**ABSTRACT.** Adults of *Sitona lineatus* (pea leaf weevil, PLW) feed on foliage of several Fabaceae species but larvae prefer to feed on nodules of *Pisum sativum* L. and *Vicia faba* L. Indirectly, through their feeding on rhizobia, weevils can reduce soil and plant available nitrogen (N). However, initial soil N can reduce nodulation and damage by the weevil and reduce control requirements. Understanding these interactions is necessary to make integrated pest management recommendations for PLW. We conducted a greenhouse study to quantify nodulation, soil and plant N content, and nodule damage by weevil larvae in relation to soil N amendment with urea, thiamethoxam insecticide seed coating and crop stage. PLWs reduced the number of older tumescent (multilobed) nodules and thiamethoxam addition increased them regardless of other factors. Nitrogen amendment significantly increased soil available N (>99% nitrate) as expected and PLW presence was associated with significantly lower levels of soil N. PLW decreased plant N content at early flower and thiamethoxam increased it, particularly at late flower. The study illustrated the complexity of interactions that determine insect herbivory effects on plant and soil nutrition for invertebrates that feed on N-fixing root nodules. We conclude that effects of PLW on nodulation and subsequent effects on plant nitrogen are more pronounced during the early growth stages of the plant. This suggests the importance of timing of PLW infestation and may explain the lack of yield depression in relation to this pest observed in many field studies. Also, pea crops in soils with high levels of soil N are unlikely to be affected by this herbivore and should not require insecticide inputs.

**Key Words:** N-fixation, Herbivory, Nodulation, Rhizobium, Sitona

In nitrogen-fixing Fabaceae, nodulation is influenced by soil nitrogen content and invertebrate herbivory, among other factors. For example, under conditions of high soil nitrogen, pea plants (*Pisum sativum* L.) produce fewer nodules relative to those under nitrogen deficient conditions (Vankosky et al. 2011a) or have a delayed peak in nodulation (Gibson and Harper 1985). A similar pattern of high nodulation under low N conditions was reported for *Mimosa pigra* L. seedlings (McIntyre et al. 2007). Feeding by specialized or generalist herbivores can affect plant nutrition and residual soil fertility. In turn, the soil fauna is influenced directly by nutrient fluctuations in the soil or indirectly through bottom-up trophic cascades (Knight et al. 2005). Techau et al. (2004) showed that high levels of simulated herbivory to above-ground *P. sativum* in combination with phosphate deficiency increased arbuscular mychorrhizal colonization and populations of bacteriophagous nematodes. However, rhizobia were only stimulated by addition of phosphate.

Broad nosed weevils (*Sitona* spp.) feed primarily on the foliage of several legumes and to a lesser extent on nonlegumes as adults (Jackson 1920, Greib and Kleingauf 1977), but their larvae specialize on root nodules of a few species (Goldson et al. 1987, Vankosky et al. 2009). Adults of *S. lineatus* maximize their fertility only on *P. sativum* and *Vicia faba* L. (Schotzko and O’Keeffe 1986) and the larvae feed on nodules of these hosts (George 1962, Fisher and O’Keeffe 1979, Vankosky et al. 2011a). For *S. lineatus* in peas, it is generally accepted that yield losses result primarily from larval feeding on root nodules and not from adult defoliation (George et al. 1962, Lee and Upton 1992, Lohaus and Vidal 2010, Vankosky et al. 2011b), hence making larvae the target of pest control actions (Seidingelanz et al. 2010, Cárcamo et al. 2012). Few studies have attempted to distinguish the effects of adult and larval feeding on pea yield. George (1962) found no significant differences in nitrogen contents of pea seeds from plants subjected to artificial defoliation up to 50% during the seedling stage, which is considered an extreme value for most field conditions. Williams et al. (1995) conducted a field cage study but stated that some oviposition, and potential larval feeding, may have confounded adult feeding damage. Nevertheless, these authors also reported no significant yield differences associated with various levels of defoliation by adults. Both of these studies, however, noted a nonsignificant trend of lower yield from plants with higher defoliation compared with the controls without adults or lower levels of defoliation.

The potential consequences to nitrogen fixation from the interactions among soil fertility, the plant host and the herbivore have been explored under field, and to a lesser extent, under controlled conditions, but have yielded mixed results. El-Dessouki (1971) reported inconsistent effects of *S. lineatus* larvae on nitrogen content of *P. sativum* and *V. faba* in pot experiments. Jensen et al. (1989) showed a reduction of nitrogen fixation rates in pea plants subjected to female herbivory and egg laying compared with male feeding or controls without weevils. Also, they reported increases in N fixation and crop yield when furathiocarb or nitrogen was applied at seeding in a field study. These authors also attempted to isolate the role of weevil larvae that feed directly on nodules; however, that portion of the study failed due to poor egg viability. In an on-farm descriptive field study of organic peas, Corre-Hellou and Crozat (2005) reported a substantial decrease in the proportion of nitrogen derived from fixation and the nitrogen status of the plants that exhibited increasing levels of foliage damage by the weevils; weed abundance also affected these parameters. More recently, under more controlled plot and/or cage experiments, Lohaus and Vidal (2010) and Vankosky et al. (2011a,b) also have explored effects of *S. lineatus* on yield and plant nitrogen. Both research teams concurred that increasing weevil density in cage studies or foliage damage did not appear to have a consistent effect on crop yield or nitrogen content of the seed (all studies) or soil nitrogen balance postharvest (Lohaus and Vidal 2010). They speculated that intraspecific competition among weevil larvae likely masked density effects on host plants, and suggested that other environmental
factors, such as soil moisture, influence nodulation and nitrogen dynamics.

In the southern Prairie Provinces of Canada (Alberta and Saskatchewan), the pea leaf weevil (PLW) continues to expand its range from west to east (Olfert et al. 2012) and growers are increasingly applying insecticides to their pea or faba bean crops in response to visible foliage damage and the potential of yield losses. In some cases, growers are no longer planting peas because of the pest concern or considering control actions. The primary objectives of the present study were to quantify, under controlled greenhouse conditions, plant nitrogen content and residual soil nitrogen at two plant stages (early and late flower) and nodulation in relation to (1) presence of PLW larvae, (2) high level of nitrogen soil amendment at seeding, (3) insecticide seed treatment, and (4) interactions of these factors and crop stage.

Materials and Methods

Insect Stock. Adults used to obtain eggs for this study were collected from 17 to 24 Aug. 2009 from a cage study used to assess weevil density effects on field pea yield, near Vauxhall, Alberta (Canada). No insecticides were used in that study (Vankosky et al. 2011a). In the laboratory, adults were fed alfalfa foliage ad libitum, and placed at 10 °C and 12:12 (L:D) h, and ambient relative humidity around 30%. A single pea seed was placed in the middle of each pot with two rows of preweighed ESN pellets buried at a depth of 2 cm beside the seed. A water tube was inserted near the corner of each pot to allow automated watering in pulses lasting 5 s every 3 min for as many cycles as required. Water requirements were manually determined by feeling the outside of the pot for moisture depth, and the automatic system was started. This method resulted in no visible runoff and no leaching of nitrogen; the amount of water added was estimated by inserting one water tube from each of the five watering lines into a 2 liters beaker with a plastic lid. The water volume was measured three times per week. Soil nitrate and ammonium were estimated at early flower (47 d after planting) using Plant Root Simulator (PRS) cation/anion probes (Western Ag Innovations Inc., www.westernag.ca) placed in five pots of each treatment 9 d after planting—the day prior to the addition of the PLW eggs. The PRS probes remained in the soil until the early flower assessment. Total plant nitrogen content was measured at early flower and at late flower (57 d after planting) using the Dumas method on the Carlo-Erba NA 2100 Elemental analyzer (Carlo Erba Strumentazione, Milan, Italy). At both sampling dates, roots from each plant were washed carefully and the intact plants were stored at 5 °C in darkness for a maximum of 14 d before all nodules were counted and characterized with regard to their form (tumescent or simple) and whether damaged by the weevil. Storing nodules under these conditions does not impede their accurate assessment (Cárucamo et al. 2012). The physiological status of the nodule in terms of expression of leghaemoglobin, was also determined by its color (i.e., pink or not). Nodules were excised from the roots during assessment, dried at 55 °C and then weighed using an analytical balance (Denver Instrument SI 114, Denver Instruments, www.denverinstrument.com). Plant material was dried at 55 °C and ground using a Cyclone Mill 0.5 mm screen (UDY Corp., www.udyone.com).

Statistical Analysis. Data collected during both crop stages, such as nodule counts and nitrogen plant content were analyzed as a split-plot mixed ANOVA using the Proc Mixed of SAS (version 9.2) with crop stage, weevil presence, urea amendment, thiamethoxam coating and their interactions as fixed factors and the interaction of replicate by crop stage as the random factor. Nitrogen content was calculated by multiplying the plant tissue concentration by the total plant dry mass and analyzed, after arc-sine transformation, as a split plot to assess sampling stage effects and explore interactions with the other factors manipulated (soil nitrogen and insecticide). The Proc Univariate in SAS was used to inspect the data for normality and presence of outliers, which were removed before analysis. To assess treatment effects on PLW abundance or nodule damage, treatments without weevils were removed to avoid zero values.

Results

The number of PLW of all stages collected at late flower were insufficient for statistical analysis probably due to completion of development and escaping the pot; therefore, only those collected during the early flower stage were analyzed. Pots with urea soil amendment had significantly fewer weevils than those without it (Fig. 1; F1,12 = 12.75, P = 0.0038). There were no other significant main effects or interactions.

Total nodules per plant or the number that appeared physiologically active by their pink appearance or those damaged by the weevil were not affected significantly by any treatment (Table 1). However, older tumescent (multilobed) nodules were significantly more numerous in plants grown from insecticide treated seed relative to plants grown from untreated seed (22.35 vs. 17.83, respectively, P < 0.05). Furthermore, weevil feeding reduced the number of these older nodules per plant.
Nitrogen treatment effect: \( F_{1,12} = 12.75, P = 0.0038 \).

(mans for pots with and without weevils: 18.0 and 22.15, respectively, \( P < 0.05 \), Table 1); there were no interactions among any factors. Nodule weight followed an opposite pattern to that observed for tumescent nodule counts: presence of weevils significantly increased total nodule weight (0.12 vs. 0.10 mg, \( P = 0.011 \)).

The urea soil amendment and presence of PLW influenced soil N (Fig. 2). Pots with urea amendment, as expected, had more available N (trapped in the root simulator membranes) than those without it (\( F_{1,24} = 15.18, P = 0.0007 \)). Adding PLW eggs to pots decreased soil N available to seedlings compared with controls without weevil eggs added (Fig. 2; \( F_{1,24} = 19.29, P = 0.0002 \)). Furthermore, there was a significant interaction between weevil presence and urea amendment (\( F_{1,24} = 7.72, P = 0.0104 \)). Urea amendment significantly increased available soil N, only when weevils were absent.

As anticipated from the higher biomass of plants at late flower than early flower, nitrogen content was also higher in these plants (Fig. 3). Plants grown from thiamethoxam treated seed, accumulated consistently more nitrogen than those from untreated seed (\( F_{1,56} = 9.6, P = 0.003 \)) but there were no interactions among factors. Analysis by sampling date showed that the difference between insecticide treatments was only significant at the late flower stage (\( F_{1,28} = 6.73, P = 0.015 \)). However, PLW presence significantly reduced plant N content only at the early flower stage (\( F_{1,28} = 4.79, P = 0.037 \)). No interactions among any factors were observed.

### Discussion

Interactions among herbivores, nitrogen fixing symbionts and their host plants can lead to very complex interactions that vary with crop stage and soil fertility. The consequences of these interactions may influence crop yield and sometimes require pest control intervention to reduce economic losses. The main objective of this greenhouse study was to improve our understanding of these types of complex interactions involving a recent invasive insect pest of field peas in the Canadian Prairies—PLW. We manipulated PLW larvae, nitrogen soil amendment in the form or urea (Ecologically Smart Nitrogen pellets) and thiamethoxam seed treatment insecticide and measured a number of biologically and chemically relevant parameters at early flower and late flower in field peas. Previous field and laboratory studies have suggested effects on parameters such as nodule formation, nitrogen in the soil and yield, but results have been inconsistent or have not isolated immature weevil effects. Under field conditions, both adult and larval
damage occur, however, adult damage is most critical during the early
seedling stage (2n node) when they can consume up to 11% of the area
(Cárcamo et al. 2012), but pea plants do not suffer significant yield loss
even when 15–50% of the stipule area is consumed (George et al. 1962, Williams et al. 1995). Therefore, it is generally accepted that
plants can compensate for moderate levels of defoliation inflicted by
adults so that most studies focus on mitigation of larval damage
(George 1962, Lee and Upton 1992, Lohaus and Vidal 2010, Vankosky et al. 2011a,b, Cárcamo et al. 2012).

In our study, weevil effects on plant nitrogen content were limited to
the early flower stage and it is consistent with the finding that weevils
only had a significant negative effect on the number of older tumescent
nodules. It appears that as the plant matures, the negative impacts of
weevil feeding on nodules decreases. This is consistent with our finding
that weevil larvae had completed their development during the early
flower stage of the plant. This made it difficult to find sufficient individ-
uals at late flower for analysis. Therefore, weevil larvae were no longer
actively feeding and destroying root nodules at later growth stages.
Also, as mature nodules senesce, younger nodules continue to fix N
and compensate for the loss of older nodules. In a greenhouse study,
Groten et al. (2005) observed decreasing N fixation (nitrogenase
enzyme activity) in nodules during the sampling period that started 3
wk after planting and ended 11 wk after planting. To our knowledge,
our study is the first report incorporating a time component in the meas-
urement of nitrogen plant dynamics in relation to weevil feeding. Our
findings can help explain results from field studies that have measured
pea protein content in seed and have generally found no effects of either
weevil or thiamethoxam (Vankosky et al. 2011a,b). Furthermore, we
hypothesize that relative to P. sativum, V. faba should be able to better
compensate for S. lineatus feeding damage because of its longer N-fixa-
tion duration that extends into seed maturity (Buttery and Gibson 1990).

Coating seed with thiamethoxam insecticide significantly affected
plant N accumulation at the late flower stage. This chemical has been
shown to directly enhance nodulation in pea plants (Seidenglanz et al.
2010; Vankosky et al. 2011b) as observed for counts of older tumescent
nodules in the present study. In our current study, thiamethoxam did not
interact with weevil herbivory although it is known to kill ~50% of
weevil larva (Cárcamo et al. 2012). However, increased nodulation
could be a direct effect of the chemical or an indirect effect of the chem-
ical killing the weevil larvae.

Residual soil nitrogen during the flower stage when plants were
sampled destructively was affected by PLW larval feeding and the ini-
tial N input in the form of urea. In the absence of weevils, addition of
urea created a large pool of residual nitrogen of almost 100 μg, almost
twice as much compared with the pots without the urea amendment.
Adding weevils reduced the pool in the amended treatment by about
half, but only by ~20% in the treatment without urea amendment.
These results suggest that when weevil larvae were feeding on the plant
below ground, the plant had to rely more heavily on the soil nitrogen to
make up for the loss of nitrogen fixed by bacteria. This is consistent
with the studies that reported decreases in N-fixation rates (Jensen et al.
1989), or N proportion derived from fixation (Corre-Hellou and Crozat
2005) associated with PLW presence or foliage damage levels in their
laboratory and field studies, respectively. In our study, the total number
of weevils retrieved at the end of the experiment (early and late flower),
was lower in the pots that had urea amendment than in those without it.
These results lend further support to the hypothesis of density inde-
pendent effects of PLW on plant processes (Lohaus and Vidal 2010;
Vankosky et al. 2011a,b).

Linking nodule parameters to nitrogen dynamics, however, remains
a challenge even in controlled studies. Of all the nodule parameters
measured, only the number of older tumescent nodules responded to
the treatments in a predictable manner in our study and in agreements
with the field results by Vankosky et al. (2011b). These nodules were
the dominant type and are large with multiple lobes compared with the
single more spherical younger nodules. Pea nodules are initially spheri-
cal when the plants are ~3 wk old and they develop branched structures
at 6–11 wk (Groten et al. 2005). Our results for overall nodule weight
per plant contradicted the pattern observed for the abundance of tumes-
cent nodules. Total nodule weight was higher in plants with weevils
than those without weevils. Tumescent nodules lose dry matter as they
change from a carbon sink to a source (Van de Velde et al. 2006) and
could be lighter than smaller younger nodules. If this is the case, then
our results would suggest some form of compensatory plant response to
weevil feeding by increasing the biomass of young nodules. This
hypothesis deserves further study and it contrasts with the compensa-
tion mechanism observed in alfalfa with S. hispidulus (F.) where the
plant compensated by producing additional nodules (Quinn and Hall
1992). Future studies of S. lineatus’ effects on nodulation need to
include data on nodule demography.

Thiamethoxam insecticide coating to pea seed increased the number
of tumescent nodules as reported in similar investigations (Seidenglanz
et al. 2010; Vankosky et al. 2011; Cárcamo et al. 2012). This pattern
likely results from a combination of factors. First, based on foliage
damage (Cárcamo et al. 2012) the insecticide is only expected to be
active in the plant and provide protection against the weevil during the
first 4 wk. Also, S. lineatus eggs take at least 10–12 d to hatch at a
temperature of 20–25°C (Lerin 2004); therefore, only the initial cohorts of nodules produced when plants were around 3 wk old would be protected. The second possibility that may act in combination with the chemical is that larvae that survive the insecticidal may preferentially feed on the new nodules. Third, the younger nodules produced during the flowering stages may not be harmed because weevil larvae have already completed their feeding and are ready to pupate. Our study is the first to demonstrate experimentally a significant negative effect of weevils on the number of older tumescent nodules. In a field study, the number of damaged nodules was only slightly lower in plants treated with thiamefoxthion than in those untreated, and adding nitrogen to the soil only caused a slight reduction in total nodulation relative to the number of damaged nodules. Weevil larvae have flowering stages may not be harmed because weevil larvae have no nodules produced when plants were around 3 wk old would be significantly reduced in total nodulation relative to the process of the roots and are therefore, underestimated.

Conclusion
Our study demonstrated that below-ground herbivory on field peas by PLW larvae significantly reduced plant nitrogen content during the early flower stage. Also, our study suggested that larvae feeding can significantly reduce the pool of soil available nitrogen during flowering and potentially impact soil fertility for subsequent crops. We anticipate that for soils with high nitrogen content at planting, such as those where manure has been applied, adding an insecticide seed treatment will not influence plant nutrition and subsequent yield. Assessing these interactions under local field conditions remains a major challenge that will require manipulation of planting date and periodic destructive plant sampling to obtain a detailed time series of the weevil population and demography of the symbiotic nodules as well as plant and soil nitrogen analysis.

Acknowledgments
We gratefully acknowledge financial support from the Alberta and Saskatchewan Pulse Grower Commissions, the Alberta Crop Industry Development Fund, Matching Investment Initiative Funds of Agriculture and Agri-Food Canada and in-kind contributions from Syngenta Crop Protection Canada. We thank D. Pearson, K. Burgess, T. Larson and X. Wu for technical help and R. De Clerck-Floate for her comments on a draft of this article.

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Received 1 August 2013; accepted 15 April 2015.