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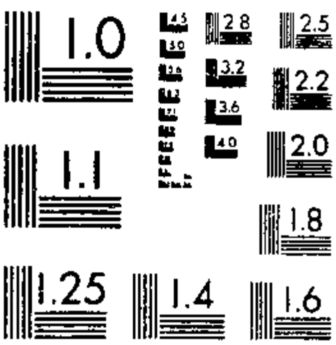

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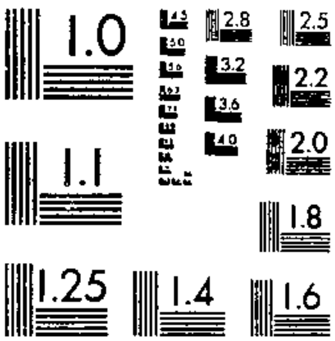

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STEM SAWFLIES
of ECONOMIC IMPORTANCE
in Grain Crops in the United States

By L. E. Wallace and F. H. McNeal

Technical Bulletin No. 1350

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Contents

STEM SAWFLIES

OF ECONOMIC IMPORTANCE

in Grain Crops in the United States

By L. E. WALLACE, *Entomology Research Division*, and F. H. McNEAL, *Crops Research Division, Agricultural Research Service*

Three stem sawflies of grasses are economically important pests of wheat production in Canada and the United States. *Cephus cinctus* Norton is endemic to the Western Hemisphere. *Cephus pygmaeus* (L.) and *C. tabidus* (F.) have been unintentionally introduced from Europe. The larvae of these species mine wheat stems during the summer and cut them close to the ground before harvest in the fall. *C. cinctus* (wheat stem sawfly), which occurs in the West, has transferred from its wild grass hosts to wheat as the grasslands were cultivated. *C. pygmaeus* (European wheat stem sawfly) and *tabidus* (black grain stem sawfly) perhaps have made this same transfer, but so long ago that it has not been documented in the literature.

In 1900, research was undertaken to control these pests in Canada and the United States. This work has been coordinated by the two countries. It is the purpose of this bulletin to bring together the published and unpublished data on this research so as to clarify future endeavor in controlling these sawflies.

TAXONOMY

Sawflies belong to the order Hymenoptera (wasps and bees), and they have been placed by taxonomists in the more primitive division Chalastogastra or Symphyta. Nearly all members of the Symphyta are plant feeders in the larval stage. Many female adults possess a sawlike ovipositor, which can be inserted into plant tissue for the purpose of oviposition. In the family Cephidae, which includes the three species under discussion, all larvae are miners of grass stems or the tender shoots of trees and shrubs.

The family Cephidae is further divided into tribes, and these three species are included in the grass-boring tribe Cephini. The adults of this group are slender insects, which are usually found among the grasses in which they lay their eggs. They are represented throughout the world, but the largest number of species is found in Europe and Eurasia (*8*, *12*, *45–47*, *173*, *174*, *184*, *200*, *201*).[1] They are weak fliers and remain hidden in plant foliage during rains or

[1] Italic numbers in parentheses refer to Literature Cited, p. 37.

windy weather. The adults of *Cephus* are commonly collected on yellow-flowered weeds, such as mustard, which grow near grainfields.

Nomenclatorial designations of sawflies have undergone changes through the years. To illustrate this, the nomenclatorial history of *C. cinctus* Norton is presented. Norton (*156*) described *C. cinctus* in 1872 based on specimens collected from Colorado with cotypes from Nevada and California. In 1890, Koebele (*103*) noted the larvae working in grass stems at Alameda, Calif. He reared some adults from the grass and sent them to Riley, who in a joint publication with Marlatt (*176*) described them as *Cephus occidentalis* Riley & Marlatt in 1891. Six years later Ashmead (*6*) described new specimens as *Cephus graenicheri* Ashmead. The first valid name employed, *C. cinctus*, is the correct one, and all others are considered synonyms.

Similarly, *C. pygmaeus* (L.) was described by Linnaeus in 1766 as *Sirex pygmaeus* L., has borne nine synonyms, and has been placed in the new genus *Cephus*.

C. tabidus (F.) was described by Fabricius in 1775 as *Sirex tabidus* F., has borne five synonyms, and now is placed in the genus *Cephus*. The genus *Sirex*, in which the last two species were originally placed, has been more narrowly delineated and now applies to species of hymenoptera that are borers in trees in the larval stage; thus, the new genus *Cephus* was erected for the grass stem-boring sawflies.

DESCRIPTION OF ADULTS AND LARVAE

The stem sawfly adults are slender insects, about 10 times as long as wide. The legs are long and slender, and the two pairs of well-developed wings when at rest extend beyond the end of the abdomen. The length, exclusive of the antennae, ranges from one-fourth to three-fourths inch. The antennae are approximately one-half the body length. The overall appearance is wasplike, but the abdomen is broadly joined to the thorax and not constricted as in wasps. (Fig. 1.)

The three species are comparable in size but vary in coloration. In general, they are distinguishable by the amount of yellow on a shiny black background. *C. cinctus* has the most yellow, *pygmaeus* a little less, and *tabidus* very little. The following key, prepared by P. R. Meyers and presented in Ries' article (*173*), illustrates this difference in pigmentation of the adults:

1. Abdomen without dorsal, transverse, yellow bands; ovipositor sheaths when viewed dorsally, swollen or laterally enlarged toward their apices; males with horseshoe-shaped depressions on last two apical ventral segments ---- *Cephus tabidus* (F.)

   Abdomen with dorsal, transverse, yellow bands; ovipositor sheaths when viewed dorsally, not swollen or laterally enlarged toward their apices; males without horseshoe-shaped depressions on last two apical ventral segments ---- 2

2. Stigma and costa dark brown, of uniform color; mesepisternum black; femora black; apical tergite and venter black; face and scutellum black (face of male with yellow spots) ---- *Cephus pygmaeus* (L.)

   Stigma in greater part and costa yellow; mesepisternum with upper angle yellow; femora mostly yellow; apical tergite and usually venter in part yellow; face and scutellum of female usually black but occasionally with yellow spots ---- *Cephus cinctus* Norton

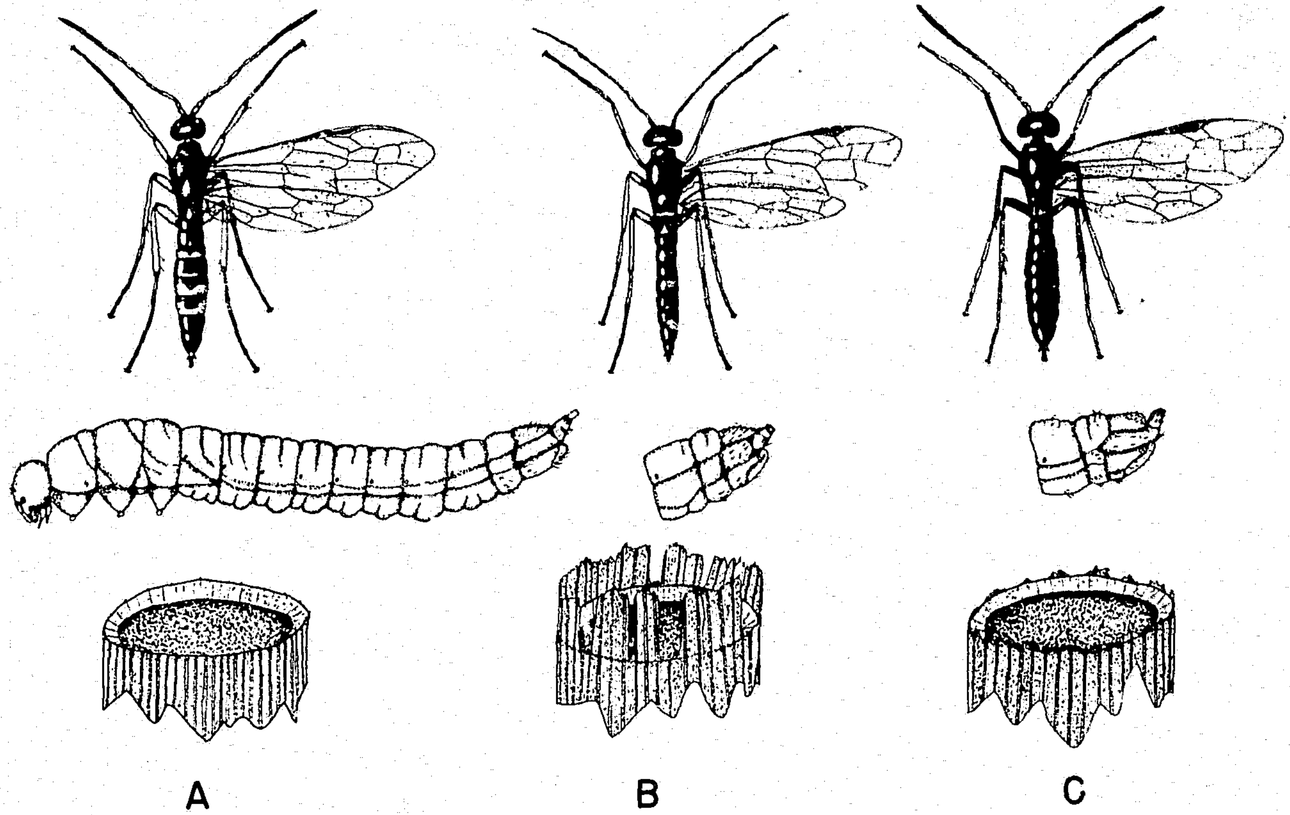

FIGURE 1.—Adults, larvae, and cut stems of three species of sawflies: *A*, *Cephus cinctus*; *B*, *C. pygmaeus*; *C*, *C. tabidus*.

The larvae are more difficult to separate. They are slender, legless, and S-shaped, with a brown head capsule and mandibles. The posterior end is armed with stiff bristles (fig. 1), which aid in locomotion up and down the host stem (*64, 199, 246*). The following key by Gahan (*64*) gives the distinguishing characters:

1. Dorsal anal lobe of 10th tergite viewed from side, triangular, sloping gradually from base to apex, and anterior end of lobe much thicker than posterior end, which is more or less acute. Spines on anal prong each arising from small, more or less chitinized tubercle and closely grouped about apex of enlarged fleshy part just basad of short chitinized apical ring. Eighth and ninth tergites apparently glabrous 2

   Dorsal anal lobe viewed from side not triangular, not sloping gradually from base to apex but convexly rounded, posterior end of lobe as thick dorsoventrally as anterior end and nearly perpendicular. Anal prong completely encircled by two irregular series of widely separated, short, stiff spines, which do not arise from chitinized tubercles. Eighth and ninth tergites each with transverse row of distinct short hairs ..... *Cephus tabidus* (F.)

2. Anal prong terminating in short chitinized ring, which is not as long as broad. Spines basad of chitinized ring few in number, confined to single transverse row on dorsal surface. Dorsal, lateral, and ventral lobes sparsely hairy *Cephus pygmaeus* (L.)

   Anal prong terminating in chitinized tubelike process, which is distinctly longer than broad. Spines basad of apical tubelike process numerous, arranged in two irregular contiguous series completely encircling base of tube. Anal lobes distinctly hairy .... *Cephus cinctus* Norton

HISTORY AND DESCRIPTION OF DAMAGE

Sawflies damaging grain in the Western Hemisphere were first reported in 1887, when *pygmaeus* was noted at Ithaca, N.Y., (*24*) and in eastern Canada in the same year (*20, 69*). *C. cinctus* was reported in 1895 damaging grain near Moose Jaw, Northwest Territories, (*3*) and *tabidus* in 1899 at Riverton, N.J., (*223*).

C. cinctus has become the most serious pest of the three species. In 1895, it was noted in wheat by John Wenman at Souris, Manitoba. He obtained specimens from his farm at Souris and sent them to Fletcher (*61*) for identification. Specimens from Moose Jaw were sent in the following year (*61*). The insect was found at Bozeman, Mont., in 1900 (*144*). After 1900, the study of this potential pest attracted the attention of entomological workers.

In 1902, Fletcher wrote in a letter that he had found *cinctus* larvae in many grasses in the Northwest Territories (*3*). In 1905 and 1906, G. L. Reeves found the larvae in *Agropyron* grasses in Wyoming and the Dakotas and in wheat at Kulm, N. Dak., (*3*). In 1907, E. O. G. Kell found this sawfly in wheat at Minot, N. Dak., (*3*). In 1908, Fletcher found damage in wheat in Manitoba and Saskatchewan (*3*). In 1909, B. B. Penhallow reported severe damage around Minot (*4*). In 1910, economic damage was reported in Montana at Bainville (*144*). Criddle (*27*) started concentrated studies on the sawfly in Canada in 1907, and Ainslie (*3*) began studies in the Dakotas and other States in 1911. Ainslie found *cinctus* feeding in native grasses in a number of States in the area and predicted it could well become a major pest of cereal crops, as had Riley and Marlatt (*176*) in 1891. Serious losses were reported in Canada in 1926 (*102*), 1931 (*7*), and 1943 (*2*). From 1943 to 1946, this sawfly was found to be increasing its area of economic importance in Montana (*144*) and North Dakota (*142*). A similar report was made from Canada in 1955 (*10*). Through the years numerous authors have mentioned the damage caused by *cinctus* (*16, 23, 26, 28–30, 32, 34, 37, 39, 40, 43, 54, 55, 62, 66, 74, 79, 131, 239–241*).

The history of *pygmaeus* is not so well documented as that of *cinctus*. *C. pygmaeus* has been reported damaging grain in southern Russia from 1893 to 1914 (*44, 104, 158, 224–227*). In 1918, a serious outbreak was reportedly held in check in Russia by the parasite *Collyria calcitrator* (Gravenhorst) (*12*). Serious outbreaks and damage were reported in North Africa in 1897 (*179*), in France in 1914 (*125*), in Germany in 1930 (*203*), and in Spain in 1921 (*1*). The insect was found in eastern Canada and in New York in 1887 (*223*). The area in Canada has not increased. However, in the United States infestations were reported from Maryland in 1915 (*25*) and from Pennsylvania in 1919 (*173*). Serious damage occurred in New York in 1921 (*173*). Some damage has resulted in areas of the East where *pygmaeus* occurs (*60*), but parasites introduced in the early 1930's have prevented this species from causing much loss.

C. tabidus has long been a pest of cereal grains in Europe. Competition undoubtedly occurs between *tabidus* and *pygmaeus* since they inhabit the same areas. *C. tabidus* contributes to the loss attributed to *pygmaeus*, but it is seldom given credit in the literature for damage it caused. Collections of *tabidus* were made prior to 1899 at Riverton, N.J., and during the next 20 years adults were reared or collected from scattered localities in Pennsylvania, Maryland, Delaware, and Virginia (*64*). The insect appeared in Ohio in 1934 and caused spotty damage there (*70*).

The loss due to sawfly infestation is twofold. When the larvae tunnel the stems, they interfere with nutrient transfer and also weaken the stem. This injury causes a smaller and lighter kernel (*197*). The larvae also girdle the stem at the base when preparing for hibernation. Girdled stems break off and lodge or fall to the ground (fig. 2). Some of the fallen heads are lost in harvesting, and occasionally wet weather causes molding or germination of their seeds. The losses in kernel weight and cutting of the stem are similar for all three species. The loss from reduced kernel weight ranges from 5 to 30 percent, but the estimated loss from fallen heads is not available.

Damage to the cereal grains by sawflies is caused solely by the larvae. The female adult punctures the stem to oviposit (fig. 3, *B*), but this does not permanently injure the stem nor has it been noted to produce an avenue for disease penetration to any great extent. The larvae, on the other hand, feed by tunneling up and down inside the stem (fig. 3, *A*). This tunneling, feeding, and ultimate cutting of the stem cause the loss. Ainslie (*3*), referring to *cinctus*, stated, "The quality of grain from the fallen straw is naturally somewhat below normal since the work of the larvae in the stems produces some injury in the heads as they fill." Losses due to tunneling by *cinctus* may range from 10 to 20 percent (*138, 197*).

Seamans et al. (*197*) found that a bushel of wheat weighed 2 pounds less from infested than from uninfested stems and usually rated one grade below the latter. For *pygmaeus*, this loss has been placed at

FIGURE 2.—Sawfly cutting of susceptible wheat variety.

6–20 percent (*117, 210, 228, 229*). Golembiowska (*67*) estimated the loss at 7–27 percent based on a 3-year study in Russia, and losses of 27.9–33.1 percent were found in Italy (*123*). Such losses for *tabidus*-infested grain also have been indicated, inasmuch as this species is found in the same areas as *pygmaeus* and often in the same fields in the Eastern Hemisphere.

Comparison of yield from heads of infested and uninfested stems contains a built-in pitfall (*173, 197*). Larger stems are usually infested, whereas slender tiller stems are not. Therefore, heads on infested stems often produce more grain than heads on uninfested stems, as has been found by some workers (*148–150*).

"White top" of wheat and grasses has been attributed to the tunneling and feeding of the sawfly larvae; however, this apparently occurs rarely and is of minor importance (*197, 245*). White top or yellowing of the head is most often the product of root rot rather than the result of sawfly tunneling.

The loss due to fallen heads depends on the infestation, number of plants per square foot, and wind and precipitation before harvest. In a thin stand and severe infestation nearly the entire crop might break and fall to the ground, whereas in a thick stand and light infestation only a very few heads might fall. Fallen heads are difficult to pick up for threshing and much of the fallen grain may be lost if heavy rains occur. Shattering may also occur in the process of picking up the fallen grain.

The monetary loss from sawflies varies from year to year, and is often difficult to determine. Losses caused by *cinctus* were estimated at 1,917,484 bushels for Montana and North Dakota in 1951 (*144*) and 20 million bushels annually for Canada (*164*). King (*102*) calculated

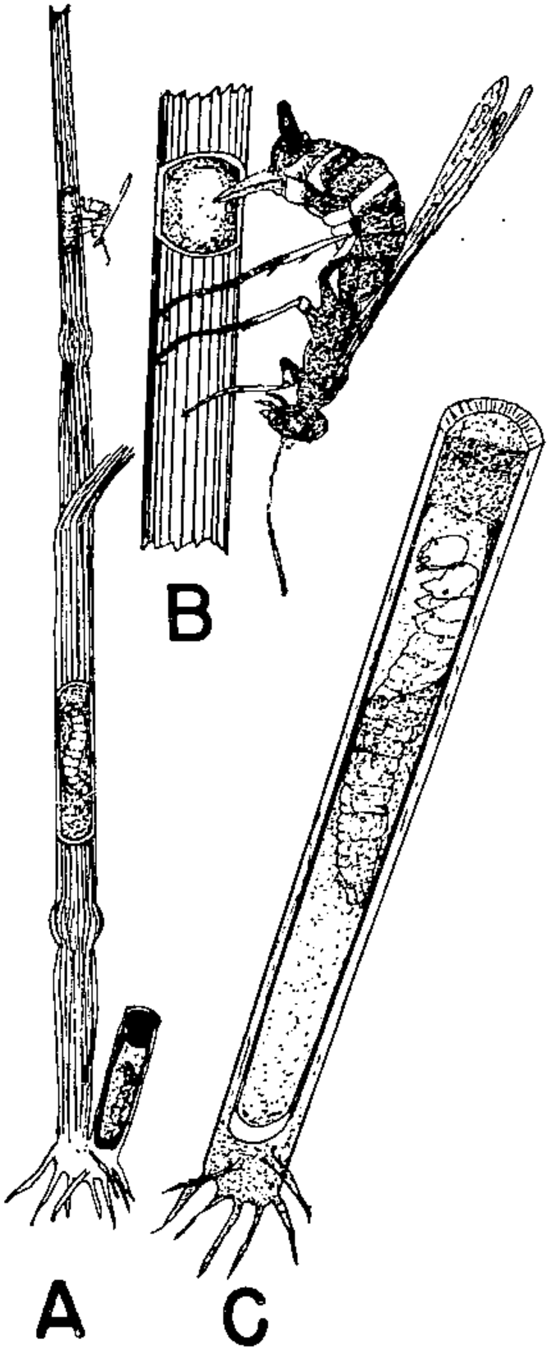

FIGURE 3.—Damage caused by wheat stem sawfly: *A*, Oviposition and larval feeding in wheat; *B*, ovipositing female (enlarged); *C*, overwintering larva in cocoon in stub (enlarged).

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the loss over a 5-year period in Canada at 2,468,000 British pounds and stated that much of the loss occurred in the 1926 outbreak. These estimates are based on surveys of infestation and cutting by the sawfly.

Attempts to determine the damage by sawfly populations have not met with success. Unpublished studies conducted in 1951–54 in Montana by W. V. Campbell, formerly with the Entomology Research Division, and R. L. Gallun, of this Division, showed that an increase of over three females per square foot added little to the ultimate cutting. Work in Canada showed little difference between 1.5 and 3 females per square foot (*85*). Variability of the season and its effect on the crop complicate this type of study. For example, in dryland farming, scant rain during the growing season produces a rapidly maturing crop, and many of the larvae may be destroyed before cutting occurs. Similarly, excess moisture may reduce larvae survival in the stems. A better understanding of the effect climatic conditions have on the sawfly larvae and the effect of the larvae on the host plants under these conditions is necessary.

DISTRIBUTION OF SAWFLIES

C. cinctus is widely distributed in the United States west of the Mississippi River (fig. 4). Its southern limit seems to be about the 36° parallel. Ainslie established the locations of collections in the United States and noted they were in the States west of the Mississippi, except Arkansas, Louisiana, Oklahoma, Texas, and Arizona (*3, 4, 175*). In Canada the range is listed as southeastern Alberta, the Peace River area of Alberta, southern Saskatchewan, and the southwest corner of Manitoba (*145*). In spite of the wide range of this insect, Davis (*38*) noted that economic loss is limited to a small part of this area.

The established distribution of *cinctus* in Canada is the area of economic loss, except in the Peace River area, whereas in the United States serious losses have been reported only in northern Montana, North Dakota, and pockets of South Dakota, Wyoming, and Nebraska. Of course, the areas of economic importance in the United States are by no means constant. Cultural practices, climatic conditions, and phenology of the hosts affect sawfly survival. This is apparently true in Canada also, as indicated by a study in 1923–27, when *Triticum aestivum* L., which is often cut 70 percent or more, was found to be cut only 33.7 percent (*143*).

C. pygmaeus and *tabidus* occupy about the same area in the Eastern Hemisphere. They are widespread and can be found in England, Scandinavia, Russia, Germany, Holland, France, Italy, Spain, Algeria, Arabia, and Iraq (*154, 155, 159, 170, 171, 173, 178, 179, 202, 224, 225, 236, 246*). In the United States both are confined to the Eastern States (fig. 4). *C. pygmaeus* was reported near Ottawa, Canada, and in New York in 1887 and has since spread into Massachusetts, Pennsylvania, Maryland, and Delaware (*64*). *C. tabidus* can be found in Pennsylvania, New Jersey, Delaware, Maryland, Virginia, eastern West Virginia, and eastern Ohio (*70–73, 93, 184, 223*). These two European species in the United States still fluctuate and may eventually occupy a larger area than they now do.

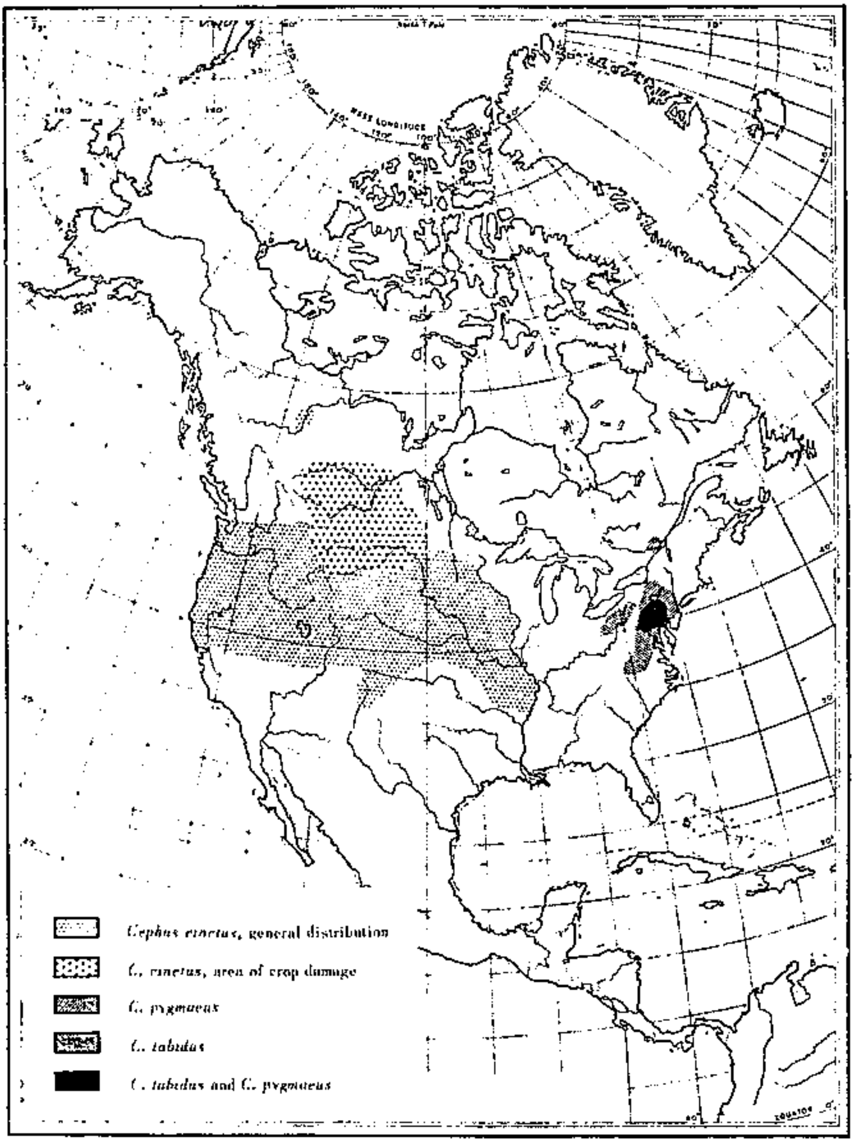

FIGURE 4.—Distribution in United States and Canada of three species of grain-infesting sawflies.

HOST PLANTS

C. cinctus is very flexible in host possibilities. Among the cultivated grains, nearly all are accepted as hosts, although wheat seems to be preferred. Solidness of stem is a deterrent in wheat, but in oats, which is hollow stemmed, the larvae fail to develop. The species of cultivated grains in which *cinctus* larvae can develop are as follows: *Hordeum vulgare* L., *Secale cereale* L., *Triticum aestivum* ssp. *aestivum*, ssp. *compactum* (Host) MacKey, ssp. *spelta* (L.) Thell., ssp. *sphaerococcum* (Perc.) MacKey, *carthlicum* Nevski, *dicoccum* Schübl., *durum* Desf., *monococcum* L., *polonicum* L., *timopheevii* (Zhuk.) Zhuk., and *turanicum* Jakubz. *T. monococcum* is a slender stemmed wheat and is not readily chosen for oviposition. *H. vulgare* and *S. cereale* do not allow many of the larvae to develop. *T. durum*, *polonicum*, and *timopheevii* show some resistance to larval development.

In addition to the cultivated hosts there are many wild grasses that allow development of *cinctus* larvae to some extent. Following is a list of grasses, with notations on the host suitability and the author of the notation indicated: *Agropyron caninum* (L.) Beauv. (*3*), *cristatum* (L.) Gaertn. (*52*) (has slender stems in dense stands), *dasystachyum* (Hook.) Scribn. (*3*), *elongatum* (Host) Beauv. (*52*) (solid stem, deleterious to larvae), *griffithsii* Scribn. & Smith ex Piper (*52*), *intermedium* (Host) Beauv. (*41*, *42*), *repens* (L.) Beauv. (*3*, *168*) (large stem, more suitable than *smithii*), *smithii* Rydb. (*31*, *42*) (half of stems too slender for oviposition), *subsecundum* (Link) Hitchc. (*3*),[2] *trachycaulum* (Link) Malte ex A. F. Lewis (*168*) (slender stem, some cutting) (*3*, *33*, *41*, *42*) (75-percent infested and 35-percent parasitized), *Beckmannia syzigachne* (Steud.) Fern (*52*), *Bromus inermis* Leyss. (*3*, *36*) (parasitism high in this grass), *secalinus* L.,[2] *tectorum* L. (larger stems cut in greenhouse),[3] *Calamagrostis* sp. (*3*), *Calamovilfa longifolia* (Hook.) Scribn. (*41*, *42*), *Deschampsia* sp. (*3*), *Elymus canadensis* L. (*3*), *cinereus* Scribn. & Merr. (many dead larvae, some cutting),[3] *condensatus* Presl (*3*), *dahuricus* Turcz. (*52*), *glaucus* Buckl. (many dead larvae, some cutting),[3] *innovatus* Beal. (*3*), *macounii* Vasey (*3*), *Festuca* sp. (*3*), *Hordeum jubatum* L. (*3*)[2] (stems rarely large enough for larval development), *montanenses* Scribn.[2] (stems rarely large enough for larval development), *Phleum pratense* L. (*3*, *52*) (bulbous spring growth crushes larvae), *Stipa viridula* Trin. (*52*) (solid stem, very little cutting).

Criddle (*31*) stated that *Agropyron* species were preferred by *cinctus* as host plants prior to the commercial production of wheat. Mills (*140*, *141*) stated that apparently the gramas (*Bouteloua*), bluegrasses (*Poa*), and fescues (*Festuca*) are little infested. From observation and reports in the literature, slender stemmed grasses are shunned by the female sawfly. There is also the possibility of mechanical resistance of the stem to oviposition, but there is no definite evidence. Also, the phenology of the grasses at the time of sawfly emergence affects host selection. Criddle (*31*) believed that cultivated grains were unsuitable hosts. He noted that small adults were produced and that the population dissipated. However, research workers are well aware that since these observations in 1917 the sawfly has adapted to wheat.

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[2] MANGLITZ, G. R., and BENTON, CURTIS. INVESTIGATIONS OF THE WHEAT STEM SAWFLY IN THE WINTER WHEAT BELT OF THE UNITED STATES. U.S. Dept. Agr. Res. Serv. Spec. Rpt. W-17, 13 pp. 1954.

[3] Personal observation by L. E. Wallace.

C. pygmaeus and *tabidus* have a much smaller host list and are restricted largely to cultivated grains. The first will attack *Bromus secalinus*, wheat, barley, rye, and oats (*64, 173, 231*). The second attacks wheat, barley, rye, and oats. Indications are that both originally attacked wild grasses, probably those closely related to the cultivated grains of today. The reduction in host plasticity is perhaps a result of a long period of development in cultivated grains. This is borne out to some extent by the fact that the *Cephus* species are most prevalent in the Mediterranean area and the Eurasian steppes (*8*). In this area there are many species attacking grasses, but only the two mentioned are a problem in cultivated grains. Other grasses are attacked by unidentified species of *Cephus* in Russia (*177*).

Oats and flax are examples of plants where sawflies deposit eggs, but fail to develop (*53, 89*).

EMERGENCE AND HABITS OF ADULTS

Emergence of the adults varies with the latitude. An adult of *cinctus* was swept from alfalfa in Utah as early as April 26 (*3*). In Montana and Canada the adults usually appear in the middle of June. At Ithaca, N.Y., *pygmaeus* appears about the first of June (*173*) and *tabidus* about a week later (*223*). In Poland the time of emergence of *pygmaeus* is also the first of June (*11*). The factors that affect emergence are similar in all three species, but they have been most studied in *cinctus*.

The weather, soil temperature, and soil moisture affect emergence (*195*). The weather must be sufficiently warm to induce the adults to emerge, soil moisture must be high enough for transformation to pupae, and there must be enough rainfall to prevent desiccation and killing of the pupae. Ideal conditions have been summarized by Seamans (*195*): A warm, moist May, a hot June with sufficient moisture to insure good plant growth, and enough dry weather to allow the sawflies to emerge. Peaks of emergence occur 2–4 days after a heavy rainfall (*124*). Warm, dry weather following snowmelt was noted as most conducive to emergence of *pygmaeus* (*173*).

The duration of adult emergence is also affected by these same conditions. Excessively hot weather coupled with drying winds tends to shorten the emergence period. More moderate conditions allow the emergence to continue into mid-July. These same conditions also affect the longevity of the adults. The lifespan has been estimated as 5–8 days for *cinctus*, and this has been extended by furnishing the sawflies with sugar water. H. W. Somsen, Entomology Research Division, stated in an unpublished report that he retrieved a marked adult 12 days after release. Thus, the length of the adult life can be shortened or lengthened depending on the moisture available, activity due to climatic conditions, and possibly plant exudations.

Reproduction in the sawflies is usually arrhenotokous (*122, 208*), with unfertilized females producing only males. Mackay (*122*) found 18 chromosomes in females of *cinctus*, with only the haploid number in the males. In this species, however, a thelyotokous parthenogenetic race appears sporadically. One was reported in Canada in 1938 (*51*).

No males were found in one area, but females were abundant. This situation persisted for more than a year and finally disappeared. Mackay (*122*) examined females of this race and found no cytological difference between the arrhenotokous and thelyotokous races. Smith (*208*) expressed some doubt of the actual existence of such a race.

Since female sawflies are usually produced only from fertilized eggs, the sex ratio and habits of the male have a direct bearing on the number of females produced. In the field the sex ratio varies as the season progresses (*58*). Early in the sawfly flight there is a predominance of males, but as the flight progresses the ratio becomes reversed (*90*). Thus, the later eggs oviposited have a much poorer chance for fertilization, because the males are fewer. Also, the males remain mostly in the margin of the field. The earlier eggs oviposited produce 50 to 60 percent females, whereas those oviposited toward the end of the flight or in the center of the field produce less than 50 percent females.

The ability to selectively fertilize the eggs cannot be demonstrated in the three species of sawflies. Wall (*234*) and Munro et al. (*150*) obtained a larger number of males from thinner stems, and McGinnis [4] found more males produced in Thatcher than Red Bobs. These findings indicated there might be some selective fertilization; however, Holmes and Peterson (*90*) were able to explain the larger number of males on the basis of later oviposited eggs. They further pointed out that time of oviposition is not always the complete picture, because sometimes these early eggs and larvae do not survive and the later oviposited eggs do.

Copulation can take place immediately after adults emerge both in captivity and in the field. The location seems of little importance, although it has never been observed while the insects were flying. Ries (*173*) found *pygmaeus* copulating almost entirely on yellow flowers, and the same habit is indicated for *tabidus*.

During copulation the male clings to the back of the female with his abdomen curved down and under the female ovipositor. This position is held for about 1 minute in *cinctus* (*3*), and Ries (*173*) placed it at 10 minutes for *pygmaeus*. However, the duration may vary in both species. Even though the duration of copulation may be long in some cases, there is no indication that a large amount of sperm is stored by the females. In fact, their acceptance of other males after copulation indicates very little storage.

There is some competition between the males, and in confinement their antagonism is shown in snipping off each other's antennae.

Adult activity is associated with weather conditions. None of the three species are active during cloudy or windy conditions. Mating can take place in *cinctus* at 63° F., but sunny days with temperatures of 68° or higher are necessary for oviposition (*195*). On sunny days a wind over 20 m.p.h. causes cessation of activity. Temperatures above 90° also inhibit activity. The most activity has been noted on warm, sunny days when there is a 3- to 5-m.p.h. wind. The males are active at lower temperatures than are the females. With cessation of activity,

[4] McGINNIS, A. J. SEX RATIO ON THE WHEAT STEM SAWFLY CEPHUS CINCTUS NORT. 1950. [Unpublished doctor's thesis. Copy on file in Library, Mont. State Col., Bozeman.]

the sawflies rest on the leaves and stems of the host plant, clinging with all legs and closely adhering to the plant.

Adults spend little time in feeding, since they apparently do not need nourishment. However, *cinctus* has been noted to take moisture from damp sand (*3*). Farstad, in unpublished notes, observed that this species did feed on mustard flowers.[5] European authors (*59*, *200*) give yellow flowers, alfalfa, and other blue flowers as favorite congregating and resting sites for *pygmaeus*.

The length of time from copulation to oviposition has not definitely been established, but it is usually several hours for *cinctus*. It could be as short as 1 hour, but during periods of inactivity it could be much longer. Females make their way to a suitable host and begin to seek an oviposition site shortly after copulation.

The adults of all three species are weak fliers and do not move far from the emergence site. *C. cinctus* has been reputed to travel as much as one-half mile if suitable plants are not available (*35*), and under ideal conditions a mile or more might be covered (*57*). In an unpublished report, H. W. Somsen recovered a marked female that had traversed 35 rods of fallow and 135 rods of grass land. These estimates are extremes. Evidence of oviposition indicates *cinctus* will accept such undesirable hosts as oats and flax rather than traverse long distances. *C. pygmaeus* follows this pattern also. *C. tabidus*, which has no known wild hosts, may make a much more concerted effort to find a suitable host.

What constitutes a suitable host and how discerning the female sawfly is are debatable. Early records on *cinctus* were contradictory. Seamans and Farstad (*196*) found that female sawflies preferred *Agropyron smithii* plants with heads, although Ainslie (*3*) stated earlier that they preferred plants without heads. Holmes and Peterson (*86*) found that preference for oviposition was related to the stage of plant growth at the time of sawfly flight. Different varieties of wheat reached their peak attractiveness at different times during the growing season. Farstad and Platt (*57*) noted that wheat was preferred over barley. Spring wheat is preferred to winter wheat, but winter wheat that is late is often heavily infested (*86*). However, the earlier emerging *pygmaeus* prefers winter wheat. Golembiowska (*67*) gave winter wheat and winter rye as the preferred hosts, and Udine (*223*) noted that *tabidus* prefers spring wheat.

The stage of plant growth that is most desirable has been clarified by Holmes and Peterson (*86*). They found that *cinctus* preferred the more tender part of the internode for oviposition. Furthermore, they found that females prefer an elongating internode. The wheat plant begins elongating in the lower internodes first and these become mature and harden first. The elongation of an internode begins at the bottom and this elongation continues in the basal part after the upper part has ceased to elongate and has become hardened. Females seek the elongating part of the lowest internode for oviposition. Thus, early emerging females oviposit lower in the stem than late emerging

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[5] HOLMES, N. D. ECOLOGY OF THE WHEAT STEM SAWFLY CEPHUS CINCTUS NORT. 1954. [Unpublished doctor's thesis. Copy on file in Library, Oreg. State Col., Corvallis.]

females. In general, more eggs are placed in plants with the largest number of elongating internodes (*86*).

Udine (*223*) stated that *tabidus* preferred the upper internodes, and Ries (*173*) stated *pygmaeus* preferred the third internode below the head. These variations indicate that plant maturity affects the selection of an oviposition site in these species also. There is some indication that the hollow part below the node in solid-stemmed wheats is selected for oviposition (*86*).

Diameter of the stem is another important factor in host selection. Large stems are preferred by *cinctus* and *pygmaeus* (*3*, *85*, *200*) and the more slender stems are shunned. This selection is very likely practiced by *tabidus* as well.

Female selectivity is apparent only when a diverse source of host material is available. Ainslie (*3*) and Seamans (*195*) both reported 3–4 eggs of *cinctus* in short spring grain with only one internode. Farstad (*54*) reported fewer eggs in solid stems. However, this selectivity can be explained on the basis of rate of plant growth rather than solidness of stem (*86*).

There seems to be some resistance to oviposition. The female may exercise some selectivity in choosing an oviposition site. Stem diameter and stage of development are more important factors in determining oviposition sites than is solidness of stem.

Ainslie (*3*) working with *cinctus* and Ries (*173*) working with *pygmaeus* described oviposition, and both descriptions are similar. Udine (*223*) reporting on *tabidus* did not describe oviposition, but indicated it was similar to that of *pygmaeus*. The adults alight on or crawl to the wheat plant and crawl up to the top, usually stopping now and then to clean the body antennae and legs. They then descend the plant in a slow, hesitant, antennal-exploring fashion. After selecting a suitable spot, they usually preen themselves and test the stem with their ovipositor while maintaining a head-downward position. The ovipositor may be forced into the stem in several spots before a suitable site is selected for oviposition. If the site is satisfactory, the female usually lays an egg and then flies to another stem. (Fig. 3, *A*, *B*.)

The ovipositor is composed of two pairs of laterally compressed appendages with serrated backward-directed teeth at the tip on the dorsal side and two rows of teeth on the ventral side. These appendages appear as an inverted sword protruding from the eighth and ninth sternites and are enclosed in a sheath.[6] The dorsal pair of appendages functions together and is connected on the dorsal side for about one-half its length. This pair meets the ventral pair along its ventral surface. The ventral pair can be operated independently of each other and of the dorsal pair. By sliding these pairs on one another the plant tissue is penetrated.

Females do not saw a hole in the tissue, but rather force their way between the cells; however, the ovipositor is such a coarse tool in relation to plant cell size that some of the cells are ruptured. The oviposi-

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[6] MANSON, G. F. THE EXTERNAL ANATOMY OF THE ADULT WITH SOME NOTES ON BIOLOGY OF CEPHUS CINCTUS NORT (WESTERN WHEAT STEM SAWFLY) (HYMENOPTERA: CEPHIDAE). 1932. [Unpublished master's thesis. Copy on file in Library, Univ. of Saskatchewan, Saskatoon.]

tor is forced into the plant tissue and withdrawn several times before it remains inserted, and then the sawfly remains motionless for a few seconds. The egg is probably deposited in the stem during this motionless period.

Ries (*173*) reported that the egg of *pygmaeus* is deposited in the lumen of the stem on the side opposite the puncture. Kreasky [7] showed by slides that *cinctus* deposits the egg on the same side as the puncture or in the pith of the solid stem.

The number of eggs the sawfly will deposit apparently varies with the vigor of the adults. Ainslie (*3*) found that the eggs deposited and those remaining in the sawfly averaged about 50 in *cinctus*. This same number has been reported for the other two species (*173*, *223*). Other workers studying *cinctus* observed 16 to be the exact number laid (*234*). The potential number of eggs is apparently between 40 and 50. The number deposited in the host stems may be affected by longevity of the female, hosts available, and size of the female (*234*).

Ainslie (*3*) observed that the *cinctus* female deposited a single egg in each stem. He observed that the female always left the stem after oviposition. Ries (*173*) found about the same thing for *pygmaeus*. Udine (*223*) indicated a similar habit for *tabidus*. Therefore, the pattern of a single egg laid per stem seems to be the rule. However, in a heavy infestation several females may oviposit in the same stem. Evidence of oviposition by a prior female is ignored by subsequent females who visit the stem.

DESCRIPTION AND DEVELOPMENT OF EGG

Ainslie (*3*) described the egg of *cinctus* as follows: "The egg is, when laid, decidedly crescent-shaped, glassy in appearance, milky-white in color, usually quite symmetrical, the ends of the crescent tapering and rounded. It is marked by very faint, short, longitudinal lines or wrinkles, placed without regard to order or pattern." The size of the egg varies with the size of the female. Ainslie (*3*) gave the range of 1–1.25 mm. long and 0.33–0.42 mm. wide. Ries gave 1.05–1.19 mm. long and 0.42–0.56 mm. wide for *pygmaeus* (*173*). Ainslie worked with dissected eggs. Ries stated that the largest egg hatched before he could make a second measurement.

The most complete description of the development of *cinctus* eggs has been given by Ainslie (*3*).

> A few hours after the egg leaves the oviduct the milk-white contents of the egg, which at first completely filled the envelope, shrinks a little from each end leaving a transparent space or vacule. Gradually the interior mass of exceedingly minute particles coalesces until about the second day when a series of faintly discernible cells arranging themselves along a central axis begins to appear. Early on the third day the form of the larvae can be dimly seen, the head being almost transparent and filling one end of the egg sac. The body is looped on itself, the cauda folded beneath the abdomen and extending forward nearly to the head. By the close of the third day the abdominal segments are usually well defined.

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[7] KREASKY, J. B. OVIPOSITION OF THE WHEAT STEM SAWFLY CEPHUS CINCTUS NORT. WITH SPECIAL REFERENCE TO SOME MORPHOLOGICAL CHARACTERS OF VULGARE WHEATS. 1955. [Unpublished master's thesis. Copy on file in Library, Mont. State Col., Bozeman.]

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During the fourth day, in most cases, a spasmodic intermittent heart beat may be noticed. These pulsations become more and more regular as the hours pass, and during the fifth and sixth days the heart beats with much regularity at the rate of about 120 impulses per minute. At intervals, for some unknown reason, it may slow down to 75 beats, but soon resumes its former rate.

The head appears abnormally large at this time, but although its general outlines are well defined the brown jaws and eye spots are not yet visible. Over night, at the close of the fifth day, the jaws turn brown and the eye spots appear and darken. Usually, after the fourth day, the muscular system of the larvae is in almost constant motion, shifting and adjusting, with the heart pulsating and the muscles moving, all clearly to be seen through the transparent membrane that serves as the shell.

The activity of the larva within the sac increases during the sixth day, and either on this day or the seventh it escapes from its confinement by a series of convulsive movements that rupture the delicate shell and set it free.

After the first day the egg changes shape, becomes intumescent, generally loses its crescentric shape entirely, and grows oval or reniform in outline.

Ries (*173*) did not give an incubation time for *pygmaeus*, but Udine (*223*) stated that *tabidus* eggs hatch in 4–7 days.

DESCRIPTION, DEVELOPMENT, AND HABITS OF LARVAE AND PUPAE

The newly emerged *cinctus* larva (*3*) is transparent and colorless until initial feeding, when a greenish-yellow hue develops from the plant material ingested. The head, thorax, and abdominal segments of the larva are easily identified after emerging from the egg. The head is pale brown with dark-brown four-pointed mandibles and eye spots, and can be withdrawn into the first thoracic segment. There are no legs present, but they are represented by thoracic tubercles (fig. 1). The head and last abdominal segment are sparsely pilose. A pygidium bears bristlelike setae at the base. Measurements of the larva vary, but average about 2.24 mm. long and 0.54 mm. wide at the widest part. Ries (*173*) gave a similar description for *pygmaeus*, but the measurements were 1.75 mm. long and 0.28 mm. wide.

After emergence the young larva immediately begins to feed on the pith in the stem. It feeds up and down a short distance from the oviposition site and eventually works its way down the stem (fig. 3, *A*). Holmes (*78*) studied the feeding of *cinctus* and found that parenchyma makes up the bulk of the tissue ingested as the larva moves up and down the stem. However, as the larva matures it may also ingest vascular tissue and, in some cases, chew through the hypoderma of the stem and into the leaf culm.

The number of instars is not definitely known and is difficult to determine because the larva feeds up and down the stem and reingests frass along with new plant tissue (*215*). Thus, the cast skins are destroyed. Ainslie (*3*) noted only four instars, and Farstad (*52*) claimed a doubtful five. As the larva matures it elongates and the pygidium becomes more pronounced. The pygidium aids in locomotion up and down the stem and also serves in conjunction with the ventral part of the abdomen to give the body support when feeding (*78*). The larva can turn in the stem, but as fall approaches it grows larger and is usually found facing up the stem (fig. 3, *A*, *C*).

The larva is cannibalistic, and the lower larva on encountering the one above will devour it. Because eggs are usually laid lower in the stem first, the first larva to develop is probably the one that survives. This indicates that direct competition between earlier emerging *pygmaeus* and *tabidus* may result in destruction of the younger larva of the latter. This competition is avoided in host selection and in the Eastern United States by area (*223*).

Ries (*173*) described the mature larvae of *pygmaeus* as follows:

The body is nearly cylindrical in outline. The head is of medium size, being much smaller than either of the thoracic segments. The thoracic segments are somewhat swollen; and the abdomen tapers gradually from the thorax to the caudal end. The antennae are four-segmented, and taper strongly. A short distance ventro-caudad of each antenna is a single ocelus. The labrum is prominent and slightly emarginate. The mandibles are strongly toothed. The maxillary palpi are four-segmented. There are 10 pairs of spiracles, 2 thoracic and 8 abdominal. The prothoracic spiracles are much larger than the others and are greatly elongated. The second spiracles open in the fold between the mesothorax and metathorax. The remaining spiracles are on the abdominal segments one to eight. The thoracic legs are represented by very short tubercles. There is, at the caudal end of the body, on the middle line, dorsad of the venter, a prominent tubercle. This is terminated by a chitinous ferrule-like ring, and is doubtless an organ of locomotion. On each side of the ventral lobe at the caudal end of the body there is also a stout spine. These spines probably have the same function as the tubercle just described. The body is naked except the head and caudal extremity. There are a few slender scattered hairs upon the head, and a like quantity of stronger more spine-like hairs at the caudal end.

The internal anatomy of the *cinctus* larvae has been studied by Holmes (*78*) and Maxwell (*130*). Holmes' description is as follows:

The mandibles are of the phytophagous biting and chewing type, with well-defined incisor and molar regions. The maxillae are closely associated with the labium and hypopharynx to form an "underlip complex." The ligula is a simple flap bearing the orifice of the labial glands in its ventral surface.

The head capsule is strengthened along its subgenal region by a strong pleurostomal ridge bearing the mandibular articulations. Anterior to the mandibles, a pair of epistomal bars extends to the anterior tentorial pits. These bars are connected between the pits by an epistomal ridge. The tentorium consists of a pair of anterior arms and a strong tentorial bridge, which originates in the postoccipital suture.

The labial glands are a pair of elongate tubes, which lie free in the body cavity, one on each side of the alimentary canal. Each tube is U-shaped, the posterior ends terminating near the ventricular valve. The anterior part encircles the gastric caecum and is enlarged to form a reservoir. From this, a duct leads forward to form a common tube with the corresponding duct from the other reservoir. This tube has its outlet in the ventral surface of the ligula. These glands produce some hydrolytic enzymes as well as the secretion for the construction of the overwintering case.

The stomadaeum is invaginated into the anterior end of the mesenteron to form the stomadaeal valve. Two ovate gastric caeca empty into the anterior end of the mesenteron. The peritrophic membrane is continuous with the ventricular epithelium and appears to be formed from the entire surface of the latter. At the posterior end of the mesenteron the epithelium of the ventriculus projects into the proctodaeum, forming the ventricular valve. The proctodaeum is differentiated into an anterior intestine and a posterior intestine, or rectum. In the rectum the lining projects into the lumen as six ridge-like structures.

The larva possesses 10 Malpighian tubes, which empty into the alimentary canal through a central opening in the ventral surface of the proctodaeum. All the tubes lie free in the body cavity; four extend to the anterior end of the mesenteron, four proceed caudally to the area of the rectum, and two extend in an anterior direction, reverse, and terminate in the caudal area.

The mature larvae of all three species work their way to the bottom of the stem in August and choose a place to girdle the stem on the inside (fig. 3, *A*). Ainslie (*3*) stated that this may take place 4 inches above the ground by *cinctus* in *Elymus*, and in many grasses and cultivated wheat the site is usually 1 inch or less. The last site mentioned for *cinctus* is more typical of *pygmaeus* and *tabidus*.

The process of girdling is similar in all three species. The stem is girdled nearly through to the outside, then a plug of frass is pushed up to the girdling groove (fig. 3, *A*). This plug is about one-eighth to one-fourth inch in length and is packed fairly compactly in the stem. Whether by design, accident, or selection the formation of the plug gives the stem rigidity, which forces the stem to break when pressure is applied rather than to collapse and bend. This prevents the cut end of the stem from remaining covered with a collapsed straw, which Ainslie (*3*) reported will prevent the escape of the *cinctus* adult in the spring.

The appearance of the cut stub varies with the species. Udine (*223*) presented photographs of stubs produced by the three species. The most ragged and incomplete girdling was by *pygmaeus;* a much smoother cut was made by *tabidus* and the smoothest by *cinctus* (fig. 1). The variety of wheat each was infesting was not reported, and it must be borne in mind that the texture and ribbing of the stem vary with the varieties of wheat. The observations made on many hosts and varieties of wheat indicate that girdling by *cinctus* is consistently smooth. Perhaps the other species are equally consistent on diverse hosts, but a direct comparison of the three species on the same wheat variety has not been made.

After girdling and plugging the stem, all three species spin a cocoon within the hollowed-out stub (fig. 3, *C*). This cocoon, which serves as a hibernaculum, is several times the length of the larvae so that they are free to move within.

The cocoon is composed of a thin cellophane-like material, which is poured out the labium and spread rather than spun as a thread. Adherence of the cocoon to the plug indicates this to be the starting point for spreading. The remainder of the cocoon is free from the sides of the stem and may be withdrawn from the stub with the plug. The cocoon is a thin, brown case, which affords protection from excessive drying or wetting of the larvae and pupae. It is pliable when first completed or when damp, but becomes brittle and cracks easily as it ages and dries out.

The overwintering larva is a very hardy stage that can withstand freezing and some drying (*188, 189, 191*). It is an obligatory diapausing stage and remains active as long as the temperature is not excessively cold. A period of cold is necessary to allow the larva to develop into the pupal stage in May. Salt (*189*) gave the temperature required for pupal development as 10° C. for 90 days. Church (*21, 22*) reported that moisture is also necessary at the end of diapause to insure normal development.

Church (*21*) reported that breaking of the diapause is caused by a prothoracic ganglion secretion, which is triggered by a secretion from the brain. The brain is affected by climatic conditions. If the secretion of the prothoracic ganglion has not progressed too far, subjection of the larvae to 95° F. for about a week will reinduce diapause and the larvae will lie dormant through the summer. These rediapausing larvae then require another cold period to break the diapause. Survival of rediapausing larvae is high (*80*). A second reentering of diapause is questionable.

Ainslie (*3*) held larvae in stubs enclosed in vials for 3½ years, but did not attempt to rear them to adults. Church (*22*) found that dehydration at subdevelopmental temperatures apparently permanently injured the larvae and they failed to develop even though they remained alive. No such records have been obtained on *pygmaeus* or *tabidus*, but it is logical to assume that they have a similar mechanism to tide them over unfavorable years.

Once the diapause in *cinctus* has been broken long enough to carry the larvae through to the prepupal stage, there is no returning to diapause. Dry conditions will desiccate the prepupal and pupal stages (*80*). The prepupal stage is discernible by the failure of the larvae to assume the "s" shape when disturbed.

The pupae are exarate in all three species and are capable of moving up and down the cocoon. No exact data on the duration of the pupal stage are presented in the literature. Ries (*173*) estimated the length of this stage at about a week for *pygmaeus*. This is a fair estimate for the other species also, subject to climatic conditions.

The pupae of all three species appear much like the adult when first formed, except the wing pads are short and they are entirely encased in a translucent cover (*173*, *223*). This covering is often ruptured by movements of the pupae. As the pupae develop, the eyes darken, the body becomes gradually pigmented, and the wings inflate and harden. By this time the pupal cover has usually been completely sloughed off; however, sometimes patches of it remain clinging to the body of the completely formed adult. All this development takes place in the cocoon, and the adult is capable of flight immediately after emergence from the wheat stub.

The three species of sawflies are univoltine and require at least 1 year to complete the life cycle.

CONTROL MEASURES

Control of wheat-infesting sawflies falls into three categories: Cultural, chemical, and biological. Biological control can be divided into parasites and resistant varieties of hosts.

Cultural Control

The cultural practices are varied in form, recommendation, and usefulness. One of the most obvious and among the first to be recommended is burning the stubble. This recommendation continues in literature, but its value is questionable. Criddle (*27*) found that burning the stubble for *cinctus* larval destruction was ineffective. The European recommendation (*66*, *200*) urges burning the stubble as soon after harvest as possible. This may be soon enough to destroy the larvae before they have spun cocoons, but it must be remembered that the hollow part of the stub often goes down into the soil an inch or two, and the heat from the fire does not penetrate the soil to any great extent. In addition to the uncertain value of this control, fire is a hazard to uncut grain, and soil erosion becomes a problem on burned-over fields.

Deep plowing of 5 inches or more has been recommended for all three species (*56, 194, 223*). In this method of control it was recommended that the soil be turned completely over, leaving the open ends of the stubble pointing downward. This is effective, preventing many of the adults from emerging; but wind erosion prohibits this practice in many areas of the Western States.

The use of a single blade, which would sink under the soil at the level of the stubble roots and lift them up and thus expose the larvae or pupae to desiccation, is effective. A one-way disk at a shallow depth would accomplish much the same effect. Holmes and Farstad (*80*) found that most of the larvae in stubs exposed in the fall were destroyed during the winter if there was no snow cover. Exposing the stubs from May 26 to June 4 also killed most of the prepupae and pupae of the sawfly by desiccation (*80*).

Crop rotation is an effective means of reducing the sawfly population as well as the damage it inflicts on wheat (*17, 19, 148*). Hosts unsuitable to the sawfly such as oats, flax, or mustard are useful in a crop rotation (*163*). Hosts that allow only a small number of the larvae to survive, such as most barleys, some durums, fall rye, and resistant varieties of wheat, are also instrumental in reducing the population. In years with an early harvest, winter wheat may not allow time for *cinctus* and *tabidus* to complete development, but this crop is ideal for *pygmaeus*. This is not true in Canada with relation to *cinctus*. Barley and rye are not as detrimental to *pygmaeus* and *tabidus* as they are to *cinctus*. Hanchen barley in some years is a favorable host to *cinctus* (*57*).

Because of the short-distance, low-flying habits of adult sawflies, trap crops have been suggested as a means of control. In this practice attractive hosts are planted early around the border of the field. These borders receive a very heavy infestation and can then be cut before the larvae complete development. A fallow strip is often maintained between the trap crop and the wheat to be protected. Some trap crops that are desirable to the sawfly but do not allow complete development, such as *Phleum pratense*, or that will facilitate parasitism, such as *Bromus inermis*, may be left standing. In large-block farming the trap crops have some merit, but in strip farming as practiced in Montana the loss of time and acreage is prohibitive (*192*).

Delayed seeding of winter wheat is recommended in Europe as a means of controlling *pygmaeus* (*172*). This practice has also been suggested as a means of controlling *cinctus* on spring wheat, but such a recommendation has never been made (*138*). The delay allows the sawfly populations to dissipate or move out of the field before the stems are suitable for oviposition. In the case of *cinctus*, a predominance of males is often reared from late oviposition (*94*). Late seeding is hazardous in both crops, since winter wheat may suffer winter loss and spring wheat may not mature or it may be too late to take advantage of available moisture.

Heavy seeding in the borders to prevent lodging and reduce sawfly cutting has been suggested (*121*). This produces a thick stand and affords more sawflies an opportunity to oviposit in the border rather than in the interior of the field or strip. Also, the cut stems are prevented from falling to the ground. This practice would be easily applied, but it might be hazardous in a dry year. In a year with adequate moisture the objectives of border cropping might be accomplished, but this would not reduce the sawfly population unless the border were destroyed before the sawflies cut the stems.

Swathing before sawfly cutting occurs has been practiced successfully to reduce loss from fallen heads (*197*). This practice does not control the sawfly, because the larva is usually below the level of cutting by this time. The loss of wheat due to tunneling of the stem remains a loss, and the sawfly population is not materially affected.

Fertilizing the crop to produce better yields does not decrease the sawfly population. In fact, evidence has been presented to show that phosphorus with or without nitrogen actually increases sawfly cutting (*119*).

Chemical Control [s]

Chemical control of sawflies is a difficult problem, because the adults feed very little or not at all and the eggs and larvae are inside the host stem. Because the adults oviposit shortly after emergence, the egg and larval stages within the stem are the forms that must be controlled. Insecticides have been found that are toxic to adults (*81*, *235*), but field application of them failed to prevent oviposition or reduce larval cutting. Systemic insecticides that will reach the larvae or pupal forms and kill them are not numerous. The application of such insecticides also is a problem. They must either be applied at the time of planting, which means a 2-month residual effect, or be sprayed on the plant after the eggs have been laid. At the present time no foliage spray is known to be effective.

The systemic organophosphorus insecticide phorate has given control as a seed treatment. Heptachlor and heptachlor epoxide have sometimes given good control when used as seed or furrow applications. Wallace (*235*) pointed out that although heptachlor is not considered a systemic insecticide, it must be taken up by the plant in sufficient amounts to kill the larvae wit[illegible]tem. Holmes and Peterson (*91*) reported that the lower [illegible] the plant were more toxic than the upper internodes, and [illegible] sawfly populations, oviposition in the higher internodes reduced [illegible]fectiveness of the insecticide. No recommendation has been made for control with insecticides. In Montana, Wallace (*235*) reported that with 1-foot row spacing one-half pound per acre of heptachlor in a furrow application has given from 75- to 95-percent control (fig. 5), and treatment

[s] If you use insecticides, apply them only when needed and handle them with care. Follow the directions and heed all precautions on the container label. If insecticides are handled or applied improperly, or if unused portions are disposed of improperly, they may be injurious to humans, domestic animals, desirable plants, honey bees and other pollinating insects, fish, and wildlife, and may contaminate water supplies.

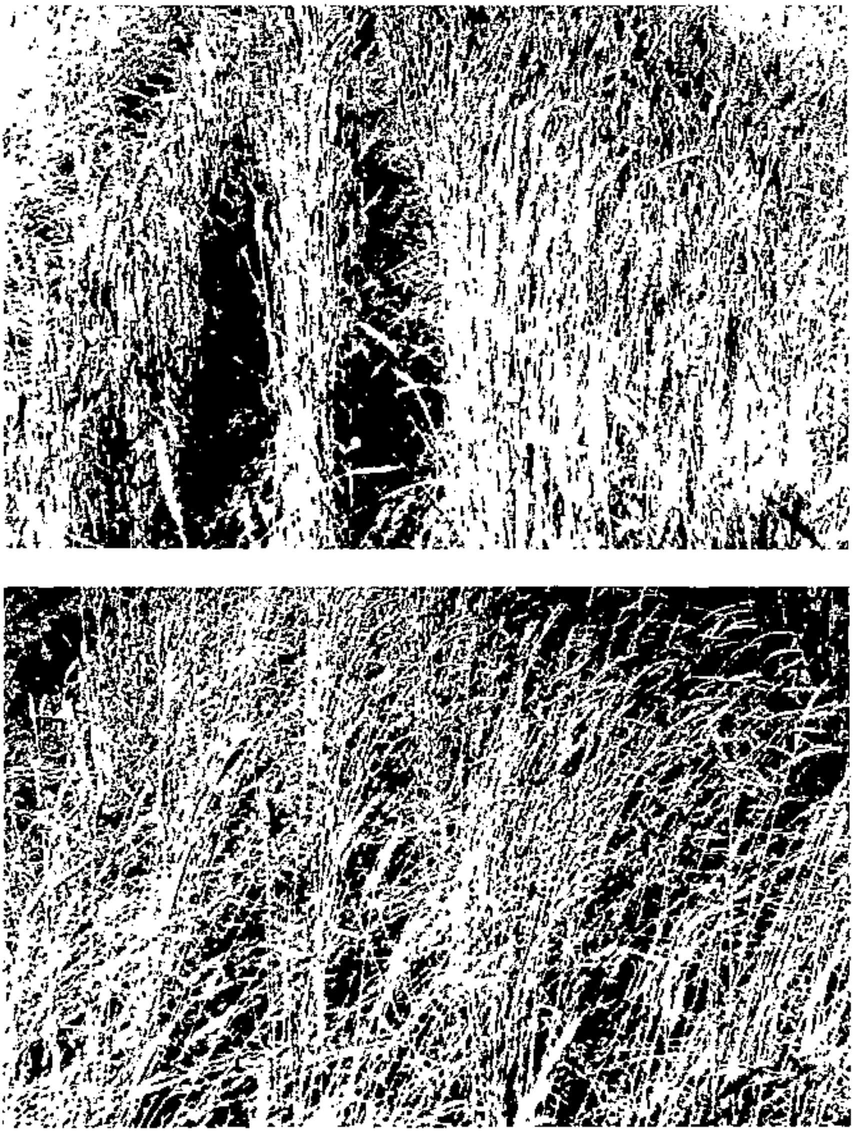

FIGURE 5.—Above, sawfly cutting in Thatcher wheat treated with heptachlor at one-half pound per acre; below, untreated.

of a 14-foot border on each strip, where infestation is heaviest, appears practical.

Several tests have been conducted and plant parts analyzed for insecticide residue. One-half pound per acre of heptachlor results in low but detectable residues in the green plant and straw. Therefore, the treated plants should not be grazed by or the straw fed to animals used for food or as a milk supply.

Biological Control

Biological control of stem sawflies has not been overwhelmingly successful. Many parasites have been recorded as infesting sawfly larvae both in the United States and in Europe. All are Hymenoptera and they are classified in six families.

The superfamily Chalcidoidea contains the most species but, in general, is the least effective, and many are hyperparasites of more efficient parasites.

The family Eupelmidae contains two species, *Eupelmus allynii* (French) and *Eupelmella vesicularis* (Retzius) (*151*). They can develop externally on other parasites. In many cases they are hyperparasites. *E. allynii* has been reared from *Bracon cephi* (Gahan) as well as from the three species of sawflies. *E. vesicularis* has been reared from *E. allynii* as well as *cinctus* and *tabidus*. Both have been reared from pupae of the Hessian fly (*Phytophaga destructor* (Say)) (*75*), and the latter is listed as a hyperparasite of *Apanteles melanoscelus* (Ratzeburg) (*147*).

The family Eurytomidae has two species that have been reared from cut wheat stubs. *Eurytoma appendigaster* (Swederus) is an ectophagous hyperparasite of *Bracon terebella* Wesmael and of doubtful benefit as a parasite of *pygmaeus*. *Eurytoma atripes* Gahan has been listed as a parasite of *cinctus* and is also a hyperparasite (*149*).

The family Pteromalidae has *Norbanus scabriculus* (Nees), which is considered a parasite of *pygmaeus;* however, the genus *Habrocytus* has a member that attacks *B. terebella*. *Norbanus* may also have hyperparasitic habits (*186*).

The family Eulophidae has two members in the genus *Pediobius*, which are apparently confined to sawfly, as no other hosts are listed. They are endophagous larval parasites and compete with the larvae of *Collyria calcitrator* (Gravenhorst). The *Collyria* larvae, however, can destroy the *Pediobius* larvae. The two species are *Pediobius nigritarsis* (Thomson), which is a European species introduced with its host into the Eastern United States, and *P. utahensis* (Crawford), which is a native species found attacking *cinctus* in the Western United States (*153*, *186*). The native species is often fairly successful in parasitizing the sawfly in grass, but does not seem to transfer to wheat (*153*). The European species is of minor importance on *pygmaeus* and *tabidus* (*65*, *185*).

The remainder of the parasites are in the superfamily Ichneumonoidea, representing two families, Braconidae and Ichneumonidae. The members of the family Braconidae are ectophagous and they represent two subfamilies. All species have no known hosts other than sawflies, except *Bracon abscissor* Nees, which parasitizes lepidoptera.

The subfamily Doryctinae contains only one species known to be a parasite of sawflies, *Heterospilus cephi* Rohwer. The hosts listed for this species are *pygmaeus* and *tabidus*, with the first considered the preferred host (*185*).

The subfamily Braconinae is represented by the genus *Bracon*, which has several species. *Bracon abscissor*, *B. stschegolevii* Telernyz (*216*), and *B. terebella* are European species that attack *pygmaeus* (*186*). *B. terebella* is one of the more important parasites of this species and also attacks *tabidus*. It has been introduced into the United States by accident with its hosts. In the United States two other species, *Bracon cephi* and *B. lissogaster* Muesebeck, are important parasites of *cinctus* in grass hosts (*63, 146, 209*).

The family Ichneumonidae has representatives in three subfamilies. The subfamily Gelinae contains a number of ectophagous parasites, but none are very abundant on sawfly larvae, and about half of them are facultative parasites that are often hyperparasites. The following species are parasites of *pygmaeus*: *Aritranis* (=*Hoplocryptus*) sp., *Bathythrix bellulus* (Kreichbaumer), *Cubocephalus unifasciatus* (Schmiedeknecht), *Gambrus tricolor* (Gravenhorst), *Gelis fallax* (Foerster), and *Hemiteles hemipterus* F. The last species is a hyperparasite of *Bracon terebella* also. *Gelis terebrator* (Ratzeburg) and *Hemiteles inimicus* Gravenhorst are hyperparasitic (*186*). Most of these species have many other hosts and do not rely on sawfly larvae for continuation of the species.

The subfamily Pimplinae contains only one species that is parasitic on the three species of sawflies. *Scambus* (*Endromopoda*) *detritus* (Holmgren) is endemic to both continents and is potentially an important parasite because it is capable of survival over all other parasites. No hyperparasites have been recorded on this parasite. However, this parasite does not reach its potentiality because it has a number of other hosts and does not heavily parasitize sawfly larvae (*77, 186*).

The subfamily Collyrinae contains the most important parasites of the grass stem sawflies. *Collyria calcitrator*, *C. iberica* Schmiedeknecht, and *C. trichophthalma* (Thomson) are endophagous and have been reared from infested stubs. *C. calcitrator* has been studied by several workers and is believed to be the most successful and best suited parasite. It attacks the egg, and the larva develops internally as the host egg and larva develop. Pupation takes place within the hibernaculum of the host the following spring (*105*). No hosts other than the three sawfly species have been discovered (*186*). *C. calcitrator* is vulnerable to all the ectophagous parasites, but is able to overpower the endophagous *Pediobius nigritarsis* and *P. utahensis*.

Salt (*186, 187*) listed the following parasites and the percent parasitization of each on *pygmaeus*, based on a field collection of cut stubs in England: *Collyria calcitrator* 62.25, *Pediobius nigritarsis* 3.95, *Bracon terebella* 2.77, *Scambus detritus* 2.12, *Hemiteles hemipterus* 0.60, *Bathythrix bellulus* 0.02, *Gelis fallax* 0.001, *Gambrus tricolor* 0.001, and *Cubocephalus unifasciatus* 0.0001. All are ectophagous except the first two species, which are endophagous.

C. calcitrator is the most efficient parasite of the European species of sawflies (*227, 228*). Introductions of *C. calcitrator* were made in 1936 to control these sawflies in the Eastern United States and Canada (*205, 214*). Introductions were also released in western Canada and Montana (*120*) to control *cinctus*. Recovery after introduction was meager and doubt exists concerning establishment in either western

Canada or Montana (*120*). The minor recoveries indicated that *C. calcitrator* could complete its life cycle in *cinctus*. *C. calcitrator* is not able to distinguish eggs already parasitized, and if the parasite population is heavy a random superparasitism can take place (*232*, *233*).

The following native primary parasites exert some biological control in the United States: *Heterospilus cephi*, *Scambus detritus*, *Bracon cephi*, *B. lissogaster*, and *Pediobius utahensis*. All are ectophagous except the last parasite, which is endophagous.

H. cephi, a parasite of *pygmaeus* and *tabidus*, has parasitized as much as 39 percent of the hosts in the Eastern United States, but this parasitization fluctuates from year to year (*76*).

S. detritus infests all three sawflies in July and usually prevents the larvae from completing tunneling. Overwintering and pupation take place above the second internode of the wheat plant, but the position depends entirely on the location of the sawfly larvae at the time of attack, since the larvae are completely paralyzed by the initial contact. This high site for overwintering makes the parasite vulnerable to destruction at harvest and also to freezing during the winter. These factors, coupled with the fact that this parasite has many other hosts, make it ineffective in sawfly control (*77*).

The other three species are parasites of *cinctus* and they unfortunately seek the host in native grasses rather than in wheat. Parasitization by *Pediobius* reaches 60–70 percent in grasses and only 1–2 percent in adjacent wheat (*153*). *B. cephi* seems to prefer hosts in *Bromus inermis*, since the long growing season of this grass enables the parasite to complete two generations (*83*, *152*). Heavy parasitization by *B. cephi* has also been reported in barley (*57*). This parasite also paralyzes the host and often overwinters in the straw and sometimes in the stub; however, it is winter hardy and can withstand extreme cold (*190*). *B. lissogaster* also prefers grass-infesting hosts rather than wheat, and repeated observations in wheat show only low parasitization (*209*).

Destruction of hosts in grass before *B. cephi* adults emerge can force the parasite into wheat (*193*). Even this will not insure success of the parasite, because there is only a partial second generation in wheat if the wheat matures too early. This plant dries out too early and the sawfly larvae migrate to the base of the plant and produce the hibernaculum. In this position they are almost free from parasitism by *B. cephi*. This loss of a second generation depletes the parasite population, and the following year it is low unless a host population in grass has maintained a high population to be forced again into wheat.

Biological control of *cinctus* is not effective because of the lack of synchronization between the wheat host and the parasites that originally parasitized the larvae in grass, and because *C. calcitrator* has not become established. More work on synchronization or a concentrated effort to understand and to establish *Collyria* seems to be the only hope of success for biological control of *cinctus*. Meanwhile, parasites of *pygmaeus* and *tabidus* seem to be holding these eastern species in check (*204–207*, *213*).

BREEDING FOR SAWFLY RESISTANCE

Immunity to attack by the sawfly has never been found in wheat, although thousands of varieties and selections have been tested under sawfly conditions in Canada and the United States. However, many workers have demonstrated that resistance to sawfly damage is associated with solidness of stem. Stem solidness is caused by the development of pith inside the stem, and although it has never been demonstrated that pith is the only factor causing a variety to be resistant, many observations do show that when a variety is less solid it is also less resistant. (Fig. 6.)

Solidness of stem imparts resistance to many of the grasses; however, other factors for resistance also occur in grasses, e.g., the crushing of sawfly larvae by the bulblike spring growth of *Phleum* (*52*). Barley also exhibits a type of resistance to sawfly development. The mechanisms of this resistance are not known, but they apparently differ from those found in wheat.[9]

Breeding programs in Canada and the United States for improving sawfly-resistant wheats have always had as a major goal the development of solid-stemmed varieties. Most programs have also included studies on inheritance of stem solidness as well as the reaction of solid-stemmed varieties to environment.

FIGURE 6.—Sawfly cutting of hollow-stemmed susceptible wheat variety in foreground; resistant solid-stemmed durum wheat in background.

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[9] ROEMHILD, G. R. MORPHOLOGICAL RESISTANCE OF SOME OF THE GRAMINAE TO THE WHEAT STEM SAWFLY (CEPHUS CINCTUS NORT.). 1954. [Unpublished master's thesis. Copy on file in Library, Mont. State Col., Bozeman.]

Shchegolev (*198*) tested the resistance of rye, barley, wheat, and oats to damage by *pygmaeus* and *tabidus*. He noted that one solid-stemmed wheat was resistant. Kemp (*100*) postulated that sawfly damage might be reduced to little or no consequence by the use of solid-stemmed wheats. He proposed that it should be possible to breed desirable wheats with a solid stem, since solid-stemmed varieties of *Triticum aestivum* L. already existed. Eckroth and McNeal (*48*) studied morphological characteristics of 180 varieties of spring wheat in relation to sawfly resistance. No plant character in common wheats, except stem solidness, appeared to contribute resistance. Some of the durum wheats showed resistance, but this resistance was not associated with any of the morphological characters studied.

Platt and Farstad (*164*) found differences in reaction to sawfly attack among susceptible, hollow hexaploid wheats, demonstrating that factors other than stem solidness may be involved in sawfly resistance. They observed that the main culms of hollow varieties were more susceptible than secondary tillers, whereas the reverse was true with solid-stemmed varieties.

McNeal et al. (*137*) studied F_2 and F_3 progenies from Rescue and Selkirk crossed to two solid-stemmed wheats from Portugal. They concluded that stem-solidness readings of F_2 plants contribute more information than do cutting percentages to the determination of sawfly resistance in the F_3 generation. They proposed that F_2 plants need not be evaluated for sawfly infestation and cutting, but that these plants be examined at harvest for stem solidness of the bottom internode and that progeny from desirable plants be evaluated for sawfly resistance in F_3.

The first commercial wheat variety to be released on the American continent with resistance to the wheat stem sawfly was Rescue, a spring wheat. This variety was developed by Canadian workers and was released for commercial production in Canada in 1946 and in the United States in 1947 (*15*, *165*). Chinook (*15*) and Cypress (*133*) spring wheats are subsequent releases from breeding programs in Canada. Sawtana spring wheat (*136*) and Rego winter wheat (*15*) are commercially grown varieties released from breeding programs in the United States.

The senior author has observed reductions in sawfly cutting to less than 1 percent by continued cropping with sawfly-resistant wheat varieties. However, there seems to be a negative correlation between stem solidness and yield of grain. Unpublished data indicate a 3-bushel loss per acre when Rescue is grown in preference to the nonresistant variety Thatcher. Farmers in the sawfly area place the yield of Rescue at 5 bushels per acre lower than that of hollow-stemmed spring wheats. If the yield of resistant varieties can be increased, a wider use of resistant wheat varieties in the sawfly areas can be expected, with a subsequent reduction in the sawfly population.

INHERITANCE OF STEM SOLIDNESS

Genetic studies of solid stem have been made in interspecific hybrids of diploids × tetraploids, tetraploids × hexaploids, and in hybrids of intraspecific crosses.

Yamashita (*242, 243*) studied many crosses between solid- and hollow-stemmed wheat varieties and species. He proposed a factor for hollowness of the entire stem and one for solidness of lower internodes in the A genome. Because of solid, partly solid, and thick-walled, hollow varieties found in the emmer series, he supposed that there must be multiple alleles for solidness and hollowness in the B genome. A factor for hollowness in the D genome that is epistatic to genes for solid stem at other loci was established by backcrossing the F_1 of a *T. durum* by *T. aestivum* cross to each parent. Yamashita did not work with solid-stemmed varieties of *aestivum*, but he postulated that in such varieties the D genome must be carrying the same factors for solidness that are present in the B genome. He suggested that it should be relatively easy to develop a cultivated *aestivum* wheat with a solid stem.

Diploids × Tetraploids

Thompson (*218*) studied crosses between 7-chromosome *T. monococcum* (hollow stem) and 14-chromosome *T. durum* (solid stem) and found the F_1 to be solid like *durum*. Examination of 50 F_2 plants revealed the hollow stem of *monococcum* in about 1 of every 15 plants.

Tetraploids × Tetraploids

Studies in 14-chromosome wheats have shown that solidness of stem is due to a single dominant factor (*169*), to a single recessive (*49*), and to complementary recessive genes (*68*). Putnam (*169*) found that the inheritance of stem solidness was unifactorial in crosses of *T. durum* and *T. turgidum* L. varieties with Golden Ball (solid stem). The solid-stem condition was partly dominant. Engledow (*49*) obtained an F_2 ratio of three hollow to one solid from crosses of Polish (*T. polonicum*) × Rivet (*turgidum*). However, peculiar ratios from a Polish × Kubanka (*durum*) cross caused the author to conclude that stem solidness is not a morphologically simple character. Engledow and Hutchinson (*50*) studied crosses of Rivet with Kubanka (*durum*) and classification of F_2 plants suggested a single factor difference, although the authors reported that some crosses seemed to indicate multiple factors. In contrast to Biffen (*9*), they concluded that a greater amount of pith is dominant to a lesser amount.

Bozzini and Avanzi (*14*) presented data on the inheritance and culm anatomy of a solid-stem mutant induced in Cappelli *T. durum* by X-irradiation. Data from F_2 plants of a cross between the mutant and Cappelli showed 23.1 percent of the plants to be completely hollow stemmed, whereas the remainder had some solidness (3 : 1 segregation, $P=0.5\text{–}0.3$). They concluded that irradiation eliminated or neutralized a gene for hollow stem; the hollow-stemmed gene normally is epistatic to all stem-solidness promoting factors in the A and B genomes of *durum* when homozygous.

Tetraploids × Hexaploids

Crosses between tetraploid and hexaploid wheats show that solid stem varies from recessive (*9, 95, 96, 212*) through intermediate (*230*) to dominant (*49, 50, 221, 222*). F_2 segregations have been interpreted as monohybrid (*9, 49, 50, 95, 96*) or multifactorial (*221, 222, 230*). Biffen (*9*) in one of the first recorded reports on the inheritance of stem solidness studied crosses of Rivet (*T. turgidum*, solid in the top internode) with hollow varieties of *T. aestivum* and found that hollow stem was dominant. Engledow and Hutchinson (*50*) studied crosses of Rivet with Chinese (*aestivum*) and concluded that stem solidness was dominant and did not appear to be associated with any other character of the wheat plant. Vavilov and Jakushikina (*230*) found solid-stem intermediates in hybrids of 14- and 21-chromosome wheat, and the F_2 segregations were interpreted as multifactorial.

Cytogenetic studies of crosses between hollow-stemmed hexaploids and solid-stemmed tetraploids showed that the D genome tends to produce a hollow stem (*5, 101, 128, 129, 167, 212, 217, 219, 220, 238*), but that differences in solid stem between the two are partly determined by genes in the A and B genomes (*5, 101, 126, 127, 211, 217, 219, 220*). A chromosome in the D genome producing a hollow stem was identified as chromosome 2D (*128, 129, 243, 244*).

Arnason (*5*) examined hybrids of Marquis (*T. aestivum*) with Iumillo (*T. durum*) and Vernal (*T. dicoccum*) for stem solidness. Marquis is hollow and the other two are solid. Since the hollow stem of Marquis was not found in the *durum* or *dicoccum* condition in 21-chromosome segregates, it was presumed to be conditioned by genes from the D genome. Kihara (*101*) studied hybrids of 14-chromosome wheat with 21-chromosome wheat and showed that the D genome tends to produce a hollow culm, but that differences in stem solidness are also partly determined by genes in the A and B genomes.

Platt and Larson (*167*) attempted to transfer the stem solidness of Golden Ball (*T. durum*) into *T. aestivum* wheat, but the differences obtained in segregating progenies were not put on a definite factor basis. No solid-stemmed *aestivum* segregates were obtained. Failure to transfer stem solidness was attributed to a gene for hollowness in the D genome that is described by Yamashita (*242, 243*) as being epistatic to genes for solid stem at other loci.

Stevenson (*211*) studied hybrids from the cross of Velvet Don (*T. durum*) with Quality (*T. aestivum*). Velvet Don was solid in the top internode and Quality was hollow. The F_1 plants were intermediate between the parents in stem solidness. One hexaploid F_3 plant was found to have the *durum* solidness, but this was regarded as an irregularity. All other hexaploid F_3 plants were classified as having a hollow stem.

Thompson (*217*) pointed out that *T. durum* varieties usually have solid stems, though some have hollow stems with thick walls; most *T. aestivum* varieties have hollow, thin-walled stems, though a few are solid. He classified F_2 plants from a cross of Iumillo (*durum*) × Marquis (*aestivum*) for stem solidness as 9 *aestivum*-like, 25 intermediate, and 23 *durum*-like. Thompson et al. (*219*) found no tetraploid hybrids with the hollow, thin-walled stem characteristic of *aestivum* while working with crosses between hollow-stemmed *aestivum* and the solid-stemmed *durum*, *T. dicoccum*, and *T. carthlicum* (= *T. persicum* Vav.) species. They suggested that there is a factor for hollow stem in either the A or B genomes of *aestivum* and that at least one additional factor for hollow stem must be present in the D genome to produce the hollow stem and thin wall of Marquis. Thompson and Hollingshead (*220*) classified F_2 plants of the cross *dicoccum* (solid) × *aestivum* (hollow) for stem solidness and found 46 *dicoccum*-like, 29 intermediate, and 2 *aestivum*-like.

Watkins (*237, 238*) examined results from interspecific crosses and concluded that some plant characters, such as hollow straw, are usually associated with high chromosome number. He supposed that a character rare in one group of wheats and common in another cannot usually be transferred by crossing. Matsumura (*128, 129*) identified chromosome 2D in the D genome as being responsible for the production of hollow stem, as did Yamashita (*243, 244*).

Larson (*109*) examined plants of the cross Rescue (*T. aestivum*) × Golden Ball (*T. durum*) for stem solidness. No F_4 line was found with a top internode as solid as that of Golden Ball combined with the morphological characters of *aestivum*. She assumed this was probably because the D genome present in Rescue but absent in Golden Ball inhibited the expression of pith. A few lines were found to have pith patterns different from those of either parent, but these differences were ascribed to segregation of genes in the A and B genomes. Larson (*110*) also analyzed F_5 lines from this study. She concluded that chromosome 3D in Rescue carries a gene (or genes) that inhibits the transfer to hexaploid segregates of the more solid top culm internode of Golden Ball. A few hexaploid segregates were found to be more solid than Rescue in the top internode, but it was assumed that none would be found with a top internode as solid as that of Golden Ball.

McNeal (*135*) crossed hollow-stemmed segregates of Rescue × N1315 to Golden Ball (*T. durum*) and evaluated the *T. aestivum*-like selections for stem solidness and sawfly resistance. Some selections nearly equaled Golden Ball in stem solidness, but they had less sawfly resistance. Differences in stem solidness between the selections and Golden Ball were found in the two top internodes. McNeal concluded that genes for stem solidness must have been transferred from Golden Ball, since some of the segregates were much more solid than the *aestivum* parent. However, an examination of F_2 plants from a cross of two of these segregates with Rescue did not reveal major differences in stem solidness among the three parents, indicating the solidness genes obtained from Golden Ball may be the same as those in Rescue.

Larson and MacDonald (*114*) examined F_8 lines, with different solid-stem indices, which had been selected from F_5 hexaploid plants of a Rescue × Golden Ball cross. The occurrence of aneuploids in solid-stemmed progenies suggested that the more solid selections were less stable cytologically and probably contained chromosomal aberrations, thus accounting for the difficulty in stabilizing stem solidness in later generations. Their work further suggests that a major gene for the Golden Ball type of solid top internode is on chromosome 3B.

Larson and Perkins (*115*) studied plants nullisomic for chromosome 3D and suggested that the presence of chromosome 3D tends to make the hybrid more like Rescue, whereas its absence causes the hybrid to revert to the Golden Ball constitution.

Hexaploids × Hexaploids

Platt et al. (*161, 162*) studied crosses of S–615 and S–633 (solid stem) with Thatcher and Renown (hollow stem). They obtained a ratio of 63 hollow and intermediate types to 1 solid for all crosses except that of Thatcher × S–633–23. Only plants having the three factors in a recessive condition had stem solidness. They suggested that the factors were cumulative and that four or more dominant genes would produce phenotypically hollow plants.

McNeal (*134*) studied plants from a cross of Thatcher and Rescue and concluded that the two parents differed by one major factor pair and possibly two to four minor factors for stem solidness. The major factor pair was found to have an effect 2½ times that of the minor factors.

McNeal et al. (*139*) examined F_2 plants from crosses between Rescue and four solid-stemmed wheat introductions from Portugal. They concluded that each of the Portuguese wheats possesses the same major factor (or factors) for stem solidness that occurs in Rescue. However, three of the Portuguese wheats differed slightly from Rescue. This difference was ascribed to the action of minor genes affecting stem solidness.

Larson (*106–108*) compared monosomic F_2 lines of Chinese Spring × S–615 with normal F_2 lines for stem solidness. She found in Chinese Spring that chromosomes 2A, 2D, 6D, and 7D carry genes for hollow stem and chromosome 4B has a gene for solid stem. Chromosome 2B, a member of homeologous group 2 that also includes 2A and 2D, may also contribute to hollowness of stem, but the data were inconclusive. Larson proposed that chromosome 2D carries gene O_D, identified by Yamashita (*242–244*) and Matsumura (*127–128*), for hollowness of stem; and that chromosome 2B probably carries gene M_A and chromosome 2A the M_B locus for hollow stem as reported by Yamashita (*242, 243*). No genes for stem solidness were located in S–615, indicating that solidness genes in this variety are probably recessive.

Larson and MacDonald (*111*) found in monosomic lines of S–615 that chromosomes 3B, 3D, 5A, 5B, and 5D carry genes for solid stem, whereas chromosomes 2D, 6D, and 7D have genes for hollow stem. Lines monosomic for 3B and 3D were less solid in the top internode, and lines monosomic for 5A, 5B, and 5D were less solid in the bottom four internodes. Chromosome 2A, which in Chinese Spring had a gene for hollow stem (*108*), did not affect the amount of pith in S–615. The concept was advanced that culm phenotype in a given environment is a result of the interaction of genes promoting pith development with those opposing it.

Larson and MacDonald (*113*) developed monosomic lines of Rescue by crossing to monosomics and nullisomics of Chinese Spring and then backcrossing the monosomic hybrids to Rescue for seven generations. They found that Rescue has fewer chromosomes affecting stem solidness than S–615, since 3D, 5B, and 5D did not make the stem more solid and chromosomes 2D and 7D did not make the stem more hollow as in S–615. They also reported that chromosome 3B failed to make the stem more solid. However, more recent work has revealed that chromosome 3B of Rescue does have a very important gene for solidness.[10] Chromosomes that do seem effective in Rescue are 6A and 6D, which tend to make the culm more hollow, and 5A, which makes the culm solid, especially in the lower internodes.

METHODS OF EVALUATING STEM SOLIDNESS

Exact measurements have never been formulated for evaluating the wheat stem for solidness. Present measurements are at best only an approximation of the genetic expression for this plant character. However, some method of evaluating stem solidness is needed and some of those used seem to fit individual tests.

Putnam (*169*) split the stems lengthwise and recorded them as solid, intermediate, or hollow. Biffen (*9*) made a cross section in the center of the top internode. Arnason (*5*) made a cross section 2 cm. below the head, and Engledow and Hutchinson (*50*) studied solidness in the top and bottom internodes.

Larson (*108*) placed the evaluation for stem solidness on a more thorough method of rating. She classified the three longest culms from each plant and recorded an average of the three observations. Three cross sections were taken in the top internode and one in the center of each of the other internodes. Cross sections in the top internode were taken at the center, 5 cm. below the head, and 5 cm. above the node. Each cross section was rated from 1 to 5 as follows: (1) Thin walled, hollow: (2) thick walled, hollow; (3) intermediate; (4) very small lumened; and (5) solid. McNeal (*134*) used this same method, except that the three cuts in the top internode were made in the center, 1 inch below the head, and 1 inch above the node. In a later test McNeal et al. (*139*) reduced the cross sectioning in the top internode to one cut and this was made in the center. O'Keefe et al. (*157*) suggested two cuts per internode, one at the top and one in the center.

Holmes et al. (*82*) made a study of longitudinal splitting as compared to the cross-sectioning method. They concluded that each method gave accurate estimates and that splitting the stem had a greater degree of sensitivity, but this method was not worth the extra time necessary to make the readings. A rating of the complete stem gives better data for interpreting genetic composition in relation to solidness; however, the top-internode rating used by early workers was perhaps adequate for the studies they were conducting.

ENVIRONMENTAL EFFECT ON STEM SOLIDNESS

Putnam (*169*) observed that the growth rate of the stem wall exceeded that of the pith in the upper and later developing internodes. The slower pith development thus caused stems to be partly hollow. He stated that this differential growth was affected by both environmental and genetic factors.

[10] Personal communication from Ruby I. Larson dated June 15, 1964.

Platt (*160*) and Platt et al. (*166*) found that stem solidness of *T. aestivum* wheats was affected by variation in light, temperature, moisture supply, and spacing of plants. Under greenhouse conditions the solidness of S–615 and S–633 was almost completely inhibited. Artificial shading inhibited the solidness of S–615, but had little effect on plants of Golden Ball, a variety of *T. durum*. Roberts (*181*) also showed differences under greenhouse conditions.

Luginbill and McNeal (*121*) found that the stem solidness of Rescue decreased as seeding rate was increased and as row spacing was narrowed.

Holmes et al. (*82*) found that shading Rescue wheat at the initiation of elongation shortened the internodes, whereas shading at a later date caused them to elongate. Solidness of the bottom internode was reduced by shading from the two-leaf to boot stage. Lodging occurred when shading was used from the boot to heading stage. Kolar [11] also found that shading and moisture supply affected stem solidness.

Roberts and Tyrell (*183*) found that Rescue maintained solidness in the greenhouse with 4,000 foot-candles of supplemental light but not with 1,500 foot-candles.

Larson and MacDonald (*112*) studied the relationship between stem solidness and culm dimensions using monosomic lines of S–615 for examination. Most monosomics of S–615 were shorter than normal. Many had thinner culms, but monosomics 2A and 3D had thicker culms. The differences in stem solidness between monosomics and normal lines of S–615 were found to be due to the loss of chromosomes affecting stem solidness and not to changes in culm dimensions. However, within lines of genetically similar plants there was a small but consistent association between short culm and solidness, between thin culm at the tops of internodes I, III, and IV and hollowness, and between thin culm in the center and lower parts of internode I and solidness.

Luginbill and McNeal (*119*) studied the effect of fertilizers on Rescue and Thatcher spring wheats and Yogo winter wheat. Phosphorus (P) applied alone caused an increase in sawfly cutting on both winter and spring wheats. Potassium applied with nitrogen (N) and P tended to decrease sawfly cutting, whereas N alone had little effect on sawfly cutting.

EFFECT OF RESISTANT VARIETIES ON SAWFLIES

Resistance in wheat, as related to the sawfly, can be divided into three categories: (1) Lack of appeal to the ovipositing female and resistance to oviposition, (2) suppression of egg hatching or larval tunneling, and (3) nutritional requirements of the larvae (*85, 87, 88, 180*).

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[11] KOLAR, J. J. THE INFLUENCE OF ENVIRONMENTAL FACTORS ON THE DEGREE OF STEM SOLIDNESS EXPRESSED BY SELECTIONS FROM CROSSES INVOLVING RESCUE WHEAT. 1952. [Unpublished master's thesis. Copy on file in Library, Mont. State Col., Bozeman.]

The first category is a matter of selection on the part of the female sawfly. Holmes and Peterson (*85*) reported increased oviposition in larger stems by *cinctus*. Shchegolev (*200*) reported the same for *pygmaeus* and *tabidus*. As would be expected, slender stems are shunned. Farstad (*52, 54*) found this to be the case with *cinctus*, and Shchegolev (*200*) obtained similar results with *pygmaeus* and *tabidus*. Roberts (*182*) presented evidence that Rescue wheat deters oviposition as it approaches flowering.

In the matter of selecting a host, Ries (*173*) and Udine (*223*) indicated that both *tabidus* and *pygmaeus* do not oviposit in oats. However, Shchegolev (*198, 200*) stated that both species attack oats and that *tabidus* likes oats best. *C. pygmaeus* has been reported to show a varietal preference when infesting barley in July in Denmark (*116*). Borodin (*13*) found no preference for barley over wheat by *pygmaeus*. Farstad (*54*) found slender stems would be accepted if the sawflies were caged on them, and he (*53*) also reported *cinctus* larvae in flax. Neither oats nor flax will allow the larvae to complete their development. Farstad (*54*) noted that fewer eggs were laid in solid-stemmed than in hollow-stemmed wheat, especially in the main stems of the solid variety. In light of available data, host selection appears to be of minor importance, since the wheat varieties being grown will be infested by any and all sawflies present.

The second category concerns the egg and larvae within the host. Any condition in the plant that is a detriment to these stages may be considered a resistance factor. Holmes and Peterson (*87, 88*), studying the susceptibility of *cinctus* eggs to destruction, found them vulnerable to desiccation and to immersion in water. They also listed crushing of the egg by plant tissue as a resistance mechanism. In relating these facts to plant resistance, the increased moisture-holding capacity of Golden Ball stems is believed to hinder hatching, though possible drying out in other solid stems, such as Rescue, was suggested. In the latter, it has been noticed that lignification of cells surrounding the egg sometimes occurs (*157, 195*).

Larvae are also susceptible to desiccation and immersion in the first instar. Holmes and Peterson (*89*) suggested that the pith may cause the small larvae to starve before they can devour enough cells to start growing. However, the largest larval mortality occurs in solid-stemmed wheat after the larvae have completed feeding (*89*). This may be due to impediment of the larvae by frass and solid stem and to desiccation before the larvae reach the bottom of the stem to complete their overwintering cell.

The types of resistance already discussed may be thought of as mechanical in nature. Attempts to link nutritional deficiencies with resistant wheats has not met with much success. McGinnis and Kasting (*131*) could find no differences in dry matter or nitrogen content of the pith of resistant varieties or in the walls of hollow-stemmed wheats. They believed that the solid-stemmed wheats killed the mature larvae by desiccation. They did find a higher moisture content in the pith of Golden Ball and accepted the hypothesis that the eggs are drowned in this wheat (*98*). Their subsequent studies have led them to postulate nutritional imbalance or toxic substances in Rescue wheat (*99*).

Since *cinctus* larvae are unable to complete development in hollow-stemmed oat plants, some nutritional deficiency or toxic substance must occur in this plant. This inability to develop in oats may be shared by the other two species of grain-infesting sawflies, in view of the varied reports on oviposition and larval tunneling. McGinnis and Kasting (*131*) were unable to show a difference in dry matter or nitrogen content between wheat and oats.

The nutritional requirements of the larvae are under study. Holmes (*78*) tested sawfly larvae for digestive enzymes. He found the larva contains enzymes capable of hydrolyzing starch, sucrose, and cellulose. Amylase and sucrase were found in the midgut and labial glands but not in the hindgut. These two enzymes are also present in the wheat stems. Tests for maltase, lactase, pepsin, and trypsin gave negative results. Lipase may be present in the larval gut, but results were not conclusive. Kasting and McGinnis (*97*, *132*) are attempting to rear sawflies on artificial media. Lopatecki et al. (*118*) examined the sugar content of the wheat plant and found that the stem contained glucose, fructose, sucrose, some reducing oligosaccharides, and one water-soluble oligosaccharide.

Reports of one or more of the sawfly species being most prevalent on such grains as barley and rye are possibly peculiarities of the area in which the insect occurs. The stage of plant development and the proximity of various hosts to the sawfly source can affect host selection. However, reports of host preference have caused some workers to suspect the existence of different races. If there are true races, then perhaps these may be capable of developing in solid-stemmed wheats. Callenbach (*18*) investigated differences in sawfly cutting in Rescue at various locations. He concluded that the differences were due to variation in stem solidness rather than to races of sawflies. Holmes and Peterson (*84*) reared a sawfly population continuously on Rescue and Thatcher for five generations and reduced the population to zero on Rescue; however, the population had also decreased in size on Thatcher. In another study, Holmes et al. (*92*) found a difference between two strains of sawflies in their ability to cut Golden Ball.

SUMMARY

Some grass stem borers of the hymenopterous family Cephidae are pests of cultivated grains in Europe, the United States, and Canada. *Cephus cinctus* Norton, *C. pygmaeus* (L.), and *C. tabidus* (F.) are economically important in the United States and Canada. *C. pygmaeus* and *tabidus* are European species accidentally introduced into the Eastern United States and Canada. *C. cinctus* is a native insect, which has transferred from wild grass hosts to cultivated grain.

The larvae of these sawflies damage the grain by tunneling the stems and girdling them near the ground before harvest. The tunneling reduces the grain quality and yield, and the girdling allows the heads to fall to the ground where they may mold or germinate in wet weather.

The loss attributed to sawflies varies from year to year. Losses caused by *cinctus* were estimated at 4,917,484 bushels in Montana and North Dakota in 1951, and in 1946 Canada estimated an annual loss of 20 million bushels. The damage caused by the European species in the Eastern United States is not so great as that caused by *cinctus* in the West.

The endemic species causes damage in Montana, North Dakota, South Dakota, Wyoming, Nebraska, and in the wheat-growing area of Canada north of Montana and North Dakota. The two European species cause damage in eastern Canada, New York, Pennsylvania, Massachusetts, Maryland, Delaware, New Jersey, Virginia, West Virginia, and Ohio.

The sawflies are univoltine, adults appearing from June 1 to July 15 in the areas of wheat infestation. At this time the eggs are laid in the stems and the larvae develop through the summer. In August the larvae work to the base of the plant, where they cut the stem and prepare an overwintering cell below the cut. A cocoon is formed within this cell and encloses the overwintering larva. Pupation occurs in May of the following spring. A description of the egg, larval instars, and pupal stage is recounted.

Cultural practices do not give a consistent level of sawfly control, and some are difficult to put into effect. Cultivation that will bring infested stubs to the surface is effective. Larvae in the exposed stubs are killed during the winter if the snow cover is light. Stubs exposed in May after the larvae have entered the prepupal stage allows desiccation of larvae and pupae unless heavy rains occur.

Crop rotations that utilize resistant crops such as durum wheat, barley, oats, flax, and mustard are effective in controlling the sawfly. Such practices as deep plowing, delayed seeding, and trap crops are also of some value; however, they are impractical in areas of strip farming as practiced in Montana. Burning of stubble and swathing are not effective means of sawfly control.

Chemical control using heptachlor as a furrow application is effective under some conditions. One-half pound per acre has given from 75- to 95-percent control in 1-foot row spacings. No formal recommendation has been made, but treatment of a 14-foot border on each strip, where infestation is heaviest, appears practical.

Biological control is effective for the European species and may be effective for the endemic species. Establishment of an internal parasite of *pygmaeus* and *tabidus*, *Collyria calcitrator* (Gravenhorst), offers the best possibility. The native parasites of *cinctus*—*Bracon lissogaster* Muesebeck, *B. cephi* (Gahan), and *Pediobius utahensis* (Crawford)—exert some control in grass hosts but are negligible in grain.

Resistant varieties of wheat offer the best means of controlling sawflies. The solid stems of these varieties appear to inhibit the development of the larvae. The solid-stem character is often associated with lower yields, and for this reason resistant varieties are not grown universally in the sawfly areas. Resistant varieties grown throughout the sawfly areas would greatly decrease the populations. If new varieties with better yields were available, growers would be more easily induced to use this means of controlling the sawfly. Resistant varieties presently in use are the spring wheats Rescue, Chinook, Cypress, and Sawtana and the winter wheat Rego.

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