



Spatial and biotic interactions of the wheat stem sawfly with wild oat and Montana dryland spring wheat

by Sharlene Elizabeth Sing

A dissertation submitted in partial fulfillment of the requirements of the degree of Doctor of Philosophy in Land Resources and Environmental Sciences

Montana State University

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Abstract:

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), has been a significant pest of wheat in the northern Great Plains since the inception of small grain production by homesteading farmers. Biological constraints associated with both the larval and adult stages of the sawfly have thwarted the development of effective chemical control of this stem-boring pest. To date, management of sawfly relies on cultural and ecologically-based strategies. Foremost among these was the development of sawfly-resistant wheat varieties.

Sawfly damage is estimated to have reduced profits to Montana wheat producers by \$20.4 million during the 1995-1996 growing season. Many Montana spring wheat fields are also impacted by the grassy weed wild oat, *Avena fatua* L. (Poaceae: Gramineae). Reduced yield, grain dockage and herbicide treatment costs are the primary sources of economic loss due to wild oat infestation of wheat fields and cost Montana farmers approximately \$20 million annually.

An accurate characterization of the spatial pattern and distribution of adult and larval stages of sawfly in sawfly-resistant spring wheat was developed to enhance existing management tools. Contrary to the conventionally held perception that sawfly is an edge-effect pest, sawfly infestation was not found to be predominantly focused at field margins. The influence of wild oat on sawfly spatial distribution was also examined. Although sawfly larval mortality was 100% in all infested wild oat stems examined, sawfly acceptance of this host plant was not rare. However, sawfly host plant preference was significantly higher for spring wheat than for wild oat hosts based on the relative densities of each species. Sawfly attack on the small number of spring wheat stems within wild oat patches at a higher rate than spring wheat in weed-free areas further emphasizes sawfly host plant preference for spring wheat.

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APPROVAL

of a dissertation submitted by

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This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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*January 9, 2002*

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## ABSTRACT

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), has been a significant pest of wheat in the northern Great Plains since the inception of small grain production by homesteading farmers. Biological constraints associated with both the larval and adult stages of the sawfly have thwarted the development of effective chemical control of this stem-boring pest. To date, management of sawfly relies on cultural and ecologically-based strategies. Foremost among these was the development of sawfly-resistant wheat varieties.

Sawfly damage is estimated to have reduced profits to Montana wheat producers by \$20.4 million during the 1995-1996 growing season. Many Montana spring wheat fields are also impacted by the grassy weed wild oat, *Avena fatua* L. (Poaceae: Gramineae). Reduced yield, grain dockage and herbicide treatment costs are the primary sources of economic loss due to wild oat infestation of wheat fields and cost Montana farmers approximately \$20 million annually.

An accurate characterization of the spatial pattern and distribution of adult and larval stages of sawfly in sawfly-resistant spring wheat was developed to enhance existing management tools. Contrary to the conventionally held perception that sawfly is an edge-effect pest, sawfly infestation was not found to be predominantly focused at field margins. The influence of wild oat on sawfly spatial distribution was also examined. Although sawfly larval mortality was 100% in all infested wild oat stems examined, sawfly acceptance of this host plant was not rare. However, sawfly host plant preference was significantly higher for spring wheat than for wild oat hosts based on the relative densities of each species. Sawfly attack on the small number of spring wheat stems within wild oat patches at a higher rate than spring wheat in weed-free areas further emphasizes sawfly host plant preference for spring wheat.

## CHAPTER 1

## INTRODUCTION

The Wheat Stem Sawfly

The wheat stem sawfly (*WSS*), *Cephus cinctus* Norton, is an economically significant wheat pest throughout the northern Great Plains. A 1995-1996 producer survey indicates that *WSS* causes an estimated annual loss of \$20.4 million to Montana wheat producers (Blodgett 1997).

The origin of *WSS* is uncertain. The first description of *WSS* was made from specimens collected in Colorado (Norton 1872). Ainslie's (1920) chronology of *WSS* records supports the hypothesis that *WSS* is an indigenous graminivore that experienced a significant shift in host plant association away from native grasses to the abundance of hosts concentrated within wheat fields. Davis (1955) suggests that wheat became an important *WSS* host as small grain cultivation expanded throughout the northern plains following the 1862 Homestead Act. Ivie (2001) refutes the native status of *WSS*, claiming the pest was introduced to North America in contaminated wheat roots and straw from northeast Eurasia.

*WSS* belongs to the Cephidae family of the Hymenopteran suborder Symphyta. Larval Cephidae tunnel and feed within small twigs of woody plants and grass stems (Smith 1987). Benson (1946) suggests that the archtypal Cephidae adaptation to feeding on the pith of steppe plants was a specialization exploiting a unique feeding and habitat

niche that facilitated survival through summer drought conditions. *WSS* larvae feed on vascular and parenchymous stem tissue of Graminae (Holmes 1954; Ainslie 1929).

### Wild Oat

The grassy weed, wild oat (*WO*), (*Avena fatua*), is thought to have originated in Eurasia (Whitson *et al.* 1996) and been disseminated throughout North America by human activity. *WO* frequently inhabits Montana dryland spring wheat (*SW*) fields infested by *WSS*. Criddle (1923) reported that *WSS* eggs were found in samples of *WO* and domesticated oat, *Avena sativa*, collected in 1922. *WO* infestation reduces annual revenues to Montana wheat producers approximately \$20 million (R.N. Stougaard, *pers. comm.*). Many Montana wheat producers are economically impacted by infestations of *WO* and *WSS* within the same fields.

### Yield Loss Due to *WSS*

There are two sources of yield loss due to *WSS* infestation: diminished wheat kernel count and weight in individual infested plants, and a reduction in the number of mature heads successfully harvested in an infested field (Luginbill, Jr. and McNeal 1954). *WSS* larval feeding causes a direct yield loss of 10.8 - 22.3% in wheat (Holmes 1977). Grain head fill, kernel weight, average protein content (Holmes 1977), and mean head weight (Morrill *et al.* 1992) are reduced because feeding diverts nutrients and water from the development and maintenance of reproductive structures in host plants (Seamans *et al.* 1938; Wallace and McNeal 1966; Weiss and Morrill 1992).

Indirect losses occur when the *WSS* larva girdles the inside of a host stem at ground level, severing the stem and causing it to fall to the ground (Munro *et al.* 1947). Yield loss due to unharvested, *WSS*-cut stems has been estimated at 2.7-15.5%. Loss varies according to the rate of infestation and the proportion of stems lodged (Weiss and Morrill 1992); if wet weather causes grain in lodged heads to mold or germinate (Wallace and McNeal 1966); as a function of wind velocity (Munro 1945); and is impacted by how effectively the combine header can recover the prostrate stems (Munro 1945; Mills 1945; Munro *et al.* 1947).

#### *WSS* Status as an Edge-effect Pest

*WSS* is conventionally perceived to be an edge-effect pest by producers and scientists alike (Mills 1944; Munro 1945; Pesho *et al.* 1971; Holmes 1982). The edge effect characterization is supported by the observation that high levels of stem lodging occur on field margins and decline toward the interior of the field (Holmes 1982). Stem cutting and lodging in mature wheat has been accepted as an obvious and reliable gauge of *WSS* infestation (Farstad 1942; Platt and Farstad 1946; Davis 1952,1953; Luginbill, Jr. and McNeal 1958). Furthermore, the assumption has been made that the pattern and intensity of *WSS* infestation follows that of lodging (Munro 1947).

Montana wheat producers have traditionally seeded wheat in long, narrow fields ('strips') oriented perpendicular to the direction of the prevailing westerly winds to minimize soil erosion. Field orientation, crop – fallow rotation, no-till production using herbicides to manage weeds, and intensive soil cultivation were adopted to retain topsoil

or conserve soil moisture (Weiss and Morrill 1992). The edge effect is potentially enhanced in crop-fallow strips because the sources of adult *WSS*, neighboring fallow strips, are typically located on one or both sides of the cropped strip (Munro 1945). When the number of invading *WSS* adults is high, narrow strip fields may reduce the pronounced edge effect by favoring *WSS* migration across the entire strip, resulting in high, uniform levels of infestation (Holmes, 1982). Infestation levels of 25% or more produced enough adult *WSS* in the following spring to generate uniformly high levels of infestation across neighboring fields (Criddle, 1922). Runyon (2001) notes a trend in Montana where producers are switching from strip to block fields, thereby reducing total edge vulnerable to *WSS* infestation for the same area cropped.

Edge effects are attributed to the unique properties of the ecotone, the transitional zone or boundary between two distinct habitat types (Gosz 1991). Cropped fields typically border fallowed fields on one or both sides in the crop – fallow rotational cropping system. The edge between these two habitats is abrupt, possessing few of the unique abiotic and biotic properties that distinguish an ecotone in the conventional sense (Wiens *et al.* 1985). The effect of wind on the more exposed stems at the edge of the field is likely to be higher than on those more sheltered in the field interior. This may in part explain the higher incidence of lodging on the field margins. The wheat field edge is therefore distinguished from the field interior largely because it is more vulnerable to vectorial forces (Hutchinson 1953) such as wind and contains the more accessible host stems.

Fallow fields, where *WSS* emerge from wheat stubble, offer few potential oviposition sites beyond infrequent stems of volunteer wheat or grassy weeds. Reproductive success is contingent upon migrating out of the effectively sterile emergence habitat to a habitat containing more readily encountered suitable host stems. Edge stems have a higher probability of encounter because they must be passed over or around by any *WSS* adults penetrating the field interior from that edge (Criddle 1922). Otherwise, the field edge simply marks the beginning of the wheat stems.

#### *WSS* Flight

Increased levels of infestation at field margins have been attributed to *WSS*'s reportedly poor flying abilities and lack of need to fly farther than necessary to find a host plant (Ainslie, 1920; Mills, 1944). Observations of *WSS* flying up to half a mile in order to oviposit in suitable host stems (Criddle, 1922) along with the documented capture of radioactively-labeled *WSS* one mile from the release point (Anonymous 1955) challenge the 'poor flier' explanation of *WSS* edge effect (Mills 1944). There is some confusion between robust flight and distance traversed; *WSS* repeatedly flies short distances close to the ground but can do so for a considerable distance (Farstad and Jacobson 1945).

An alternative to the 'poor flyer' mechanism driving the 'edge effect' may also be found in the interaction of climatic perturbations with restrictions on the energetic budget of the sawfly. Adult *WSS* are thought to live for 5-8 days after adult emergence (Wallace and McNeal 1966). During this time, they are not known to feed (McNeal 1954). Flight and all other activities must be fueled by endogenous energy reserves.

Johnson (1974) found that flight duration in many insect species increased to a maximum relatively soon after adult emergence and diminished with age and maturation of the ovaries. Unfavorable climatic factors also significantly reduce *WSS* flight duration and frequency. Cloudy, cool ( $< 17.2$  °C), and/or windy conditions halt *WSS* flight completely (Wallace and McNeal 1966). *WSS* adopts a characteristic resting posture in inclement weather conditions with the head downward and body held parallel to the leaf or stem perch which during rainfall allows water to collect in the wings, delaying flight until the wings dry (Seamans 1945).

### *WSS* Control Methods

#### Chemical Control

Insecticides are generally available for the control of pervasive and economically significant pests (Metcalf 1982; Knipling 1979). This option is currently not available for effective control of *WSS*. Confounding features of *WSS* phenology and biology provide an ecological refuge from chemical control of this pest (Wallace 1962, Anonymous 1997). *WSS* emerges and oviposits over a protracted period on a regional scale, beginning in late May and ending in mid- or late June. The larval stage of *WSS* is spent either feeding within the protective confines of the host stem, or protected in the hibernaculum (Ainslie 1929).

Foliar treatment of adult *WSS* with insecticides is not cost-effective because it requires either repeated applications or a highly persistent compound (Holmes and Hurtig 1952, Anonymous 1955, Luginbill, Jr. and McNeal 1955). Application of

insecticidal dusts ranging from chlordane, DDT, toxaphene, parathion, BHC and DDD were not found to be effective in reducing *WSS* damage (Munro *et al.* 1949). A greenhouse study, based on field observations linking 2,4-D applications to increased larval *WSS* mortality, found that treatment was effective if applied exactly at the time of oviposition, but efficacy declined rapidly with increased time between oviposition and herbicide application (Gall and Dogger 1967). The authors did not determine the mechanism of 2,4-D activity against *WSS* eggs or early instar larvae. Treatment with 2,4-D is impractical because the frequency and cost of application during the 4-6 week *WSS* flight and oviposition period is prohibitive.

Systemic pesticides functionally penetrated the protective barrier of the larval *WSS* host stem when applied with the seed or in-furrow (Wallace 1962, Skoog and Wallace 1964). Treatment with systemic insecticides has not been widely adopted against *WSS* because control was not reliable: chemicals did not persist at effective rates over the entire oviposition period, and insecticide was not effectively translocated to the preferred nodes for oviposition and feeding.

### Ecologically-based Control

The history of *WSS* control is unique because the lack of effective insecticides has forced producers to develop a number of ecologically-based control methods. Trap strips that are strategically placed around crop fields to absorb maximum oviposition pressure and to take advantage of the perceived *WSS* oviposition edge effect (Farstad 1942). Shallow fall tillage of harvested wheat fields has been used to expose the hibernaculum and enclosed *WSS* larva to dessication and freezing (Mills 1944). The dry, impenetrable

pith of *WSS*-resistant wheat varieties compromises late instar larval water relations and mechanically impedes tunneling and construction of the hibernaculum (Holmes and Peterson 1962). Inclusion of reported non-host species rotations such as flax, barley and oat is thought to significantly reduce local *WSS* populations (Callenbach and Hansmeier 1945). Temporal escape of crops from *WSS* infestation can be mediated by late seeding *SW* (Jacobson and Farstad 1952; Weiss *et al.* 1987; Morrill and Kushnak 1999).

The interaction of *WSS* population dynamics with environmental stochasticity has the potential to compromise most of these ecologically-based *WSS* management approaches. As Morrill and Weiss (1992) note, only seeding to *WSS* resistant varieties and non-host rotations remain in favor, although producers risk economic penalties with often lower valued crops or marketing difficulties. Significant research efforts in recent years have focused on the re-evaluation of *WSS* cultural control methods (Goosey 1999; Morrill and Weiss 1992; Morrill *et al.* 2001; Weiss *et al.* 1987) for inclusion in a more integrated management approach.

### Trap Crops

Trap crops have been suggested by many researchers as a cultural control method for *WSS*. A trap strip is a narrow area bordering the crop field that is seeded to a *WSS*-accepted host plant species. Temporary traps are effective because the phenological stage of trap stems is advanced relative to the crop field stems. Crop field stems are rejected because they have not elongated to the degree required for *WSS* acceptance for oviposition. Permanent trap crops are areas seeded to perennial grasses such as smooth brome (*Bromus inermis*). *WSS* readily oviposits in the stems but larvae are reported to be

unable to reach maturity in these hosts (Mills 1944). In some cases a bare-earth strip 10-20 feet wide separates the trap strip from the cropped field (Farstad 1942). Adult *WSS* are retained in the trap strip because host stems are at an optimal developmental stage for oviposition compared to the crop field, or because the bare earth strip deters movement between the trap strip and the crop. The trap strip is generally cut or disked under once the *WSS* flight period has ended but before the larvae have left the upper regions of the stem to construct the hibernaculum (Farstad 1942).

Holmes (1978) advocated the use of trap strips based on the finding that female *WSS* emerged in a higher proportion from the stubble at the margins of wheat fields than from the interior (Holmes and Peterson 1963). The trap strip is effective when it targets female *WSS* offspring and eliminates them from the breeding population before they can reproduce. Control with trap strips is most reliable when trap plants are seeded at a high enough density to retain the number of *WSS* attacking the field and when trap strip host stems are at an appreciably advanced developmental stage compared to those in the crop (Criddle 1923, Morrill *et al.* 2001). Trap strip control is not widely favored because it reduces profits: harvestable acres are lost, soil moisture reserves are diminished in non-productive cultivation, and seed, fuel, and labor are generally input without return. However, Morrill *et al.* (2001) report the successful harvest of a trap strip seeded with *WSS*-resistant winter wheat which was used to protect a field of *WSS*-susceptible *SW*. The use of trap strips is recommended only where infestations are low to moderate, a priori information not readily available to farmers. When the number of emerging adults is high, migration continues across the trap and bare earth into the crop (Holmes 1982).

### WSS-resistant Wheat Varieties

Seeding fields to *WSS*-resistant wheat varieties is considered one of the best methods currently available to reduce yield loss. Farstad (1940) found that wheat stem solidness in the amount and consistency of the stem pith conferred mechanical resistance to *WSS* larval feeding. Stem solidness, even in solid-stem varieties, is not consistently expressed. Variability has been attributed to environmental factors. Reductions in light intensity associated with prolonged overcast conditions and shading by closely spaced conspecifics had the greatest impact on stem solidness (Platt 1941). In contrast, increased *WSS* infestation rates occurred in *SW* fields sowed at a low seeding rate with wide row spacing (Luginbill and Munro 1958, Miller *et al.* 1993). Unfortunately, stem solidness in *WSS*-resistant *SW* varieties is best expressed when rows are widely spaced and the seeding rate is relatively low (Luginbill and Munro 1958, Miller *et al.* 1993).

### Management Thresholds for *WSS*

*WSS* control methods are largely prophylactic rather than reactive in nature, targeted at reducing the economic impact of an unknown density of reproductive adults invading cropped fields in the spring. Because the level of *WSS* infestation and resulting yield loss are difficult to assess, the net fiscal benefit of instituting any of the currently available *WSS* management practices has not been directly measured. As a result, credible economic injury levels and economic thresholds for *WSS*-infested wheat do not presently exist.

The development of a *WSS* threshold has been hampered by two primary sources of uncertainty universally encountered in the generation of thresholds. Uncertainty

arises in: 1) estimating the pest population density, especially if sampling accuracy is confounded by the non-random spatial distribution of the organism, and 2) defining the precise shape and dynamic behavior of the crop loss function (Auld and Tisdell 1987). My study addresses aspects of uncertainty arising from population estimation. Small plot and greenhouse experiments to quantify direct yield loss due to *WSS* infestation are being conducted by the sawfly research group at Montana State University – Bozeman. These studies were undertaken to address fundamental uncertainties regarding the shape and dynamic behavior of a *WSS* yield loss function.

The results from the fore-mentioned studies will provide essential information for the future development of a credible economic threshold for *WSS*. Wheat producers affected by *WSS* infestation would benefit from the development of a predictive *WSS* bio-economic model based on this newly available and accurate economic and biological information. However, because indirect yield loss attributable to stem lodging from *WSS* infestation is strongly influenced by unpredictable climatic factors such as wind, rain, and hail just before or during harvest. Accurate economic impacts are difficult to estimate from pest densities and direct yield losses alone.

#### *WO* Control

Effective *WO* management uses a bifurcated strategy with two primary objectives to: 1) prevent seed production, and, 2) foster controlled seed germination thereby depleting existing seed reserves (Anonymous 1995). The first objective is attained by bolstering crop competitive ability, assuring that essential resources such as space, light,

moisture and nutrients are utilized by established crop plants and not appropriated by weeds (Carlson and Hill 1985).

Crop competitiveness, increased through a variety of cultural and chemical control methods, is especially important during the 'critical period' (Nieto *et al.* 1986) when crop yield loss due to weed competition cannot be reversed by subsequently instituted management practices. Soil incorporated herbicides such as the meristematic inhibitors trifluralin (Treflan™) and triallate (Far-Go™) kill germinated *WO* before they emerge (Dewey *et al.* 1999). Foliar herbicides including the lipid synthesis inhibitors sethoxydim (Poast™) and tralkoxydim (Achieve™) and the amino acid synthesis inhibitor metsulfuron (Ally™) (Dewey *et al.* 1999) are applied to seedling stage *WO* before *SW* emergence, significantly reducing interspecific competition for resources.

Cultural control measures that increase crop competitiveness include optimizing the timing of crop sowing, choosing more competitive crop rotations or cultivars, and increasing the crop seeding rate (Chancellor and Peters 1976). Fertilizing *WO*-infested fields helps in accomplishing both management objectives. Early fertilization increases *WO* germination, thereby depleting the seedbank, and allows for safe and effective herbicide treatment before *SW* seedling emergence (Anonymous 1995). Additionally, fertilizer applications may increase the competitive ability of the standing crop (Chancellor and Peters 1976).

## Mechanisms of Plant Resistance to Herbivory

### Definitions

Plants have evolved both indirect and direct mechanisms to counteract herbivorous attack. Tolerance traits such as compensatory growth are indirect means of reducing the impact of herbivory on plant fitness. Resistance traits reduce herbivory directly and impact herbivore fitness (Tiffin 2000). In this context herbivore fitness defines the food quality of a plant (Crawley 1983). Antixenotic resistance traits affect herbivore behavior by potentially reducing herbivory through avoidance. Antibiotic resistance traits impact herbivore fitness through plant-herbivore incompatibility.

Antibiotic defenses are either constitutive, present at all times, or induced, synthesized in response to stress such as herbivore feeding or fungal attack (Litvak and Monson 1998). Host plant antibiosis is manifested in the food quality of host plants which are: nutritionally devoid and lacking in the full compliment of dietary components, including water, necessary for growth and development of the herbivore; nutritionally unavailable, either mechanically incompatible with the insect's feeding habit or physiologically inedible due to enzymatic digestive inhibition; or, contain compounds which function as contact or stomach toxins.

### Potential Sources of *WO* Resistance to *WSS*

Although *A. sativa* resistance to *WSS* has been reported in the literature (Criddle 1923; Holmes and Peterson 1964, Wallace and McNeal 1966), the specific mechanism of resistance has not yet been identified. A review of related literature suggests that *A.*

*sativa* and *WO* resistance to *WSS* may be serendipitous, an additional benefit of a suite of traits evolved to increase oat fitness across two trophic levels: allelopathy for competitive advantage with other plant species at the same trophic level, and elicited responses to counteract parasitic phytopathogens.

### *WO* Allelopathy

Allelopathic compounds in *WO* may contribute to *WSS* mortality. *WO* produces several phenolic compounds with known allelopathic activity: the coumarin scopletin, and the phenolic acids *p*-coumaric acid, vanillic acid, and ferulic acid (Schumacher *et al.* 1983). Crop-associated weeds such as *WO* benefit from the competitive advantage afforded by allelopathy when both species are at the seedling stage and engaged in intense competition to establish and dominate. Phenolics in seedling stage *WO* root exudates inhibited root and coleoptile growth (Perez and Ormeno-Nunez 1991) and reduce leaf and root dry weight (Schumacher *et al.* 1983) in *SW* seedlings. Wheat midge resistant wheat lines were found to synthesize two phenols, *p*-coumaric acid and ferulic acid, in high constitutive levels which were augmented by rapid induction in response to larval feeding. These compounds suppress larval development and result in high levels of mortality in lines which synthesize phenols at toxic concentrations (Ding *et al.* 2000).

The identification, quantification and characterization of phenolics in *A. sativa* has been focused on the edible groats (Collins 1986) and in *WO* on seedling root exudates. *WSS* researchers at Montana State University are currently working to determine the identity and concentration of phenols in *WO* interior stem parenchyma and vascular tissues and their potential role in larval *WSS* antibiosis.

### *A. sativa* Elicited Responses to Pathogens

*A. sativa* accumulates avenacin, a saponin, in an induced response to attack by phytopathogenic fungi including take-all disease of wheat and barley (Maizel *et al.*, 1964), *Puccinia coronata* spp. crown rusts (Mayama *et al.* 1981), and the root-infecting fungus *Gaeumannomyces graminis* (Bowyer *et al.* 1995). Saponin enzymatic activity against fungal membranes confers oat resistance (Bowyer *et al.* 1995). Wheat is susceptible to these pathogens because it does not produce saponins. The degree to which *WO* saponins may affect *WSS* larval membrane integrity has not yet been evaluated.

### *A. sativa* Constitutive Antibiotic Capabilities

*A. sativa* has evolved resistance traits significantly limiting its nutritional value to specific herbivores. *A. sativa* leaf sap has deleterious effects on insect herbivores. Hypermodulation of digestive proteinases in response to *A. sativa* leaf proteinase inhibitors is thought to cause significant growth depression, weight loss, and mortality in the lesser migratory grasshopper, *Melanoplus sanguinipes* (Hinks and Hupka 1995). *WO* stem tissue has not been evaluated to determine if proteinase inhibitors are present, or if they are present at sufficient concentrations to affect larval *WSS* in a similar fashion. High concentrations of glutamic acid in phloem sap were correlated with low suitability in *A. sativa* varieties for the bird cherry-oat aphid, *Rhopalosiphum padi* L. (Weibull *et al.* 1990).





















































































































































































































































































































































