Wheat stem sawfly parasitism in varying field sizes and tillage systems in dryland wheat in Montana
by Justin Blake Runyon

A thesis submitted in partial fulfillment of the requirements of the degree of Master of Science in Entomology
Montana State University

Abstract:
The wheat stem sawfly, Cephus cinctus Norton, is a major pest of wheat in the northern Great Plains. Sawfly-infested plants have lower yields and usually lodge, reducing the amount of grain that can be harvested. In 1995 and 1996, annual losses because of sawfly infestations were estimated to exceed $25 million in Montana alone. Two parasitoids, Bracon cephi (Gahan) and B. Iissogaster Muesebeck, attack the wheat stem sawfly in wheat, but provide satisfactory control only in isolated cases. The effects of selected conventional dryland wheat production practices on sawfly parasitism were examined. Sawfly parasitism levels in tilled vs untilled, and block vs strip fields were compared. The effect of sawfly parasitism on kernel weight was investigated.

In general, little difference was found in sawfly parasitism between tilled and untilled fields. However, parasitism was significantly lower in intensively tilled fields. No difference was found in sawfly parasitism between strip fields and block fields. Sawfly parasitism was uniform across block fields, even though sawfly infestation levels were often lower in the middle of blocks. Intensive tillage prevents successful biological control of the wheat stem sawfly by reducing the total number of sawfly parasitoids. Replacing intensive tillage with minimum tillage or chemical fallow will better conserve sawfly parasitoids and result in a cumulative increase in sawfly parasitism over time. Planting block fields instead of strips should have little effect on sawfly parasitism and should decrease sawfly infestations. Kernels of stems containing parasitized sawflies were generally heavier than those containing unparasitized sawflies, indicating that parasitism may provide some protection against yield loss caused by sawfly feeding.

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APPROVAL

of a thesis submitted by

Justin Blake Runyon

This thesis has been read by each member of the thesis 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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ABSTRACT

The wheat stem sawfly, *Cephus cinctus* Norton, is a major pest of wheat in the northern Great Plains. Sawfly-infested plants have lower yields and usually lodge, reducing the amount of grain that can be harvested. In 1995 and 1996, annual losses because of sawfly infestations were estimated to exceed $25 million in Montana alone. Two parasitoids, *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck, attack the wheat stem sawfly in wheat, but provide satisfactory control only in isolated cases. The effects of selected conventional dryland wheat production practices on sawfly parasitism were examined. Sawfly parasitism levels in tilled vs untilled, and block vs strip fields were compared. The effect of sawfly parasitism on kernel weight was investigated.

In general, little difference was found in sawfly parasitism between tilled and untilled fields. However, parasitism was significantly lower in intensively tilled fields. No difference was found in sawfly parasitism between strip fields and block fields. Sawfly parasitism was uniform across block fields, even though sawfly infestation levels were often lower in the middle of blocks. Intensive tillage prevents successful biological control of the wheat stem sawfly by reducing the total number of sawfly parasitoids. Replacing intensive tillage with minimum tillage or chemical fallow will better conserve sawfly parasitoids and result in a cumulative increase in sawfly parasitism over time. Planting block fields instead of strips should have little effect on sawfly parasitism and should decrease sawfly infestations. Kernels of stems containing parasitized sawflies were generally heavier than those containing unparasitized sawflies, indicating that parasitism may provide some protection against yield loss caused by sawfly feeding.

CHAPTER 1

INTRODUCTION

In Montana, the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), has been the most economically important chronic insect pest of wheat since cultivation began more than a century ago (Weiss and Morrill 1992). Within the northern Great Plains of North America this insect has caused devastating losses in spring wheat, and more recently, winter wheat (Weiss and Morrill 1992, Morrill and Kushnak 1996). Estimated annual losses in 1995 and 1996 exceeded $25 million in Montana alone (Anonymous 1997). Sawfly-infested plants have reduced yields and usually lodge, making harvest difficult (Ainslie 1920, Platt and Farstad 1946, Holmes 1977). Sawflies are difficult to control because eggs, larvae, and pupae are enclosed within host plants. Current management practices do not provide adequate levels of control. Solid-stemmed wheat cultivars provide some measure of control; however, stem solidness varies with environmental factors (Platt 1941). Resistant cultivars have lower yield potentials and reduced disease resistance (Weiss and Morrill 1992). Tillage implements to bury sawflies or to expose overwintering sawfly larvae to unfavorable winter conditions do not kill enough sawflies to affect populations the following year (Weiss *et al.* 1987, Goosey 1999). Sawflies are difficult to control with insecticides because residues are not active long enough to protect crops throughout the adult emergence period (Holmes and Hurtig 1952).

The original hosts of the wheat stem sawfly are grasses (Ainslie 1929, Wallace and McNeal 1966, Morrill *et al.* 1992) where sawfly larvae are attacked by nine species of parasitoids (Criddle 1923, Nelson 1953, Holmes *et al.* 1963, Morrill 1997). Only two of these, *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae), have been found in significant numbers in wheat (Morrill 1998). Levels of parasitism vary greatly among fields but provide satisfactory control only in isolated cases (Morrill 1997, 1998). Seasonal phenology of wheat plays a major role in parasitoid success. Wild grasses remain green longer than wheat and sawfly parasitism is maximized; in wheat, sawflies complete development sooner and avoid parasitism by second generation parasitoids (Morrill *et al.* 1994, Morrill 1997).

The effects of wheat production practices on levels of parasitism are unknown. The goal of this research was to ascertain the effects of tillage practice and field size on sawfly parasitoids and to identify practices that would conserve naturally occurring beneficial insects in the wheat agroecosystem.

Objectives

The objectives of this project were to identify wheat production practices that can be used to enhance populations of two parasitoids of the wheat stem sawfly, reduce severity of sawfly infestations, and minimize crop loss. Practices compared were tilled and untilled fallow fields, and block and strip fields. The hypothesis that sawfly infestation, cut stems, and parasitism of untilled and tilled fields were equal was tested. The hypotheses that sawfly infestation, cut stems, and parasitism were the same at the edge and middle of block fields, and that sawfly infestation, cut stems, and parasitism of the block edge, block middle, and the strips at each location were equal were tested.

Sawfly-infested stems produce lighter kernels than similar sized uninfested stems. However, nothing is known about the yield of sawfly-infested plants that have been parasitized. The hypothesis that kernel weights of uninfested, sawfly-infested, and sawfly-parasitized stems were equal was tested.

History of the Wheat Stem Sawfly

In 1890, when wheat stem sawfly adults were first reared from grasses in California, Riley and Marlatt (1891) predicted, "The economic importance of this species arises from the fact that it may be expected at any time to abandon its natural food source in favor of the small grains, on which it can doubtless successfully develop." Five years later, wheat stems containing *C. cinctus* larvae were found at Souris, Manitoba (Fletcher 1896), fulfilling this prediction. After the early infestation at Souris, there were continuous increases in the amount of damage and the area involved (Farstad 1940). Heavy infestations occurred in wheat at Minot, North Dakota, in 1907 (Wallace and McNeal 1966, Holmes 1978). By 1926, sawfly damage was widespread and extensive; annual losses in wheat were estimated at 25 million bushels in Montana and Canada (Wallace and McNeal 1966). In 1951, grain loss caused by the wheat stem sawfly in Montana and North Dakota was valued at over 10 million dollars (Davis 1952). Cropping systems developed in an attempt to solve problems of drought, wind erosion, and plant diseases, made the control of the wheat stem sawfly much more difficult (Farstad 1940). Alternate-year summer fallow, strip cropping, and a major increase in wheat production encouraged sawfly populations and increased crop damage (Weiss and Morrill 1992, Morrill 1997).

Sawflies are continuing to adapt to wheat. Originally, infestations were primarily in spring wheat because winter wheat usually matured early enough to avoid losses (Davis 1955). However, by the 1980's, both winter and spring wheat were heavily infested in Montana. The recent increase in susceptibility of winter wheat to attack by *C. cinctus* is a result of earlier emergence of adults (Morrill and Kushnak 1996).

Taxonomy and Distribution of the Wheat Stem Sawfly

Edward Norton first described the wheat stem sawfly as *Cephus cinctus* in 1872 from one male collected in Colorado (Norton 1872). In 1890, Albert Koebele reared *C. cinctus* adults from grass stems near Alameda, California (Koebele 1890), which Riley and Marlatt (1891) described as *C. occidentalis*. Six years later, Ashmead described a female from Wisconsin as *C. graenicheri* (Ashmead 1897). The first name given, *Cephus cinctus* Norton, is valid and all others are considered junior synonyms.

The wheat stem sawfly is known from the Pacific Coast states and British Columbia, south to Arizona and east to Ontario and Georgia (Ainslie 1929, Ivie 1996, Wallace and McNeal 1966); however, it is of economic importance only in the northern Great Plains (Weiss and Morrill 1992). In recent years, it has been suggested that *C. cinctus* was introduced from northeast Asia; unfortunately, the taxonomy of the genus *Cephus* is poorly understood and a world revision is needed to understand species limits (Ivie 1996).

Biology of the Wheat Stem Sawfly

Adult emergence begins in late May or early June and lasts three to four weeks (Weiss and Morrill 1992, Morrill and Kushnak 1996). The wheat stem sawfly is reported to be a weak flier; females usually deposit eggs in stems near the emergence site (Criddle 1911, 1915, Ainslie 1920, Salt 1947, Mills 1945, Holmes 1975, 1982). Adults are active when it is sunny, the temperature is above 17° C, and wind speeds are minimal (Seamans 1945). Females prefer to oviposit in the uppermost internode of the largest diameter stems from which the head has not yet emerged (Holmes and Peterson 1960). Morrill *et al.* (2000) and Morrill and Weaver (2000) demonstrated that the sex ratio is male-biased in small diameter stems and female-biased in larger stems. Adult size, fecundity, and longevity increase with stem size.

Eggs hatch in approximately seven days, and larvae feed on parenchyma and vascular tissue within the stems (Ainslie 1920, Holmes 1954). Because of cannibalism, only one sawfly per stem completes development (Ainslie 1920, Holmes 1954, Weiss and Morrill 1992). There are four or five instars, depending on the host (Ainslie 1920, Farstad 1940). Upon completion of development, the larva migrates to the lower region of the stem and cuts a V-shaped notch around the perimeter of the stem, usually at or a little above ground level. The larva retreats to the region of the stem below the notch and plugs the stem with frass; this provides an easy exit for the adult the following spring. The stem usually breaks at the notch, leaving a "stub" that serves as an overwintering chamber (Ainslie 1920, Wallace and McNeal 1966, Weiss and Morrill 1992). The "stub" is hollow and lined with a silk hibernaculum, allowing the larva to overwinter below the soil surface and thus protecting it against severe winter weather (Ainslie 1920, Salt 1946a, 1946b, Holmes and Farstad 1956, Weiss and Morrill 1992).

C. cinctus overwinters as a larva that can withstand freezing and some drying (Salt 1946a, 1947, 1961, Morrill *et al.* 1993). A diapause of 10° C for 90 days is necessary before pupation can take place (Salt 1947). The following spring, changing climatic conditions trigger pupation (Salt 1947, Church 1955), the pupal stadium lasts 7-14 days (Criddle 1922); adults emerge by chewing through the frass plug (Ainslie 1920).

<u>Wheat Stem Sawfly Damage</u>

Sawfly infestation reduces yield in two ways. The most obvious loss is the result of lodging prior to harvest (Morrill *et al.* 1992). High winds and precipitation increase lodging of cut stems (Ainslie 1920, Weiss and Morrill 1992). Supplementary harvest techniques, such as swathing and lowering header height, are required to recover lodged stems. The potential for equipment damage and harvest time increase, and lower stubble height affects field moisture levels because of less snow retention (Caprio *et al.* 1982, Goosey 1999). Weiss and Morrill (1992) estimated that there would be a total yield loss of 15.5% in a field where 50% of the stems were cut, assuming that 85% of the cut stems could be retrieved during harvest.

The second source of loss is a direct reduction in yield of infested plants. Feeding by wheat stem sawfly larvae affects yield by physically interrupting the flow of nutrients and water to the developing kernels (Morrill *et al.* 1992). Reports concerning the reduction of head weight caused by larval feeding range from "no significant effect" (Munro 1945) to >20% reduction (Seamans *et al.* 1944, McNeal *et al.* 1955, Holmes 1977). Sawflies prefer to oviposit in large stems, which inherently produce the heaviest heads. Accurate estimations of loss can be determined only by comparing infested and uninfested stems of similar size (Morrill *et al.* 1992). This may explain why early research failed to detect a yield loss. Holmes (1977) found that there was a yield reduction of 11-22% attributable to decreases in the number and weight of kernels in *C. cinctus* infested plants. Seamans *et al.* (1944) estimated that sawfly infestation reduced the amount of grain produced by two kernels per head, a 10% crop loss in an average season. Morrill *et al.* (1992) showed a head weight reduction of 3-10%, depending on cultivar, due to larval feeding.

Wheat Stem Sawfly Control

Resistant Cultivars. Solid-stemmed wheat cultivars have been available since 1945 (Stoa 1947, Roberts 1954, Morrill *et al.* 1994). Kemp (1934) was the first to relate stem solidness to wheat stem sawfly resistance. Stem solidness is a result of pith production inside the stem. Pith dries early during plant maturation; this may result in desiccation of sawfly eggs and larvae (Holmes and Peterson 1961, 1962). In stems completely filled with pith, larval movement appears to be physically impeded. Larvae that hatch from eggs completely surrounded by pith don't survive (Farstad 1940). The degree of stem solidness is strongly tied to environmental factors; elongating stems fail to fill with pith during cloudy conditions (Platt 1941, Holmes 1984).

Sawflies are able to infest and cut solid-stemmed cultivars. Sawfly infestation in solid-stemmed cultivars ranged between 16 and 47% in 1991 (Morrill *et al.* 1992). However, there is greater mortality of overwintering larvae in solid stems (Morrill *et al.* 1994). Mortality factors included desiccation (Holmes and Farstad 1956) and freezing of larvae that were unable to migrate below the soil surface (Holmes and Peterson 1962, Morrill *et al.* 1993).

Although sawfly-resistant cultivars reduce sawfly losses, their lower yield potential, reduced disease resistance, and lower grain quality have resulted in limited grower acceptance (Weiss and Morrill 1992). New resistant winter wheat lines, 'Vanguard' and 'Rampart', were produced by back crossing with solid-stemmed spring wheats (Bowman *et al* 1998). As a result, the new winter wheat cultivars are more susceptible to winter kill (Morrill *et al.* 1994).

Insecticides. The biology of the wheat stem sawfly makes control with conventional insecticides difficult and uneconomical. Sawfly larvae spend all of their development inside the host plant and are protected from insecticides. Because adult emergence and oviposition lasts up to six weeks, multiple insecticide applications are necessary (Holmes and Hurtig 1952). Systemic insecticides and seed treatments were also shown to be ineffective (Wallace 1962, Holmes and Peterson 1963, Skoog and Wallace 1964, Blodgett *et al.* 1996). No insecticides are currently labeled for wheat stem sawfly control.

Cultural Control. Cultural practices that could be used to manage the wheat stem sawfly were first evaluated in the early 1900's. Suggestions included mowing grassy borders that could act as sawfly reservoirs, trap strips, leaving grasses that could act as reservoirs for sawfly parasitoids, early harvesting, and deep plowing (Criddle 1915, 1917, 1922). Tillage, trap crops, swathing, and planting date modifications are practices currently suggested to control sawflies.

Tillage is commonly used to kill weeds in fallow fields, and has been extensively evaluated as a control method for sawflies (Farstad *et al.* 1945, Callenbach and Hansmeier 1944, 1945, Mills 1945, Holmes and Farstad 1956, Morrill *et al.* 1993, Goosey 1999). Tillage that exposes sawfly-infested stubs on the soil surface showed potential as a control tactic (Holmes and Farstad 1956). Freezing and desiccation were important mortality factors for larvae in exposed stubs (Salt 1946a, 1961). Although there is high mortality in exposed stubs (Holmes and Farstad 1956, Morrill *et al.* 1993), current tillage methods do not expose enough stubble to affect sawfly populations the following year (Goosey 1999).

Trap crops are used to concentrate sawflies into a small percentage of the total crop. The trap crop can consist of planting a susceptible or resistant cultivar around the border of the crop being protected (Morrill *et al.* 2001). The susceptible trap crops are destroyed after sawfly oviposition (Callenbach and Hansmeier 1945) and resistant trap crops can be harvested (Anonymous 1997, Morrill *et al.* 2001). Trap crops are not widely used because producers are reluctant to destroy grain (Goosey 1999) and drought conditions sometimes preclude the vigorous plant growth needed to retain dispersing sawflies (Farstad and Jacobson 1945).

Modifications in planting dates can reduce sawfly damage by disrupting synchronization of sawfly emergence and plant development (Weiss *et al.* 1987). Morrill and Kushnak (1999) showed that late-planted spring wheat had lower levels of sawfly infestation than winter wheat and sometimes avoided attack completely. They suggested that fields with a history of the heaviest sawfly infestations be planted last. A disadvantage of late planting in semiarid regions is the loss of critical early season moisture (Morrill and Kushnak 1999).

History of Sawfly Parasitoids

Sawfly populations in feral grasses were impacted by at least nine species of hymenopterous parasitoids (Criddle 1923, Morrill 1997) where parasitism levels sometimes approached 100%. However, parasitism levels were usually less than 2% in wheat (Criddle 1923, Neilson 1949). Until recently, parasitoids have made little progress in following the sawfly into wheat; only two, *Bracon cephi* and *B. lissogaster,* have been reared from sawflies in wheat (Holmes 1953, Davis *et al.* 1955, Somsen and Luginbill 1956, Morrill *et al.* 1994). Slow adaptation of parasitoids to wheat may be due to lack of synchrony between parasitoids and host, because feral grasses remain green longer than wheat. *C. cinctus* larvae usually escape parasitoid attack once they move to the lower underground regions of mature plants in preparation for overwintering (Morrill *et al.* 1994). Both *B. cephi* and *B. lissogaster* have two generations. Therefore, unless there is an unusually long growing season caused by cool wet weather, thus prolonging plant senescence and sawfly activity, the second generation of parasitoids cannot survive in wheat because they are unable to locate their hosts in their underground "stubs" (Holmes *et al.* 1963, Morrill *et al.* 1994). *B. cephi* has effectively suppressed sawfly populations in wheat in Canada (Nelson and Farstad 1953, Holmes *et al.* 1963) and Montana (Morrill *et al.* 1994).

Attempts at introducing other biological control agents have been unsuccessful. A release of 6,000 adult *Collyria calcitrator* (Gravenhorst) (Hymenoptera: Ichneumonidae), a parasitoid of the European wheat stem sawfly, *Cephus pygmaeus* L., was made in Saskatchewan in 1930, but they did not become established. Further releases of *C. calcitrator* over a nine-year period were unsuccessful (Clausen 1978). Releases of 17,000 *C. calcitrator* and 3,000 *Bracon terebella* Wasmael (Hymenoptera: Braconidae) were made in North Dakota and Montana during 1952-1954, but neither became established (Smith 1961). Smith (1961) hypothesized that the releases failed because of the parasitoids' specific adaptations for the European species.

Taxonomy and Distribution of *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck

In 1918, A. B. Gahan described *Bracon cephi* (as *Microbracon cephi*) from two males and five females from North Dakota and Manitoba. Specimens were reared from *Cephus cinctus* infested stems of wild grasses. *Microbracon cephi* was later transferred to the genus *Bracon* (Muesebeck and Walkley 1951).

In 1953, C. F. W. Muesebeck described *Bracon lissogaster* from 17 females and 28 males reared from *C. cinctus* infested wheat in Teton County, Montana.

Bracon cephi is recorded from Alberta, Saskatchewan (Nelson and Farstad 1953), Manitoba, North Dakota (Gahan 1918), British Columbia, Iowa, Kansas, Minnesota, Montana, Nebraska, South Dakota, Wyoming, and southwest United States (Krombein *et al.* 1979).

Bracon lissogaster is found in the north-central Montana counties of Cascade, Chouteau, Glacier, Hill, Liberty, and Pondera (Somsen and Luginbill 1956), and Teton and Toole (Muesebeck 1953). It was released and is established in south-central Montana (Morrill 1998) and was recently released in northeastern Montana, but its status there is uncertain (Morrill *et al.*, unpublished).

Runyon *et al.* (2001) give morphological characters that can be used to separate adults of *B. cephi* and *B. lissogaster.*

Biology of *Bracon cephi* and *B. lissogaster*

Bracon cephi. *Bracon cephi* has two generations per year (Criddle 1923, Nelson and Farstad 1953, Morrill 1997). The occurrence of a complete second generation apparently depends on how late in the season the first generation females continue to oviposit. Eggs deposited by first generation parasitoids in June or July pupate and emerge as second generation adults, whereas those laid in August overwinter as larvae (Holmes *et al.* 1963). First generation adults emerge in late June and may still be found when second generation adults appear in mid August. Second generation adults are present at harvest and have been found in late September (Nelson and Farstad 1953). There is a preoviposition period of one to three weeks for the first generation (Nelson and Farstad 1953, Holmes *et al.* 1963). Whether this delay is required for maturation of eggs (Nelson and Farstad 1953) or for sawfly larvae to develop sufficiently to permit parasitoid development (Holmes *et al.* 1963) is unclear. Females of the second generation begin oviposition almost immediately upon emergence (Holmes *et al.* 1963).

A number of parasitoids respond to odors released by the feeding activity of their hosts (Lewis and Tumlinson 1988, Whitman 1988, Dicke and Sabelis 1989, Turlings *et al.* 1990, Vinson 1991, 1999). Turlings *et al.* (1990, 1991a, 1991b) found that a chemical alicitor in the saliva of the fall armyworm caterpillar causes the host plant (corn) to release chemicals, which attract fall armyworm parasitoids. These chemicals are released not only from the site of attack, but systemically by the entire plant (Turlings and Tumlinson 1992). It is logical that *B. cephi* females locate sawfly-infested stems using chemical cues. "It can fly for considerable periods and, on a very calm day, may be observed flying above the crop, but with no specific directional tendency" (Nelson and Farstad 1953). Indeed, without air currents to direct these chemical cues *B. cephi* has nothing to orient toward.

Once an infested plant is found, the sawfly larva within the stem must be located. Nelson and Farstad (1953) observed "females walking up and down the stem, stopping periodically and straddling the stem with the antennae and remaining in this position for several seconds". Substrate vibration is often used by parasitoids, especially those attacking concealed hosts (Wharton 1984, Lawrence 1981, Glas and Vet 1983, Meyhofer *et al.* 1994). Richerson and Borden (1972) demonstrated that oviposition by a braconid bark beetle parasitoid could be induced by scratching the undersurface of the bark with a pin. *C. cinctus* larvae in wheat stems also produce detectable sounds (Mankin *et al.* 2000). It is likely that *B. cephi* uses the vibrations and sounds produced by sawfly larval feeding and movement to locate its host within the stem.

Once the host has been located, the female inserts her ovipositor into the stem, paralyses the sawfly larva, and deposits an egg. Typically, only one egg is placed per host (Holmes *et al.* 1963); however, the oviposition of two eggs has been observed (Nelson and Farstad 1953). Paralysis probably occurs prior to oviposition and is achieved by the injection of a toxin (Clausen 1940, Piek 1986, Shaw and Huddleston 1991). Parasitoids that do not allow the host to continue functioning (paralysis is permanent or the host is killed) after being parasitized are called idiobionts (Vinson 1975, Wharton 1993). *B. cephi* is an idiobiont parasitoid (Morrill 1998, Runyon *et al.* 2001), and must complete development using the host resources present at oviposition. A related and well-studied parasitoid, *Bracon hebetor* (Say), injects two proteins into its host, which act presynaptically at neuromuscular junctions. The venom paralyzes the host, which may live for several weeks after the attack without moving or molting (Godfray 1994).

B. cephi places the egg on or near the host. The larva hatches in one to two days, locates the host, attaches itself with its mandibles, and immediately begins to feed. Development is completed in approximately 10 days; usually little is left of the host except the integument. The mature larva spins a cylindrical cocoon that is attached lengthwise to the inside of the stem at each end by a disc-like plate. First generation cocoons are often loosely woven; those of the second generation are tightly woven (Nelson and Farstad 1953). Most *B. cephi* larvae overwinter above ground in uncut stems. Unlike sawfly larvae, which are below the soil surface, *B. cephi* larvae are more exposed to unfavorable winter conditions, making cold-hardiness necessary. They avoid freezing and are able to survive if they do freeze because of large concentrations of glycerol in the haemolymph (Salt 1959). Larvae pupate in the spring and adults emerge by chewing a neat, circular hole in the stem wall.

Bracon lissogaster. The biologies of *B. lissogaster* and *B. cephi* are similar. In general, the preceding discussion also applies to *B. lissogaster.* Somsen and Luginbill (1956) described the biology of *B. lissogaster* in some detail; with the following differences: *B. lissogaster* has two complete generations. Each female lays one to four eggs per host. Four larvae have been observed to successfully develop on a single host (Runyon, personal observation). Larvae hatch in 66 hours at 23° C and 78% relative humidity. They feed on the outer surface of the host, sucking juices from minute lacerations made with the mandibles. Larval development is completed in six to eight days. When three or four larvae feed on the same host, the development period is shorter and adults are smaller, probably because of food limitations. The sex ratio appears to be 2:1 (male:female) (Somsen and Luginbill 1956).

Wheat Production Practices

Summer Fallow. Summer fallow is a practice to replenish soil water reserves during one growing season for use by the crop grown the following season (Troeh *et al.* 1999). In the semiarid regions of the northern Great Plains, water availability is a major factor limiting plant growth (Willis *et al.* 1983). Summer fallow helps conserve water and reduce the risk of poor yields. Yields of spring wheat and winter wheat are 40-50% higher after fallow than with continuous cropping in dryland areas (Krall *et al.* 1965, Willis *et al.* 1983). Tillage and chemical fallow are common practices used to manage weeds on fallow land in Montana. Weeds must be controlled on fallow land to obtain maximum water storage and to reduce future weed problems (Willis *et al.* 1983).

Tillage. Tillage, disturbance and perturbation that results in the inversion of soil, is used to prepare seedbeds and control weeds. Tillage kills seedlings and mature weeds (Troeh *et al.* 1999). However, intensive tillage that leaves the soil surface free of crop residue increases water loss and soil erosion (Young *et al.* 1983).

Chemical Fallow (No-Till). During the fallow period weeds are controlled with herbicides; the soil is left undisturbed and the crop is seeded directly into the residue of the previous crop (Blevins and Frye 1993). Chemical fallow maximizes soil surface residue, thus decreasing soil erosion and increasing moisture by trapping snow (Larney *et al.* 1994). Crop residue also conserves water by decreasing evaporation and run-off (Wiese *et al.* 1967). The absence of tillage in chemical fallow reduces machinery repair and maintenance costs, and cuts fuel bills in half (Unger *et al.* 1977). Wicks and Smika (1973) demonstrated that chemical fallow plots stored more water and had higher yields than conventionally tilled plots. Crop emergence is typically superior in chemical fallow due to improved soil structure and more favorable moisture (Perry Miller, personal communication). Also, winter wheat seeded into standing stubble has a better chance of winter survival because snow caught by stubble protects the young plants against low temperatures and freezing (Larney *et al.* 1994). The developments of a wide variety of new and improved herbicides (Weise 1983), and of new seeding equipment that can penetrate heavy crop residue and compact soils (Larney *et al.* 1994) have reduced the need for tillage.

Field Size

Strip Farming. Strip farming is a method of wind erosion control that consists of narrow adjacent strips, oriented perpendicularly to the prevailing wind, which are alternately cropped and fallowed (Troeh *et al.* 1999). Strip farming began in the early 1920's after the drought years of 1917-1919 resulted in serious erosion problems (Howard 1959, Larney *et al.* 1994). Typical strip widths range from 50 to 100 meters.

Disadvantages of the use of strips are the susceptibility of the multiple, long, exposed borders to disease and insect attacks, and to the desiccating effect of hot, dry winds in arid regions (Troeh *et al.* 1999), and to overlap inefficiencies during machinery operation. The efficiency of chemical fallow in reducing soil erosion has diminished the need for strip farming.

Block Farming. Block farming is the planting of large rectangular fields (Figure 3). Block farming is better suited to the efficient use of large farming equipment (Larney *et al.* 1994) and presents fewer borders to diseases, insects, and desiccation from hot, dry winds (Troeh *et al.* 1999).

CHAPTER 2

MATERIALS AND METHODS

Research Sites

Research sites were located in the north-central and south-central wheat producing regions of Montana (Figure 1, Table 1). Study sites were selected to examine either the impact of tillage (Table 2) or the effect of field size (Table 3) on sawfly parasitism levels. Sites were sampled with a sweep net to ensure the presence of sawflies. Each site was assigned a number, since fields were sampled in different years and differed in production practices.

Table 1. Research site locations and production practices compared.

Site	Comparison	County	Latitude	Longitude
1	nt / t [1]	Chouteau	N 47° 50'	W 111° 17'
2	nt / t	Chouteau	N 48° 00'	W 111° 13'
3	nt / t	Chouteau	N 48° 00'	W 111° 16'
4	nt / t	Chouteau	N 47° 58'	W 111° 22'
5	b / s [2]	Stillwater	N 45° 41'	W 109° 11'

Table 1. Research site locations and production practices compared (cont.).

Site	Comparison	County	Latitude	Longitude
6	nt / t b / s	Stillwater	N 45° 45'	W 109° 07'
7	b / s	Stillwater	N 45° 59'	W 109° 15'
8	b / s	Golden Valley	N 46° 10'	W 109° 16'
9	nt / t	Cascade	N 47° 41'	W 111° 37'
10	nt / t b / s	Teton	N 47° 57'	W 111° 47'
11	nt / t	Toole	N 48° 16'	W 111° 49'
12	nt / t	Chouteau	N 47° 50'	W 111° 19'
13	nt / t	Chouteau	N 48° 00'	W 111° 08'
14	b / s	Cascade	N 47° 42'	W 111° 34'
15	b / s	Teton	N 47° 51'	W 111° 40'
16	b / s	Pondera	N 48° 02'	W 111° 39'
17	b / s	Chouteau	N 48° 05'	W 111° 29'

Table 1. Research site locations and production practices compared (cont.).

Site	Comparison	County	Latitude	Longitude
18	nt / t b / s	Cascade	N 47º 39'	W 111º 35'
19	nt / t	Teton	N 47º 49'	W 111º 59'
20	b / s	Teton	N 47º 50'	W 111º 34'

[1] nt / t = no-till / tilled
[2] b / s = block / strip

Figure 1. Approximate locations of research sites.

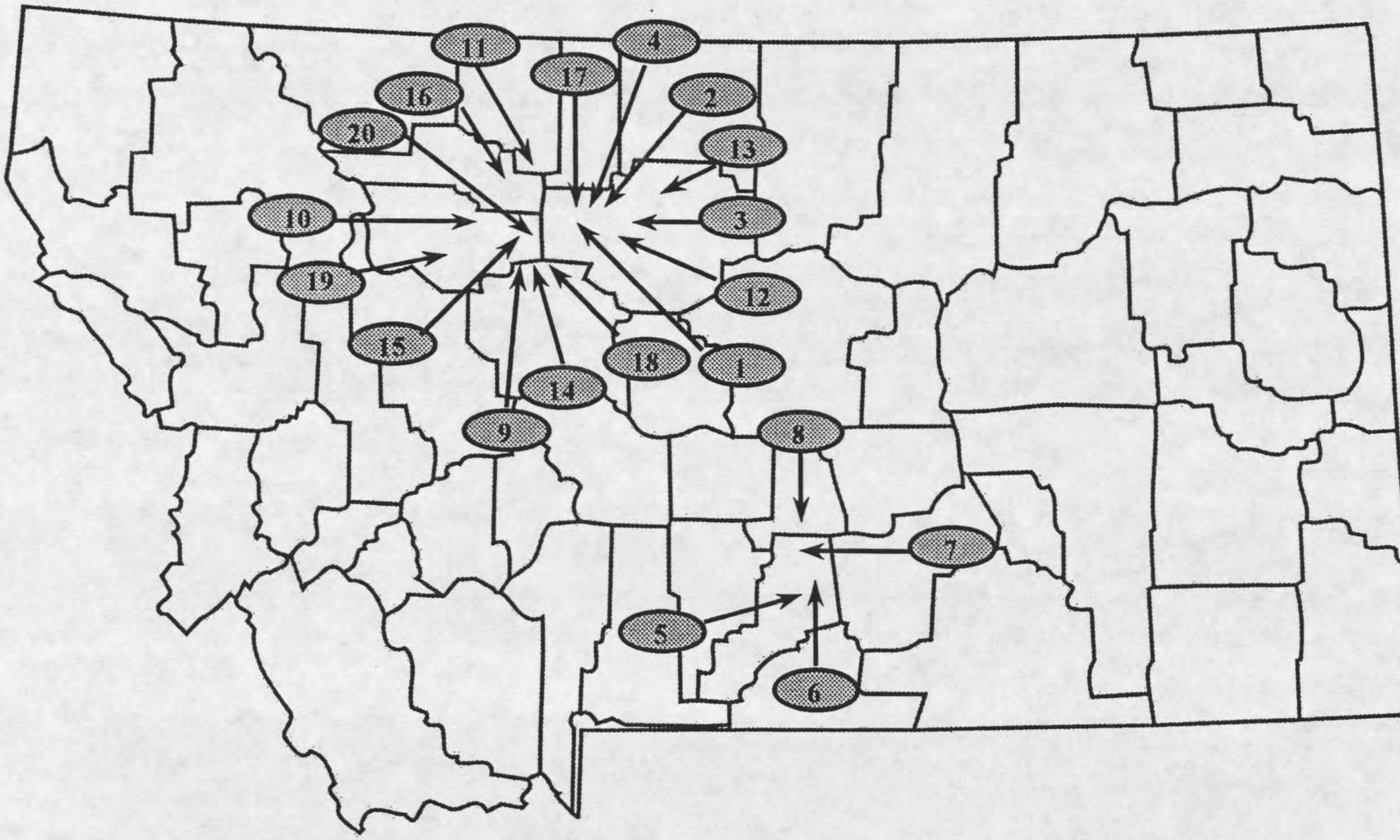

Table 2. No-till / tilled fields: Year sampled and production practices.

Site	Year	nt / t [1]	Tillage Type	sw / ww [2]	h / s [3]	b / s [4]
1	1998	t	N / A	ww	s	s
1	1998	nt		ww	s	b
2	1998	t	N / A	ww	h	s
2	1998	nt		ww	h	b
3	1998	t	N / A	ww	h	b
3	1998	nt		ww	h	b
4	1998	t	min [5]	ww	h	s
4	1998	nt		ww	s	b
9	1998	t	min	ww	s	s
9	1998	nt		ww	s	s
10	1998	t	min	ww	s	s
10	1998	nt		ww	s	b
11	1998	t	int [6]	sw	s	b
11	1998	nt		sw	s	b
6	1999	t	int	ww	s	s
6	1999	nt		ww	s	s
12	1999	t	int	ww	s	s
12	1999	nt		ww	s	s
4	1999	t	mod [7]	ww	s	s
4	1999	nt		ww	s	s
13	1999	t	int	ww	s	s
13	1999	nt		ww	s	s
9	1999	t	min	ww	s	s
9	1999	nt		ww	s	s
18	2000	t	mod	ww	s	s
18	2000	nt		ww	s	s
19	2000	t	int	ww	h	b
19	2000	nt		ww	h	b

[1] nt / t = no-till / tilled
[2] sw / ww = spring wheat / winter wheat
[3] h / s = hollow / solid-stemmed
[4] b / s = block / strip field
[5] min = minimum
[6] int = intense
[7] mod = moderate

Table 3. Block / strip fields: Year sampled and production practices.

Site	Year	nt / t [1]	sw / ww [2]	h / s [3]
5	1998	t	ww	h
6	1998	nt	ww	s
7	1998	t	ww	h
8	1998	t	ww	h
10	1998	t	ww	s
5	1999	t	ww	h
14	1999	nt	ww	s
15	1999	nt	ww	s
16	1999	nt	ww	s
17	2000	nt	ww	s
15	2000	nt	ww	s
20	2000	nt	sw	s

[1] nt / t = no-till / tilled
[2] sw / ww = spring wheat / winter wheat
[3] h / s = hollow / solid-stemmed

Stem Sampling

Plant samples were collected at each location to determine sawfly infestation, sawfly cutting, and sawfly parasitism levels. Mature plant stems were collected immediately before harvest. Stems were collected by uprooting entire plants to ensure that the sawfly 'stubs' were obtained. The plants were then secured with twine, labeled, and transported to the lab for processing. The wheat type (spring or winter, solid or hollow) was determined, but the exact cultivar was sometimes unknown. Locations in which the wheat cultivar was not known were selected to match hollow or solid-stemmed, and winter or spring wheat. Only fields with the same wheat cultivar or stem character were selected for comparison at each location.

Tillage System Comparison

Neighboring fields that were as similar as possible, except for differences in tillage system, were chosen at each location. The tillage type was categorized by the amount of crop residue on the soil surface. Tilled fields with >90% of the stubble remaining on the soil surface were designated as "minimum tillage", fields with approximately half of the stubble remaining were "moderate tillage", and fields with no visible stubble were labeled "intensive tillage". Four samples were taken at each location. The first sampling location was randomly assigned, and sample spacing along the long axis of the field was constant thereafter. Samples were taken in two fields, one that bordered an untilled and one that bordered a tilled summer fallow field (Figure 2, ☆ 's). Samples were taken from the same side of each field (i.e., from the east edge) at each location because adults fly upwind to existing crops, possibly causing sawfly infestation and parasitism levels to vary between opposing field edges. In 1998, samples consisted of four replicates of approximately 100 randomly selected stems located within 1-5 m of the field border. In 1999 and 2000, samples consisted of four replicates of all stems in a 30 cm length of a row located within 1-5 m of the field border.

Block / Strip Field Comparison

Strip fields adjacent to a block field were chosen at each location, which matched stubble management practice and cultivar type. In 1998, a single strip field was paired with a block field. In 1999 and 2000, four strip fields were matched with a single neighboring block field. Mature plant stems were collected as described above. For every strip at each location, eight samples were taken. Four samples at the field edge and four corresponding samples were taken in the center of each strip. The first sampling location was randomly assigned, and sample spacing along the long axis of the field was constant thereafter. In 1998,