



Impact of nitrogen fixing and plant growth-promoting bacteria on a phloem-feeding soybean herbivore



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ABSTRACT

In soybean (*Glycine max* L.) production systems, growers often inoculate seeds with the symbiotic N-fixing species *Bradyrhizobium japonicum* along with other bacterial species or chemicals intended to enhance plant growth and yield. However, microbes associated with plant roots can also impact the biology of above-ground insect herbivores through influencing various aspects of plant physiology, with effects dependent on the bacterial species. Because rhizobial seed inoculants can potentially affect densities of soybean herbivores, we investigated the performance of phloem-feeding soybean aphids (*Aphis glycines* Matsumura) on: (1) soybeans receiving one of four commercially available rhizobial seed inoculants, (2) non-inoculated soybeans associated with existing soil bacteria, or (3) non-inoculated soybeans receiving high levels of fertilizer to suppress N-fixation while still providing adequate N as nitrate. We quantified effects of inoculants and aphid presence on parameters associated with plant growth, N-fixation, and foliar N levels, and explored relationships between aphid densities and these plant parameters. Regardless of inoculation treatment, aphid presence negatively affected plant biomass, pod density, and total N concentration in aerial plant tissues, although, effects on the concentration of ureide N (primary products of N-fixation) were not significant. Inoculant identity significantly impacted aphid populations in both short- (1 week) and longer-term experiments (2 months), with pest densities negatively related to the number of root nodules per plant. This research indicates that nodulation status of soybeans can influence above-ground herbivores.

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1. Introduction

Plants often form close mutualistic associations with soil microorganisms such as bacteria and fungi, with the relationship between legumes (Fabaceae) and nitrogen (N) fixing bacteria being one of the most well known. In this case, both types of organisms directly benefit from the relationship, however, there can be indirect effects on organisms at different trophic levels, such as on herbivorous insects (Dean et al., 2009; Thamer et al., 2010; Ballhorn et al., 2013). Root-associated bacteria (i.e., rhizobia) and mycorrhizal fungi can aid plants by increasing resistance to above-ground herbivores via defensive compounds; however, concomitant increases in plant growth and nutrition due to these

associations may make plants more susceptible to other herbivores (Koricheva et al., 2009; Pineda et al., 2010).

Commercial soybean (*Glycine max* L.) production requires less N input than non-leguminous crops due to the plant's ability to obtain biologically fixed N via a symbiotic relationship with *Bradyrhizobium japonicum* (Bradyrhizobiaceae), a bacterial species in a group of N-fixing taxa associated with legumes collectively referred to as rhizobia (van Rhijn and Vanderleyden, 1995). The bacteria are located within root nodules and convert atmospheric N₂ into nitrogenous compounds called ureides (Schubert, 1986). In general, ureide N is correlated with N-fixation (van Berkum et al., 1985; Schubert, 1986). Several factors can impact the strength of rhizobial-plant associations and subsequent nodulation and N-fixation rates, most notably soil N (e.g., nitrate) levels (Streeter and Wong, 1988). When a soil contains adequate N, either from organic matter or synthetic fertilizer, a plant will use these sources before associating with rhizobia (Evans, 1982; Ohshima et al., 2009).

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The source of N used by soybeans (from fertilization or N-fixation) can impact the identity and concentration of nitrogenous compounds within plant tissues (Pate, 1980; McNeil and LaRue, 1984), with the total N within xylem sap of nodulated soybeans consisting of 60–95% ureides (McClure and Israel, 1979). The other major form of N translocated from roots to the shoots is asparagine (ASN), which is an amino acid present within the xylem, regardless of whether the plants obtain N from N-fixation or fertilizer, although more of this amino acid results from the latter scenario (Streeter, 1972; McClure and Israel, 1979; Schubert, 1986; Shelp and Da Silva, 1990).

Rhizobia are an integral part of the soil microbial community and can remain viable in soil for years, even when their legume host is not present (Bottomley, 1992). However, because the most suitable species may not occur in high densities, many soybean growers use commercially available rhizobial seed inoculants to increase N-fixation and boost yield (Bottomley, 1992; Keyser and Li, 1992). These commercial inoculants, typically applied to seeds before planting, contain *B. japonicum*, but often have additional components intended to increase yield (e.g., other biological organisms or growth-promoting factors). The other chemical and biotic components in these inoculants may affect plant physiology in various ways, including by enhancing seedling emergence, root nodulation, N-fixation, and plant growth (Dénarié, Dobbelaere et al. et al., 1996; Dénarié, Dobbelaere et al. et al., 1996; Dénarié, Dobbelaere et al., 2003; Dénarié, Dobbelaere et al., 2003; Cassán et al., 2009; Rodríguez-Navarro et al., 2011; Sindhu et al., 2010).

Rhizobial species identity, root nodulation, and N-fixation impact the behavior and biology of above-ground herbivorous arthropods, including those that feed on legumes (Wilson and Stinner, 1984; Dean et al., 2009; Kempel et al., 2009; Thamer et al., 2011; Katayama et al., 2011a). In addition, in some legume systems, rhizobia can alter induced plant defenses, i.e., the production of volatile organic compounds associated with herbivore plant preference (Ballhorn et al., 2013). Effects of rhizobia on herbivores may depend on the latter's feeding habit, as chewing herbivores seem to be affected to a greater degree than sucking herbivores, such as phloem-feeding aphids (Kempel et al., 2009; Katayama et al., 2011a). Although there is mixed evidence for effects of rhizobia on aphids (Kempel et al., 2009; Katayama et al., 2011a), one study indicated that results might depend on the species of rhizobia associating with the plant (naturally occurring versus commercially available; Dean et al., 2009). Thus, it is possible that specific inoculants may differentially affect aphids that feed on legumes, including soybean aphids (Hemiptera: Aphididae: *Aphis glycines* Matsumura).

Soybean aphids overwinter on buckthorn (Rhamnaceae: *Rhamnus*), and in the spring, winged females migrate to soybean, the preferred summer (secondary) host on which females reproduce asexually and give birth to live nymphs (Ragsdale et al., 2004). These reproductive strategies facilitate rapid aphid population growth, and densities can quickly become high enough to surpass economic thresholds (Ragsdale et al., 2007). Several plant factors and aphid behaviors are involved in host plant selection and acceptance (reviewed by Powell et al., 2006), including visual, olfactory, and gustatory cues.

To investigate the impact of rhizobial seed inoculants on soybean aphid establishment and reproduction on soybean plants, we conducted greenhouse and field studies with six treatments: four different commercially available inoculants, a non-inoculated control in which plants associated with existing soil rhizobia, and a high N treatment, in which additional fertilizer was used to suppress nodulation and N-fixation while still providing adequate N (as nitrate) for plant growth. Because aphid feeding can impact plant growth and physiology, in field experiments two cages were erected in each plot (with and without aphids) in order to explore main and interactive effects of inoculant treatments and aphids on plant parameters associated with growth, foliar N levels, and

reliance on N-fixation. We also used correlation analysis and multiple linear regression to assess relationships between aphid density and various plant parameters related to plant growth, N-fixation and foliar N content, in order to explore what parameters were the most important drivers of aphid populations.

2. Methods

2.1. Field experiment

2.1.1. Experimental design

Field experiments were conducted in 2010 and 2011 in Carrington, ND at the North Dakota State University (NDSU) Research and Extension Center. The exact location of experimental plots (1.5 × 7.6 m) within the research farm changed between years. Within a replicate, plots were separated by same-size soybean buffer plots, with replicates separated by 1.5 m fallow strips. In late June of both years, ammonium sulfate (2.3 l/ha) was mixed with glyphosate (3.5 l/ha) and applied to plots for weed control. Plots were not sprayed with any other chemicals for the duration of the experiment.

There were six experimental treatments: CNTL (a non-inoculated control), N (a non-inoculated high nitrogen treatment), and four types of commercially available seed inoculants, B (*B. japonicum*, N-DURE, peat formulation, INTX Microbials, LLC, Kentland, IN), B+D [*B. japonicum* + *Delftia acidovorans* (Comamonadaceae), BioBoost[®] Plus, liquid formulation, Brett Young, Winnipeg, MB, Canada], B+L [*B. japonicum* + lipo-chitooligosaccharides, Optimize[®] 400, liquid formulation, Novozymes, Brookfield, WI] and B+A [*B. japonicum* + *Azospirillum brasilense* (Rhodospirillaceae), PRIMO, liquid formulation, INTX Microbials].

Azospirillum brasilense is a known nitrogen fixer and research has indicated it can enhance the effectiveness of *B. japonicum* (Groppa et al., 1998) and increase nodulation and N-fixation of several legumes (Dobbelaere et al., 2003). In addition, some *A. brasilense* strains can produce phytohormones and enhance growth of soybean seedlings (Cassán et al., 2009). *Delftia* spp. (syn. *Comamonas*) are known as bioremediators of environmental pollutants (Ubalde et al., 2012). *Delftia acidovorans* is considered a plant growth promoter and can produce phytohormones, such as indole-3-acetic acid (Barazani and Friedman, 1999), and protect grape roots from harmful nematodes (Aballay et al., 2013). Related species have also been shown to fix N (Han et al., 2005) and increase the effects of some legume inoculants (Morel et al., 2011). Lipo-chitooligosaccharides, or Nod factors, are bacteria-produced plant signaling molecules essential to establishing the symbiotic relationship between N-fixing bacteria and legume roots (Dénarié et al., 1996). They have been associated with plant growth promotion, including enhanced germination and root growth of soybean (Souleimanov et al., 2002; Prithiviraj et al., 2003) and protection against root pathogens (Duzan et al., 2005).

In 2010, each treatment was replicated six times, while in 2011 there were only five replicates of each treatment. Treatments were randomly assigned to plots within replicates. Soybean seeds (indeterminate, Dairyland 401RR, Dow AgroSciences, Indianapolis, IN) were inoculated according to package instructions (ml product kg⁻¹ seed): B, 74 per 23 (2 × 10⁸ viable *B. japonicum* cells g⁻¹); B+D, 104 per 45 (2 × 10⁹ viable *B. japonicum* and 1 × 10⁷ *D. acidovorans* g⁻¹); B+L, 83 per 45 (includes liquid additive, 5 × 10⁹ viable *B. japonicum* cells g⁻¹, 2 × 10⁻⁷ % lipo-chitooligosaccharide); B+A, 125 per 45 (includes liquid additive, 3 × 10⁹ viable *B. japonicum* cells and 1 × 10⁸ *A. brasilense* g⁻¹). Seeds were planted on 20 May 2010 and 2 June 2011 using a Hege 1000 research plot planter at a rate of approx. 543,630 viable seeds ha⁻¹, with 17.8 cm between-row and 10.4 cm within-row seed spacing. For high N plots, 67.3 kg N fertilizer ha⁻¹ was applied shortly after planting by

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