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Rapid evolution to host plant resistance by an invasive herbivore: soybean aphid (*Aphis glycines*) virulence in North America to aphid resistant cultivars

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Introduction

Rapid evolution by insects to resistant crop cultivars is a concern for applied entomologists, who seek to expand the tools available for managing herbivores. Efforts to prevent this evolution drives the development of Insect Resistance Management (IRM) plans for crop pests [1], which require a greater understanding of plant–herbivore interactions to produce effective plans for sustained use of host plant resistance. Efforts to delay resistance includes using highly lethal toxins (i.e. a high dose), combining multiple resistance traits in one cultivar (i.e. pyramids), and using susceptible plants (e.g. a refuge) within or near plantings of the resistant crop. To date, IRM plans have successfully prevented the frequency of resistant insect pests reaching levels that would allow populations to overcoming crops bred to be resistant to them, but failures have occurred, often when an IRM plan is not fully implemented [2]. Even if fully implemented, theoretical models suggest that IRM plans for asexually-reproducing insects (e.g. aphids) may not limit the frequency of resistance to provide sustainable use of a pest-resistant cultivar [3•]. This is particularly worrisome as an invasive aphid (*Aphis glycines* Matsumura) that reproduces asexually on soybean is challenging US agriculture [4]. To manage this pest with tools beyond insecticides, there is a need to ensure that the financial effort needed to develop alternatives, like aphid-resistant soybeans, will result in a tool that can be used beyond a limited number of growing seasons (currently estimated as <10 insect generations per theoretical predictions [3•]). Here, we discuss empirical evidence that suggests interactions between an aphid and plant, along with associated natural enemies, may prevent increases in virulence to aphid-resistant soybeans. Expanding upon existing IRM models with more system-specific data suggests increased durability of aphid-resistant soybeans beyond what is predicted from general models. Q3

Thirteen years after it was noted [5] that entire guilds of herbivores, like phloem-feeders, were missing from soybean fields in the western hemisphere, *A. glycines* invaded North America [4]. This invasive insect is the leading pest in the main soybean producing region of the US, being the only aphid in North America to produce large, persistent colonies on soybeans resulting in yield losses as high as 40% [6]. A community of endemic natural enemies commonly found in soybean fields [7] are a source of significant mortality to *A. glycines* but an inconsistent source of biological control [8]. Since 2001, frequent outbreaks of *A. glycines* are responsible for a 140% increase in foliar-applied insecticide use on soybeans, counter to trends observed for other major field crops in the US like corn and cotton [9••].

In an attempt to offer an alternative management tactic, soybean breeders in the US discovered genes that confer resistance to *A. glycines* (referred to as *Rag*-genes) in soybean germplasm [10]. Many of the terms used to describe features of an aphid-plant system that involves host plant resistance to herbivory are defined in Table 1. Commercial cultivars containing *Rag1* were first sold in 2010, yet adoption was limited, in part because of survival by virulent *A. glycines* on resistant cultivars occasionally at economically damaging levels [11]. Additional efforts by breeders [12] produced soybean cultivars with a pyramid of more than one *Rag* gene (i.e. *Rag1* + *Rag2*), resulting in protection from economic levels of *A. glycines* without the use of seed-applied and foliar-applied insecticides [13•]. Current availability of a *Rag1* + *Rag2* cultivar is limited to a company that provides non-genetically modified (GM) cultivars. These cultivars are used mostly for organic soybean production, which is a small percentage of the total amount of soybean grown in the US. Such a limited usage would likely not contribute to selection pressure for virulence.

Even though a *Rag*-pyramid did not allow large populations of *A. glycines* to develop and reduce soybean yield, plants were not free of aphids. Additional virulent biotypes were discovered in the US, including a biotype capable of surviving on a *Rag1* + *Rag2* pyramid [14] (i.e.

Table 1

Glossary of terms used to describe components of aphid-plant interactions.

Rag-genes	Genes in soybean germplasm that confer resistance to *Aphis glycines*, the soybean aphid, resulting in phenotypes that produce both antibiosis and antixenosis. The name is an acronym of Resistance *Aphis glycines*.
Biotype	Subpopulations of herbivore species that vary in their capacity to survive on differing cultivars of a host plant. Subpopulations of *A. glycines* have been classified as different biotypes based on their ability to survive on soybean cultivars containing vary types and number of *Rag* genes.
Virulence	A subpopulation of an insect herbivore capable of surviving on a plant species with genetic variation in its value as a host for that species. For example, biotype-4 of *A. glycines* survives on soybean plants with multiple Rag-genes. Biotype-4 is considered virulent to *Rag* 1 and *Rag* 2. Virulence by a biotype to a plant trait is analogous to a subpopulation of an insect being resistant to an insecticide.
Avirulence	A subpopulation of an insect herbivore incapable of surviving on a plant species with genetic variation resulting in resistance to that insect species. For example, biotype-1 of *A. glycines* cannot survive on soybean plants with any *Rag* genes. Biotype-1 is considered avirulent to *Rag* 1, *Rag* 2, *Rag* 3, and *Rag* 4. Avirulence is analogous to a subpopulation of an insect being susceptible to an insecticide.
Induced susceptibility	A general phenomenon in which a plant is physiologically altered by the feeding of an insect herbivore, resulting in an improvement in the fitness of conspecific's in a subsequent colonization. This susceptibility can be due to feeding by conspecifics with the same (i.e. feeding facilitation) or differing genotypes (i.e. obviation of resistance), in which the initial colonization is by a virulent biotype.
Feeding facilitation	Insect herbivores can have a systemic impact on host plants such that the physiology is altered resulting in the plant being a better host for the herbivore. This phenomenon has been observed with spider mites [23], aphid species [21,24,27]. These examples of improvement in the herbivore's fitness on the colonized plant appears to be density dependent but not limited to biotypes or subpopulations within a given species.
Obviation of resistance	Capacity for subpopulations of insects to overcome resistance to herbivory that is specific to a species. For example, virulent biotypes of *A. glyinces* are capable of obviating *Rag*-resistance in soybeans such that avirulent biotypes can survive on these aphid-resistant cultivars. Similar examples have been observed with a beetle [25], other aphid species [27,28] and a fly [29]. Improvement in the herbivore's fitness may be density dependent and shared with avirulent conspecifics, but producing this obviation is limited to biotypes virulent to a resistant trait.

Biotype 4). Occurrence of virulent biotypes was reported in North America before commercial use of *Rag*-genes [15] and the aforementioned pyramid, with observations documented from multiple locations within the US [16]. This is remarkable given evidence that like most invasive species, *A. glycines* passed through a genetic bottleneck [17] when it was transported from Asia (likely northern China) to North America. Explanations for how virulent biotypes of *A. glycines* established and persist in the US have to also account for limited selection pressure, as *Rag*-genes have not been widely or persistently used in commercial soybean production. A lack of genetic distinction among biotypes found in its expanded range suggests that the occurrence of virulence on aphid resistant soybeans in the US is either due to a complex of genes that are widely distributed in the aphids expanded range or has a non-genetic (i.e. epigenetic) basis [18]. The later explanation would complicate the study of virulence in *A. glycines* as biotypes are currently defined based on their phenotype (a phenotype based solely on the aphids capacity to feed on Rag-containing soybeans) and not their genotype. If this later explanation is possible than it is unclear to what extent field observations of *A. glycines* on a *Rag1* + *Rag2* pyramid plants indicate the presence of virulent biotypes.

Induced susceptibility — an alternative explanation for the appearance of virulent aphids on resistant plants

We explored a series of hypotheses to account for alternative explanations for the occurrence of persistent, often large (i.e. above economic population levels) populations of *A. glycines* on *Rag*-containing soybeans. Our overall hypothesis was that feeding by the aphid alters the quality of the soybean plant such that it becomes a better host, increasing the aphid's intrinsic growth rate. In general, aphids are strongly nitrogen limited and the quality of a plant as a host tracks with nitrogen availability in phloem. For example, aphid intrinsic rate of growth is highest during periods of vegetative growth and senescence [19] (i.e. periods when nitrogen is most available in phloem). Nitrogen availability in soybeans can also be affected by stress, in the form of limited nutrient availability in soils, resulting in significant changes in the intrinsic rate of growth of *A. glycines* [20]. When soil nutrients are controlled, direct feeding by *A. glycines* is correlated with changes in nitrogen availability in the phloem [21], suggesting that the stress of aphid herbivory itself alters soybean physiology resulting in a more nutritious host. The expression 'induced susceptibility' has been used to describe when a plant is altered by insect herbivore in such a way that it is improved as a host [22]. Such changes have been observed on plants both susceptible [23–27] and resistant [28,29] to a specific herbivore. We tested if the susceptibility of soybean plants to *A. glycines* could be altered by its herbivory alone. Since avirulent and virulent biotypes of *A. glycines* have been captured in the same locations within the US [18], there is the potential that both can co-occur on the same plant. To what extent such facilitation by conspecifics results in improved performance of an avirulent biotype on a resistant plant was a subhypothesis.

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