989). While such research clearly indicates floral trait plasticity in response to abiotic factors, few, if any, studies have attempted to explore how such plasticity might alter pollinator behavior, and consequently plant reproductive success (as proposed in Majetic et al., 2009b).

One abiotic factor that is known to drive phenotypic plasticity for a range of plant traits is soil nitrogen concentration. Given the important role that nitrogen plays in plant development, it is unsurprising that many species display alterations to vegetative phenotype when exposed to different concentrations of nitrogen (Garnier, 1998; Navas and Garnier, 2002; Poorter and Nagel, 2000; Reynolds and Dantonio, 1996; Schlichting, 1989). Explorations of the impacts of nitrogen on floral trait plasticity are less common (El-Mokadem Hoda and Mona, 2014; Schlichting, 1989), but knowledge of floral trait development suggests that some traits should respond significantly and in predictable ways to the addition or loss of soil nitrogen. Pollinator attraction traits such as display size and flower dimensions (corolla width and length) might be expected to increase with increased levels of soil nitrogen, as additional nitrogen would allow for greater resource allocation to reproductive units. Pollinators are known to respond to increases in floral display size and floral dimensions (Conner and Rush, 1996; Grindeland et al., 2005; Harder and Johnson, 2005; Mitchell, 1994; Mitchell et al., 2004), thus creating the potential for plasticity in these traits to impact reproductive success.

Pigmentation production could also be positively impacted by increases in soil nitrogen. Anthocyanin, one of the most common floral pigment groups, is produced from the amino acid precursor phenylalanine in the shikimic acid pathway (Rauscher, 2008); thus, production of these pigments would require soil nitrogen for synthesis (Gretewold, 2006). An increase in soil nitrogen could therefore result in an increase in pigmentation in floral tissues. Given the known role of pigmentation in attracting pollinators (Fenster et al., 2004; Frey et al., 2011; Hoballah et al., 2007; Jones and Reithel, 2001; Schemske and Bradshaw, 1999; Stanton, 1987), any plasticity in pigmentation could lead to a range of possible changes in pollinator response and consequently plant reproductive success.

Finally, changes in soil nitrogen content could alter production of floral scent, a known pollinator attraction characteristic with potentially important impacts on plant reproductive success (Dudareva and Pichersky, 2006; Majetic et al., 2009a; Parachnowitsch et al., 2012). In particular, benzenoid and phenylpropanoid volatile compounds are synthesized, like anthocyanins, from the amino acid phenylalanine through the shikimic acid pathway (Dudareva and Pichersky, 2000; Majetic et al., 2008). Thus, plants exposed to higher levels of soil nitrogen may show an increased synthesis of such volatiles. Given the role of these particular compounds in the attraction of a wide range of pollinators (Raguso, 2004, 2008), such plasticity should have important impacts on pollinator behaviors. Furthermore, some (although

not all) other classes of volatile compounds found in the floral scent bouquet, such as terpenoids or fatty acid derivatives, should remain unaffected by the increased nitrogen concentration in the soil, as such compounds are not derived from phenylalanine or other nitrogen-based compounds (Dudareva and Pichersky, 2000; Majetic et al., 2008).

Despite substantial knowledge on floral trait plasticity, the potential for floral traits such as those described above to be plastic in response to soil nitrogen and the subsequent impact such plasticity is likely to have on pollinator behavior and plant reproduction remains poorly investigated. We thus explored this possibility using a two-tiered hypothesis. First, we hypothesized that floral dimensions, floral display size, benzenoid/phenylpropanoid scent emission, and anthocyanin pigmentation levels should display phenotypic plasticity in response to changes in soil nitrogen levels. Specifically, we predicted that all of these traits should increase in the presence of increased nitrogen; increased nitrogen levels should allow for increased allocation to these morphological and biochemical characteristics. Second, we predicted that insect visitors should change their behavior in response to these altered floral characteristics. In particular, increased floral size, display size, and floral scent could increase visitation to plants grown in high-nitrogen conditions; pollinators often show increased landings in response to additional flowers, larger flowers, or increased scent (Conner and Rush, 1996; Harder and Johnson, 2005; Majetic et al., 2009a; Mitchell et al., 2004). The impact of increased pigmentation is less clear. If increased pigmentation drastically increases color saturation, putative pollinators may be more apt to visit (e.g., Lunau, 1990). However, changes in behavior would be more likely if the type of anthocyanin expressed was altered, as shown with plants that change their pigmentation post-pollination (e.g., Weiss, 1995; Weiss and Lamont, 1997), in the *Mimulus* hybridization work of Schemske and Bradshaw (1999), and as predicted by pollination syndrome patterns (e.g., Fenster et al., 2004) – a less likely outcome of increased nitrogen availability alone.

2. Materials and methods

2.1. Study species

Petunia hybrida Vilm. is an annual member of the Solanaceae family. While the progenitors of this species are native to South America (Ando et al., 1999; Schuurink et al., 2006), *Petunia hybrida* is commonly used as a garden ornamental in the Northern Hemisphere and many cultivars representing unique floral genotypes have been developed (Rhodus, 2003). These true-breeding genetic lines display a range of colors (shades of purple, magenta, red, pink, blue, white, violet, and yellow), a flared and trumpet-shaped corolla that can vary in size, and a sweet but variable fragrance (Rhodus, 2003). Due in part to the ease of cultivation and annual life history, *Petunia* has become a model system in recent years, with studies using both hybrid genotypes and wild true-breeding species for research on floral scent (Boatright et al., 2004; Colón et al., 2010; Colquhoun et al., 2011; Schuurink et al., 2006; Verdonk et al., 2005), floral color patterns (Ando et al., 1999), and pollination ecology (Hoballah et al., 2005, 2007; Kessler et al., 2013; Klahre et al., 2011; Stuurman et al., 2004). Previous work on *Petunia hybrida* response to chemical fertilizers suggests that at least one genotype responds to increases in soil fertilizers with increased vegetative and floral trait sizes, indicating the potential for plastic responses to nitrogen alone (El-Mokadem Hoda and Mona, 2014). With such substantial information available, *Petunia* presents a unique opportunity to closely test the plasticity of well-characterized floral traits in a controlled setting.

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