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Phenology of goatweed, Hypericum perforatum, in relation to the behavior of goatweed beetles, Chrysolina gemellata and C. hyperici, in western Montana

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THE PHENOLOGY OF GOATWEED, Hypericum perforatum,
IN RELATION TO THE BEHAVIOR OF GOATWEED BEETLES,
Chrysolina gemellata AND C. Hyperici, IN WESTERN
MONTANA.

by

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Dean, Graduate School

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Date
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INTRODUCTION

St. Johnswort, Hypericum perforatum L., commonly known as goatweed or Klamath weed, is a perennial, woody stemmed, noxious range weed. It is indigenous to Europe, Asia, and North Africa. Goatweed has been introduced into Australia, North America, and, according to Mr. H. D. Sandvig of the Food and Agriculture Division of the United Nations, it is reported to occur in Chile. The plant appeared in California during the 1860’s and by 1924 it had entered Montana.

Goatweed beetles, Chrysolina gemellata Rossi. and C. hyperici Forst., phytophagous insects that are host specific on goatweed, are found in Europe. The population center of C. gemellata is in southern France, while that of C. hyperici is in England (17). There are seventeen insects that parasitize goatweed, as natural enemies of the plant, in the Var District of southern France. Certain of these, including Chrysomelid beetles, were introduced into Australia in an attempt to control goatweed by beetle feeding. C. gemellata and C. hyperici were brought from Australia to California for the same purpose. The first beetle colonies were introduced into Montana by the Montana Extension Service from California in 1948. During the years 1950 and 1951 more colonies were introduced.

Observations on the behavior of beetle colonies in Montana have been of a general nature since the time of their introduction. The general objective of this study was to observe, at short intervals, beetle behavior as it related to plant development throughout a period of one year, and to learn the ability of the beetle to control the plant. The following specific objectives were selected: a study of goatweed phenology, insect phenology, the synchronization of plant and insect activ-
ities, the feeding characteristics of larval and adult beetles, beetle population density during all life stages, and plant mortality.

LITERATURE REVIEW

Intensive studies of goatweed and the numerous insects parasitizing it were carried out by Wilson in France (17). Results growing out of that study led to the introduction of goatweed beetles into Australia in the 1930's. A number of studies, both of the beetles and the plant, have been conducted by Clark and others (1,3,5,14). The successful use of beetles in goatweed control in Australia led to their introduction into California in the 1940's. A number of studies and reports from California by Holloway, Huffaker and others testify to the success of goatweed control through beetle feeding in that area (6,7,8,9,10,11,12,13).

The word control, in reference to plant death or reduction of plant population by biological methods, has many meanings. Since opinion regarding its meaning is controversial, the following statement by Clausen describes control as it is referred to in this study: "Full commercial control may be defined as that degree of control beyond which other methods of control are not required or economically practicable". He goes on to say that "A species that is fully effective in its country of origin, yet fails to achieve equal control in a new location, may likely attribute its effectiveness to climate directly or indirectly. Biological control is less frequent in temperate than in tropical climates" (4). Climate, therefore, probably is an important factor relating to goatweed and particularly to goatweed beetle
activity.

The Var District of France has a Mediterranean climate characterized by summer temperatures around seventy degrees Fahrenheit, and those of winter approaching forty degrees. Precipitation falls as rain, the major portion occurring during the autumn season. Summers are dry. Total annual precipitation approximates 22.3 inches (18). In the Owens Valley of Australia, a principal area of goatweed infestation, the winters are cold with frequent and severe frosts. Summers are warm, although maximum temperatures rarely exceed 100 degrees Fahrenheit. Total annual precipitation varies from 33.3 inches to 54 inches, most of it falling between May and October. Frosts are reported to be frequent but no reference is made regarding precipitation occurring in the form of snow (3).

Goatweed occurs in the foothills of southern France in scattered stands of cork oak and other trees, along roadsides and railway areas, embankments and waste areas. It is found typically in forest clearings, gradually yielding place to other plants (17). In the Bright District of Victoria, Australia, goatweed invades formerly cultivated soils, abandoned gold dredgings, and eucalyptus and pine stands (1). Goatweed occurs as a pest on range and pasturelands of northern California. It crowds out clovers, and nearly all grasses, wherever it is found (16).

In France, goatweed development during the year has the following pattern: An abundant basal rosette of procumbent stems is present in January. The plant grows rapidly in February and begins to form
upright stems which develop flower buds in April. Shortly afterwards the first flowers appear at the top of the upright stems and by mid-June the plant is in full bloom. During April and May the procumbent stems die. In June the leaves become less succulent, and by July or August complete defoliation occurs. Heavy rains of late August or early September cause the plant to renew growth and new basal stems appear at that time. Procumbent stems at the base of the plant sometimes reach a length of one foot by the end of September. Foliage continues to develop throughout the winter although growth is delayed by low temperatures. Seed capsules begin to open at the end of September but the seeds are not completely shed until the end of November (17).

Plant growth begins during April and May in Australia. The first growth phase consists of basal, procumbent stems which form a close carpet in dense stands. A second growth-phase follows with development of erect fertile stems which reach heights of one to four feet. After flowering, growth is checked by drought and, as stems dry, the leaves fall off. The dried, erect stems often persist for several years (2).

After fall rains begin in California, goatweed develops a prostrate rosette of basal foliage. Growth continues slowly during the winter months and by May or June the plants are in flower. The period from late June to October or November is a relatively dormant one for the plant. Seeds ripen and fall during this period and most of the leaves become dry and are shed. The stems become hard and woody (6).
In France adult beetles emerge from March until mid-June. They aestivate from July to September, when they become active again. Oviposition occurs from October to May. Larvae are present from mid-October until the following summer. The first full-grown larvae appear in December and new adults emerge in late March (17).

Adults begin to emerge in September in Australia. By late November they have emerged and major feeding has been completed. Aestivation extends from that period until May when seasonal rains stimulate them to emerge, copulate, and commence oviposition. Eggs are laid until September. Larvae occur from May through October, and pupae during August, September, and October (1).

Goatweed beetles emerge during April and early May in California. By late June or early July they return to the soil and go into aestivation until fall rains begin. Copulation and oviposition commence in mid-October. Eggs, larvae, and adults are present during the winter. By spring most of the eggs have hatched, larvae are approaching maturity, and pupation begins (7).

Adults and larvae, feeding instars of the beetle, appear in France when goatweed is in a green and succulent stage. There is a close synchronization of larval feeding with basal plant growth development. Adults emerge from pupal cells to feed on plants which are then flowering. At the time that foliage becomes less succulent, beetles enter into aestivation (17). The synchronization of beetle and plant activities in Australia, France, and California is close. In California, synchronization is believed to be directly related to control of the plant. C. hyperici, less well synchronized with plant growth than
C. gemellata, is less able to control goatweed stands in California (7).

It was found in Australia that very young and large, old crowns of goatweed were readily destroyed by beetle feeding, but mortality of moderate-sized crowns was relatively low (2). The susceptibility of mature goatweed to defoliation depends on environmental conditions, e.g. the condition of the soil, which determine the life span of the individual crown and the rate and amount of vegetative reproduction. C. hyperici is highly destructive only in stands characterized by large crowns and limited vegetative reproduction; whereas C. gemellata can eliminate any type of stand occurring in treeless areas (3).

Large numbers of larvae and adults attack goatweed for nine or ten months of the year in France (17). It is reported from Australia that C. gemellata usually keeps goatweed defoliated from four to six months (1). In the Bright District of Victoria, Australia, it was found that the growing period of goatweed was longer than the feeding period of the beetle. Plants must be kept leafless for several months to be killed. Partial defoliation for longer periods or complete defoliation for shorter periods will not kill them (1). In California, insect feeding extends over an eight month period. It was observed that plants stripped of foliage for five months renewed growth if sufficient moisture was supplied to them. Third and fourth instar larvae completely destroyed basal growth in California and complete defoliation extended over several months (7).

The principal factors which adversely affect the population of C. gemellata in France are firstly, parasites and predators and, secondly,
the absence at certain times of the year of an adequate food supply (17). Beetle losses in Australia are due to both density dependent and density independent factors. Destruction of food and reduction of protective cover are the only density dependent factors operative. Adults and larvae are subject to predation by birds. Very little parasitism occurs and is mostly confined to larvae (2). Small losses are reported from California, because of parasites, but no major reduction of the beetle population occurs (10). Some adult beetle losses are attributed to winter frosts and to overheating in summer in Australia (2).

PROCEDURE

Three geographically distinct areas in western Montana were studied. The Bison Range, on grassland, was one of these. The other two were at Hamilton and Thompson Falls, both in open forest. In each area beetle colonies had been established for a minimum period of three years. Eleven goatweed stands were studied, of which ten were colonized with C. gemellata and one stand with C. hyperici. Two forested areas were selected. Two goatweed stands were studied on each of these. One area, consisting of seven goatweed stands, was selected on grassland.

The most northern area studied was at Thompson Falls. Annual precipitation during the 1941-1950 decade averaged 19.5 inches, falling principally during the winter months as snow. Average air temperatures varied between 68 degrees Fahrenheit in July and 21 degrees in January. One southern and one western exposure were studied, both occurring in
an open stand of larch-Douglas fir.

The Hamilton area was situated approximately 120 miles south of Thompson Falls. Annual precipitation during the ten year period from 1941-1950 averaged 11.2 inches. Spring is the wettest season. Temperature levels closely approximate those of Thompson Falls throughout the year. As in Thompson Falls, goatweed stands on western and southern exposures were studied at Hamilton. Dominant vegetation at the Hamilton area was Ponderosa pine, occurring as an open growth stand.

The Bison Range is located geographically between Thompson Falls and Hamilton. Average annual precipitation from 1941 to 1950 was 15.2 inches at the nearby weather station at St. Ignatius. Spring is the wettest season. Summers are warm and winters are cold. Two goatweed stands were studied on northern, eastern and western exposures, and a single stand on the southern exposure.

The smallest examination unit was an individual plant. The collection of necessary data required the removal of each plant examined. Goatweed stands were examined along a straight line from the lower border to the upper border of the stand. Plants were selected for examination at regular intervals. Since the goatweed stands varied in size, the intervals between plants examined were varied to accommodate that difference. The interval between plants examined within each stand remained constant.

Observations were taken weekly or bi-weekly, except during a short period of plant and beetle inactivity during late summer. One goatweed stand at the Bison Range was examined weekly from April 27th through December 4th, 1954. Remaining goatweed stands at the Bison Range and
all of those at Thompson Falls were examined from June 6th to December 4th. Those at Hamilton were examined from May 9th through November 14th, 1954. Qualitative observations at irregular intervals continued through January and February, 1955.

The number of plants to be examined per observation was determined by Chi-square analysis. A base sample of 50 plants was examined. The numbers of eggs, larvae, and adults present were tabulated for each plant examined. Sample sets of 40, 20, 10, and 5 plants were compared with the base sample of 50 plants to determine the ratio of individuals present in each life stage of the various sets compared. It was found that the examination of 20 plants yielded approximately the same ratio of life stages of the beetle and the same number of individuals per plant as did an examination of 50 plants. Thus, twenty plants were examined per goatweed stand per observation. A total of 4,860 plants were examined during the course of the study.

Qualitative data were taken on the phenological stages of goatweed including crown bud development, flower bud formation, full bloom, seed capsule formation, seed shedding, maximum height growth, and defoliation. Quantitative data were collected on the number of stems per plant and their average length. Goatweed manifests two distinct vegetative growth phases. The first phase is one of procumbent basal growth development. The other phase is the vegetative development of upright stems. There is no sharp distinction between the two phases. In this study the separation of these two growth phases was made at the time of greatest basal growth formation, as determined by the maximum number of basal stems present, and is referred to as the maximum rosette
RESULTS

Corrections made per established stand.

Observations made. Temperature values were averaged for the vicinity of each plot, and each plant examined at each temperature. Periodic measurement measurements were taken. Root temperatures were

At the end of the threeyear study, a random sample was taken and

occurred in a sample of twenty

root system and expressed in terms of  the percentage of dead plant

that had dead plant. Mortality was determined by examination of the

plant mortality measurements were made on all exposed stands.

exposed

were taken on the number of edges of all lateral branches of

pores, mortality, and percentage data from

resting habit; population, initial reading and reading, photosynthesis; res-

beetle behavior observed included copulation, larval feeding and

development.
Five Phenological Development Phases of Foothood at the Bison Range, Thompson Falls, and Hamilton 1954
bud formation and flowering occurred within a few days on all areas. Maximum height growth was achieved after the flowering period was over. Fall bud formation began during July and August but growth was not rapid. Fall rosette development was more rapid on the grassland area.

**Beetle Phenology**

Forest areas were quite similar with respect to both beetle numbers and phenology. Figure II shows the numbers of insect eggs, larvae, pupae, and adults per plant, that were observed during the course of the study. For the purpose of comparison, two goatweed stands on each of two forest areas were combined in Figure II to describe the phenology of beetles under forest conditions. Figure III presents similar information regarding beetle phenology on seven goatweed stands of the grassland area.

Adults were present in goatweed litter when first observations were made on grassland goatweed stands in April, 1954. Copulation was observed intermittently during the spring season and in the fall after the aestivation period was completed. Oviposition commenced during the latter part of April with larvae appearing in the last week of the month. Eggs were found principally on spring basal growth. In the absence of such growth, eggs had been laid on annual grass and other seedlings, on litter, rocks, or on the soil. Eggs occurred singly or in groups of two or more, attached to leaves or other material by a glue-like substance. Eggs were first observed at Hamilton the week of May 9th, and at Thompson Falls during the week of June 6th, 1954. Goatweed basal growth was advanced on forest areas beyond that of the Bison Range and eggs were found mostly on goatweed leaf and stem surfaces.
The average number of eggs, larvae, pupae, and adult beetles present per plant on chestnut occurring in forest areas.
The average number of eggs, larvae, pupae, and new adults present per plant on goatweed occurring on the grassland area.
With the development of ample fall growth on all areas in 1954, eggs were found almost exclusively on the basal rosette.

Figure IV presents information relating to incubation periods and larval development in the fall of 1954. Eggs appeared the latter part of September on forest goatweed stands and five weeks later the first larvae were seen. The incubation period on forest goatweed stands was approximately equal to that on northern exposures of grassland goatweed stands. Soil temperatures over the period from May to December are presented in Figure V.

Forest areas had larvae when initial examinations were made. Larvae were first observed on the Bison Range during the last week of April. The four larval instars differed principally in size. First instar larvae typically fed on leaf tips, remaining there until they reached the second instar stage. Second and succeeding larval instar stages fed on basal growth at night, and crawled to the surface litter during the day where they became inactive. They were found in litter at the base of plants or on the root crown, singly or in groups. Larval feeding habits changed as fall temperatures approached the freezing point. At that time it was found that larvae were inactive during the early morning and late afternoon. Feeding took place only during the warmest portion of the day.

Pupae were noticed on forest goatweed stands the first week of June and those on grassland appeared two weeks later. After fourth instar larvae completed feeding they burrowed into the soil and remained inactive for a short period. A simple, unlined pupal cell was formed in soil at the base of goatweed plants. Pupal cells were found from
Insect Developmental Stages Plotted Against Time Showing the Differences in Development Rate Between Exposure and Forest and Gravel Road Areas.
Average Monthly Soil Temperatures, Taken One Inch Deep, for the Bison Range, Thompson Falls, and Hamilton.
one half to two inches deep on forest areas, and from one to three and one half inches deep on grassland. One goatweed stand on the Bison Range had fall pupae on November 7th, 1954. Fall pupae were not found elsewhere.

Adult beetles were present on all areas in the spring of 1954. While ovipositing, adult beetles were difficult to find. New adults began to issue from pupal cells during the third week of June on forest areas and a week later on grassland. Newly emerged adults were positively phototrophic, and attacked the terminal portions of goatweed plants. They fed voraciously during the first weeks following emergence. Adults aggregated on the plants in clusters of as many as fifty individuals. They remained there continuously, feeding and summing themselves. On several occasions adults were seen to fly.

Aestivation began slowly, commencing on forest goatweed stands the first part of August, and a week or two later on the grassland area. Beetles sought favorable aestivation sites away from goatweed stands. An occasional beetle was found in the litter of goatweed stands but the vast majority were found under bushes and in forest duff. Aestivation coincided with conditions of high temperature and low soil moisture.

The fall of 1954 was unusually wet in western Montana. Rains started the second week of August and continued intermittently through November. Beetles came out of aestivation on the grassland area after 1.7 inches of precipitation fell; on the forest area at Hamilton after 1.4 inches had fallen; and after 2.7 inches had fallen at Thompson Falls. Surface litter was scant at both Hamilton and the Bison Range. At
Growth development started at approximately the same time on all areas. Four to six weeks after planting, Compared with the plastic-hilled areas, Plant Protection was delayed by six weeks at Thompson Falls and many
Feed the plants were chosen for the plant protection development. Beans sprouting Growth and maximum interval
the maximum and advanced stages were feeded at the time of seedling area in late June. On all Goodseed stands Interval numbers were near
were obtained through development stages in late May, and the Gradient of the grass when the beans rose to reach maximum development. Percent
Spray Growth has an average stem length of approximately 5 feet

Sprout evaluation

Evaluation was performed at the same time, Find all
Heterotrophs were counted with the Goodseed stands, more in all
In the spring of 1966, beetles were increased from the same scenario. Beetles were found on the soil surface and within the surface litter. During the last week of November and the early part of December

Alt temperatures were near freezing which on dead Goodseed stems and other plants during the day. Although
Ocuppied on at a slightly higher altitude by ecosystems alike. Beetles remained
from distribution. The perennial leaves of seaweed found in water
advice to stay away from phototropism been at the front of emergence

from distribution (18)

7 Deoe of 1967 and 1968 very intense rain fell on the Mission Plateau. There were no indications of surface litter. Durning the
When larvae first appeared on forest areas, fall plant growth averaged one inch of stem length at Thompson Falls, and 3/4 inches at Hamilton. Goatweed growth on forested areas did not reach the maximum rosette developmental stage in the fall of 1954.

Larvae were present on grassland goatweed stands when fall plant growth averaged a half inch in length. There was a rapid increase in larval numbers at the time when plant growth reached two inches of stem length. Heavy larval feeding during October caused widespread and often complete defoliation of basal plant growth. In the absence of sufficient foliaceous food, larvae fed on stem tissues thereby causing a reduction in the average stem length of basal plant growth. Plant rosettes did not reach the maximum developmental stage in the fall of 1954. The larval population passed its peak of numbers and was on the decline the first week of December on the grassland area.

Flower buds formed on all areas during the first week of July. Forest and grassland areas were in full bloom the last week of July. New adults began to emerge from pupal cells on all areas in the last week of June. New adults fed on terminal goatweed leaves in preference to green flower buds. By the end of July the plants were in full bloom and beetle feeding was nearing its end. Adult feeding on goatweed flowers was light and not well synchronized with plant flowering.

**Insect Feeding and Population Density**

Larval and adult feeding started on forest areas before field observations began. By the third week of June larvae had disappeared from goatweed stands at Thompson Falls, and a week later there were none at Hamilton. New adults appeared at Thompson Falls on June 20th,
and were feeding until July 25th. New adults emerged June 13th at Hamilton, and disappeared August 15th. There was no overlap of larval and new adult feeding in the Hamilton area nor at Thompson Falls. Fall larvae were first observed at Thompson Falls on October 24th, and at Hamilton on November 14th. Since spring larval feeding had commenced when first observations were taken on forest areas, the time of initial spring larval feeding was unknown.

Beetle activities extended over a longer period on grassland goatweed stands than on those in forested areas. The following table shows the length of time, in weeks, that beetles in various life stages were present on goatweed stands in forest and grassland areas.

Table 1. The Period of Time, in Weeks, that Various Life Stages of the Beetle were Present on Goatweed Stands of Forest and Grassland Areas.

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Spring</th>
<th>Fall</th>
<th>Total</th>
<th>Spring</th>
<th>Fall</th>
<th>Total</th>
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<tbody>
<tr>
<td>Eggs</td>
<td>15</td>
<td>11</td>
<td>26</td>
<td>13</td>
<td>13</td>
<td>26</td>
</tr>
<tr>
<td>Larvae</td>
<td>12</td>
<td>5</td>
<td>17</td>
<td>12</td>
<td>12</td>
<td>24</td>
</tr>
<tr>
<td>Pupae</td>
<td>4</td>
<td>-</td>
<td>4</td>
<td>4</td>
<td>-</td>
<td>4</td>
</tr>
<tr>
<td>Adults</td>
<td>16</td>
<td>12</td>
<td>28</td>
<td>16</td>
<td>13</td>
<td>29</td>
</tr>
</tbody>
</table>

The total larval feeding period at Thompson Falls was at least 12 weeks, and at Hamilton at least 8 weeks, during 32 weeks of observation. New adults were present for five weeks at Thompson Falls and for nine weeks at Hamilton.

Larval feeding started on the grassland area on April 25th. By the second week of July larvae had disappeared from goatweed stands at the Bison Range. New adults were seen at the Bison Range the week of June 27th and remained on the plants until August 15th. There was a
six week overlap of larval and new adult feeding in the Bison Range area. Fall larvae appeared on the grassland area the week of September 12th and were still present when observations ceased on December 4th. The total larval feeding period on the Bison Range lasted 24 weeks during 32 weeks of observation. New adults were present for six weeks.

The average number of spring larvae per plant at Hamilton was slightly less than one, when larvae were present in greatest numbers. Grassland goatweed stands had an approximately equal larval density at that time. Thompson Falls had the lowest spring larval density but observations began as larvae were disappearing.

At Thompson Falls the greatest numbers of fall larvae were found early in December and averaged approximately three individuals per plant. When observations ceased, larvae were only beginning to appear at the Hamilton area. Larvae occurring on grassland goatweed stands reached a peak of seven individuals per plant in the third week of October. The population density of new adults was approximately equal on forest and grassland areas with an average of less than one individual per plant. Figure VI presents information on the length of the feeding period and population densities on the three areas studied.

**Plant Mortality**

Three quarters of the grassland goatweed stands examined had dead plants at some time during the period of observation. One stand on a southern exposure had no dead plants in June, 1954. By August 22nd every plant was dead.

Four Bison Range stands had large numbers of dead plants. The average percentage of dead plants for those four stands were plotted
Figure VI

The Average Number of Larvae and New Adults Present Per Plant at the Bison Range, Thompson Falls, and Hamilton
against time from April 27th through November 28th. In Figure VII, precipitation and temperature are superimposed over the plant mortality curve to present an interesting relationship of climatic factors to plant mortality. During the active larval feeding period plant mortality increased slowly with time. At the time larval feeding ceased and adult beetles had entered aestivation, plant mortality increased rapidly. Air temperatures were highest at this time, and the soil moisture content was the lowest of the year. Plant mortality tapered off as temperatures dropped and fall rains started. It appeared that beetle feeding weakened goatweed plants, and that high temperatures or the lack of moisture, or both, were important in contributing to plant death.

**Climate**

The 1954 weather of western Montana differed somewhat from the ten year average of 1941-1950. Figure VIII shows the temperature and precipitation for three weather stations in western Montana during 1954 and their ten year averages. Climatological data used in this study were taken from weather records at Hamilton, Thompson Falls, and St. Ignatius. Hamilton is situated approximately nine miles from the goatweed stand studied. Thompson Falls lies four miles, and St. Ignatius three miles from goatweed stands at Thompson Falls and the Bison Range respectively. Temperature and precipitation are expressed in monthly averages. The climatological data from these sources is therefore of limited value. Soil temperature and precipitation measurements were taken within goatweed stands at each of the three areas to supplement the weather station data.
In the Upper Graph Accumulated Moisture is Plotted Against the Percentage of Dead Plants Found in a Sample of Twenty. Below, Soil Temperature is Plotted Against Dead Plants.
The Average Monthly Precipitation and Temperature at St. Ignatius (Bison Range), Thompson Falls, and Hamilton are Shown for the Ten Year Period 1941-1950 and for 1954.
Air temperatures were almost identical, by monthly averages, throughout the year at all three areas. Average soil temperatures taken in the field showed the Thompson Falls goatweed stands to be generally cooler than those of Hamilton and the Bison Range. Bison Range soil temperatures were the warmest of the three areas and Hamilton was intermediate. Figure V shows soil temperatures of the three areas.

The hypergraphs of Figure IX describe graphically the climate of Hamilton, Thompson Falls, St. Ignatius, and Marsiellas, France. They were constructed from weather data covering a ten year period for the Montana stations and a fifty year period for France. The principal difference among the three Montana areas is the amount of winter precipitation that the Thompson Falls area receives compared with the relatively small amounts that fall at Hamilton and the Bison Range. Average monthly temperatures throughout the year are quite similar at the Bison Range, Thompson Falls, and Hamilton. Larval activity occurs between temperatures of 35 and 75 degrees Fahrenheit in France and Montana. Larvae are active during the warm and humid months of the year both in France and Montana. Since France is generally warmer and more humid for a longer period of time than any of the western Montana areas, the larval feeding period is consequently longer.

DISCUSSION

Some beetle colonies introduced into Montana have increased their numbers or maintained themselves. There are no reports that any of the beetle colonies introduced have completely disappeared. There are
Figure IX

Hythergraphs for the Bison Range, Thompson Falls, and Hamilton, compared with a Hythergraph of Larsielles, France.
colonies that have not caused the death of a single goatweed plant, particularly in forested areas. Other colonies have killed goatweed plants in large numbers. Goatweed beetles seem able to withstand the vagaries of Montana climate. When conditions are favorable, beetle density increases to a level that results in the reduction of plant vigor and eventually in the death of the plants.

Density Dependent Factors

Lack of food probably caused adult and larval losses on some of the grassland goatweed stands during the spring and early summer seasons of 1964. As the period of aestivation approached, numerous adult beetles and advanced instar larvae died. The larvae were small-bodied, with relatively large heads, and were restricted to feeding on stem tissues since no foliaceous growth was available. There were no such larval deaths observed on forest areas. Density dependent factors, other than lack of food, appear to have been relatively unimportant in reducing beetle populations in Montana.

A contrary situation occurs in France where, according to Wilson, greatest beetle losses are attributed to density dependent factors. Predation and egg parasitism are primarily responsible for reducing the beetle population. The factor of insufficient food is of secondary importance (17). Density dependent factors arise from, or are aggravated by, a very dense beetle population resulting in intraspecific competition and consequent reduction of beetle numbers.

Density dependent factors are less important in Australia where predation and parasitism are present but are not major causes of beetle losses (2). Plant defoliation through beetle feeding in Australia
resulted in larval losses due to lack of food, but most of the adult
losses were attributed to density independent factors that became ac-
tive after plant defoliation (6). Density dependent factors are not
important in the reduction of the beetle population density in
California (7).

Density Independent Factors

The density independent factors that appear to be most important
in Montana, affecting the goatweed beetle population, are those of
temperature and moisture. The cold winters of western Montana appar-
ently keep adult beetles in hibernation until spring. The spring sea-
son is characteristically wet due to precipitation and melting snow.
Rising temperatures probably stimulate adult beetles to emerge from
hibernation. Eggs laid in the fall remain in a dormant condition
through the winter and hatch in spring. Those laid in the spring hatch
later than eggs laid in the fall.

Low temperatures affect the incubation period, but are less impor-
tant in relation to egg-laying, at least on grassland goatweed stands.
Two stands on opposite sides of the same hill at the Bison Range were
apparently identical except for exposure. Beetles were present on both
stands in approximately equal numbers. Eggs appeared on the south ex-
posure one week before they did on the north exposure. Larvae were ob-
erved one week after the first eggs were seen on the southern exposure.
Larvae were observed four weeks after the first eggs appeared on the
northern exposure. Larval development was more rapid on the southern
exposure than elsewhere, and by November 7th pupae were present. Lar-
vae did not complete development on any other exposure, nor did all of
Above 100 degrees Fahrenheit caused the death of all beetles when
maintained in the litter area when temperatures were low. Temperatures
where temperatures were 2 to 6 degrees higher, adults likewise re-
tained in the litter. The litter areas were open, less resistant to low
temperatures, but litter inter-tissue were killed at temperatures of 20
degrees. However, the major cause of larval, pupal, and adult beetles
were not apparently affected by temperatures as low as 10 degrees
in contrast to western Montana; density independent factors.

In contrast to western Montana: density independent factors in

and most rapid at the plateau trend

temperature was shown at Hamilton, somewhat higher at Thompson Falls,

warmer at Thompson Falls, and warmer at the plateau trend. Thermal de-
the plateau trend. Soil temperatures were colder at Hamilton, somewhat
was successfully lower on western, eastern, and northern exposures of
mean look place most rapidly on the southern exposed, and

Larval development correlated with soil temperatures develop-

read 75-70 degrees Fahrenheit.

Raising temperature on forest floor decreased stenot when soil temperatures were-
the soil temperature level was between 55-60 degrees Fahrenheit. 1971 of 1974. Observation common on grassland exposed stands when
the

were probably not associated with temperature in the

continuous factor. Resulting in a more rapid reduction in plant matter.

ment means that cowpea bean grown is attacked earlier and reading

the larvae on the southern exposure do so. More rapid larvae develop.
they were exposed to direct sunlight (2).

There is a major climatic difference between France, where *C. gomphocephala* is indigenous, and Montana, regarding total annual precipitation. Since western Montana receives approximately 1.65 inches of precipitation per month during a three month spring larval period, and France receives an average of 2.2 inches per month during an eight month larval period, it could be expected that larval success in France might be dependent upon moisture.

In Montana spring pupal cells were observed at a depth of 2 inches on forest goatweed stands. Grassland goatweed stands had pupae occurring deeper, often to a depth of 3 or more inches during the spring season. Fall pupae, observed on one southern exposure of the Bison Range only, were found approximately 2 inches deep. It is suggested that moisture was the determining factor in regulating the depth of pupal cell formation.

It is reported from Australia that an excess of soil moisture is responsible for reducing the population of pupae. During aestivation water was a limiting factor, and insufficient soil moisture caused the death of aestivating adults (2). In California, laboratory tests of pupal survival in soils of varying moisture content demonstrated that pupae do not survive in soils containing three percent, or less, of moisture. If the soil is slightly moist, many larvae enter the soil but few emerge. Only with ample moisture do they survive the pupal stage (7). Goatweed stands in France, Australia, and California occur in areas that receive more precipitation than Montana. Pupal cells are formed at an average depth of 2 inches in those areas (2,7,17).
Beetles in Montana were in aestivation at the Bison Range and at Hamilton by the third week of August, and by the last week of July at Thompson Falls. Throughout this period, ample food was available, in a green state, on the areas under study. Since aestivation took place in the presence of sufficient food, there was no association of aestivation with lack of food supply in western Montana.

Beetles migrated out of goatweed stands to aestivate. They were found concentrated in plant litter around the base of trees and bushes. Soil adjacent to such plants appeared to be more moist than soil within goatweed stands. Aestivation was preceded by a dry period of high temperatures on all areas. No correlation was apparent between air temperature levels and the commencement of aestivation. It is believed that the lack of moisture within goatweed stands was responsible for beetle migration to more favorable sites for aestivation.

Adult beetles emerged from aestivation at Thompson Falls only after 2.7 inches of precipitation had fallen. This quantity of moisture required for beetles to emerge from aestivation at the Thompson Falls area, greater by sixty percent than Hamilton or the Bison Range areas, is believed to be associated with the relatively more abundant surface litter at that site. It appears that beetles emerge when sufficient moisture reaches the litter level in which they aestivate, usually at the soil surface. This condition would occur more rapidly on areas having a shallow litter layer. It is suggested that fall moisture stimulates beetles to emerge from aestivation. Figure X presents rainfall data taken on each of the three areas.

In France aestivation apparently occurs when goatweed becomes dry
Figure X

Average Bi-weekly Precipitation from June 6th to November 14th at the Bison Range, Thompson Falls, and Hamilton. Estimation Periods are shown for each area.
and the leaves are lost (17). Aestivation takes place during the dry period in Australia, and low soil moisture is reported to be responsible for some beetle losses during aestivation (1).

The climate of western Montana is characterized by winter snows and spring rains that provide ample soil moisture, usually into the month of June. Spring plant growth and larval development are active and well synchronized during this period. Moisture becomes important and perhaps sometimes critical in late June and July when pupae are in the soil. A dry summer followed by a dry fall probably causes beetles to enter aestivation and remain dormant throughout the fall and winter. Emergent fall plant growth does not develop without fall rain or ample moisture in the soil. With sufficient fall precipitation on the grassland area, goatweed sends out basal shoots and beetles emerge from aestivation. The Thompson Falls area typically receives fall rain and Mr. I. C. Puphal, United States Forest Service District Ranger at Thompson Falls reports that eggs have been observed every fall at that location. It appears that rainfall distribution is an important regulator of plant and beetle activities, particularly on the grassland area where more than one generation of beetles can be active in a single year if the autumn season is wet.

Grassland goatweed stands were found to have increasing numbers of dead plants as the spring and summer seasons progressed. Figure VII shows the relationship of temperature and moisture to plant mortality. It will be seen that the greatest number of plants died at the time when larvae had disappeared and adult beetles were in aestivation. With the advent of fall rains, plant mortality tapered off. Since
greatest plant mortality occurred under conditions of high temperature and low soil moisture, and in the absence of beetle feeding, it appears that these factors were important in contributing to the death of goatweed plants.

In Montana the only areas showing any significant or measurable kill of plants were of the lower two thirds of a large stand on grassland at the Bison Range, and partial or complete stand mortality on small, scattered goatweed stands in the same vicinity.

It is reported from Australia that beetle feeding can eliminate any goatweed stand that occurs in open country. There plants must be kept leafless for several months to effect goatweed stand control (1). In California large areas of goatweed have been cleared by beetle feeding. Annual and perennial grasses have returned to the cleared areas (12). In Idaho, beetles controlled sixty acres of goatweed in three years, and the plant cover was replaced entirely by annual bromes (16).

Comparison of Forest and Grassland Areas

The phenology of goatweed on forest and grassland areas differs annually according to the rainfall pattern. Hamilton and the Bison Range sometimes have fall precipitation, and sometimes not. Wet fall seasons cause goatweed basal shoot development. If there is insufficient moisture in the fall, basal growth forms root buds but does not appear above ground until the following spring. Thompson Falls typically has fall precipitation, and basal shoot development follows.

Goatweed at Thompson Falls developed basal shoot growth in the fall of 1953. Grassland goatweed stands developed basal growth in the spring of 1954, but not in the fall of 1953. Goatweed flowered
at approximately the same time on forest and range areas. Seed capsule opening occurred earlier on grassland goatweed stands than on forest stands. In 1964 goatweed phenology passed from maximum rosette development to the period of seed capsule opening in 11 weeks at the Bison Range. At Thompson Falls an equal plant development took 19 weeks, and at Hamilton 22 weeks. Goatweed root crown buds appeared on forest and grassland areas at approximately the same time, but the basal growth rate on grassland goatweed stands was nearly twice as fast as it was on forest goatweed stands.

Adults and larvae are the life stages of the beetle that parasitize goatweed plants. Goatweed stands occurring in forested areas were subjected to approximately 12 weeks of larval feeding and 26 weeks of adult feeding in 1954. Grassland goatweed stands sustained 24 weeks of larval feeding and 39 weeks of adult feeding during 1954. Larval density was approximately equal on forest and grassland areas during the spring season. In fall, the grassland area supported up to three times as many larvae per plant as did goatweed stands in forested areas.

The aestivation period on the grassland area averaged 4 weeks in length; that on forested areas 6 weeks. Beetles on the grassland area migrated as far as 200 feet to aestivate under bush or tree litter. Beetles on forested areas migrated less than 50 feet and aestivated under coniferous forest litter, sometimes into the forest proper a distance of 25 feet.

There were no dead plants observed on forest goatweed stands of this study. Most grassland goatweed stands had dead plants, and four
stands had large numbers of them. The degree of plant defoliation by newly emerged adults appeared to be approximately equal on grassland and forest areas and portions of several stands in each area suffered complete defoliation. Forest goatweed stands had relatively low larval and adult population densities in the spring of 1954. Only a few of the grassland goatweed stands were similar in that respect. The remaining grassland stands had dense populations of egg-laying adults and larvae. Feeding pressure was so great on those stands that goatweed basal growth was kept trimmed at or below the soil surface and no leaves formed. Adults typically fed on terminal portions of the shoots sometimes below the soil surface. Larvae fed principally on the sides of basal shoots.

Goatweed stands that were subjected to heavy feeding were the ones that had large numbers of dead plants. So long as the moisture level of the surface soil was sufficient, basal growth continued. As feeding continued, goatweed apparently responded by sending out more basal shoots. Emergent growth developed from lateral roots as far as a foot from the original root crown. After larval feeding ceased and adult beetles entered into aestivation, basal growth was able to grow above the surface and send out leaves. It seems likely that surface soil moisture was rapidly exhausted since many plants suddenly dried up and died. During this period, while no feeding occurred and leaves were forming, the greatest mortality of plants took place.
GOATWEED IS WELL ADAPTED TO WESTERN MONTANA CONDITIONS AS EVIDENCED BY THE VIGOROUS STANDS PRESENT IN THE STATE. GOATWEED BEETLE COLONIES RELEASED UNDER A VARIETY OF COVER, EXPOSURE, ELEVATION, AND SOIL DIFFERENCES HAVE BECOME ESTABLISHED. MANY GOATWEED PLANTS HAVE BEEN KILLED AND A FEW SMALL GOATWEED STANDS HAVE BEEN KILLED OUT, DIRECTLY OR INDIRECTLY, AS A RESULT OF BEETLE FEEDING.

Both the goatweed plant and the beetles became active with the advent of spring or fall moisture. Likewise, both were active within approximately the same temperature range. Consequently there was a close synchronization of plant basal growth and larval feeding. High temperature and dry soil seemed to curtail insect activities before the plant was so affected. Goatweed continued to grow while beetles were in aestivation. Beetles issuing from pupal cells completed their major feeding before flowers appeared. Thus, there was an asynchronizaton of adult feeding and plant flowering.

Certain factors were critical in regulating the density of beetle populations. Insufficient food, a density dependent factor, was probably important in reducing larval density on a few grassland goatweed stands. Density independent factors appeared to be principally responsible for insect losses. Since pupal cells occurred near the surface on forest areas, it seems likely that pupal survival was greater there than on the grassland area. Beetles on forest and grassland areas demonstrated a remarkable reaction to unfavorable aestivation conditions within goatweed stands by migrating to sites with a more
favorable microclimate. Low temperatures and frost restricted fall larval feeding and caused the death of some larvae. The Bison Range area was examined for the presence of larvae during the winter months. In late February no live larvae were found, leading to the conclusion that larvae are unable to overwinter in that form on the grassland area.

Beetle feeding, and the indirect effects developing from it, were perhaps the only deleterious effects that goatweed was subjected to in Montana. The time of beetle feeding was important. If the insect population was sufficiently large to keep goatweed from producing spring leaves, for a prolonged period of several months, the plant was seriously weakened. Yet the total volume of plant tissue consumed at that time was probably small. If the plant was able to send up fertile stems, the partial or complete defoliation that occurred through newly emerged adult feeding appeared to be much less effective in weakening the plant. Goatweed seemed to suffer more from spring and fall basal growth larval feeding than early summer defoliation of upright stems.

All areas had a synchronization of basal plant growth and insect feeding. However well synchronized these activities may have been, plant mortality apparently became possible only when the feeding period lasted for several consecutive months, and the insect population was large. Forest areas had a synchronized basal shoot development and insect feeding period, but the length of the feeding period was relatively short and the density of the feeding population was relatively light compared to the grassland area. The grassland area had a similarly
well synchronized plant growth and beetle feeding period, but in addition, it had a long feeding period by a dense feeding population. It appears that goatweed plant mortality is more likely to occur where all three factors are operative instead of a single one. The direct cause of plant death appears to have been related to climatic factors that were able to kill plants weakened by beetle feeding.

It is concluded that goatweed stands on grassland areas in western Montana are more likely to be killed by goatweed beetle feeding than are goatweed stands that occur on forested areas.

**SUMMARY**

Goatweed plant phenology in western Montana was found to be correlated with the rainfall distribution pattern in 1964. Plant development on the grassland area started in the spring season, the plants flowered in July, and seeds began to be shed in September. Plant development commenced during the fall of 1963 at Thompson Falls, flowering occurred in July, and seed capsules opened in October.

Goatweed beetle phenology followed plant development closely. Eggs appeared on the grassland area in April, new adults emerged in June, and adult aestivation started in August. The aestivation period lasted four weeks. Fall eggs appeared in September and fall larvae passed their maximum density in November.

On forest areas eggs and larvae were present when first observations were made in April, leading to the conclusion that the eggs were laid in the fall of 1963. New adults emerged in June. Aestivation commenced in August and lasted six weeks. Fall eggs appeared in
October. Larval development was slow on forest areas and by December the larval density was less than one third the larval density on the grassland area.

Coatweed basal growth was well synchronized with larval feeding and development during both the spring and fall seasons on forest and grassland areas. New adults emerged prior to the plant flowering period and their major feeding activity was completed before large numbers of plant flowers appeared. New adult feeding was thus not well synchronized on either forest or grassland areas with respect to plant flowering.

The length of the larval feeding period on the grassland area was 24 weeks in 1954. New adults fed for a period of 7 weeks and adults were present for a total period of 29 weeks. On forest areas larvae fed for 12 weeks and new adults for an average of 7 weeks, with adults present on the plants for a total period of 26 weeks. The population density of spring larvae was approximately equal on forest and grassland areas. The fall larval population was three times more dense on the grassland area than it was on forest areas. The population density of new adults was approximately equal on forest and grassland areas.

Plant mortality was observed on the grassland area exclusively. Coatweed stands occurring on the warmer exposures, and subjected to long periods of larval feeding by a dense larval population, suffered the greatest plant mortality. The rate of plant mortality increased when temperature was highest, soil moisture lowest, and when no beetle feeding took place.

Beetle colonies introduced into Montana have maintained themselves
or increased their numbers for six years. Density dependent factors were not important in reducing the beetle population except on a few goatweed stands on grassland that were completely defoliated. Density independent factors reduced the beetle population by extremes of temperature and by low soil moisture conditions. The same factors governed the activity of the beetle population in time. Temperature affected the incubation period, and rainfall pattern determined the time of adult emergence from aestivation.

Goatweed mortality occurred only on those areas that were subjected to heavy larval feeding for a period of several months and closely synchronized with basal growth development. These conditions were present only on grassland goatweed stands.
LITERATURE CITED


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