

REVIEW

Morning glory as a powerful model in ecological genomics: tracing adaptation through both natural and artificial selection

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Many diverse questions in ecology and evolution have been addressed using species belonging to the genus *Ipomoea*, commonly referred to as the morning glory genus. *Ipomoea* exhibits a wide range of diversity in floral color, growth form, mating system and tolerance to environmental factors, both within and among species, and as such has been a focal group of many investigations in the last 80 years. In this review, we highlight recent work to which *Ipomoea* species have contributed—from studies of the mating system,

molecular evolution, plant–herbivore and plant–parasite interactions to their impact on and importance to agriculture. Genomic resources for this group are currently under development, and given the breadth of studies and history of this group, combined with an expanding genetics toolkit, we argue that *Ipomoea* should provide the next model organism for ecological genomics.

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The term ‘morning glory’ is often used to describe an ephemeral nature or something that shows an impressive start but quickly fades. This characterization can be traced to the flowering habit of *Ipomoea* or the morning glory genus—the flowers of many morning glory species open early in the day but wilt by the afternoon. However, this trait, as well as rampant flower and seed production, rapid generation time and ease of growth in both greenhouse and field conditions have facilitated *Ipomoea*’s use in ecological genetics. Although the current incarnation of morning glory work began and has continued since the late 1970’s, morning glory species have been prominent in the scientific literature for ~80 years. Japanese workers in the early 1930’s produced one of the first plant genetic maps using flower color variants of *Ipomoea nil* (Imai, 1934), and recent work has positioned morning glory as a model genus for understanding the genes involved in the floral color pathway (Durbin *et al.*, 2000, 2003; Zufall and Rausher, 2004; Streisfeld and Rausher, 2009). Given the persistence of morning glories in both basic and applied science, it is interesting that the term ‘model’ has yet to be consistently applied to this group.

The emerging models in plant ecological genomics, *Mimulus*, *Helianthus* and *Aquilegia*, are quickly joining the rank that was singly held by *Arabidopsis* as little as

5 years ago. Emergent models from these genera have a long history in the literature and are now enjoying the benefit of increased genomic resources. They are excellent groups for elucidating the genetics of speciation, domestication and local adaptation. However, there are themes in plant ecological genetics and evolutionary biology for which *Ipomoea* species currently serve as excellent study organisms. For example, *Ipomoea* species, and *I. purpurea* in particular, have a history as being used to study the evolutionary process of adaptation to various ‘interactions’—whether with herbivores, pollinators, parasites or even human-mediated influences (Epperson and Clegg, 1987a; Rausher and Simms, 1989; Simms and Triplett, 1994; Baucom and Mauricio, 2004)

Current work with *Ipomoea* species addresses a range of evolutionary questions that are applicable to many organisms and biological processes, from the evolution of the mating system to plant–herbivore and plant–parasite interactions (Chang and Rausher, 1999; Kniskern and Rausher, 2006a; Simonsen and Stinchcombe, 2007). Further, species within the genus are both noxious crop weeds as well as important crop species, highlighting its unique applicability to agriculture. Members of *Ipomoea* are invasive in the United States, exhibit a range of mating systems from selfing to obligately outcrossing both within and among species, and vary in form from vines to shrubs to trees. The genus itself is large, encompassing more than 600 species that are distributed worldwide (McDonald, 1991; Austin and Huaman, 1996; Wilkin, 1999; see Manos *et al.*, 2001 for a phylogenetic tree of 45 species). Thus, *Ipomoea*, in addition to providing a focal species in multiple laboratories, presents

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both the attributes of a model system and also an incredible range and diversity of evolutionary scenarios.

The purpose of this review is to highlight recent work using *Ipomoea* and present the case that morning glory is a powerful model for tracing the genetics of adaptation to natural and human-mediated selection. We first briefly review the diverse evolutionary questions that have been addressed with *Ipomoea* species, from molecular pathway evolution, mating system evolution, and the evolution of plant defense to herbivores, pathogens and herbicide. We then discuss the conceptual leaps that increased genetic and genomic resources can provide these areas of study. We believe that morning glory's history in the literature, phylogenetic placement (sister to Solanaceous crop species) and broad ecological relevance positions this genus as a unique model in both ecological and weedy plant genomics. Our overarching goals are to pique the interest of a wide range of researchers, to strengthen the *Ipomoea* community, and make the case for increased genomic resources for this group.

Ipomoea and the evolution of the plant mating system

Morning glories have been a model genus for studying the ecology and genetics of plant reproduction for the past four decades (Durbin *et al.*, 2003). Many of these studies focused on variation in flower color and its interaction with pollinators, whereas others examined the consequences of variation in other floral traits on the fitness of individual plants (Ennos and Clegg, 1983; Chang and Rausher, 1999). The extreme variation in flower color is perhaps one of *Ipomoea*'s most prominent characteristics. Within the genus, flower color ranges from white to darkly pigmented red and purple corolla (Figure 1), and much of this variation is present within a single species, the common or tall morning glory, *I. purpurea* (Ennos and Clegg, 1983; Epperson and Clegg, 1987c, 1988, 1992).



Figure 1 The genus *Ipomoea* contains a range of diversity in floral color. The species pictured here (approximately clockwise from left) are *I. purpurea* (white, purple and light purple flowers present), *I. nil*, *I. lobata*, *I. quamoclit* and *I. lacunosa* (small white corolla pictured bottom left). Photo credit: Shu-Mei Chang.

The maintenance of floral color polymorphisms in *I. purpurea* in the Southeastern US has received intensive investigation (Epperson and Clegg, 1986, 1987a, b, 1988, 1992; Rausher and Fry, 1993; Fry and Rausher, 1997; Mojonner and Rausher, 1997). One of the most interesting results from this work was that natural pollinators discriminate against white color morphs when they are rare—a result that was not uncovered for pigmented flowers, suggesting that pollinators do not treat color morphs equally (Epperson and Clegg, 1987b; Rausher and Fry, 1993). Besides impacting pollinator visitation, flower color was shown in these studies to influence selfing rate or the proportion of progeny produced through self-fertilization. Because of low visitation that they received, white flower individuals were found to self at a higher rate—potentially influencing mating system evolution, individual fitness and the distribution of genetic variation in populations.

Although selfing may have the advantage of doubling genetic transmission compared with outcrossing (Fisher, 1941), it can lead to inbreeding depression if progeny derived from selfing have lower fitness than the ones derived from outcrossing. By taking advantage of anther–stigma separation (another trait affecting selfing rates) in *I. purpurea* (Figure 2), Chang and Rausher (1998; 1999) studied selfing's deleterious effects. They showed that even though plants with higher selfing rates (or those with smaller anther–stigma distance) may enjoy a transmission advantage, inbreeding depression could counteract it (Chang and Rausher, 1998; Chang and Rausher, 1999). However, the magnitude of inbreeding depression was not sufficient to completely counteract selfing advantage or to maintain an evolutionarily stable mixed mating system (Rausher and Chang, 1999).

An important finding of these studies was that inbreeding depression was expressed not only in seed production (female fitness) but also in pollen production (male fitness). They also uncovered negative frequency dependence in pollen success of two groups of plants contrasting in their anther–stigma distance. More specifically, anther–stigma distance genotypes that tended to



Figure 2 *Ipomoea purpurea* exhibits genetic variation for anther–stigma distance (ASD), or anther–stigma distance, a trait that is measured by the distance between the stigma and anthers. This trait has been studied in context of the maintenance of a mixed mating system: plants with lower ASD self-pollinate more often than plants with greater ASD. In this picture, ASD is higher for the flowers of the genotype on the right relative to the genotype in the middle. Photo credit: Shu-Mei Chang.

have higher than expected outcrossing success when at low frequency had lower than expected outcrossing success when at high frequency. The presence of frequency-dependent selection involving pollen success highlights the importance of including male fitness components in understanding the maintenance of genetic variation in both floral traits and selfing rates in natural populations (Chang and Rausher, 1998; Rausher and Chang, 1999).

A recent series of studies involving another morning glory species, *I. hederacea*, identified another potential benefit for selfing. Flowers of this species have five anthers that cluster around its stigma, a trait that has been suggested to convey high selfing rates. In contrast, in *I. purpurea*, a sympatric species, anthers are at various heights, but often at some distance away from stigmas (Chang and Rausher, 1998). Because pollen transfer from *I. purpurea* reduces seed set in *I. hederacea*, Ennos (1981) suggested that anther clustering in *I. hederacea* functioned to reduce the effects of interspecific pollen transfer.

Studies designed by Smith and Rausher (2007; 2008a,b) support the Ennos hypothesis: clustering of anthers around stigma in *I. hederacea* flowers indeed offers protection against hybridization from *I. purpurea* pollen through both mechanical interference and through high selfing rates. Smith and Rausher (2007; 2008a,b) further demonstrated experimentally that the presence of *I. purpurea* altered the pattern of natural selection on anther clustering in *I. hederacea* flowers. Specifically, directional selection for anther clustering was only found when *I. purpurea* was also present in their experimental population. Although population selfing rates for *I. hederacea* vary significantly elsewhere in the range (Tennessee and Alabama; Hull-Sanders *et al.*, 2005), it is unclear whether such variation was related to anther–stigma distance or the presence of *I. purpurea*.

Ipomoea's contribution to the study of molecular evolution

Targeting genes by selection

Natural selection often has ‘a choice’ of which genes to target to produce any particular novel phenotype. An unanswered question in evolutionary biology is whether in such cases natural selection differentially targets different types of genes (Wray *et al.*, 2003; Carroll, 2005a,b; Hoekstra and Coyne, 2007; Lynch and Wagner, 2008; Stern and Orgogozo, 2008). Investigations on the genetics of flower color evolution in *Ipomoea* are yielding insight into this issue.

Most species of *Ipomoea* have blue/purple, bee-pollinated flowers. In several clades, however, red, hummingbird-pollinators have evolved independently. In three species, parallel evolution at the phenotypic level is associated with parallel evolution at the biochemical level: shifts from blue to red flowers are accomplished by producing pelargonidin-based rather than cyanidin-based anthocyanins (Zufall and Rausher, 2004; Streisfeld and Rausher, 2009). In addition, in all three species, there is no change in the type of anthocyanins produced in vegetative tissues, suggesting that the genetic change involved is regulatory rather than functional. The regulatory hypothesis has been supported for *I. quamoclit* and *I. horsfalliae*: in both

species, production of pelargonidin-based anthocyanins in flowers is due to a downregulation of the pathway branching enzyme F3'H (Des Marais and Rausher, 2008; Streisfeld and Rausher, 2009). In *I. quamoclit*, downregulation is accomplished by a mutation in the *cis*-regulatory region of *F3'H*; a similar mechanism is likely for *I. horsfalliae*, but has not been definitively proven. Two potential explanations for this genetic parallelism are: (1) regulatory mutations are more common than functional mutations that can produce the same red phenotype and (2) regulatory mutations are more likely to be fixed than functional mutations because they incur less deleterious pleiotropy. Streisfeld and Rausher (2009) demonstrate that explanation (1) can be ruled out because spontaneous mutations causing shifts from blue to red flowers all involve functional inactivation of anthocyanin enzymes rather than regulatory changes.

Another common flower color transition is from flowers containing anthocyanin pigments to white or yellow flowers that lack anthocyanins. Investigations in *Ipomoea*, as well as in *Petunia*, *Antirrhinum* and *Mimulus*, have all revealed that genetic changes associated with this transition are also regulatory, involving modification of transcription factors rather than enzyme-coding genes (Quattrocchio *et al.*, 1999; Durbin *et al.*, 2003; Schwinn *et al.*, 2006; Whittall *et al.*, 2006). The pattern of transcription factor mutations contrasts with that of spontaneous mutations, approximately half of which involve functional inactivation of enzyme-coding genes (Streisfeld and Rausher, 2011). As with transitions from blue to red flowers, a commonly proposed mechanism that regulatory changes incur less deleterious pleiotropy than functional mutations, as the latter eliminate production of anthocyanins, and more generally flavonoids, in tissues other than flowers (Quattrocchio *et al.*, 1999; Rausher, 2006; Rausher *et al.*, 2008). Some experimental support for this assumption is provided by investigations of pleiotropy associated with regulatory and functional flower color mutants in *I. purpurea* (Coberly and Rausher, 2008).

Variation in rates of amino-acid substitution

Proteins vary markedly in the rate of amino-acid substitution (Li *et al.*, 1985). The traditional explanation for this variation is that proteins are under different degrees of selective constraint (Kimura, 1977; Li, 1997). It has been very difficult, however, to understand and predict the degree of constraint that any particular protein experiences.

One recent hypothesis is that constraint will be greater in genes products of which are more ‘connected’ to other gene products, and a number of recent studies using genomic approaches have tended to corroborate this hypothesis (Fraser *et al.*, 2002; Hahn and Kern, 2005; Vitkup *et al.*, 2006). One of the earliest examinations of this hypothesis was a study by Rausher *et al.* (1999) on anthocyanin pathway genes in three taxonomically disparate species including *I. purpurea*. Rausher *et al.* (1999) found that downstream enzymes evolve at higher rates than upstream enzymes, and suggested differential constraint as the mechanism. Differential constraint could arise for either of two reasons: (1) upstream enzymes are used to produce physiologically and

ecologically important flavonoids other than anthocyanins or (2) because upstream enzymes are likely to have the greatest control over pathway flux, mutations in them are less likely to be quasi-neutral than that in downstream genes. Two subsequent investigations using just *Ipomoea* species (Lu and Rausher, 2003; Toleno *et al.*, 2010) confirmed the latter by showing that dN/dS is higher for downstream genes. Finally, Rausher *et al.* (2008) demonstrated that the rate differences are caused by differential constraint rather than accelerated rates of adaptive substitution in downstream genes. These investigations suggest that location of a gene product in a pathway or network likely influences degree of constraint, and hence rates of substitution.

Analyses of transcription factor evolution in *Ipomoea* also suggest that differences in substitution are caused by differences in 'connectedness', where connectedness is assessed in terms of the number of proteins with which the transcription factor interacts. In *Ipomoea*, the bHLH anthocyanin transcription factor exists as two copies. Based on studies of orthologs of these two genes in *Petunia* (Kroon, 2004), bHLH1 interacts with more proteins than bHLH2 and exhibits a lower amino-acid substitution rate. Consistent with the 'connectedness' hypothesis, bHLH1 in *Ipomoea* evolves more slowly than bHLH2 (Streisfeld and Rausher, 2007). In addition, the *myb* anthocyanin transcription factor *Ipmyb1* evolves faster than either *bHLH* gene (Chang *et al.*, 2005), and the number of other proteins the products its ortholog in *Petunia* interacts with is lower than that of either *bHLH* gene (Kroon, 2004), providing further support for the 'connectedness' hypothesis.

Morning glories and plant–herbivore interactions

The common morning glory, *I. purpurea*, and the ivy leaf morning glory, *I. hederacea*, have become model systems for plant–herbivore evolutionary ecology. Studies in these species have tested fundamental hypotheses about whether insects impose natural selection on plants, costs and benefits of plant defense strategies (including constitutive resistance, induced resistance and tolerance), and the nature of multispecies coevolution (Rausher and Simms, 1989; Rausher *et al.*, 1993; Hougen-Eitzman and Rausher, 1994; Tiffin and Rausher, 1999). Both are annual, widely distributed and easily collected, and fed upon by a wide and taxonomically disparate suite of enemies that leave distinctive patterns of damage (Simms and Rausher, 1989; Stinchcombe and Rausher, 2001).

Early studies by Rausher and Simms (Rausher and Simms, 1989; Simms and Rausher, 1989) provided strong evidence that insects can impose natural selection on plant resistance to damage in *I. purpurea*. Although this finding might seem non-controversial now, at that time, there was serious debate about whether insect populations were either of sufficient density or imposed enough damage to lead to natural selection on resistance traits. In an early use of the Lande and Arnold (1983) framework for estimating selection gradients, Rausher and Simms (1989) showed that there was significant directional selection for increased resistance to herbivores—plants that were more resistant had higher fitness. By including an insecticide treatment, Rausher and Simms (1989) also

showed that plants set more seed and had significantly higher fitness in the absence of insects, and that plants in the insecticide treatment showed no additive genetic variation in fitness and thus were unable to evolve.

Follow-up studies have examined the diversity of defenses in *Ipomoea* (for example, constitutive versus induced defenses; Rausher *et al.*, 1993; Simonsen and Stinchcombe, 2007), and tested whether tradeoffs exist between different modes of defense. One area that has been intensively investigated is whether there is a tradeoff between resistance—which determines the amount of damage a plant suffers—and tolerance—which determines the fitness consequences of damage. Such a tradeoff has been predicted on theoretical grounds, because a plant that is highly resistant (and suffers little damage) would receive no benefit from tolerance but still express the costs (Meijden *et al.*, 1988). Fineblum and Rausher (1995) provided evidence of a genetic tradeoff—in the form of a negative genetic correlation—between resistance and tolerance to apical meristem damage in *I. purpurea*. Using empirical data and theory, they showed how understanding the evolution of resistance required understanding the evolution of tolerance—and vice versa.

Tiffin and Rausher (1999) subsequently examined whether costs of tolerance to apical meristem damage and leaf damage were present in *I. purpurea*, and how selection acted on these traits. They found evidence that both traits exhibited fitness costs—genotypes that were more tolerant to damage had lower fitness in the absence of damage. Tiffin and Rausher (1999) also showed that correlational selection (favoring combinations of traits) was acting on resistance and tolerance, and that natural selection on both traits was likely to fluctuate with herbivore abundances. Collectively, these studies of tolerance to herbivory—which were themselves inspired by a study of tolerance to pathogen damage in *I. purpurea* (Simms and Triplett, 1994)—have provided a model for studying the evolution of resistance and tolerance to other forms of damage (for example, frost: Agrawal *et al.*, 2004; herbicide: Baucom and Mauricio, 2004, 2008, 2010; One important distinction exists between the evolutionary literature and the herbicide resistance literature in the use of tolerance and resistance—in the evolutionary literature, these terms distinguish between the amount of damage and the fitness consequences of damage, whereas in the herbicide resistance literature, they refer to whether a weed has evolved to make the herbicide ineffective. We prefer the former definitions, as they emphasize the different biological processes underlying the traits, whereas the latter approach will necessarily depend on a current population's or species' evolutionary trajectory and allele frequencies, even with the same underlying traits).

A final area of plant–herbivore interactions that has been intensively studied in *Ipomoea* has been multispecies coevolution. Approximately 30 years ago, Janzen (1980) and Fox (1981) suggested that coevolution among suites of interacting species was likely to be qualitatively different than between pairs of species. The resulting distinction between diffuse and pairwise coevolution thus reflects the degree to which ecological complexity—the number and abundance of interacting species—affects the coevolutionary dynamics between a pair of species (Stinchcombe and Rausher, 2001).

Species interactions between *I. hederacea* and *I. purpurea* and their associated competitors and herbivores have been examined in this context. To date, the balance of evidence suggests that diffuse coevolution predominates. For instance, Stinchcombe and Rausher (2001; 2002) showed that natural selection on resistance and tolerance to deer herbivory was dependent on the presence of insect herbivores in *I. hederacea*. Likewise, Tiffin (2002) showed that herbivory in *I. purpurea* had significantly greater negative effects on fitness in the presence of an interspecific competitor. Similarly, Smith and Rausher (2007; 2008a,b) have shown that the presence of *I. purpurea* significantly alters selection in *I. hederacea* floral morphology, and in a way that promotes selfing in *I. hederacea*. One exception to this trend comes from Hougen-Eitzman and Rausher (1994), who found that the presence or absence of tortoise beetles and sweet potato leaf miners, respectively, failed to alter the fitness consequences of damage by the other species. Collectively, however, the balance of data from *Ipomoea* suggests that any coevolution is likely to be diffuse—the community context of plant–herbivore interactions is essential to understand evolutionary and coevolutionary dynamics.

Ipomoea and the evolution of plant–parasite interactions

Research programs on the evolution and ecology of wild plant–pathogen interactions are still relatively new, spurred in large part by the pioneering work of Burdon and colleagues in the 1980s (for example, see Burdon, 1987). Although wild relatives of crops have long been known to possess polymorphism in pathogen resistance (Wahl, 1970; Zimmer and Rehder, 1976), work in the 1980s documented that wild plant populations possess extensive natural genetic variation in resistance to their natural pathogens (Burdon, 1980; Burdon and Marshall, 1981; Harry and Clarke, 1987; Parker, 1988). Because pathogens are expected to generate strong selection on plant resistance, these observations implied that there may be general costs or tradeoffs that could constrain resistance evolution and thereby promote the maintenance of genetic variation (Parker, 1988, 1990). One of the major contributions of *Ipomoea* to plant–pathogen evolutionary studies has come from this line of investigation.

For example, Simms (1993) showed that populations of *I. purpurea* possess both quantitative and qualitative genetic variation in resistance to two of its natural pathogens, *Colletotrichum dematium* and *Coleosporium ipomoeae*, respectively. In field experiments, *I. purpurea* provided some of the first evidence that quantitative resistance to *C. dematium* is genetically correlated to quantitative resistance to an insect herbivore (Simms and Rausher, 1993), although as the authors note, it is not clear if this correlation is sufficiently large to alter insect resistance evolution. Simms and Triplett (1994) further explored how the evolution of quantitative resistance to *C. dematium* might be influenced by the evolution of tolerance, a trait that reduces the negative fitness effects—but not the amount—of disease, and may be negatively correlated with resistance.

More recently, Kniskern and Rausher (2006a) showed that qualitative and nearly complete resistance to

C. ipomoeae is conferred by a single gene, *Rci1*. Polymorphism at this locus was observed in several wild populations, and field experiments revealed a large fitness cost of *Rci1* in some years, which may help to explain persistence of *Rci1* polymorphism in populations where this pathogen can generate strong reductions in plant fitness (Kniskern and Rausher, 2006b; Kniskern and Rausher, 2007). Together, these studies reveal how the evolution of resistance to pathogens may be constrained by a variety of tradeoffs, which, in turn, could shape larger patterns of plant–pathogen coevolution.

Although these studies focused on microevolution, this system provides tantalizing evidence linking microevolution of resistance within species to larger species level patterns of host specificity. Isolates of the oomycete *Albugo ipomoeae-panduratae* and *A. ipomoeae-hardwickii* infect a range of *Ipomoea* species, including *I. nil*, *I. hederacea*, *I. lacunosa* and *I. purpurea*. These isolates exhibit strong patterns of host specialization; strains collected from one host species cannot infect others in reciprocal inoculations (Sato *et al.*, 2009). The ability of *Albugo* to infect *I. purpurea* in Japan is interesting because in wild mixed populations in the Southeastern US, *Albugo* is a common pathogen of *I. hederacea*, but it is never observed on *I. purpurea* (J Kniskern and J Stinchcombe, personal observations), implying that these isolates are similarly specialized, in this case lacking the ability to infect *I. purpurea*. Likewise, strains of another major pathogen of *Ipomoea*, *C. ipomoeae*, also exhibit evidence of host specialization in wild populations of the Southeastern US (T Chappell, personal communication). For example, in controlled growth chamber infections, isolates of *C. ipomoeae* collected from a single plant population were only able to infect 8 of 22 *Ipomoea* species (JM Kniskern and RE Miller, unpublished data), yet many of the uninfected species are known hosts of *C. ipomoeae* in the wild. The genes that confer these patterns of host specialization are poorly characterized, yet the ability to generate interspecific crosses with different pairs of hosts would open the door to genetic analysis of host range factors in *Ipomoea*.

The agricultural relevance of *Ipomoea*

Baker (1974) noted that the same traits that make species good models of adaptation and microevolution—high abundance, fast growth to reproduction and high seed output—are also traits that make for weedy species. Annual morning glories exhibit many of Baker's 'weediness' traits and it is likely that these characteristics have allowed morning glories to become especially noxious in agricultural crops. Morning glories have been listed as 'troublesome' by weed specialists and farmers since the early 1970s; in 1995, morning glory species were considered the first, second and fourth most troublesome weeds of soybean, cotton and peanut in the Southeast USA, respectively (Webster and Coble, 1997). *Ipomoea* species have remained prominent in the weed science literature since that time, highlighting their continued importance to agriculture. Currently, 30 species of morning glory are considered to be weeds in North America by the Weed Science Society of America (<http://www.wssa.net/>).

Morning glory infestations can have severe economic impact: For example, competition between common and

ivy leaf morning glories and row crops such as cotton can reduce yield by as much as 80–88% (Howe and Oliver, 1987; Stoller *et al.*, 1987). Infestations of morning glories cause declines in crop quantity and quality, and also reduce harvesting efficiency, a problem that sometimes leads to complete loss of a crop.

Farmers use various means to control weed infestations, with the most general mechanism being herbicide use. The acceptance and wide spread use of RoundUp Ready technology, in which a crop species is transformed with a gene conferring RoundUp tolerance, has led to skyrocketing use of glyphosate, the active ingredient in the herbicide RoundUp (Dill, 2005). Unfortunately, morning glory species are also notoriously difficult to control with this herbicide, and are becoming more prominent in glyphosate resistant crops (Culpepper, 2006).

Morning glories are not currently considered to be 'resistant' to glyphosate by weed science standards (<http://www.weedscience.org>). When glyphosate is applied, they generally suffer significant leaf loss if not death. However, genetic lines of *I. purpurea* exhibit the ability to re-grow following glyphosate damage and produce progeny, a trait termed 'tolerance' (Baucom and Mauricio, 2004). The presence of genetic variation in glyphosate tolerance, as well as their increased prominence in glyphosate resistant crops, makes *I. purpurea* an exceptional model for the study of herbicide defense evolution. Most examples of herbicide resistance come from cases in which the plant shows a very high level of resistance; this research generally finds resistance to be conferred by mutations in the single, (in)completely dominant gene responsible for the enzyme that interacts with the herbicide (Neve, 2007). In contrast, morning glory's tolerance to RoundUp provides a different model for the evolution of crop weeds. Although the genetics of glyphosate tolerance are currently unknown, it is likely under polygenic control, as tolerance is measured as an aspect of plant fitness following damage, and fitness has been suggested to be the ultimate Fisherian trait (Mauricio, 2001).

The evolutionary dynamics of glyphosate tolerance have recently been investigated in a series of field and greenhouse experiments. Tolerance to glyphosate in *I. purpurea* is genetically variable (Baucom and Mauricio, 2004, 2008) and can potentially respond to selection. Further, tolerance has been shown to provide a fitness benefit—genetic lines that are more tolerant are also more fit in the presence of herbicide, suggesting that selection *via* glyphosate can act to increase the level of tolerance over time (Baucom and Mauricio, 2004). One evolutionary force that might constrain this potential increase in tolerance is a fitness cost—that is, if highly tolerant lines have lower fitness in the absence of glyphosate than less tolerant lines. A fitness cost of glyphosate tolerance has been uncovered in two field experiments, suggesting potential constraints on the evolution of tolerance, and, further, that crop rotations are a valid mechanism of mitigating an increase in the level of tolerance (Baucom and Mauricio, 2004, 2008).

Morning glories have been indicated in 'weed shifts' in response to increased planting of glyphosate resistant crops within the past 10 years. Their prevalence in weed shifts presents the possibility that, in addition to tolerance, they might quickly adapt to glyphosate use through mechanisms of 'ecological defense,' such as

shifts in phenology, seed dormancy or increased growth rate. Baker (1974) hypothesized that the evolutionary synthesis of 'generalist' genotypes across a range of environments could pre-adapt certain species to be highly tolerant of new environments and thus allow them to become weedy. The many infestations of morning glory populations, and species, in agricultural fields presents a unique opportunity to investigate this hypothesis, especially the relative importance of each type of 'ecological defense' trait, and the genetic basis of such traits.

Future work in *Ipomoea*: the next line of investigation

With a rich history of previous ecological investigation, we are now poised to ask questions that will rely on genomic tools. For example, the development of a genetic map and introgression lines would provide the ability to discriminate among several competing hypotheses regarding the evolution of herbivore defense, such as: are genetic correlations among resistance traits generated primarily by pleiotropy or linkage disequilibrium? Is resistance to herbivory determined by a few major effect loci, or several loci of smaller effect? Are the effects of polymorphism in Mendelian traits (flower color, leaf shape: Simms and Bucher, 1996; Campitelli *et al.*, 2008) on herbivory due to the pleiotropic effects of those genes, or closely linked genes? Are molecular signatures of balancing selection detected on genes where classical ecological genetics suggests selection is maintaining stable polymorphisms? Although answering these questions is non-trivial (Stinchcombe and Hoekstra, 2007), they are largely inaccessible with quantitative genetics approaches that have been used to date.

Furthermore, sequence-based analysis of loci putatively involved in adaptation to agricultural regimes would allow us to address such questions as: which loci are involved in herbicide defense, and are the same loci involved in multiple populations? Are the loci underlying herbicide defense the same as those indicated in adaptation to other forms of damage, such that there are 'generalist damage response' loci (photosystem, re-growth, detoxification and so on)? The answers produced by such investigations can be integrated into practical aspects of weed control regimes.

Finally, the use of *Ipomoea* as a model plant–pathogen system, and development of genomic resources for this group, would bolster the current research on economically important plant pathogens. A newly characterized pathogen of *Ipomoea* named *Phytophthora ipomoeae* has recently been discovered in Mexico (Flier *et al.*, 2002; Badillo-Ponce *et al.*, 2004). *P. ipomoeae* is closely related to *P. infestans*, the infamous causal agent of potato blight, while other members of this genus, like *P. capsici*, are devastating pathogens of other Solanaceous crops, in this case pepper (*Capsicum annuum*). In *Ipomoea* and *Solanum*, for example, comparative studies could investigate how evolutionary change at orthologous resistance genes is associated with patterns of pathogen specialization. Knockout and transgenic manipulation of genes identified in this manner could be coupled with the types of studies described above to reveal how host resistance drives pathogen specialization to the point of race formation and eventual speciation.

Morning glory as a model group in ecological genomics
Ecological genomics has been defined as a 'scientific discipline that studies the structure and functioning of a genome with the aim of understanding the relationship between the organism and its biotic and abiotic environments' (Straalen and Roelofs, 2006). The broad goal of understanding the evolutionary processes that both create and maintain genomic and phenotypic diversity is best addressed using species or interfertile groups that exhibit many interesting evolutionarily and ecologically relevant traits, yet are also easy to grow in both the greenhouse and field, have a short generation time and high fecundity—all traits that promote ease of study (Wu *et al.*, 2008). Logistically, *Ipomoea* is an excellent choice for a model in ecological genomics as the generation time of two well-studied members, *I. purpurea* and *I. hederacea*, is approximately 8–12 weeks, and both are amenable to greenhouse and field conditions. Further, as this review has highlighted, *Ipomoea* enjoys a long history of research in 'ecological interactions,' and thus there exists a wealth of information regarding the ecological context of certain traits.

Ipomoea is a predominant group in other plant science fields. A Web of Science search using the term '*Ipomoea*' restricted to titles and abstracts returns >2100 references since 1965, with many of these citations found within the agricultural sciences. Roughly, 30 species of *Ipomoea* are considered noxious weeds in the United States and thus are a focus of weed management studies. On the other side of the agricultural spectrum, *Ipomoea batatas* (sweet potato) is a major agricultural crop that provides 170 million tons of food for human and animal consumption per year (FAO). Further, morning glories are closely related to other agricultural species. The morning glory genus is a member of the Convolvulaceae, which is related to Solanaceous species such as tomato and tobacco—the genomes of which are currently in the process of being sequenced. Interestingly, the genome size of *I. purpurea* is approximately the same as that of tomato, a moderately-sized 980 Mb. Given the range of interest in *Ipomoea*, its history in the literature, its relatedness to other important crop species and its moderately-sized genome, we suggest it is time to fully develop and amplify the genetic and genomic resources for this group. Expanded resources such as a sequenced genome, the ability to transform genetic lines with mutant alleles and extensive genetic linkage maps will allow for continued integration of knowledge about natural environmental forces impacting phenotypic variation and their underlying, causative genetic mechanisms: the basic goal of ecological genomics.

Although genetic and genomic resources exist and are being developed for the above-mentioned relatives of *Ipomoea*, there are currently few resources for morning glories. It is ironic that in a genus in which we have plentiful ecological and quantitative genetic data, for example, on the identity of herbivores, the strength of selection they impose on populations, how they interact with the rest of the community—we have few genomic resources. Genetic and genomic tools are in the process of being developed for this group, but more work is needed. Current genomic resources for morning glory species include a completely sequenced chloroplast genome (*I. purpurea*), a set of ~60 000 expressed sequence tag for *I. nil*, and sequenced transcriptomes

of nine morning glory species—*I. purpurea*, *I. hederacea*, *I. coccinea*, *I. quamoclit*, *I. nil*, *I. pubescens*, *I. lobata*, *I. lindheimeri* and *I. indica*, provided by the Beijing Genomics Institute as part of the 1kp plant transcriptome project (<http://www.onekp.com/project.html>). A highly comprehensive database of transposable elements from the *I. purpurea* genome has been developed from random shotgun library, sequenced using Titanium FLX 454 technology (RS Baucom and JL Bennetzen, unpublished results). These 454 sequences have also been mined for microsatellite repeats, and marker development is currently underway. Different labs maintain populations of inbred and family lines for both *I. purpurea* and *I. hederacea*, and many species of *Ipomoea* are stored as germplasm and are available for public use (R. Miller, USL). Finally, genetic maps are currently in progress for both *I. purpurea* and *I. hederacea* (Baucom and Stinchcombe labs, http://homepages.uc.edu/~baucomra/Baucom_Lab/Home.html; <http://labs.eeb.utoronto.ca/stinchcombe/index.htm>, respectively).

Conclusions

Here, we have highlighted *Ipomoea*'s contribution to studies of mating systems, floral color pathway evolution, plant herbivore and parasite interactions, and *Ipomoea*'s importance to agriculture. Although we have presented these specific areas, we stress that there are many other lines of research that utilize *Ipomoea* species, such as studies of plant ecophysiology, comparative genomics and the evolutionary biology of transposable elements, among others. Many diverse questions can be addressed using morning glories—their ubiquity in nature, their fast, weed-like growth, and the many forms they exhibit both across and within species can equip researchers with a powerful study system. Given the historical and continued interest in this group of plants, as well as the incredible range and diversity of evolutionary scenarios this group present, it is ironic that the term 'morning glory' has symbolized an ephemeral nature, as focus and interest in these plants is unlikely to fade anytime soon.

Conflict of interest

The authors declare no conflict of interest.

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