

THE CEREAL LEAF BEETLE, *Oulema melanopus* (L.),
AND ITS INTERACTION WITH TWO PRIMARY HOSTS:
WINTER WHEAT AND SPRING OATS

Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY
STUART H. GAGE

1972



~~NOV 28 '78~~ 38
~~KVAR 2 3 '78~~ 24

~~NOV 28 '78~~ 318
~~NOV 29 '78~~ R
B — 345
~~NOV 28 '78~~
OX 8008

MAR 13 1995
~~6716912~~

OCT 08 2000

7

well

dyna

was

host

and

the

quant

visite

of the

culent

by the

feeding

the sea

instar

ABSTRACT

THE CEREAL LEAF BEETLE, Oulema melanopus (L.),
AND ITS INTERACTION WITH TWO PRIMARY
HOSTS: WINTER WHEAT AND SPRING OATS

By

Stuart H. Gage

The biology and dynamics of the cereal leaf beetle is becoming well documented but little is understood about the role of plant dynamics in this beetle's life system. The objective of this study was to quantify the interaction between the cereal leaf beetle and its hosts within a season.

Field populations of the cereal leaf beetle, 'Genessee' wheat and 'Clinton 64' oats were examined throughout a season to identify the important plant and insect components which would assist in quantifying this interaction.

The amount of leaf surface per unit area is a basic plant requisite with respect to final grain yield and is important to the survival of the cereal leaf beetle because it lays eggs and feeds on the succulent upper leaf surface.

Two estimates of the amount of foliage removed from the crops by the insect population were made. First, the actual numbers of feeding scars on the leaves were counted from samples taken throughout the season and second, the larval population was translated into first instar feeding equivalents by knowing how much each of the 4 instars

const

popu.

respe

const

were

in w

surfa

by ce

this

beetl

conte

consumes during its life. The constants for converting a larval population of known instar distribution are 1.0, 2.87, 5.97 and 24.23 respectively for the 4 instars. Knowing the amount a first instar consumes, the population can be weighted accordingly.

Estimates of 45,647 and 73,035 sq. mm. per sq. ft. of foliage were removed by 88.01 and 142.78 total larvae per sq. ft. respectively in wheat and oats. Under the conditions investigated, winter wheat surface area production was about 3.4 times that of oats at peak feeding by cereal leaf beetle larvae. Oats received more damage than wheat but this cannot be translated into yield loss.

It is suggested that the phase of defining the effect of the beetle on yield be initiated over a broad geographical area within the context of the 'cereal leaf beetle population dynamics survey'.

THE CEREAL LEAF BEETLE, Oulema melanopus (L.),
AND ITS INTERACTION WITH TWO PRIMARY
HOSTS: WINTER WHEAT AND SPRING OATS

By
Stuart H. Gage

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Entomology

1972

ACKNOWLEDGEMENTS

My sincere appreciation is extended to Dr. Dean L. Haynes under whose direction this work was accomplished. I have had respect for his scientific insight since we met at North Dakota State in 1966. His advice and assistance led me to Fredericton, New Brunswick where I worked on the Green River Project. Since coming to Michigan State to work with Dr. Haynes, my respect has been enhanced.

I would also like to thank Dr. James Webster whose work in the area of host plant resistance helped stimulate my interest in plants and Dr. Robert Barr, of the Dept. of Electrical Engineering and Systems Science, whose systems viewpoint has helped place the plant component in its proper perspective within the cereal leaf beetle management system.

Dr. Stan Wellso and Dr. Fred Stehr had important input into my program and their evaluations are appreciated. Dr. Gordon Guyer's comments from the economic entomologist's standpoint helps to bring entomology to real world situations.

Dr. Patricia Gage bravely withstood many hours while I thought about 'leaves' and her patience and understanding was remarkable during my transition from studying birds to studying plants.

TABLE OF CONTENTS

	Page
LIST OF TABLES	iii
LIST OF FIGURES	vi
INTRODUCTION	1
LITERATURE REVIEW	4
MATERIALS AND METHODS	19
Study Areas	19
Plant Sampling	19
Cereal Leaf Beetle Feeding Damage	21
Cereal Leaf Beetle Population Sampling	21
Degree-days	22
RESULTS	24
Vegetative Phase	24
Crop Height	36
Head Component	36
Root Biomass	36
Cereal Leaf Beetle Population Densities	47
Foliage Consumption Estimated from Cereal Leaf Beetle Population Densities	49
Foliage Consumed by Estimates of Leaf Damage	54
DISCUSSION	73
SUMMARY AND CONCLUSIONS	84
LITERATURE CITED	86
APPENDICES	90

LIST OF TABLES

Table	Page
1. Amount of feeding (mg.) on oat seedlings by larvae and adults of the cereal leaf beetle based on 24-hour tests (after Castro <u>et al.</u> 1965)	6
2. Shoots per winter wheat plant at different stages of growth sown at different densities (In Bunting and Drennan 1966 after Puckeridge 1962)	11
3. Accumulated heat units (base 48°F) for completion of development of cereal leaf beetle eggs, larvae and pupae	23
4. Oven dry weight (g. per sq. ft.) of the top 3 leaves, all leaves and the per cent of the total leaf weight contributed by the top 3 leaves in winter wheat and spring oats at each sample date and corresponding accumulated degree-days (base 42°F)	28
5. Leaf lengths (mm.) of the top 3 leaves of winter wheat and spring oats calculated from total leaf length per leaf type per sample divided by the total number of leaves per leaf type per sample at each sample date and corresponding accumulated degree-days (base 42°F) (n = 10; $\pm$ S.E.)	31
6. Leaf length (mm.) of the top three leaves of winter wheat and spring oats determined from subsampling 5 leaves of each type at each sample date and corresponding accumulated degree-days (base 42°F) (n = 5; $\pm$ S.E.) . .	32
7. Flag leaf lengths (mm.) collected from fields of winter wheat and spring oats at Gull Lake and East Lansing ($\pm$ S.E.)	33
8. Per cent composition of each of the top 6 leaves of the total number of the top 6 leaves in each sample of winter wheat and spring oats at each sampling date and corresponding accumulated degree-days (base 42°F) .	34

Table	Page
9. Number of plants, stems and stems per plant (per sq. ft.) in winter wheat and spring oats at each sampling date and corresponding accumulated degree-days (base 42°F) (n = 10)	35
10. Calculated surface area (sq. mm. per sq. ft.) of the top 3 leaves of winter wheat and spring oats at each sampling date and corresponding accumulated degree-days (base 42°F) (see text)	37
11. Regression equations to predict oven dry weight (g. per linear ft.) from wet sample weight (g. per linear ft.) for roots, stems, the top 4 leaves and heads of winter wheat and spring oats sampled throughout the growing season	43
12. Per cent moisture remaining in the roots, stems and the top 4 leaves at each sample date and corresponding degree-days (base 42°F) (n = 10)	44
13. Within field comparison of plant height (cm.) total wet sample weight (g.), oven dry weight of heads (g.) and number of heads in spring oats (n = 3; $\pm$ S.E.)	45
14. Within field comparison of plant height (cm.), total wet sample weight (g.), oven dry weight of heads (g.) and number of heads in winter wheat (n = 3; $\pm$ S.E.)	46
15. Amount of foliage consumed by each instar of the cereal leaf beetle and the corresponding first instar feeding equivalent conversion (see text)	49
16. Cumulative first instar feeding equivalents and the cumulative estimate of foliage consumed (sq. mm. per sq. ft.) from winter wheat and spring oats as determined from first instar feeding equivalent incidence curves	52
17. Number of feeding scars per leaf on each of the top 3 leaves and the corresponding average scar area (sq. mm.) in winter wheat and spring oats at each sample date and corresponding accumulated degree-days (base 48°F)	55
18. Cumulative amount of foliage consumed (sq. mm. per sq. ft.) from the top 3 leaves of winter wheat and spring oats	56

Table	Page
19. Final amount of foliage (sq. mm.) consumed by cereal leaf beetles as predicted by the 2 methods (see text)	58
20. Per cent utilization of the top 3 leaves of winter wheat and spring oats by the cereal leaf beetle	59
21. Per cent of available leaf surface removed from the top 3 leaves of winter wheat and spring oats by the cereal leaf beetle as determined from damage estimates	60
22. Total biomass of foliage (g. per sq. ft.) present in 3 areas at peak cereal leaf beetle larval feeding . . .	70
23. Total monthly rainfall (in.) for May, June, and July at Gull Lake and East Lansing	70
24. Accumulated degree-days from January 1 to July 31 at base 42°F for Gull Lake and East Lansing	70
25. Total amount of foliage consumed (sq. mm. per sq. ft.) calculated from cereal leaf beetle population estimates converted to first instar feeding equivalents in winter wheat and spring oats at Gull Lake and East Lansing	71
26. Prediction of larval survival and mortality and generation survival and mortality from the within-generation cereal leaf beetle model developed by Helgesen and Haynes (in press)	72
27. Observations on egg laying behavior of the cereal leaf beetle on oat seedlings in the laboratory (after Castro <u>et al.</u> 1965)	74
28. Crop growth rate of winter wheat (g. per degree-day (base 42°F)) per sq. ft. at Gull Lake and East Lansing	76
29. Crop growth rate of spring oats (g. per degree-day (base 42°F) per sq. ft.) at Gull Lake and East Lansing	77
30. Grain yields (bu. per acre) of 'Chancellor' wheat and 'Arkwin' oats for 5 levels of leaf area removal at 4 stages of plant development (after Womack and Thurman 1962)	81

LIST OF FIGURES

Figure	Page
1. Relationship between date and the number of shoots per plant in winter wheat (adapted from Bunting and Drennan 1966)	12
2. Relationship between accumulated degree-days (base 42°F) and oven dry weight of plant material above ground in winter wheat and spring oats	25
3. Relationship between accumulated degree-days (base 42°F) and oven dry weight of the top 3 leaves of winter wheat and spring oats	27
4. Relationship between leaf length and leaf surface area in winter wheat	29
5. Relationship between leaf length and leaf surface area in spring oats	30
6. Relationship between accumulated degree-days (base 42°F) and average plant height of winter wheat and spring oats	38
7. Relationship between accumulated degree-days (base 42°F) and oven dry weight of heads of winter wheat and spring oats	39
8. Relationship between accumulated degree-days (base 42°F) and the number of heads of winter wheat and spring oats	40
9. Relationship between wet sample weight and oven dry weight of spring oats	42
10. Relationship between oven dry weight of winter wheat and spring oat leaves and leaf surface area	48
11. Relationship between accumulated degree-days (base 48°F), cereal leaf beetle larvae (●) and first instar equivalents (○) on winter wheat and spring oats	51

12. Relationship between accumulated degree-days (base 48° F) and the predicted amount of foliage consumed by cereal leaf beetle larval populations on winter wheat and spring oats using the first instar equivalent method	53
13. Relationship between accumulated degree-days (base 48°F) and the amount of foliage consumed by populations of the cereal leaf beetle on winter wheat and spring oats estimated from damage to the top 3 leaves	57
14. Relationship between accumulated days from April 20, first instar feeding equivalents on winter wheat and spring oats and:	
(a) plant height	62
(b) oven dry weight of leaves	63
(c) sum of the squares of the lengths of the top 3 leaves	64
(d) the number of heads	65
15. Relationship between accumulated days from April 20, first instar feeding equivalents and oven dry weight of foliage above ground for winter wheat and spring oats at:	
(a) Gull Lake - R area	67
(b) Gull Lake - T area	68
(c) East Lansing - C area	69
16. Relationship between accumulated days from April 20, first instar feeding equivalents and per cent moisture in the top 3 leaves of winter wheat and spring oats	79

1

INTRODUCTION

The cereal leaf beetle, Oulema melanopus (L.), is potentially the most important insect pest of small grains in North America. Damaging populations of this insect have occurred in southern Michigan since 1959, after being introduced from Europe (Castro et al. 1965). As of 1971 cereal leaf beetle populations were detected as far south as Kentucky, north to Ottawa, Ontario, west to the Iowa border and east of Michigan to the Atlantic coast (USDA Detection and Quarantine Survey 1971).

The cereal leaf beetle is not considered an economically important pest of small grains throughout its range in the Old World. However, in the region of the Balkans, the Ukraine, and the Transcaucasia area of the Soviet Union, Castro et al. (1965) noted that this pest does more damage and is more constant in appearance. Miczulski (1971) studied the cereal leaf beetle in Poland from 1966 to 1971 and found that the amount of damage was non-economic and insignificant when compared with what he observed in Yugoslavia in 1967.

In southern Michigan insecticide use has been necessary to protect the spring oat crop from the cereal leaf beetle. In 1969 and 1970, 1.41×10^5 and 1.78×10^5 acres of oats, respectively were sprayed with malathion and carbaryl and unknown acreages were also sprayed with azinphosmethyl in each of these years (Ruppel personal communication).

The within-generation population dynamics of the cereal leaf beetle has been investigated (Helgesen and Haynes in press). Their model shows that two major factors account for over half of the variation in within-generation mortality: the cereal leaf beetle population level and host crop.

The principle economically important host plants of larvae and adults of the cereal leaf beetle in North America are the small grains (wheat, oats, barley and rye). This report will examine two of these crops, winter wheat and spring oats, the two small grains most important to Michigan agriculture.

The assumption underlying this investigation was that the host crops contain specific dynamic components which directly influence the cereal leaf beetle. Because the hosts of the beetle are equally as dynamic as the consumer, the plant component became the central theme of this study toward further understanding the population dynamics of the cereal leaf beetle. By modeling the insect's interaction with its primary cereal grain hosts, winter wheat and spring oats, it was hoped that relationships would be uncovered which would aid in controlling this pest.

To date little detailed published information is available concerning the relationship of cereal leaf beetle populations to natural growing cereal grains throughout a single season. Some significant work has been published relative to cereal leaf beetle feeding on plants (primarily seedlings grown in the laboratory) with regard to adult survival (Wilson and Shade 1964) and host plant resistance (Schillinger 1969, Webster and Smith 1971). Gallun et al. (1966) studied host plant resistance under field conditions using damage ratings.

In this study three principle factors were investigated: (1) the growth responses of winter wheat and spring oats, (2) the cereal leaf beetle population density in each crop and (3) adult and larval feeding damage on each crop. Limited comparisons were made between areas and within fields.

LITERATURE REVIEW

The bionomics of the cereal leaf beetle have been adequately described by Castro et al. (1965) and Wellso et al. (1970) have published a comprehensive bibliography of literature pertaining to this cereal grain pest.

The consumer-host interaction considered in this study initiates when spring adults move from their overwintering sites into winter wheat and begin feeding and laying eggs on the upper surface of the leaves. Winter wheat, having established roots the previous autumn, is one of the most abundant food sources for the adult beetles during the latter part of April and early May, although several other hosts become available later in the spring. When spring oats become available, numbers of adults appear in this crop. Ruesink (1972) suggests that there is not much movement between winter wheat and spring oats but that once in a crop, the beetles tend to remain there until death. After the eggs hatch, the larvae immediately begin feeding adjacent to the eggs on the leaf surface until the fourth instar larvae complete development and pupates in the soil.

Helgesen and Haynes (in press) developed techniques for measuring the within-generation population dynamics of the cereal leaf beetle and developed a model which predicts within-generation survival from cereal leaf beetle egg input. Their model is reiterated here to show that survival of the first instar in oats and the fourth instar in

both wheat and oats varied predictably with density and host plant:

$$S I \text{ (oats)} = 1 - (-.85 + .46 \log x), r = .78$$

$$S IV \text{ (oats)} = 1 - (-.18 + .28 \log x), r = .69$$

$$S IV \text{ (Wheat)} = 1 - (-.31 + .34 \log x), r = .54$$

where x is the total number of eggs per sq. ft. Combining the constant mortalities observed in the other life stages of the cereal leaf beetle, Helgesen and Haynes (in press) simplified the within generation survival on the two crops to:

$$S W G \text{ (oats)} = 0.03914 (4.02174 - \log x) (4.21429 - \log x)$$

$$S W G \text{ (wheat)} = 0.04794 (3.85294 - \log x).$$

Castro et al. (1965) discuss the relationships of the cereal leaf beetle and its hosts. They noted that the cereal leaf beetle preferred seedling plants and the younger growth of older plants and that the beetles were more abundant in late planted winter grains than in early planted winter grains. Table I (after Castro et al. 1965) shows the amount of feeding by larvae and adults of the cereal leaf beetle.

Wilson and Shade (1964) studied feeding by postdiapause adult cereal leaf beetles in the laboratory and found that feeding choice between wheat and rye and oats was not significant. They also noted that survival was high on small grains but low on orchard grass, tall fescue, millet, giant foxtail, grain sorghum and sudan grass.

Methods for determining the amount of foliage consumed by insects have been developed for some species and these methods (e.g. photometric, radioactive tracers) have been applied by Crossley (1963) and Pegigo et al. (1970).

TABLE I.--Amounts of feeding (mg.) on oat seedlings by larvae and adults of the cereal leaf beetle based on 24-hour tests (after Castro et al. 1965)

Stage	Number	Average wt. of insect (mg.)	Mg. of leaf consumed	
			Per day	Per life (est)
1st instar larvae	10	0.22	2.14	5.35
2nd instar larvae	25	2.68	7.80	19.5
3rd instar larvae	10	7.80	12.9	41.7
4th instar larvae	15	20.8	26.4	52.8
Adults	41	7.35	25.9	1040.

Estimates of damage to plants caused by the cereal leaf beetle are quite varied and without a reliable base for method comparison. Castro et al. (1965) rated damage from 0 to 5 based on visual estimates. Wilson et al. (1969) took 20 stems at random from each plot and classified the leaves according to per cent that had been consumed (0, trace, 10 to 100%), thereby using a rating of 12. Gallun et al. (1966) rated the damage visually from 1 to 5 with 1 being no feeding and 5 severe damage. Schillinger (1969) rated damage from 1 to 5 with 1 being highly resistant and 5 susceptible. Webster and Smith (1971) also used the visual rating system but their system ranged from 0 to 3; 0 being no damage and 3 equal to heavy damage. In Poland (Miczulski 1971) estimated the per cent of surface area consumed by the cereal leaf beetle and divided his classification as: less than 1%, 1 to 5%, 5 to 10%, 10 to 15%, 15 to 20% and more than 20%.

Larvae and adults feed almost entirely on the upper surfaces of the leaves of their hosts and seldom feed on any other portion of the plant. However, Merrit and Apple (1969) found that some feeding occurred on the leaf sheath one inch beneath the base of the leaves when the upper leaf surface was entirely consumed. Shade and Wilson (1967) found that larvae feed only on the parenchyma tissue between the leaf veins and noted that a larva feeds parallel to veins on favorable hosts and perpendicular to veins on unfavorable hosts. They attributed the reduced survival on some grasses to the leaf-vein spacing but Helma (personal communication) noted that the data could be similarly interpreted by attributing mortality differences to cool weather and warm weather grasses which have different biochemical pathways.

Wilson et al. (1969) showed that only larger larval instars consumed appreciable amounts of foliage on oats and that one larva, completing development to pupation, consumed about 20% of the leaf tissue on one stem regardless of the vigor of the plant.

Yield loss on 'Monon' wheat caused by this insect was investigated by Gallun et al. (1967) who found that up to 23% loss (kernel number and size reduction) could be attributed to the cereal leaf beetle but that such high losses would seldom occur in North America where winter wheat is grown. Wilson et al. (1969) studied yield loss in oats under field conditions. They noted that the degree of yield loss depended on the stage of development of the crop and that these losses ranged from 2.29 to 4.1 bushels per acre per larva per stem. Merrit and Apple (1969) also examined yield loss in oats and found a grain yield reduction of 48.8%, or 4.77% per larva per stem for each

of the 10.4 larvae per stem. They also note that loss in straw weight caused by the cereal leaf beetle was considerable. Womack and Thurman (1962) studied the effect of leaf removal in 'Chancellor' winter wheat and 'Arkwin' winter oats by removing 10%, 20%, 30%, 40% and no leaf removal at 1 week before the boot stage, at the boot stage, 1 week after the boot stage and 2 weeks after the boot stage. In wheat they found that 1 week before the boot stage was the most critical stage and that leaf area removal in excess of 10% was necessary to cause significant reductions in yield. The stages of leaf area removal in oats had little expressed effect on yield and that the 30 and 40% leaf removal treatments reduced yields significantly below the check. In general, Womack and Thurman (1962) conclude that reductions in grain yield due to leaf removal were primarily a result of reduction in seed size.

Blackman (1959) appraised 4 decades of research in plant growth and plant responses to environmental factors. He expressed anxiety that he had made no reference to American workers and stated:

This omission is not perverse but due to my inability to trace a body of papers where the techniques of growth analysis have been fully exploited. This divergence of interest I have discussed on previous visits to the United States, and the opinion has been expressed that the concepts are crude and yield but meager information concerning the basic physiological processes that determine the reaction of plants to the environmental factors. My reply has been that it is essential to match what is learned in the laboratory with an equal and precise knowledge of the reactions of the plant as a whole for a wide range of species and conditions. My hope is that this paper is persuasive enough to support my contention that there is a continuum between research involving the cold room and centrifuge and field experimentation seeking to assess plant performance.

The vegetative phase in cereals is taken to begin when the first leaves appear above the soil and to end when the flag leaf has died (Bunting and Drennan 1966). The leaf number attained prior to flowering

is not fixed and in field crops of wheat, barley and oats the total number of leaves formed on the main shoot of the plant is usually from 7 to 9. At spring temperatures, the plastochron (the interval between the appearance of successive primordia) in the temperate cereals is 2 to 3 days.

The flag leaf, the last to be formed on the shoot, may be determined no more than 15 to 20 days after germination or after growth of autumn-sown crops starts in the spring. In wheat grown at 20°C, 6 new leaves were initiated in 15 days after germination, in addition to the 3 leaves present in the embryo (Williams 1960 as seen in Bunting and Drennan 1966). The latter authors note that in field crops, the phyllochron (the time interval between successive leaf appearance) is always considerably longer than the plastochron, often from 5 to 7 days, but increasing with time.

Other investigators studied plant components related to environmental factors. Borrill (1959) showed that the curve obtained for the length of successive leaves along the main shoot in the Gramineae (Glyceria, Lolium and Triticum), was often of a definite shape, the curve increased to a peak and then fell until the flag leaf appeared. Leaf length trends were compared to Watson's (1947) trend in total leaf area for wheat and barley and the trends were similar. Borrill (1959) also noted that the behavior of autumn sown winter wheat revealed an overall seasonal effect. This was indicated by the difference in the general shape of the curve with respect to inflorescence initiation. This was delayed beyond the peak of the curve, to the early part of a second increase in leaf length associated with a decrease in the rate of leaf production.

Jewiss (1966) notes that the number of visible living leaves on a grass tiller is a direct result of the rate of leaf appearance and the length of life of these leaves. Ryle (1964 reported in Jewiss 1966) has shown that the number of living leaves on the main stem may vary between 3 and 6 according to genotype and environment.

Allison and Watson (1966) studied the production and distribution of dry matter in maize after flowering and noted that the leaf laminae are the chief source of the dry matter in the grain of maize. This contrasts with wheat and barley, in which laminae, sheath, and ear all make substantial contributions to the dry matter in the grain. Also, they noted that photosynthesis throughout the upper two-thirds of the leaf area of maize supplied the dry matter that fills the grain, whereas in wheat and barley the structures above the highest node supply most of the dry matter. They attribute this difference to the slower senescence of maize leaves with the lower leaves providing a much larger proportion of the total photosynthetic area after ear emergence than in wheat or barley. Finally, they note that dry matter in the grain of maize, as contrasted with wheat or barley, comes mostly from photosynthesis after flowering.

Ryle (1966) pointed out that the first component of final yield in grasses is the number of fertile tillers per unit area. In subsequent weeks, ear development proceeds until shortly before ear emergence. During this time the second component of yield, the number of florets per ear, is fixed followed by anthesis, pollination and fertilization. This determines the third component of yield, seed set. Finally the seeds swell and mature to determine the fourth and last component, seed weight.

Tillering is important during the vegetative stage and there seems to be a characteristic trend of shoot numbers, especially in wheat as pointed out by Bunting and Drennan (1966) by illustrating Kirinde's (unpublished) figure (Figure 1).

Friend (1965) studied the effect of temperature and light intensity on tillering and leaf production in wheat to determine the importance of tillering. His studies constitute an essential addition to plant growth studies conducted in North America, especially with respect to the effect of environmental components on plant growth (Friend 1966).

Puckeridge (1962) as seen in Bunting and Drennan (1966) recorded in detail the effect of density on the growth of wheat sown at a range of densities from 5.7 to 3,540 x 10³ plants per acre (Table II).

TABLE II.--Shoots per winter wheat plant at different stages of growth sown at different densities (In Bunting and Drennan 1966 after Puckridge 1962)

Initial density x 10 ³ plants/acre	Shoots/Plant					
	Weeks from sowing (23 May 1961)					
	4	10	14	17	20	26
5.7	1.8	16.4	24.9	40.5	37.0	33.0
28.3	1.9	16.1	30.0	29.5	27.0	24.5
141.3	1.8	13.7	11.9	10.6	9.5	9.9
708.2*	2.0	5.5	4.1	3.0	3.0	3.3
3,541.0*	1.3	1.6	1.4	1.2	1.5	1.2

*At these densities the populations had fallen to 623.2 and 1,808.9 thousands, respectively, by week 26.

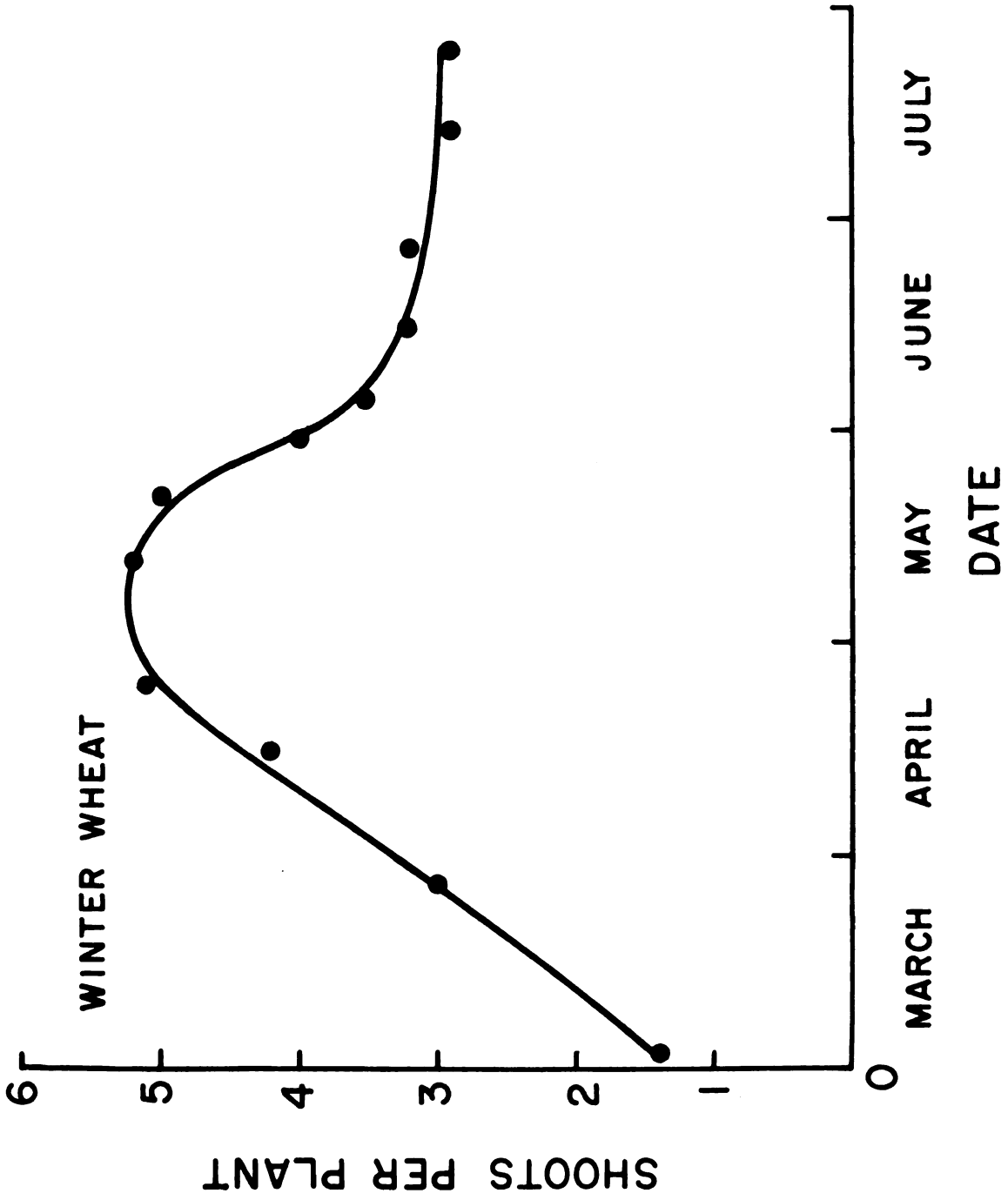


Figure 1.--Relationship between date and the number of shoots per plant in winter wheat (adapted from Bunting and Drennan 1966).

Table II shows clearly that competition between plants affected tiller numbers per plant. There must also have been competition between parts within individual plants, since the number of shoots per plant declined from a maximum (even at the widest spacing) where the number of tillers per acre was far lower than at the denser spacings (Bunting and Drennan 1966).

The yield of cereal grains depends on a great many factors over which man has little control. However, Watson (1956) considers several influences on yield of crops and concludes that,

. . . the main opportunity for increasing yield lies in the increase of leaf area. Information on the physiological cause of variation in yield is still scanty, but, so far as it goes, it indicates that cultural practices that increase yield do so wholly or mainly by influencing leaf growth.

Later in the same paper Watson (1956) continues his argument by saying,

. . . the conditions favoring high yield of grain in so far as it depends on leaf area, appear to be: a high leaf area index at the time of ear emergence, slow senescence of the leaves then surviving, which implies a long time interval between emergence and harvest. The fulfilment of these conditions practically depends on the size and longevity of the flag leaf.

This explanation has been challenged by Gregory (1956) who argues that the increase in leaf area depends on additional production of tillers because early nitrogen application increases the rate of tillering and therefore the rate of increase in leaf surface area increased. This increase does not go on indefinitely because when flower initiation occurs in the early tillers, then tillering stops. Rather than emphasizing the flag leaf, Gregory (1956) emphasized the importance of the emerging ear and the dependence of yield on the number of ears, and also the fact that late applications of nitrogen produces tillers that do not ear, therefore wasting nitrogen.

As Ryle (1966) noted, the number of fertile tillers per unit area is a significant factor in determining yield. Thorne (1966) reviewed the physiological aspects of grain yield in cereals and points out that the economic yield in cereals consists of a particular portion of the biological yield (total dry matter production usually with some water) so it does not depend on the whole photosynthetic performance of the crop. Leaves, sheathes and stems below the flag leaf node usually contribute little, about 15% of the final grain weight and it is suggested that ample leaf area after ear emergence is one of the most important attributes likely to enhance grain yield (Thorne 1966).

The analysis of plant growth under different environmental conditions has had a long and somewhat confusing history; confusion due primarily to problems in terminology. Blackman (1919) was one of the first who was able to accurately quantify growth rates of plants by applying the compound interest law to growth rates and analytical techniques have been evolving since that time.

D. J. Watson of the Rothamsted Experimental Station in England seems to have the most straight forward approach when dealing with the growth rate of crops under field conditions.

The total dry matter production by a crop may vary through a change in either the size of the photosynthetic system or its activity, as well as the length of the growth period during which photosynthesis continues. These can be expressed as photosynthetic capacity and photosynthetic efficiency (Watson 1958). The photosynthetic capacity of crops is expressed by Watson as leaf area index (L, ratio of leaf area to land area) while the photosynthetic efficiency is expressed as net assimilation rate (E, rate of increase of dry matter per unit leaf

area). Watson's (1958) primary data consisted of initial and final dry weights and leaf areas per plot of the plants harvested at the end of the experimental period. The dry weights were expressed as yields in g. per sq. m. and the leaf areas in sq. m. of land surface (i.e. leaf area index).

Calculations of the growth functions in Watson's (1958) paper were derived from the following formula:

$$\text{Mean net assimilation rate} = \frac{(W_2 - W_1) (\log_e L_2 - \log_e L_1)}{(t_2 - t_1) (L_2 - L_1)}$$

where W_1 , and W_2 are initial and final total dry weight yields, L_1 and L_2 the initial and final leaf area indices, and t_1 and t_2 the length of the time interval. The mean rate of increase of dry weight yield in g. per sq. m. of land area per unit time is:

$$\text{Crop growth rate (C)} = \frac{W_2 - W_1}{t_2 - t_1}.$$

Relative leaf growth rate per cent was calculated as

$$\frac{\log_e L_2 - \log_e L_1}{t_2 - t_1} \times 100.$$

Net assimilation rate calculations assume a linear relationship between crop dry matter production (W) and leaf area index (L). To develop a more general method of calculation. Whitehead and Meyerscough (1962) used the exponential relationship

$$W = k L^a + c.$$

The exponent a is the ratio of the mean relative growth rate (dry weight) to the mean relative growth rate in leaf area over a time interval ($t_1 - t_2$). This may be calculated from

$$a = \frac{\log_e W_2 - \log_e W_1}{\log_e L_2 - \log_e L_1}$$

The mean net assimilation rate ($\bar{E}$) may then be calculated for a time interval $t_1 - t_2$ from the more general relationship

$$\bar{E} = \frac{(W_2 - W_1) (L_2^{a-1} - L_1^{a-1}) a}{(L_2^a - L_1^a) (a - 1)}$$

Whitehead and Meyerscough (1962) present these formulas and Williams et al. (1965) use them in their analysis of the growth rate of corn describing additional uses of "a" for partitioning assimilates within the plant. Similar arguments are followed by Evans and Hughes (1962).

The growth of the plants and the final yield and quality of the grain depend very materially on the weather conditions during the year with light (radiation), moisture and temperature influencing the growth rate of the plants. For this reason studies on the growth rates of small grains have been conducted under controlled conditions to minimize the effects of weather. Unfortunately few investigations have been conducted under natural conditions because of variability caused by existing light, temperature, wind and moisture conditions as well as soil type, planting date and crop variety.

Alcock et al. (1968) described an experiment designed to show the effect of environment on the growth of a grass sward in 2 habitats in North Wales. They noted that the growth of plants is very slow at low temperatures but increases rapidly as temperature rises above a certain minimum. Alcock et al. (1968) used the threshold temperature of 5.5°C (42°F) for accumulating heat units (degree-days) and also used the maximum soil temperature at 10 cm. The correlation of degree-days above 42°F and maximum soil temperature at 10 cm. with yield (dry

matter accumulation) showed a high positive coefficient. They note that accumulation of heat above 42°F is highly correlated with time which necessitated removal by using partial correlation. Doing this, Alcock et al. (1968) were able to explain 86% of the variation in yield with these two variables. The soil temperature (at 10 cm.) was found to be the most highly correlated variable with L (leaf area index) accounting for 71 to 86% of the variation. They also found a significant relationship between $\bar{E}$ (net assimilation rate) and radiation. Alcock et al. (1968) note that the 10 cm. soil temperature is a complex factor to interpret since, particularly in the spring, it is highly correlated positively with radiation, grass minimum temperature, maximum air temperature and negatively with wind speed, relative humidity, and soil water content. The above authors suggest that wind speed may be an important factor determining the habitat differences in soil temperature and plant growth.

There has been some debate as to the usefulness of the concept of heat accumulation above a certain threshold and Wang (1960) outlines some of the problems involved. Its usefulness tends to outweigh the disadvantages as long as the investigator realizes that the method is not perfect because biological activity does not rely on temperature alone.

The accumulation of heat units is a better prediction of variations in growth in spring than temperature itself (Mc Cloud, Bula and Shaw 1964; Hogg 1965) or for that matter, date. Baskerville and Emin (1969) present a means of rapid estimation of heat accumulation from minimum and maximum temperatures assuming the sine curve as an approximation of the diurnal temperature curve. Van Den Brink et al. (1971)

note that

is perhaps

(1971) did

mean tempe:

temperatur

used for a

note that plants respond to many meteorological elements but temperature is perhaps the most significant single factor. Van Den Brink et al. (1971) did not use the sine curve approximation but simply took the mean temperature $((\text{max} - \text{min}) / 2)$ and subtracted this from several temperature bases (40°F, 45°F, 50°F, 55°F) which they suggest can be used for a range of crops.

1

MATERIALS AND METHODS

Study Areas--Detailed studies of the plant growth of 'Genesee' winter wheat and 'Clinton 64' spring oats and the interaction cereal leaf beetles feeding on these two crops were conducted at Kellogg Gull Lake Biological Research Station, Hickory Corners, Michigan in level strip-planted fields 600 ft. x 50 ft., hereafter referred to as Gull Lake - R. In other fields at Gull Lake, Gull Lake - T, about one-half mile from Gull Lake - R and different in that the fields were on rolling rather than level terrain, additional but limited measurements on plant growth and beetle feeding were made at two elevations and compared with observations from Gull Lake - R. Limited plant growth information (total biomass per sq. ft.) was also obtained from fields near East Lansing, Michigan, hereafter referred to as East Lansing - C.

In each of these 3 areas detailed population estimates of the beetle were obtained at about weekly intervals corresponding to the plant growth measurements.

Plant Sampling--Detailed plant growth measurements (Gull Lake - R) were collected by random selection of 10 samples each a linear ft. in length within each crop throughout the season. Plants were clipped 4 in. away from each end of a linear ft. row to avoid collecting additional stems. Each sample was then excavated by digging at an angle down to include as much of the root component as possible from the

center of the plant rows (which were 7 in. apart). These samples, including soil (extracted with the root systems) were placed in plastic tubs and taken to the laboratory for processing. Water was placed in the tubs and left standing overnight to allow the soil to loosen around the root systems. The plants were then washed and separated according to those stems which were connected by common root systems. These were arbitrarily called plant combinations as they contained a variable number of stems or tillers. The plant combinations were counted, measured for height of the longest stem, weighed, wrapped in moist paper toweling and placed in temporary storage at 44°F until processing the next day. The samples were removed from storage, reweighed and processed in the following manner. First, roots were clipped from each plant combination, weighed and placed in labeled paper bags. Second, stems were counted and recorded. Third, leaves were removed from each stem at the ligule where the sheath separates from the stem. Each leaf type was cut from every stem in each linear ft. sample and placed in numbered trays. Leaves were numbered from the top down so that the emerging leaves were placed in the first category (hereafter referred to as type 1 leaves), the second leaves down the stem (type 2) were placed in the second category, etc. Fourth, leaves were counted and weighed by leaf type. Generally the earlier leaves (types 6 to 8) were dessicated and these leaves were all placed in the sixth category. Fifth, the leaves were laid out in linear rows by leaf type and the number of individual leaves counted. The total length of each leaf type in each sample was measured and then placed by type into labeled paper bags. Sixth, roots, stems and heads (when present) were weighed

and placed in separate bags. Oven dry weight of each component was obtained after drying the samples in a forced air drier at 105°C for more than 24 hours.

Prior to drying the leaf type samples, 5 leaves of the first 4 leaf types were subsampled from each linear ft. sample for estimates of cereal leaf beetle damage and leaf surface area measurements. These leaves were placed on white paper, covered with clear plastic and photocopied to provide a permanent record for later measurements. After photocopying, these leaves were placed into the appropriate paper bags containing the other leaves so as not to bias the dry weight estimates.

Surface areas of individual leaves were determined by measuring the area of a number of wheat and oat leaves over a range of leaf lengths using a polar planimeter.

Cereal Leaf Beetle Feeding Damage--The permanent records of the subsampled leaves were processed by counting the number of feeding scars in each leaf. Five clearly delineated feeding scars from each leaf type for each crop and sampling date were measured with a microscope using an ocular micrometer to estimate an average feeding scar size. This information provided an estimate of feeding damage and a method of estimating foliage surface area removed.

Cereal Leaf Beetle Population Sampling--Population density estimates of the egg, larval and pupal stages were estimated in the same fields where the plants were sampled using the technique described by Helgesen and Haynes (in press).

Two linear ft. of foliage were clipped at the soil surface at 30 sites within each sample area for each host crop at each sampling date. The foliage was placed in labeled plastic bags, returned to the laboratory and placed in storage at 44°F until processing. Eggs and larvae (according to instar) were counted from each sample. The foliage from these samples was dried in a forced air drier at 105°C for more than 24 hours and then weighed. To accommodate the within-generation population model (Helgesen and Haynes in press) egg input was measured by counting and then destroying cereal leaf beetle eggs laid in each of 10 two linear ft. sample areas at about three day intervals. Egg input was measured at Gull Lake R and T and East Lansing - C.

Degree-Days--Both cereal crops and the cereal leaf beetle are strongly dependent on temperature. It was necessary to use a measure which combines both these parameters. Although there are some arguments against using degree-days for this (Wang 1960), the use of degree-days is a very practical method and is becoming generally accepted (Baskerville and Emin 1969; Van Den Brink et al. 1971). The method used to calculate the accumulation of heat units was that of Baskerville and Emin (1969).

Developmental temperature thresholds used for plant growth of grasses (Alcock et al. 1968) was 42°F and for the cereal leaf beetle larval instars the threshold and heat accumulation as determined by Ruesink (personal communication) from experiments conducted by Helgesen (1969) and Yun (1968) are given in Table III. Accumulation of heat units from January 1 to August 31 in 1970 for Gull Lake and East Lansing for bases 42°F and 48°F are provided (Appendices I and II). In addition

Appendi

and the

lected

TABLE I

Life st

Eggs

Larvae

Pupae

Total

Appendices III and IV give the date, degree-days at bases 42°F and 48°F and the number of days accumulated from April 20 when samples were collected at Gull Lake and East Lansing in 1970.

TABLE III.--Accumulated heat units (base 48°F) for completion of development of the cereal leaf beetle eggs larvae and pupa

Life stage	Degree days (base 48°F)	
Eggs	160	
Larvae	220	(@ 55 for each instar)
Pupae	<u>450</u>	
Total	830	

1

RESULTS

The cereal leaf beetle and its host plant species are ecologically inseparable. Spring adults must search for adequate hosts on which to feed and oviposit their eggs and this selection must ensure larval survival. This study will attempt to quantify the growth of the plant species which are most important from the human economic viewpoint as well as for the economy of cereal leaf beetle survival.

The basic growth characteristics of the host plants were examined to determine how the cereal leaf beetle interacts with its hosts.

Vegetative Phase--In the area examined most thoroughly (Gull Lake - R) the vegetative phase of wheat and oats differed significantly in many respects. Wheat grew more rapidly and produced substantially more foliage per sq. ft. of land area. Figure 2 shows the oven dry weight of total foliage produced (g. per sq. ft.) by wheat and oats and illustrates the basic shape of the growth curves at this site. From these samples cereal leaf beetle egg and larval populations were measured.

Additional samples, in close proximity to the previously mentioned samples, were collected to determine biomass of components which comprise the vegetative phase. The top 3 leaves at any one point in time were considered to be the most important component of the vegetative portion of the plant in growth and consumption by the cereal leaf

60

• WINTER WHEAT



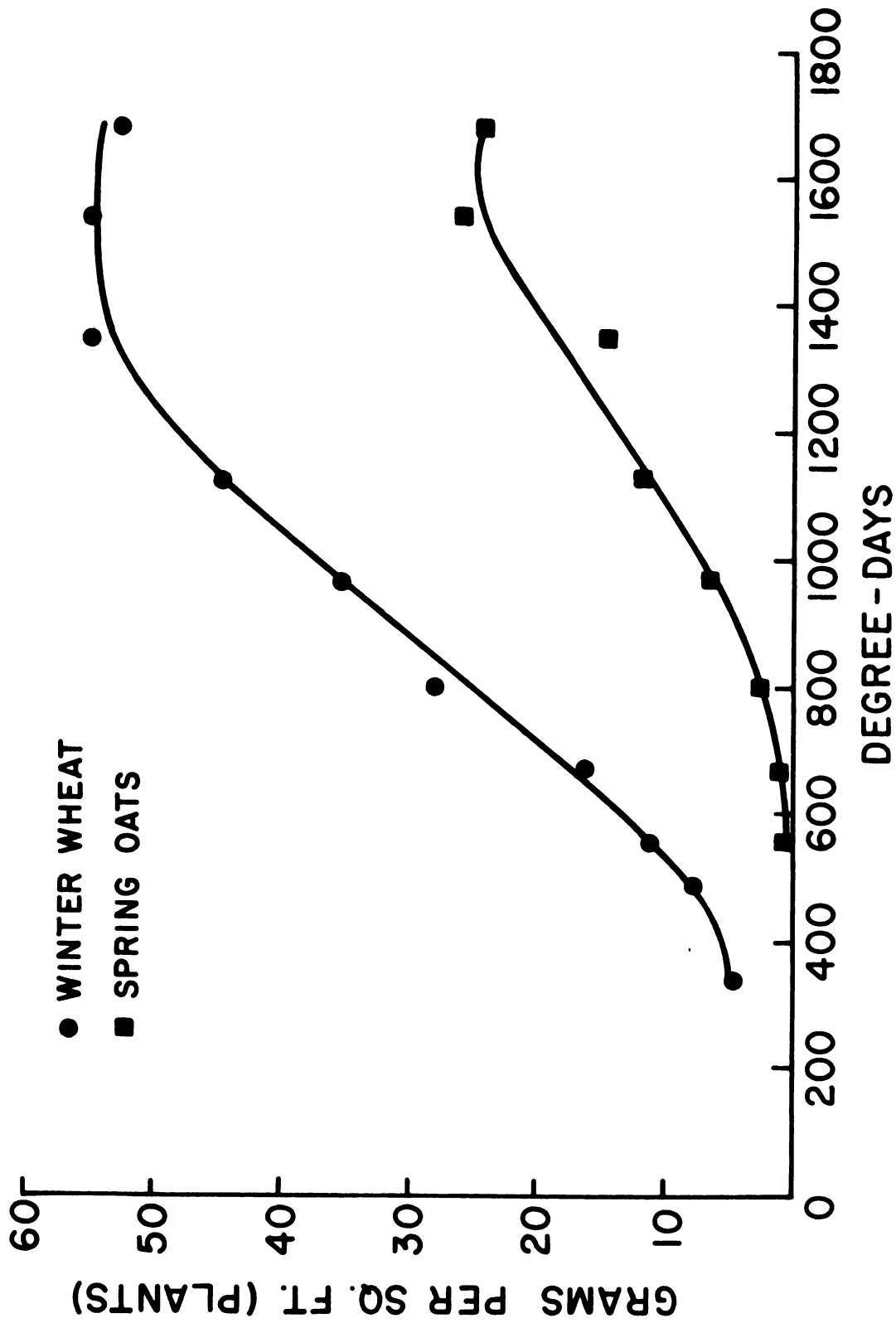


Figure 2.--Relationship between accumulated degree-days (base 42°F) and oven dry weight of plant material above ground in winter wheat and spring oats.

1

beetle. The leaves below these, in many cases tended to be desiccated, especially in wheat. Figure 3 illustrates the oven dry weight of the top 3 leaves in each crop while Table IV shows the total leaf weight and the per cent of the total represented by the weight of the top 3 leaves and shows that the proportion was greater in wheat than oats.

The surface area of individual leaves was estimated by measuring the surface area of several leaves of known length for both wheat and oats. Leaf length was squared to produce a linear relationship with surface area using

$$S A W = 24.56 + 0.037 (l_w^2); r^2 = 95.2$$

and

$$S A O = 52.15 + 0.034 (l_o^2); r^2 = 88.8$$

where S A W and S A O are the surface area (sq. mm.) and l_w^2 and l_o^2 are the leaf lengths squared (mm.) for wheat and oats respectively (Figures 4 and 5).

Determining the surface area of foliage of wheat and oats required measuring the length of each leaf type. Rather than measure all individual leaves, the total length of all leaves was measured and the total number of individual leaves counted. By dividing total length of all leaves of each type by the respective number of leaves, the average leaf length was determined and these estimates are shown in Table V. Using this method adds a bias to estimates of individual leaves (Ruesink, personal communication) and an alternate method of determining leaf length was then adopted by measuring actual lengths of leaves subsampled from each leaf type. These results are given in Table VI and these estimates of leaf length were used to compute the surface area of

• WINTER WHEAT

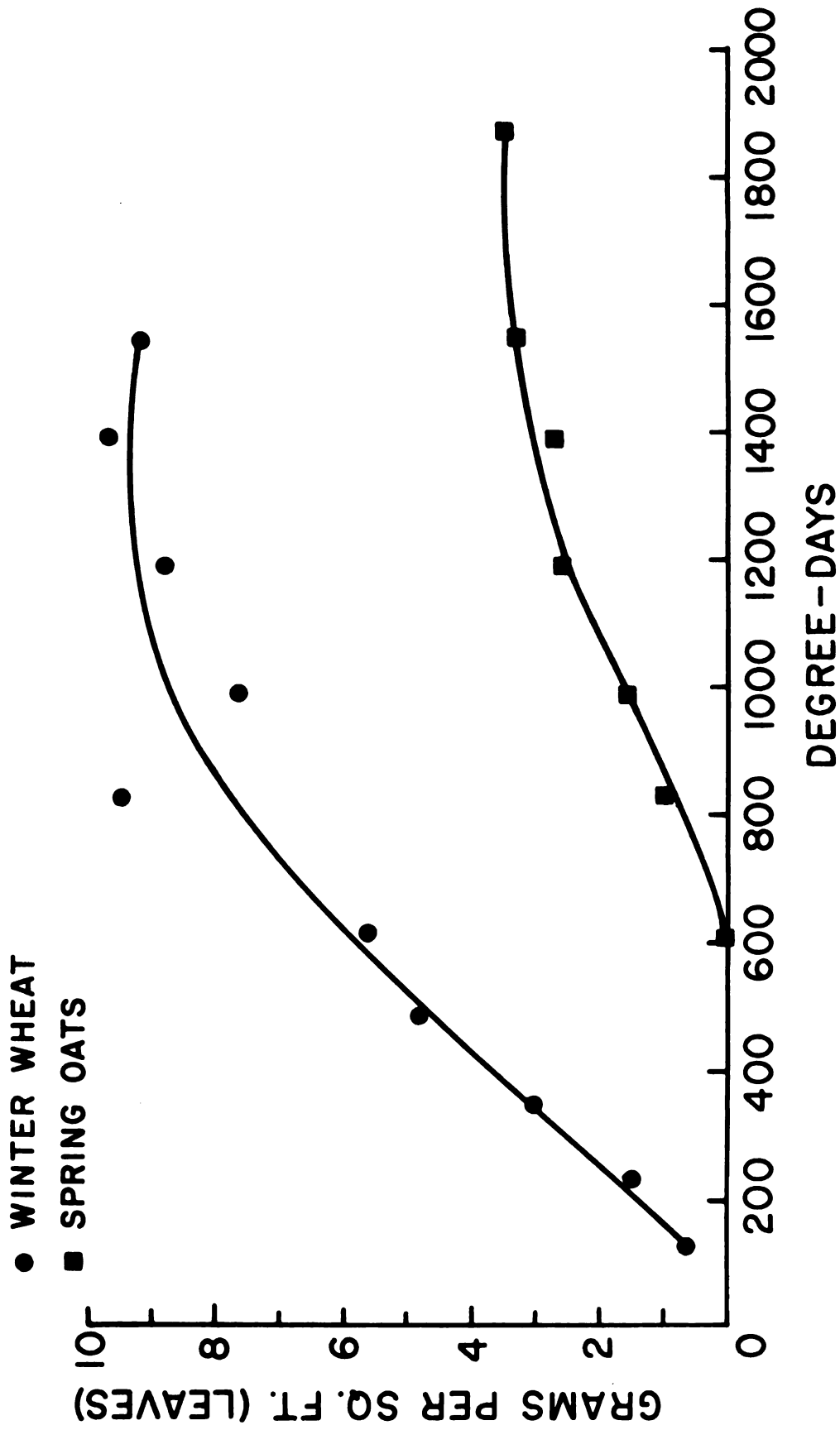


Figure 3.--Relationship between accumulated degree-days (base 42°F) and oven dry weight of the top 3 leaves of winter wheat and spring oats.

TABLE IV.--Oven dry weight (g. per sq. ft.) of the top three leaves, all leaves and the per cent of the total leaf weight contributed by the top three leaves in winter wheat and spring oats at each sample date and corresponding accumulated degree-days (base 42°F)

Date	Degree-days (base 42°F)	Oven dry wt. of top 3 leaves	Oven dry wt. of all leaves	Top 3 leaves as % of total
Wheat				
4/23	121	0.69	.86	80.2
4/29	239	1.49	1.82	81.9
5/6	342	3.06	3.76	81.4
5/13	487	4.83	5.94	81.3
5/20	608	5.61	7.75	72.3
5/29	825	9.56	12.36	77.3
6/5	986	7.71	9.66	79.8
6/12	1,193	8.86	10.09	87.8
6/18	1,383	9.68	12.10	80.0
6/25	1,540	8.15	9.54	85.4
Oats				
5/20	608	0.10	0.12	83.3
5/29	825	0.96	1.30	73.8
6/5	986	1.55	2.30	67.4
6/12	1,193	2.57	4.47	57.5
6/18	1,383	2.68	4.35	61.6
6/25	1,540	3.33	5.06	65.8
7/06	1,869	3.51	5.23	67.1
7/14	2,119	3.02	4.66	64.8
7/22	2,336	2.53	3.93	64.4

1

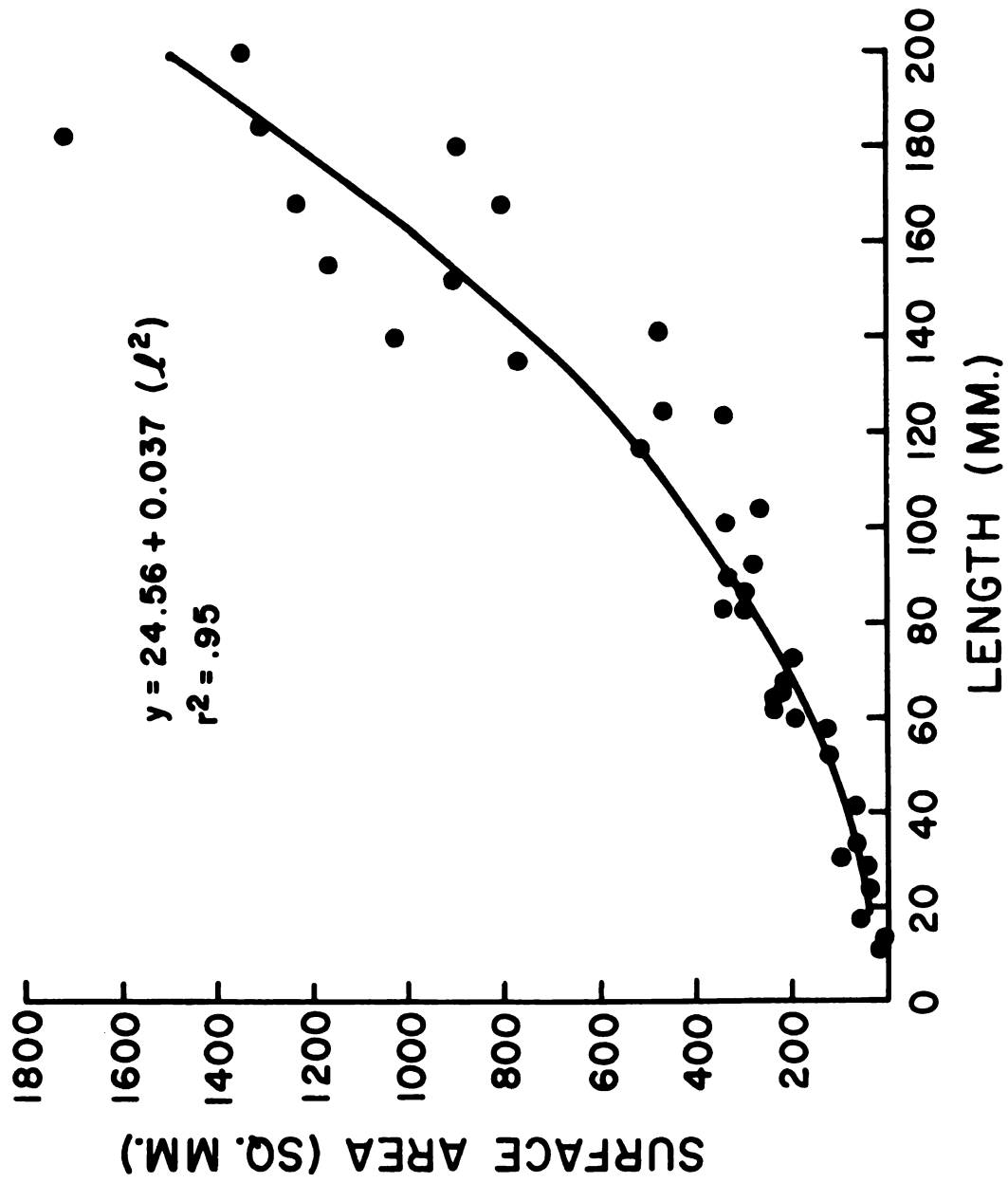


Figure 4.--Relationship between leaf length and leaf surface area in winter wheat.

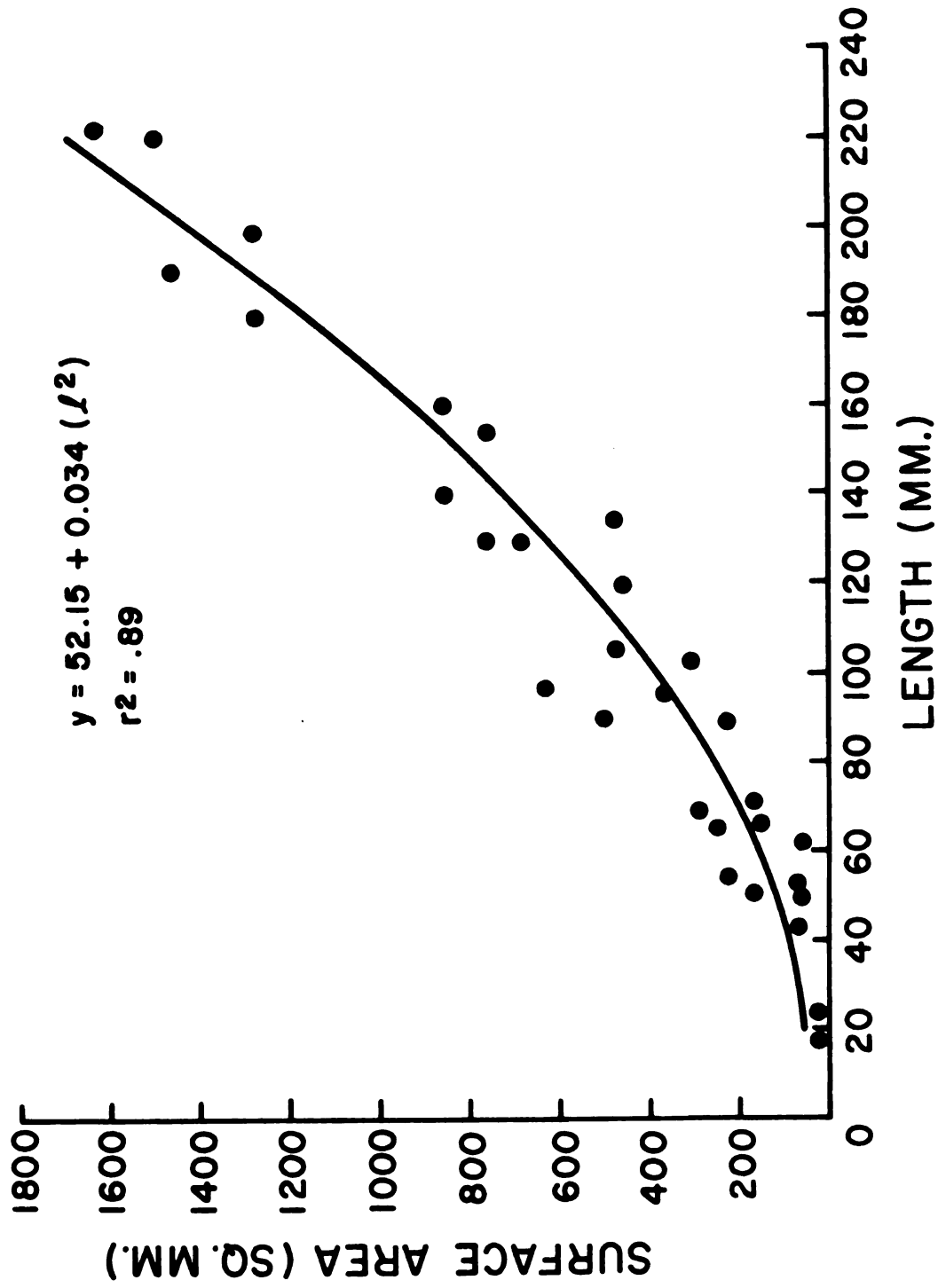


Figure 5.--Relationship between leaf length and leaf surface area in spring oats.

TABLE V.--Leaf lengths (mm.) of the top three leaves of winter wheat and spring oats calculated from total leaf length per leaf type per sample divided by total number of leaves per leaf type per sample at each sample date and corresponding accumulated degree days (base 42°F) (n = 10; $\pm$ SE)

Date	Degree-days (base 42°F)	Leaf 1	Leaf 2	Leaf 3
Wheat				
4/23	121	30.3 $\pm$ 6.5	50.6 $\pm$ 8.2	41.9 $\pm$ 4.5
4/29	239	52.8 $\pm$ 6.3	82.0 $\pm$ 9.6	53.7 $\pm$ 6.3
5/6	342	73.3 $\pm$ 5.7	116.2 $\pm$ 6.2	76.9 $\pm$ 5.7
5/13	487	80.8 $\pm$ 6.9	128.7 $\pm$ 13.7	108.8 $\pm$ 10.3
5/20	608	65.9 $\pm$ 4.0	115.0 $\pm$ 7.3	125.2 $\pm$ 5.8
5/29	825	161.0 $\pm$ 14.8	183.9 $\pm$ 15.2	154.0 $\pm$ 9.7
6/5	986	168.0 $\pm$ 10.1	204.2 $\pm$ 47.1	147.8 $\pm$ 13.8
6/12	1,193	170.2 $\pm$ 13.2	174.3 $\pm$ 17.6	151.1 $\pm$ 17.7
6/18	1,383	184.6 $\pm$ 22.1	191.5 $\pm$ 19.1	152.9 $\pm$ 22.9
6/25	1,540	160.0 $\pm$ 28.4	173.2 $\pm$ 14.8	147.3 $\pm$ 9.3
Oats				
5/20	608	51.5 $\pm$ 15.3	97.7 $\pm$ 9.8	75.5 $\pm$ 18.3
5/29	825	67.1 $\pm$ 3.9	132.1 $\pm$ 8.4	127.4 $\pm$ 9.8
6/5	986	88.3 $\pm$ 10.8	174.4 $\pm$ 13.5	146.3 $\pm$ 8.8
6/12	1,193	83.7 $\pm$ 9.9	169.6 $\pm$ 8.5	168.8 $\pm$ 8.6
6/18	1,383	106.3 $\pm$ 8.6	187.1 $\pm$ 11.8	191.2 $\pm$ 13.5
6/25	1,540	91.2 $\pm$ 21.9	154.9 $\pm$ 39.6	155.2 $\pm$ 39.7
7/06	1,869	101.1 $\pm$ 10.3	171.5 $\pm$ 14.7	181.2 $\pm$ 12.9
7/14	2,119	108.2 $\pm$ 5.7	165.0 $\pm$ 17.8	169.5 $\pm$ 15.6
7/11	2,336	109.0 $\pm$ 12.2	161.8 $\pm$ 17.6	153.7 $\pm$ 14.4

TABLE VI.--Leaf length (mm.) of the top three leaves of winter wheat and spring oats determined from subsampling five leaves of each type at each sample date and corresponding accumulated degree days (base 42°F) (n = 5; $\pm$ S.E.)

Date	Degree-days (base 42°F)	Leaf 1	Leaf 2	Leaf 3
Wheat				
4/23	121	30.2 $\pm$ 8.5	57.8 $\pm$ 3.8	52.2 $\pm$ 6.0
4/29	239	55.4 $\pm$ 7.7	83.2 $\pm$ 6.0	55.8 $\pm$ 5.4
5/6	342	92.0 $\pm$ 17.2	82.4 $\pm$ 19.0	94.2 $\pm$ 6.7
5/13	487	118.0 $\pm$ 19.0	141.2 $\pm$ 22.6	138.3 $\pm$ 13.3
5/20	608	90.4 $\pm$ 23.9	130.4 $\pm$ 14.3	126.4 $\pm$ 6.0
5/29	825	182.0 $\pm$ 32.4	168.4 $\pm$ 27.4	181.0 $\pm$ 7.0
6/5	986	196.8 $\pm$ 5.3	194.8 $\pm$ 12.4	172.8 $\pm$ 11.9
6/12	1,193	205.2 $\pm$ 12.8	191.4 $\pm$ 8.6	167.4 $\pm$ 12.9
6/18	1,383	198.4 $\pm$ 11.1	184.0 $\pm$ 4.0	176.0 $\pm$ 1.9
Oats				
5/20	208	53.4 $\pm$ 13.9	110.0 $\pm$ 14.8	107.0 $\pm$ 4.2
5/29	825	115.8 $\pm$ 6.6	156.8 $\pm$ 26.2	139.8 $\pm$ 16.0
6/5	986	139.0 $\pm$ 17.0	182.4 $\pm$ 16.9	193.4 $\pm$ 6.7
6/12	1,193	117.8 $\pm$ 11.4	213.2 $\pm$ 5.7	239.0 $\pm$ 10.1
6/18	1,383	156.8 $\pm$ 15.9	205.0 $\pm$ 14.0	198.4 $\pm$ 16.7
6/25	1,540	148.8 $\pm$ 8.9	220.8 $\pm$ 4.8	210.6 $\pm$ 12.8
7/6	1,869	154.8 $\pm$ 10.4	220.0 $\pm$ 8.6	218.2 $\pm$ 14.2

foliage. Flag leaves from each crop were collected to confirm the second method, their average lengths are given in Table VII.

TABLE VII.--Flag leaf lengths (mm.) collected from fields of winter wheat and spring oats at Gull Lake and East Lansing (+ S.E.)

	Gull Lake (R-area)	Gull Lake (T-area)	East Lansing (C-area)
	June 17	June 17	June 25
Wheat	199.1 $\pm$ 2.8 (n = 110)	199.6 $\pm$ 2.9 (n = 100)	163.2 $\pm$ 3.2 (n = 90)
Oats	165.4 $\pm$ 2.9 (n = 99)	152.3 $\pm$ 2.5 (n = 100)	166.3 $\pm$ 4.0 (n = 100)

The number of new leaves produced per unit land area varies with time, environmental conditions, and the tillering capacity of the variety. Table VIII gives the percentage of each leaf type of the total types for each sample.

As the plant matures, new leaves are produced at a decreasing rate until all leaves are formed. The discrepancy noted in oats (Table VIII) indicates that there were more than 6 leaves produced on a stem and these were placed in the sixth leaf type category.

The difference in the amount of foliage per sq. ft. in wheat and oats is not reflected in the number of leaves per stem but in the number of tillers per sq. ft. Wheat produced more stems per unit land area than oats using these varieties and under the environmental conditions in 1970 (Table IX).

TABLE VIII.--Per cent composition of each of the top six leaves of the total number of the top six leaves in each sample of winter wheat and spring oats at each sampling date and corresponding accumulated degree days (base 42°F)

Date	Degree-days (base 42°F)	% composition					
		L 1	L 2	L 3	L 4	L 5	L 6
Wheat							
4/23	121	3.4	27.5	17.5	12.0	8.0	1.5
4/29	239	29.5	26.5	18.5	11.5	8.0	6.0
5/6	342	26.0	23.5	19.5	14.5	9.5	7.0
5/13	487	24.5	22.5	18.5	14.0	10.0	10.0
5/20	608	24.5	21.0	17.5	15.5	12.0	10.0
5/29	825	18.5	18.5	18.0	15.5	14.0	16.0
6/5	986	19.5	20.0	18.0	16.0	15.0	14.0
6/12	1,193	20.0	20.0	19.0	16.5	13.0	10.5
6/18	1,383	18.0	17.0	17.0	15.5	15.0	17.0
Oats							
5/20	608	36.5	29.5	24.5	10.0	0.0	0.0
5/29	825	26.0	23.5	19.0	13.5	11.0	7.0
6/5	986	20.0	19.0	19.0	16.5	13.5	12.0
6/12	1,193	19.0	18.5	16.5	14.0	11.5	20.5
6/18	1,383	17.0	17.0	16.0	13.5	12.0	25.5
6/25	1,540	19.0	18.5	17.0	17.0	12.5	18.0

TABLE IX.--Number of plants, stems and stems per plant (per sq. ft.)
in winter wheat and spring oats at each sampling date and
corresponding accumulated degree days (base 42°F) (n = 10)

Date	Degree-days (base 42°F)	No. plants	No. stems	Stems/plant
Wheat				
4/23	121	26.4	82.4	3.12
4/29	239	28.6	115.5	3.89
5/6	342	27.3	118.8	3.98
5/13	487	32.6	128.5	3.94
5/20	608	26.3	117.2	4.47
5/29	825	29.7	98.3	3.31
6/5	986	25.0	73.3	2.93
6/12	1,193	20.2	81.4	4.03
6/18	1,383	26.6	97.4	3.36
6/25	1,540	28.8	97.2	3.37
7/6	1,869	23.7	67.9	2.86
Oats				
5/20	608	9.8	14.6	1.49
5/29	825	18.5	41.7	2.25
6/5	986	12.3	29.8	2.34
6/12	1,193	14.1	33.0	2.34
6/18	1,383	19.9	31.4	1.58
6/25	1,540	15.9	38.2	2.40
7/6	1,869	12.7	32.6	2.57
7/14	2,119	14.7	41.3	2.80
7/22	2,336	17.0	34.1	2.01

Leaf surface area (excluding leaf sheaths) was calculated from average leaf lengths (Table VI) using the equations from Figures 4 and 5 for individual leaves. This value multiplied by the number of stems per sq. ft. gives surface area per sq. ft. for an individual leaf type. For example, if the average length of a wheat leaf is 100 mm. and there are 100 stems per sq. ft. the predicted surface area would be:

$$S A w = (24.56 + 0.037 (100^2)) \times 100$$

or 39456 sq. mm. per sq. ft. Table X gives the predicted number of sq. mm. per sq. ft. of surface area of foliage for each of the top 3 leaves for wheat and oats.

Crop Height--The height attained by a crop is easily measured. Figure 6 shows the progression of height growth in wheat and oats and illustrates the growth difference under the environmental conditions at the Kellogg Farm. The shape of the acceleration phase of height growth of these crops differs and the maximum height of winter wheat was about 100 cm. whereas oats grew to a maximum height of only 75 cm.

Head Components--The total oven dry head weight per sq. ft. (including chaff, kernals and stems) was determined for each crop (Figure 7). Again the difference in head weight between the two crops is apparent although the morphological difference in head structure between wheat and oats must be considered. The number of heads per sq. ft. were also counted (Figure 8).

Root Biomass--Variations in soil compactness made estimates of root biomass difficult so they were not used in calculations. The benefit of removing roots was the separation of stems belonging to single root systems.

TABLE X.--Calculated surface area (sq. mm. per sq. ft.) of the top three leaves of winter wheat and spring oats at each sampling date and corresponding accumulated degree days (base 42°F) (see text)

Date	Degree days (base 42°F)	Surface area (sq. mm. per sq. ft.)		
		Leaf type 1	Leaf type 2	Leaf type 3
Wheat				
4/23	121	4,804	12,209	10,331
4/29	239	15,400	31,296	15,584
5/6	342	40,122	32,763	41,923
5/13	487	69,358	97,949	94,095
5/20	608	38,316	76,615	72,161
5/29	825	122,889	105,557	121,569
6/5	986	106,841	104,716	82,783
6/12	1,193	128,817	112,333	86,389
6/18	1,383	124,402	107,288	98,336
Oats				
5/20	608	2,162	6,753	6,430
5/29	825	21,145	36,991	29,843
6/5	986	21,100	35,902	39,422
6/12	1,193	17,258	52,688	65,778
6/18	1,383	27,854	46,472	43,630
6/25	1,540	30,711	65,274	59,559
7/6	1,869	26,209	55,705	50,828

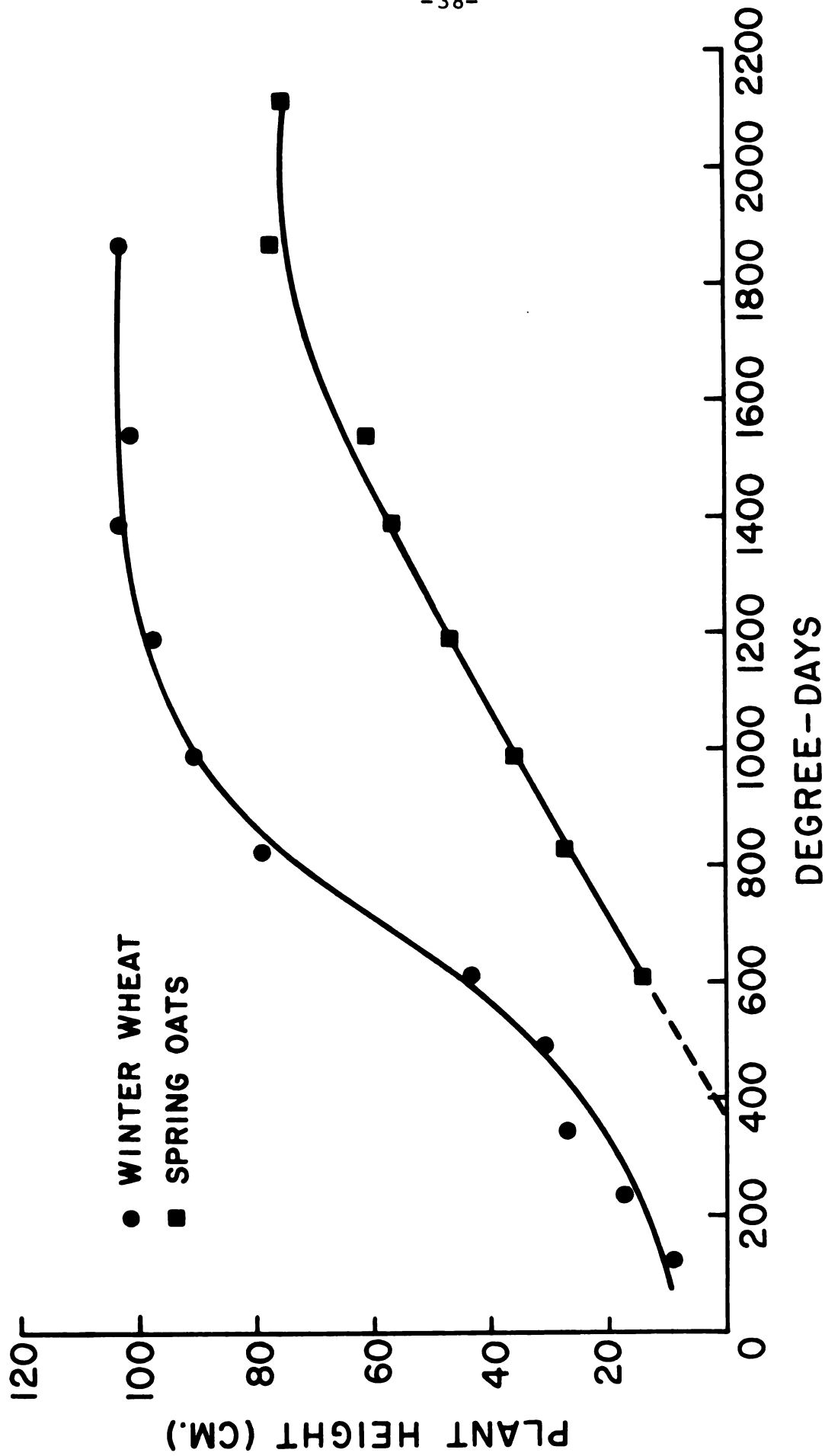


Figure 6.--Relationship between accumulated degree-days (base 42°F) and average plant height of winter wheat and spring oats.

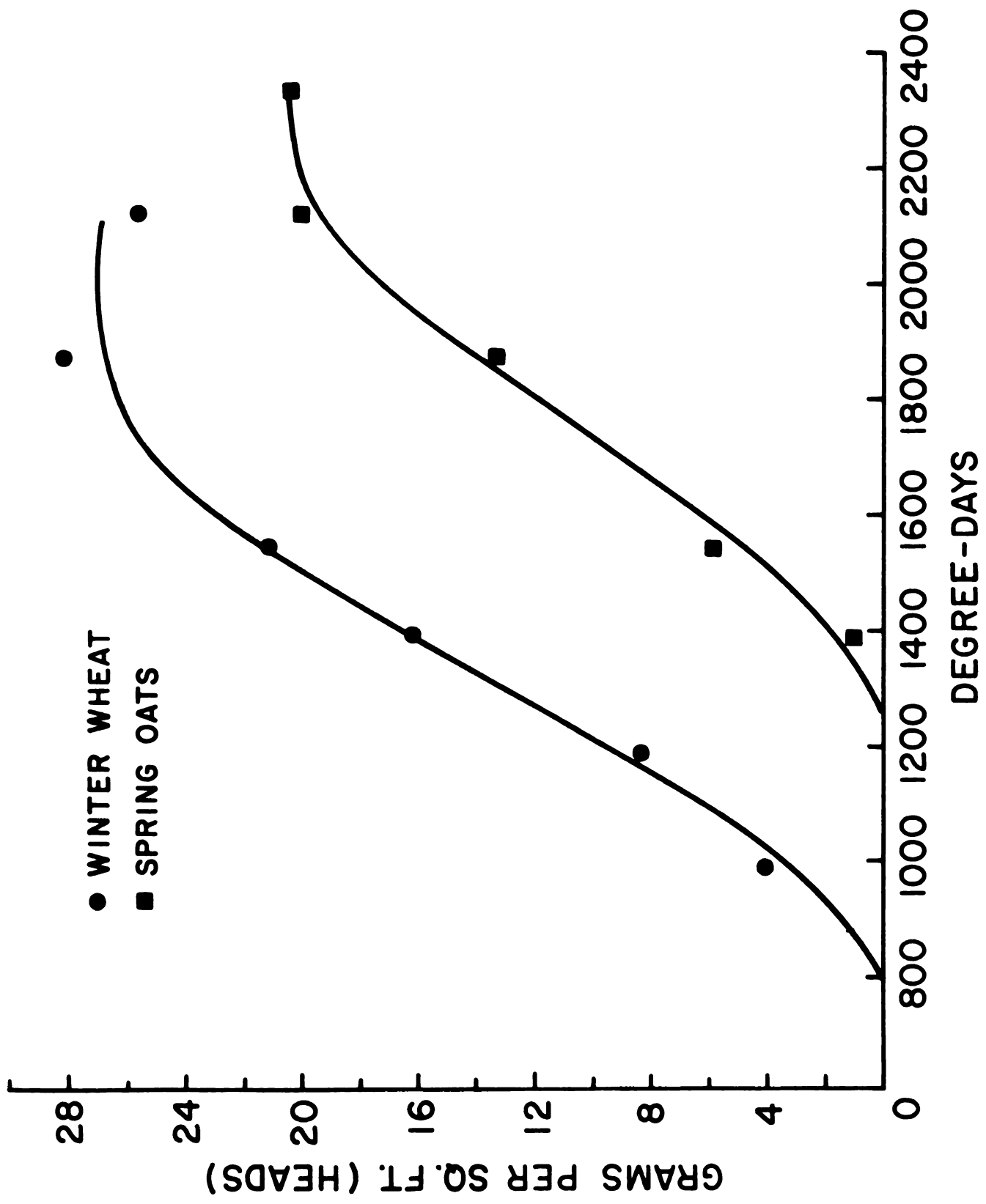


Figure 7.--Relationship between accumulated degree-days (base 42°F) and oven dry weight of heads of winter wheat and spring oats.

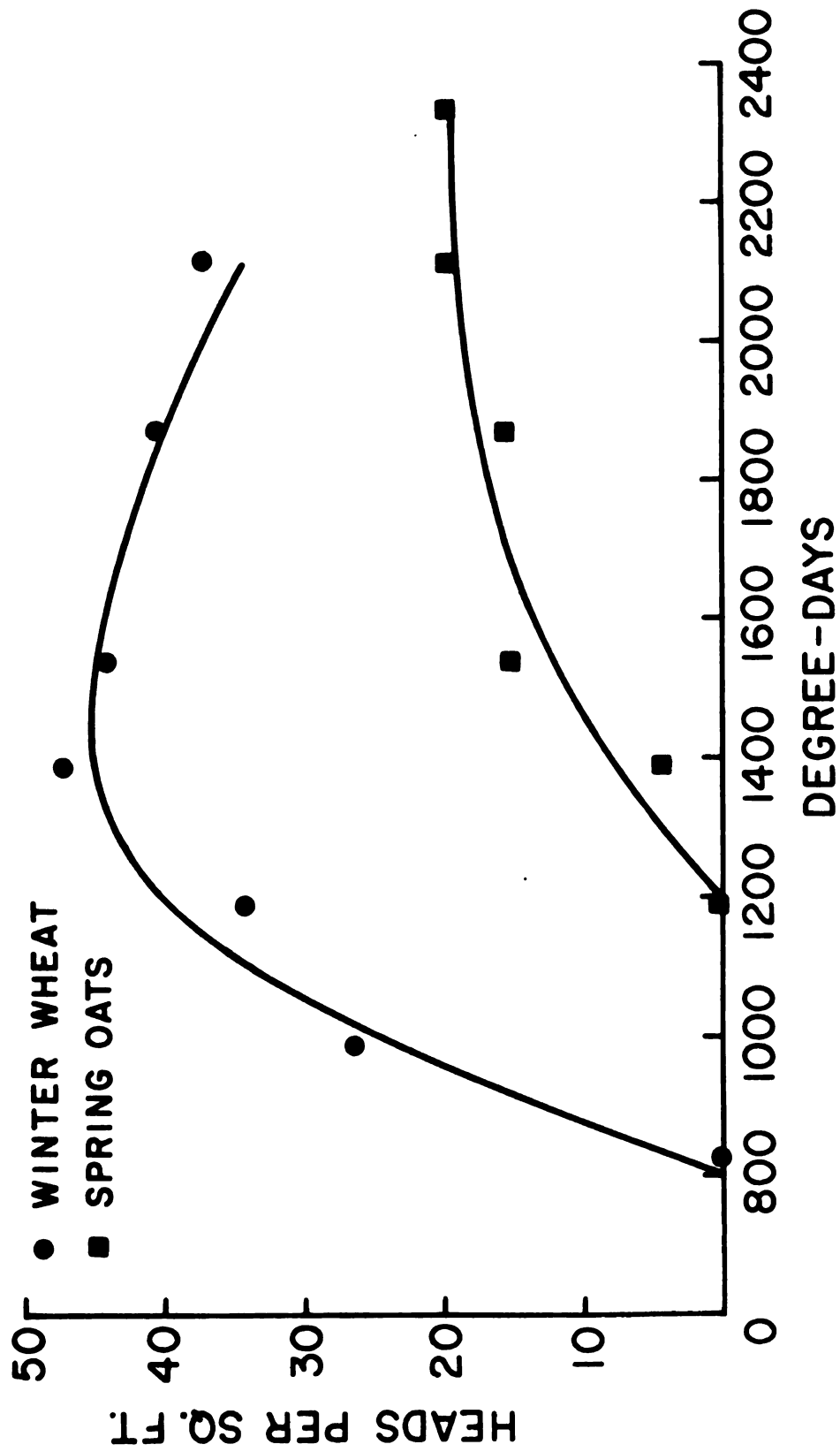


Figure 8.--Relationship between accumulated degree-days (base 42°F) and the number of heads of winter wheat and spring oats.

To develop a working relationship between wet sample foliage and oven-dry weight of foliage per sq. ft., samples were collected over a range of plant densities from Gull Lake and East Lansing on June 19 (Figure 9). Similar relationships were developed for each of the plant components collected from Gull Lake - R at about weekly intervals and are given in Table XI.

The per cent moisture in each of the components when sampled was calculated (dry wt./wet wt. x 100) and is presented in Table XII.

Plant growth is variable from one site to the next even within a single field. Plant samples were collected from fields of wheat and oats where the land was rolling (Gull Lake - T). Two sets of samples were taken; one on the top of a hill (Gull Lake - H T) and the other at a lower area of the same field (Gull Lake - V T). Table XIII illustrates the differences in plant height, wet weight of foliage, oven dry weight of heads and number of heads in wheat within the same field at the two locations. Similar comparisons are made for oats (Table XIV). The striking difference between the 2 areas within fields indicates the superiority of the low area (Gull Lake V T) compared to the hill-top samples (Gull Lake H T) in that growth was better in all the plant components shown. These differences are assumed to be related to the capacity of the lower area to hold moisture longer than the higher area.

The foliage weights (g. per sq. ft.) for the 2 areas at Gull Lake (R and T) and the area at East Lansing from which cereal leaf beetle eggs and larval were sampled are given in Appendices V, VI and VII for wheat and oats.

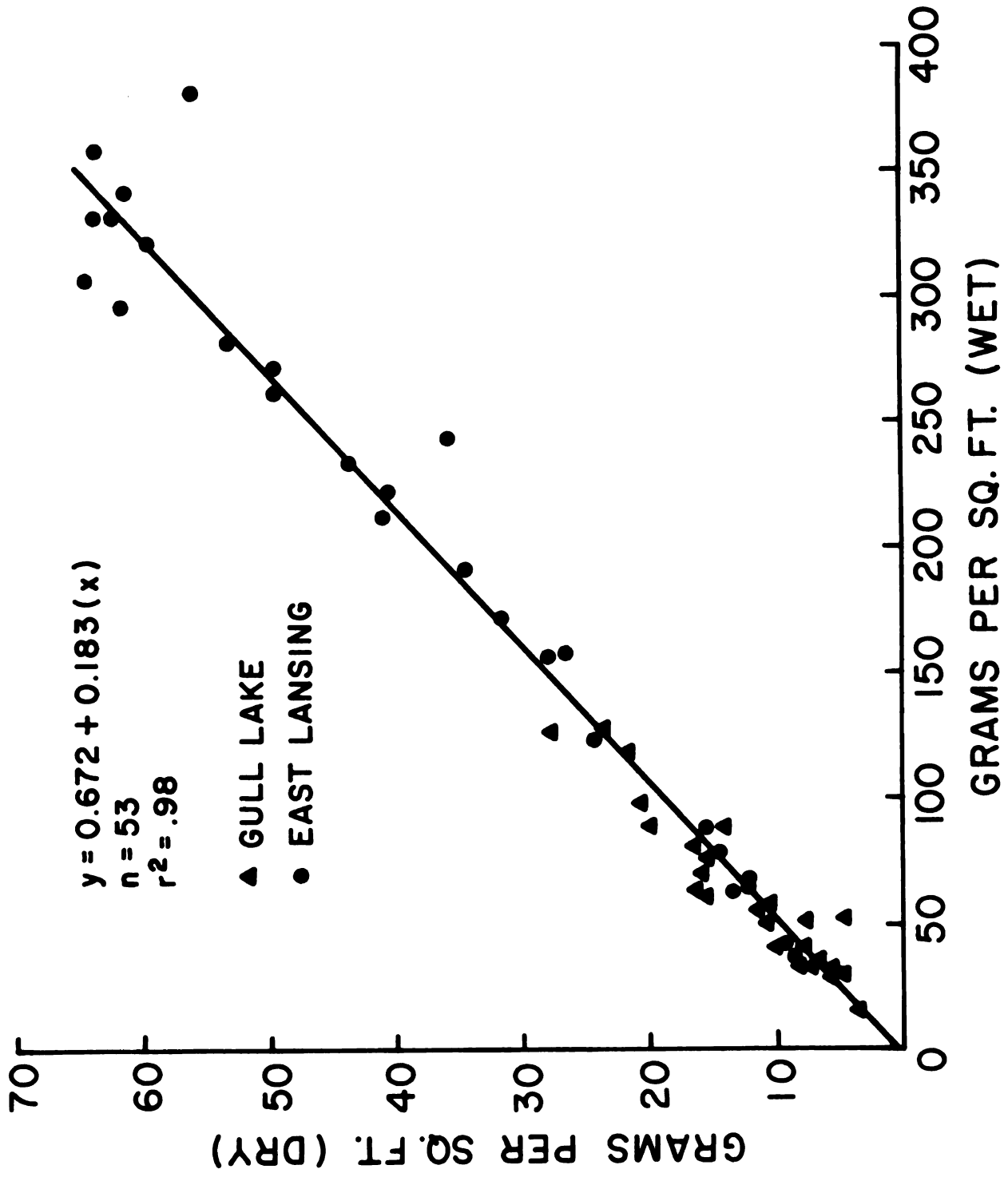


TABLE XI.--Regression equations to predict oven dry weight (g. per linear ft.) from wet sample weight (g. per linear ft.) for roots, stems, the top four leaves and heads of winter wheat and spring oats throughout the growing season

Roots		
Wheat	o.d. wt. = - .285 + .478 w.s. wt. (gms.)	n = 110, r^2 = .79
Oats	o.d. wt. = - .049 + .281 w.s. wt.	n = 90, r^2 = .81
Stems		
Wheat	o.d. wt. = .503 + .259 w.s. wt.	n = 110, r^2 = .72
Oats	o.d. wt. = - .778 + .227 w.s. wt.	n = 90, r^2 = .86
Top leaf		
Wheat	o.d. wt. = .317 + .231 w.s. wt.	n = 100, r^2 = .52
Oats	o.d. wt. = .030 + .197 w.s. wt.	n = 90, r^2 = .48
Second leaf		
Wheat	o.d. wt. = .642 + .121 w.s. wt.	n = 100, r^2 = .38
Oats	o.d. wt. = .137 + .158 w.s. wt.	n = 90, r^2 = .58
Third leaf		
Wheat	o.d. wt. = .418 + .136 w.s. wt.	n = 100, r^2 = .36
Oats	o.d. wt. = .102 + .157 w.s. wt.	n = 90, r^2 = .60
Fourth leaf		
Wheat	o.d. wt. = .233 + .164 w.s. wt.	n = 100, r^2 = .36
Oats	o.d. wt. = .065 + .157 w.s. wt.	n = 90, r^2 = .61
Heads		
Wheat	o.d. wt. = -2.38 + 0.525 w.s. wt.	n = 60, r^2 = .86
Oats	o.d. wt. = -1.59 + 0.531 w.s. wt.	n = 48, r^2 = .85

TABLE XII.--Per cent moisture remaining in plant components at each sample date and corresponding accumulated degree-days (base 42°F) (n = 10)

Date	Degree-days (base 42°F)	% moisture					
		Roots	Stems	Leaf 1	Leaf 2	Leaf 3	Leaf 4
Wheat							
4/23	121	73.1	86.9	86.6	85.5	83.4	82.9
4/29	239	68.6	88.3	87.6	87.4	87.3	86.3
5/6	342	59.8	86.6	86.0	86.0	86.2	85.2
5/13	487	56.2	85.7	83.8	83.1	83.5	85.7
5/20	608	63.0	85.3	79.6	73.5	73.8	73.0
5/29	825	66.4	81.9	77.8	80.4	75.9	67.6
6/5	986	57.3	78.7	75.6	73.8	62.3	44.1
6/12	1,193	48.2	70.7	66.6	71.7	65.6	61.4
6/18	1,383	38.8	61.7	39.8	19.4	17.5	17.0
6/25	1,540	53.3	63.8	53.8	53.6	57.3	64.3
7/6	1,869	48.7	58.3	28.8	25.2	25.7	30.0
Oats							
5/20	608	70.4	91.5	96.9	85.5	94.1	100.0
5/29	825	83.5	92.3	91.2	89.7	89.9	91.0
6/5	986	82.2	91.7	89.0	87.7	87.3	87.3
6/12	1,193	67.9	87.0	85.0	81.8	82.9	82.6
6/18	1,383	68.8	84.2	82.3	82.1	82.9	84.1
6/25	1,540	71.7	81.2	79.3	79.2	80.8	81.9
7/6	1,869	68.0	75.6	62.8	66.4	70.1	69.3
7/14	2,119	72.1	75.2	64.9	72.2	74.1	72.2
7/22	2,336	73.3	72.1	62.0	62.3	63.9	67.4

TABLE XIII.--Within field comparison of plant height (cm.), total wet sample weight of foliage (g.), oven dry weight of heads (g.) and number of heads in springs oats (n = 3; $\pm$ S.E.)

Date	Degree days (base 42°F)	Gull Lake - HT	Gull Lake - VT
Plant height			
6/15	1,280	49.46 $\pm$ 0.97	79.20 $\pm$ 1.62
6/22	1,462	60.94 $\pm$ 6.16	86.66 $\pm$ 2.09
6/29	1,637	73.32 $\pm$ 5.72	106.72 $\pm$ 0.99
7/06	1,869	79.55 $\pm$ 9.05	103.75 $\pm$ 5.52
7/22	2,336	79.66 $\pm$ 2.64	104.20 $\pm$ 1.57
Wet weight total foliage			
6/15	1,280	221.77 $\pm$ 56.18	355.69 $\pm$ 65.27
6/22	1,462	133.62 $\pm$ 13.54	418.81 $\pm$ 84.59
6/29	1,637	126.61 $\pm$ 14.24	313.83 $\pm$ 61.74
Oven dry weight heads			
7/22	2,336	19.44 $\pm$ 0.19	29.02 $\pm$ 3.41
Number of heads			
7/22	2,336	15.99 $\pm$ 1.51	26.28 $\pm$ 4.58

TABLE XIV.--Within field comparison of plant height (cm.), total wet sample weight of foliage (g.) oven dry weight of heads (g.) and number of heads in winter wheat (n = 3; $\pm$ S.E.)

Date	Degree-days (base 42° F)	Gull Lake - HT	Gull Lake - VT
Plant height			
6/15	1,280	52.60 $\pm$ 6.27	92.41 $\pm$ 6.81
6/22	1,462	49.54 $\pm$ 5.45	94.89 $\pm$ 6.47
6/29	1,637	54.67 $\pm$ 9.41	88.78 $\pm$ 9.0
Wet weight total foliage			
6/15	1,280	73.15 $\pm$ 12.97	181.07 $\pm$ 45.32
6/22	1,462	56.12 $\pm$ 7.10	189.50 $\pm$ 57.11
6/29	1,637	42.51 $\pm$ 17.62	93.48 $\pm$ 26.21
Oven dry weight heads			
6/29	1,637	12.31 $\pm$ 1.03	27.75 $\pm$ 7.71
Number of heads			
6/29	1,637	17.71 $\pm$ 1.15	39.99 $\pm$ 7.56

Further studies of cereal leaf beetle-host interactions need not include measurements of all components of plant growth. Because adult cereal leaf beetles oviposit and feed on the leaf tissue of their hosts and the larvae also feed only on the leaves, this plant component is most important. It is difficult and time consuming to separate each leaf by its respective position on the stem of the plant, determine its length and surface area. A more realistic approach is to develop relationships between plant components which are readily measurable. Therefore a method which predicts surface area of foliage available to the cereal leaf beetle would be most useful. An indirect method of predicting surface area can be determined using the dry weight of the foliage. This functional relationship is given in Figure 10 and is linear:

$$SA = 29513 + 34268 (DWL)$$

where SA is surface area (sq. mm. per sq. ft.) and DWL is oven dry weight of leaves (g. per sq. ft.).

Cereal Leaf Beetle Population Densities--To assess feeding damage to wheat and oats by the cereal leaf beetle, population estimates of eggs and each of the 4 larval instars in both crops were made within the same fields from which the plant components were measured and also from Gull Lake - T and East Lansing - C. Sampling methods for cereal leaf beetle population estimates were the same as those used by Helgesen and Haynes (in press) described under methods. Results from these samples are given in Appendices VIII, IX and X. Separate estimates of egg input were also made (Appendix XI).

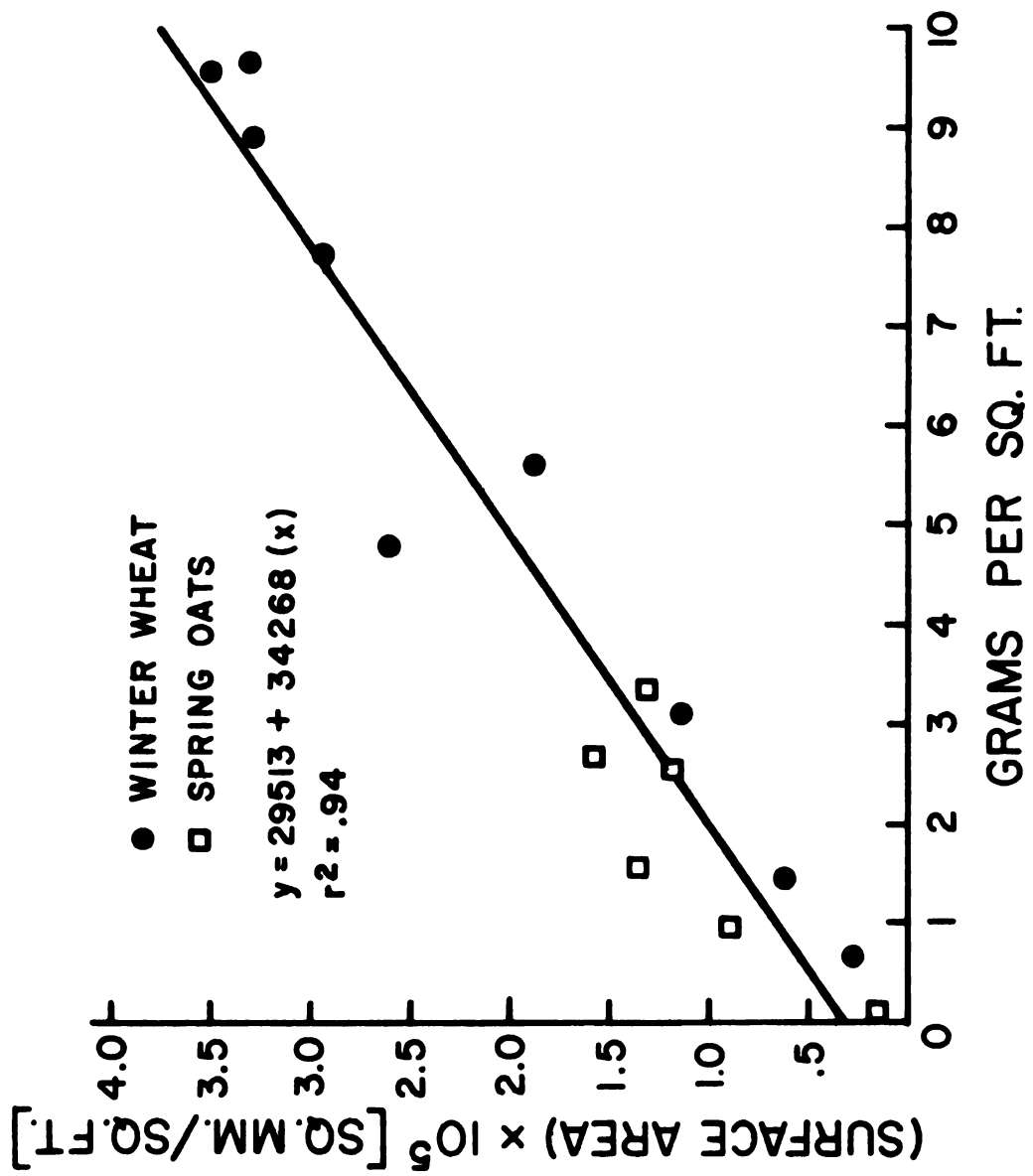


Figure 10.--Relationship between oven dry weight of winter wheat and spring oat leaves and leaf surface area.

Total feeding on each host crop by the larval population is related to the total number of larvae produced per unit area of land. This was determined by calculating the area under the total larval population curve from the population estimates given in Appendix IX. The total number of larvae produced per sq. ft. was 88.01 and 142.78 in wheat and oats respectively. Feeding, however, is not proportional to the total larvae produced because different amounts of food are required by each of the four cereal leaf beetle instars.

Foliage Consumption Estimated from Cereal Leaf Beetle Population Densities--A technique hereafter called 'first instar feeding equivalents' was developed to account for the difference in consumption by each instar. The results obtained by Wilson et al. (1969) (Table XV) were used to calculate this conversion.

TABLE XV.--Amount of foliage consumed by each instar of the cereal leaf beetle and the corresponding first instar feeding equivalent conversion (see text)

Instar	Area of foliage consumed m m ² *	First instar equivalent conversion factor
1	18.6	1.00
2	53.4	2.87
3	111.0	5.97
4	459.5	24.23

*Mean of 21 and 26°C after Wilson et al. 1969.

The conversion factor is the expression of each of the instars with respect to first instar feeding: for example the conversion factor for the second instar is $53.4/18.6 = 2.87$. These conversions effectively weight the population by their respective amount of feeding.

Each population estimate (Table XVI) was multiplied by the appropriate conversion factor and the curves in Figure 11 show the effect of the conversion. To determine the total amount of foliage consumed by the larval populations in the 2 crops, the area under the first instar equivalent curves were calculated and divided by the development time (degree-days 48°F) to give the number of first instar equivalents produced in wheat ($134976.6/55 = 2454.12$) compared with $215962.5/55 = 3926.6$ produced in oats. The respective amounts of foliage consumed in each crop was estimated by multiplying the amount of foliage consumed by a first instar larvae (18.6 mm^2). Therefore, larvae consumed 45646.6 and 73034.6 mm^2 of foliage in wheat and oats respectively.

The expression of foliage consumed through time by larvae is of particular interest and cannot be ascertained by the preceding calculations. The amount of foliage consumed through time is cumulative and therefore, the area under the first instar equivalent curve for each crop was calculated at intervals of 100 degree days 48°F , divided by the number of degree-days required for development (55 48°F) and multiplied by the area consumed by a first instar larva (18.6 mm^2). Table XVI shows the calculated values of the cumulative numbers of first instar equivalents and Figure 12 depicts the cumulative amount of foliage consumed per sq. ft. by the cereal leaf beetle larval population on wheat and oats.

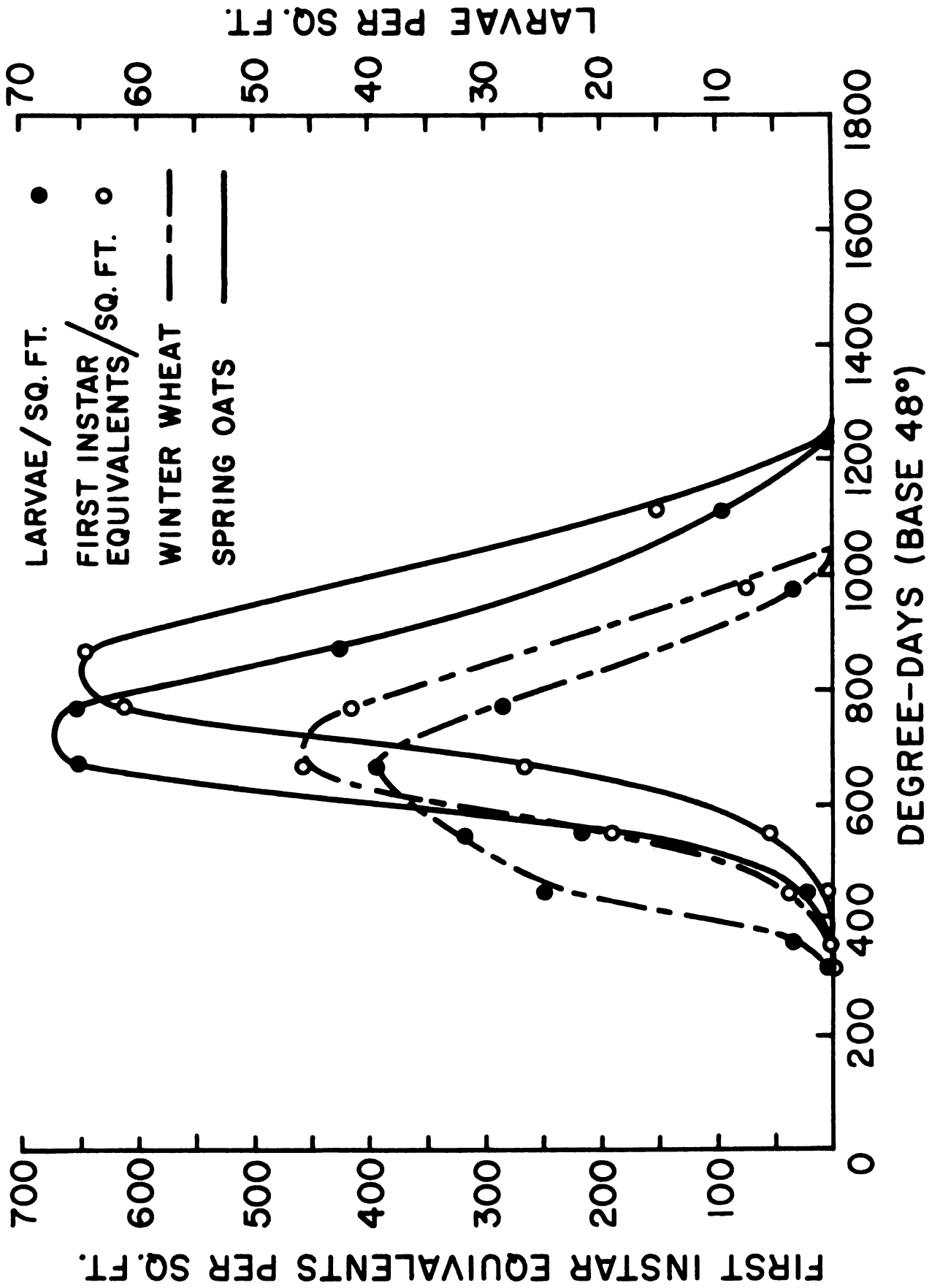


Figure 11.--Relationship between accumulated degree-days (base 48°F), cereal leaf beetle larvae (0) and first instar equivalents (0) on winter wheat and Spring oats.

TABLE XVI.--Cumulative first instar feeding equivalents and cumulative estimate of foliage consumed (sq. mm. per sq. ft.) determined from first instar equivalent incidence curves for winter wheat and spring oats

Degree day interval (base 48°F)	Cumulative first instar feeding equivalents	Cumulative foliage consumed
Wheat		
300 - 400	7.79	144.89
401 - 500	70.12	1,304.23
501 - 600	389.54	7,245.44
601 - 700	1,075.15	19,997.79
701 - 800	1,779.70	33,474.42
801 - 900	2,290.52	42,603.67
901 - 1,000	2,446.33	45,501.74
1,001 - 1,100	2,454.12	45,646.63
Oats		
400 - 500	7.79	144.89
501 - 600	54.54	1,014.44
601 - 700	428.50	7,970.10
701 - 800	1,324.45	24,643.77
801 - 900	2,399.60	44,623.56
901 - 1,000	3,217.63	59,847.92
1,001 - 1,100	3,724.05	69,267.33
1,101 - 1,200	3,903.22	72,599.89
1,201 - 1,300	3,926.59	73,034.57
1,301 - 1,400	3,926.59	73,034.57

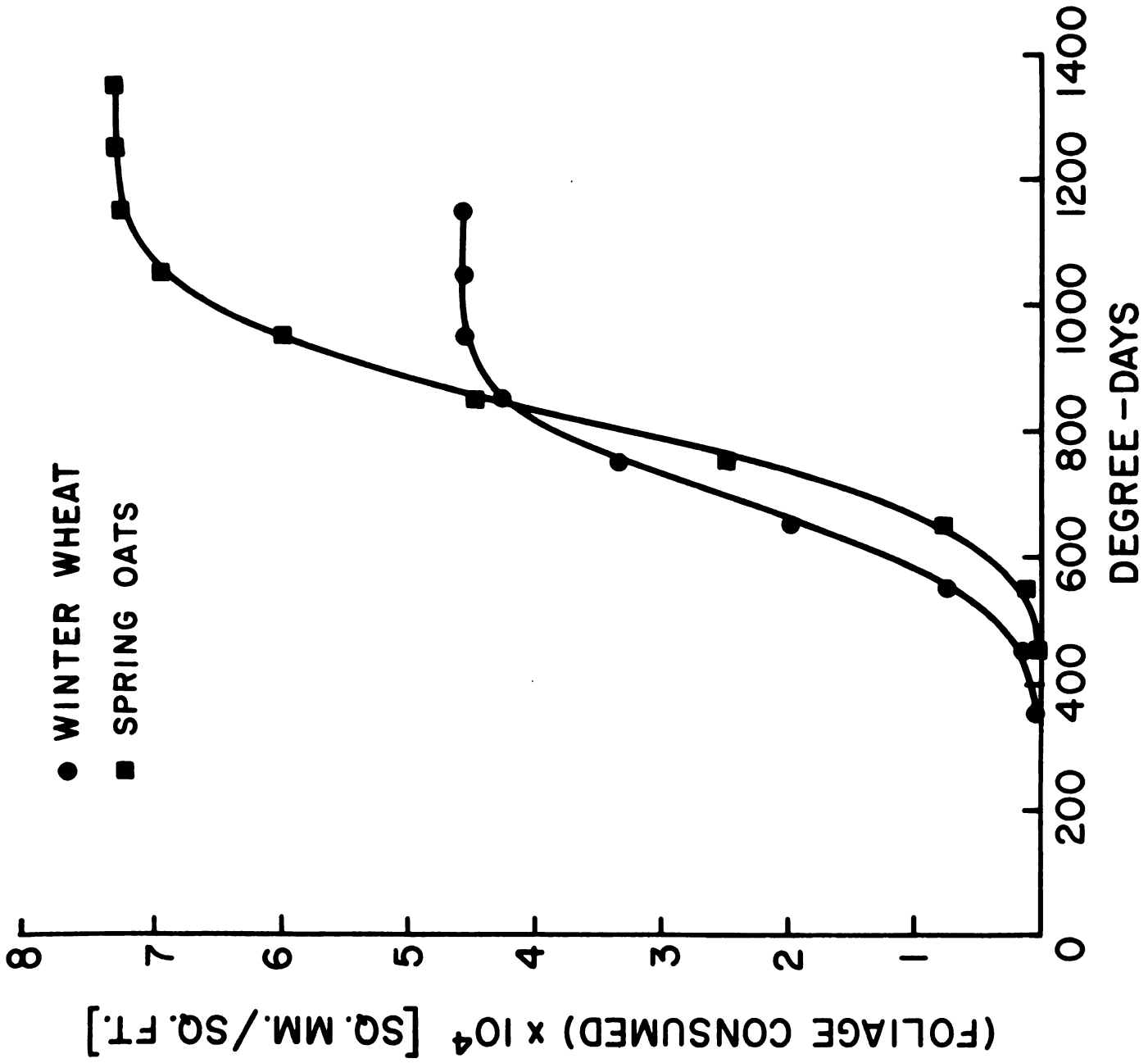


Figure 12.--Relationship between accumulated degree-days (base 48°F) and the predicted amount of foliage consumed by cereal leaf beetle larval populations on winter wheat and spring oats using the first instar equivalent method.

Foliage Consumed by Estimates of Leaf Damage--An alternate estimate of damage, independent of the number of larvae found on the plants, was made by counting the number of feeding scars, through time, on the top 3 leaves of the 2 host crops investigated. To predict the amount of feeding on the leaves of a plant, and to compare these results with the foliage consumed by a known larval population, the area of foliage consumed was measured. The number of feeding scars per leaf on each of the top 3 leaves of wheat and oats and the average scar area (sq. mm.) is given in Table XVII. The amount of surface area removed per leaf (SAR) was estimated by multiplying the number of scars by the mean scar area at each time interval. Then using the estimate of the number of leaves per sq. ft., the area of foliage removed was calculated using the following formula: $SAR = s \cdot a \cdot t$ where s is the number of feeding scars per leaf type, a is the area of the feeding scars (in sq. mm.) and t is the number of tillers (stems) per sq. ft. of land area. SAR is the surface area removed (sq. mm.) per sq. ft. of land area.

Table XVIII gives the values calculated from this equation for the first 3 leaf types. The total sq. mm. of foliage removed from these leaves for wheat and oats is shown in Figure 13. Table XIX compares these 2 methods (Figures 12 and 13) of predicting feeding damage and shows they are similar.

The first instar feeding equivalent method estimates damage to the total plant while the methods of counting holes involved only the top 3 leaves and may underestimate damage because damage occurs on leaves below the third leaf down, especially on oats. No attempt was

TABLE XVII.--Number of feeding scars per leaf on each of the top three leaves of wheat and oats and the average scar area (sq. mm.)

Date	Degree-days (base 48°F)	Number of feeding scars			Scar area (sq. mm.)
		Leaf type 1	Leaf type 2	Leaf type 3	
Wheat					
4/23	59	0	0	0	0
4/29	144	0	0.04	0.04	1.0
5/6	215	0.24	1.08	0.76	2.6
5/13	320	1.36	2.84	2.64	3.8
5/20	402	1.04	3.92	4.36	4.4
5/29	565	7.48	10.88	10.12	5.2
6/5	684	18.68	18.52	19.70	5.6
6/12	849	32.30	18.52	19.70	6.0
6/18	1,003	60.00	18.52	19.70	6.0
Oats					
5/20	402	0.42	3.80	3.70	1.0
5/29	565	3.08	14.80	16.80	2.6
6/5	684	3.45	17.30	12.30	3.8
6/12	849	5.04	23.30	38.70	4.4
6/18	1,003	18.32	34.40	41.20	5.2
6/25	1,119	25.32	39.30	64.00	5.6
7/6	1,382	49.00	182.30	130.10	6.0

TABLE XVIII.--Cumulative feeding (sq. mm. per sq. ft.) on the top three leaves of wheat and oats by a population of cereal leaf beetles

Date	Degree-days (base 48°F)	Surface area consumed (sq. mm. per sq. ft.)		
		Leaf type 1	Leaf type 2	Leaf type 3
Wheat				
4/23	59	0	0	0
4/29	144	0	5	5
5/6	215	74	334	235
5/13	320	664	1,387	1,289
5/20	402	536	2,022	2,248
5/29	565	3,824	5,562	5,173
6/5	684	7,668	7,602	8,087
6/12	849	15,775	9,045	9,622
6/18	1,003	30,240	9,334	9,928
Oats				
5/20	402	6	56	54
5/29	565	334	1,605	1,822
6/5	684	391	1,959	1,393
6/12	849	732	3,383	5,619
6/18	1,003	2,991	5,617	6,727
6/25	1,119	5,417	8,407	13,691
7/6	1,382	9,584	35,658	25,448

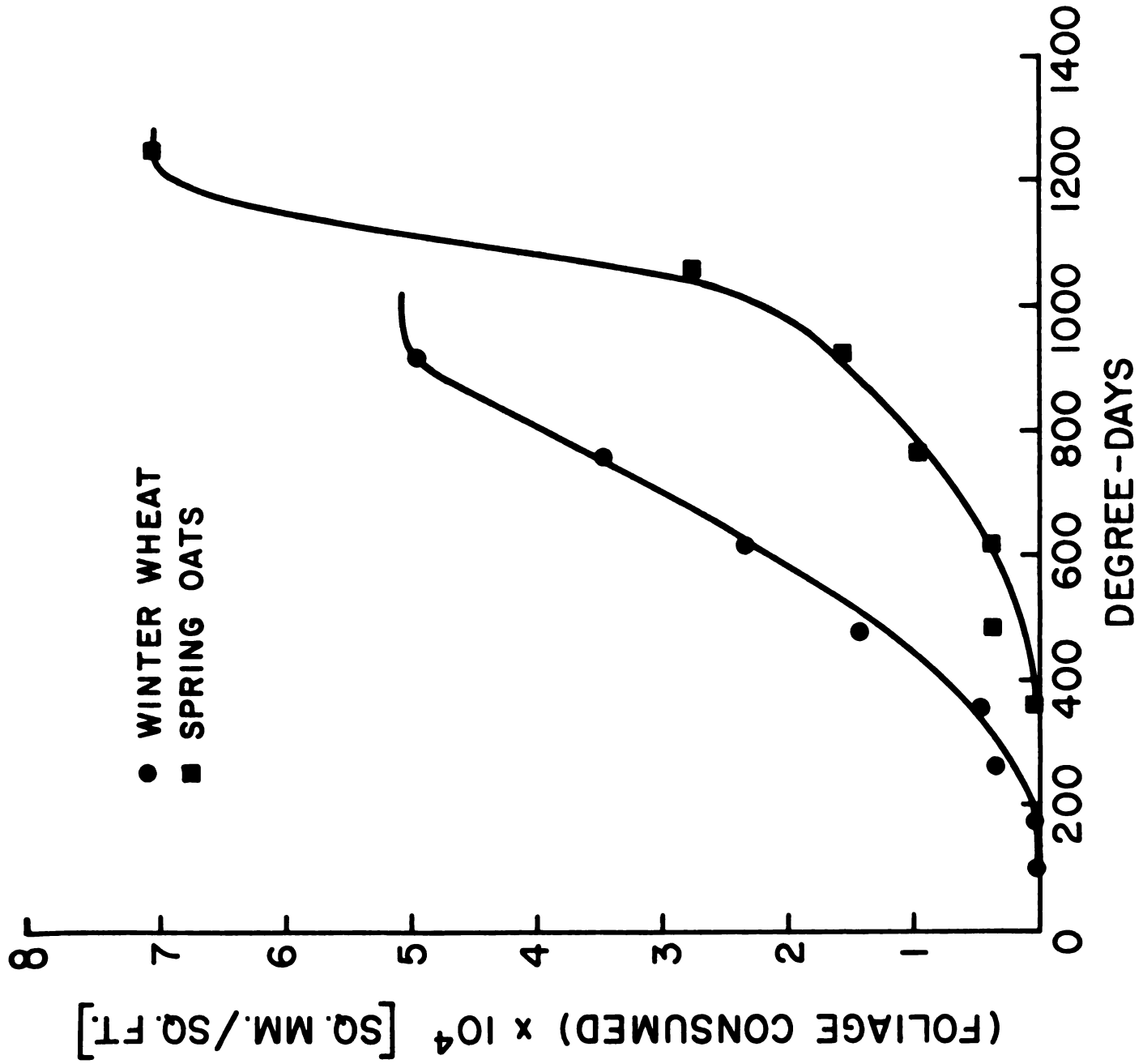


Figure 13.--Relationship between accumulated degree-days (base 48°F) and the amount of foliage consumed by populations of the cereal leaf beetle on winter wheat and spring oats estimated from damage to the top 3 leaves.

TABLE XIX.--Final amount of square millimeters of foliage removed predicted by two different methods

Method	Wheat	Oats
1st instar equivalents	45,646.6	73,034.6
Damage to leaves	49,502.9	70,689.8
Difference	- 3,856.3	+ 2,344.8

made to separate damage caused by adult feeding. However, an estimate of this is possible, especially early in the year on wheat when larvae were not yet present in the crop (up to 300 degree-days).

The number of feeding scars in each of the top 3 leaves was different within each crop and between wheat and oats. Table XX shows the per cent of the total number of scars contributed by each of the top 3 leaves. In wheat damage to the top leaf increased linearly with time a corresponding decrease in damage to the second and third leaf. A similar trend was not found in oats where damage to the second and third leaf remained higher than on the first leaf. Table XXI shows the per cent of the leaf surface available per sq. ft. consumed and a relationship similar to that given in Table IX is evident.

The importance of each of these leaves with respect to the damage inflicted on them is reflected in Table XXI by indicating that in wheat the top leaf (flag leaf this late in the season) damage is about 2.6 fold greater than on the 2 leaves below it. This is not the case in oats where damage on the lower leaves is greater than on the flag leaf.

Only by superimposing incidence the cereal leaf beetle first instar feeding equivalents in wheat and oats over respective plant

TABLE XX.--Per cent utilization of the top three leaves of winter wheat and spring oats by the cereal leaf beetle

Date	Degree-days (base 48°F)	% utilization		
		Leaf type 1	Leaf type 2	Leaf type 3
Wheat				
4/29	144	0	50.0	50.0
5/16	215	11.5	51.9	36.5
5/13	320	19.9	41.5	38.6
5/20	420	11.2	42.1	46.8
5/27	565	26.3	38.2	35.5
6/5	684	32.8	32.5	34.6
6/12	849	45.8	26.3	27.9
6/18	1,003	61.1	18.8	20.0
Oats				
5/20	402	5.0	47.9	46.7
5/29	565	8.9	43.2	49.0
6/5	684	10.4	52.3	37.2
6/12	849	7.5	34.8	57.7
6/18	1,003	19.5	36.7	43.9
6/25	1,119	19.7	30.6	49.7
7/6	1,382	13.6	50.4	36.0

TABLE XXI.--Per cent of the leaf surface available per sq. ft. consumed by cereal leaf beetles on the top three leaves of wheat and oats

Date	Degree-days (base 48°F)	% leaf surface consumed			
		Leaf 1	Leaf 2	Leaf 3	$\bar{X}$
Wheat					
4/23	59	0.0	0.0	0.0	0.0
4/29	144	0.0	0.01	0.03	0.01
5/6	215	0.18	1.02	0.56	0.56
5/13	320	0.92	1.42	1.37	1.28
5/20	402	1.40	2.64	3.12	2.57
5/29	565	3.11	5.27	4.26	4.16
6/05	648	7.18	7.26	9.77	7.94
6/12	849	12.24	8.05	11.14	10.52
6/18	1,003	24.31	8.70	10.10	15.00
Oats					
5/20	402	0.28	0.82	0.84	.75
5/29	565	1.58	4.34	6.10	4.27
6/05	684	1.85	5.46	3.53	3.88
6/12	849	4.24	6.42	8.54	7.17
6/18	1,003	10.74	12.09	15.42	13.00
6/25	1,111	17.64	12.88	22.99	17.69
7/06	1,382	36.57	64.01	50.07	53.25

growth curves can one appreciate the difference in impact of this insect on the two crop species. The cereal leaf beetle and plant growth initiate development at different temperature thresholds (plant at 42°F and cereal leaf beetle larvae at 48°F). It was therefore impractical to plot the curves over 2 thresholds simultaneously. Instead the x-axis is accumulated days from April 20 and does not detract significantly from the curves plotted over degree-days.

However, Appendices III and IV provide the necessary relationships between date, degree days (based 42°F and 48°F) and days from April 20 at the corresponding sampling intervals at Gull Lake and East Lansing.

In general it is apparent why oats is damaged more heavily than wheat. Peak feeding by the cereal leaf beetle occurs in wheat when a great deal of growth has already taken place. The wheat plant, by overwintering and receiving fall and early spring moisture, has a well established root system and therefore can probably withstand considerable defoliation. Under growth conditions in the study area, wheat leaf biomass is greater than that for oats (Figure 14 B) and could be responsible for diluting the larval population, especially during early larval stages. In oats, the plants have barely emerged from the soil with newly established root systems, often under moisture stress, when the cereal leaf beetle adults begin to feed on the newly emerged oat seedlings and oviposit eggs. Eggs hatched and larvae began feeding before the plants were 20 cm. tall (Figure 14 A). Leaves grow rapidly in oats and at peak larval feeding leaf length in both crops is comparable (Figure 14 C). The appearance of heads, on the other hand,

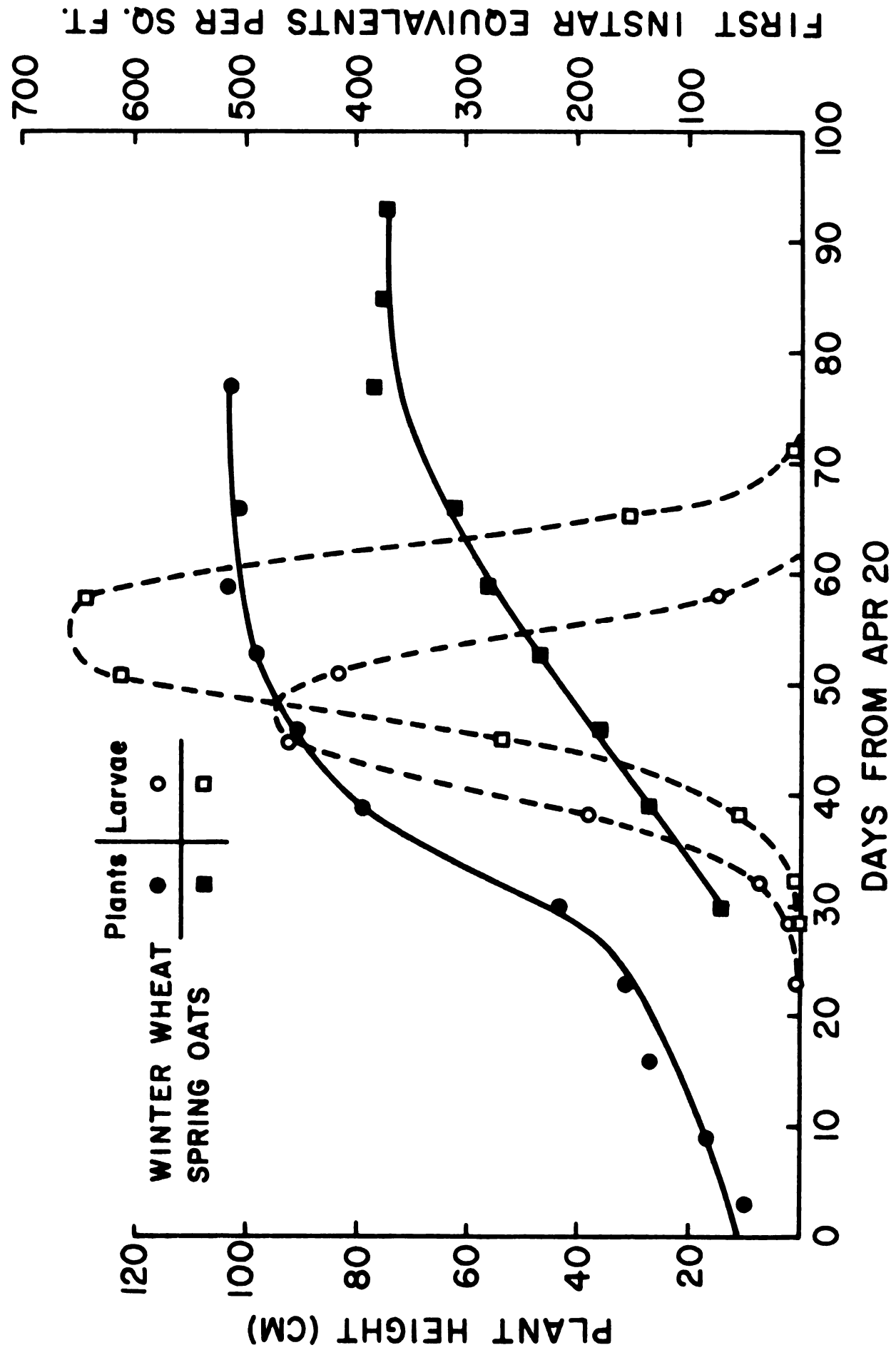


Figure 14a.--Relationship between accumulated days from April 20, first instar feeding equivalents on winter wheat and spring oats and plant height.

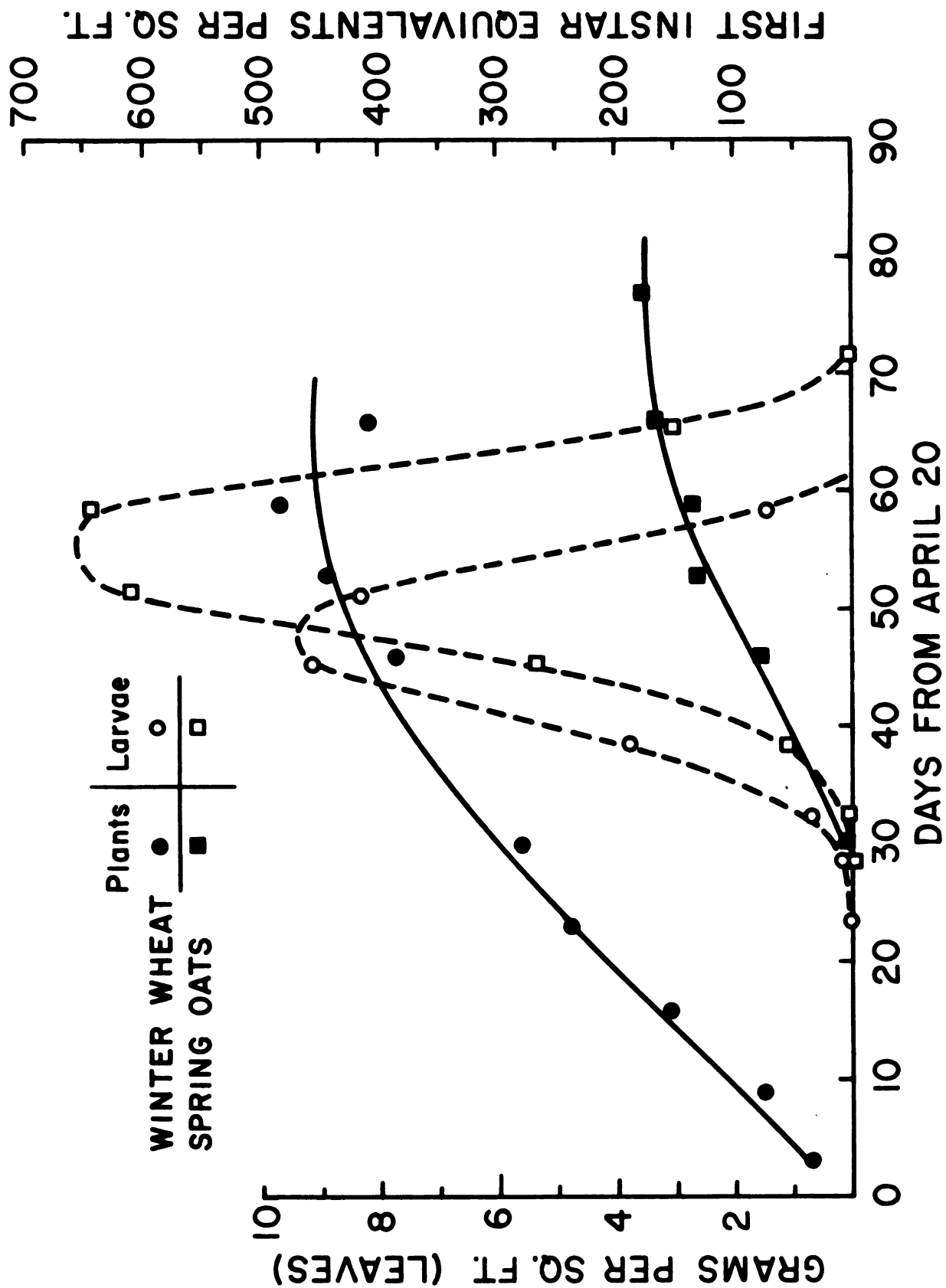


Figure 14b.--Relationship between accumulated days from April 20, first instar feeding equivalents on winter wheat and spring oats and oven dry weight of leaves.

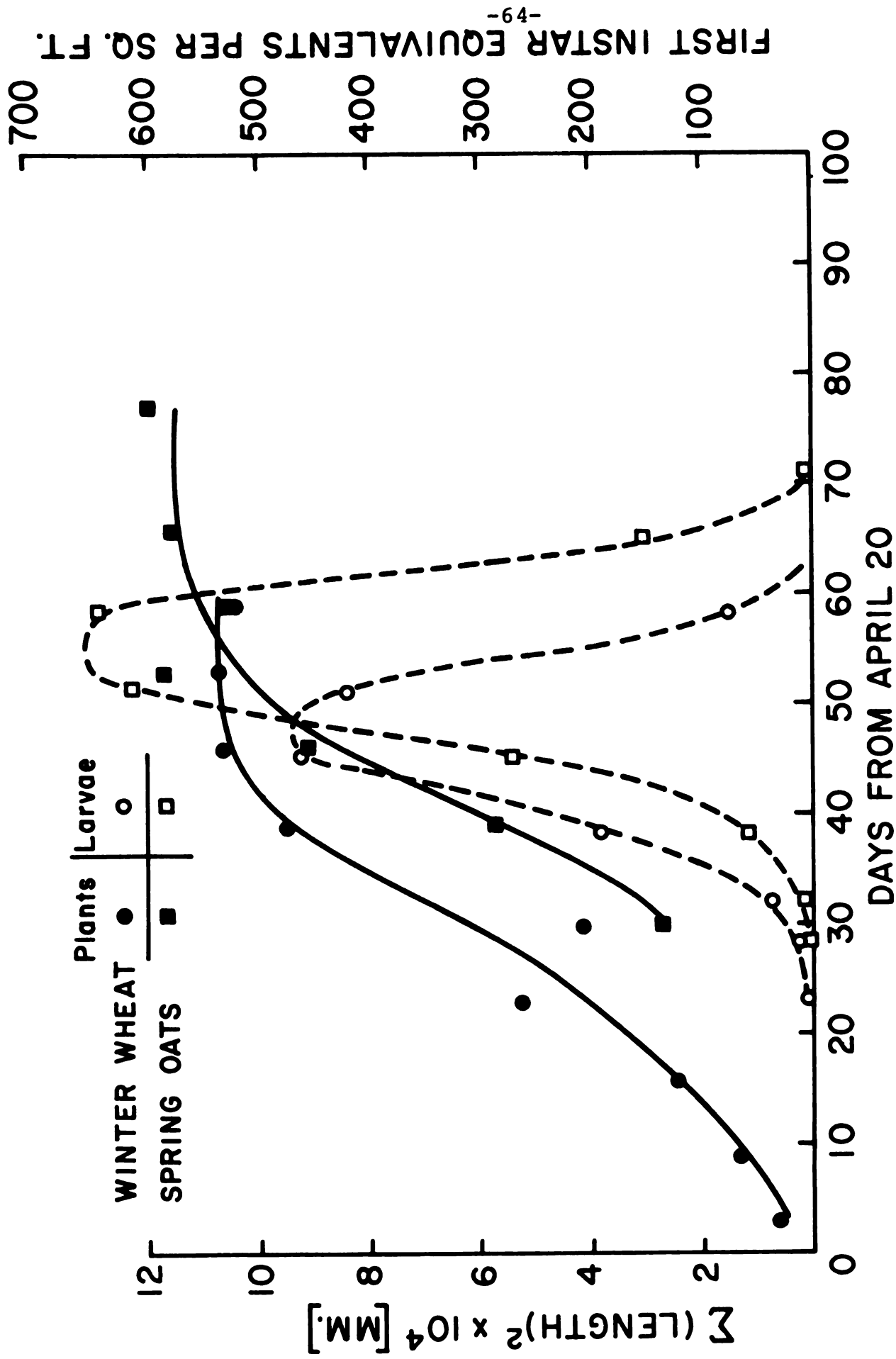


Figure 14c.--Relationship between accumulated days from April 20, first instar feeding equivalents on winter wheat and spring oats and sum of the squares of the lengths of the top 3 leaves.

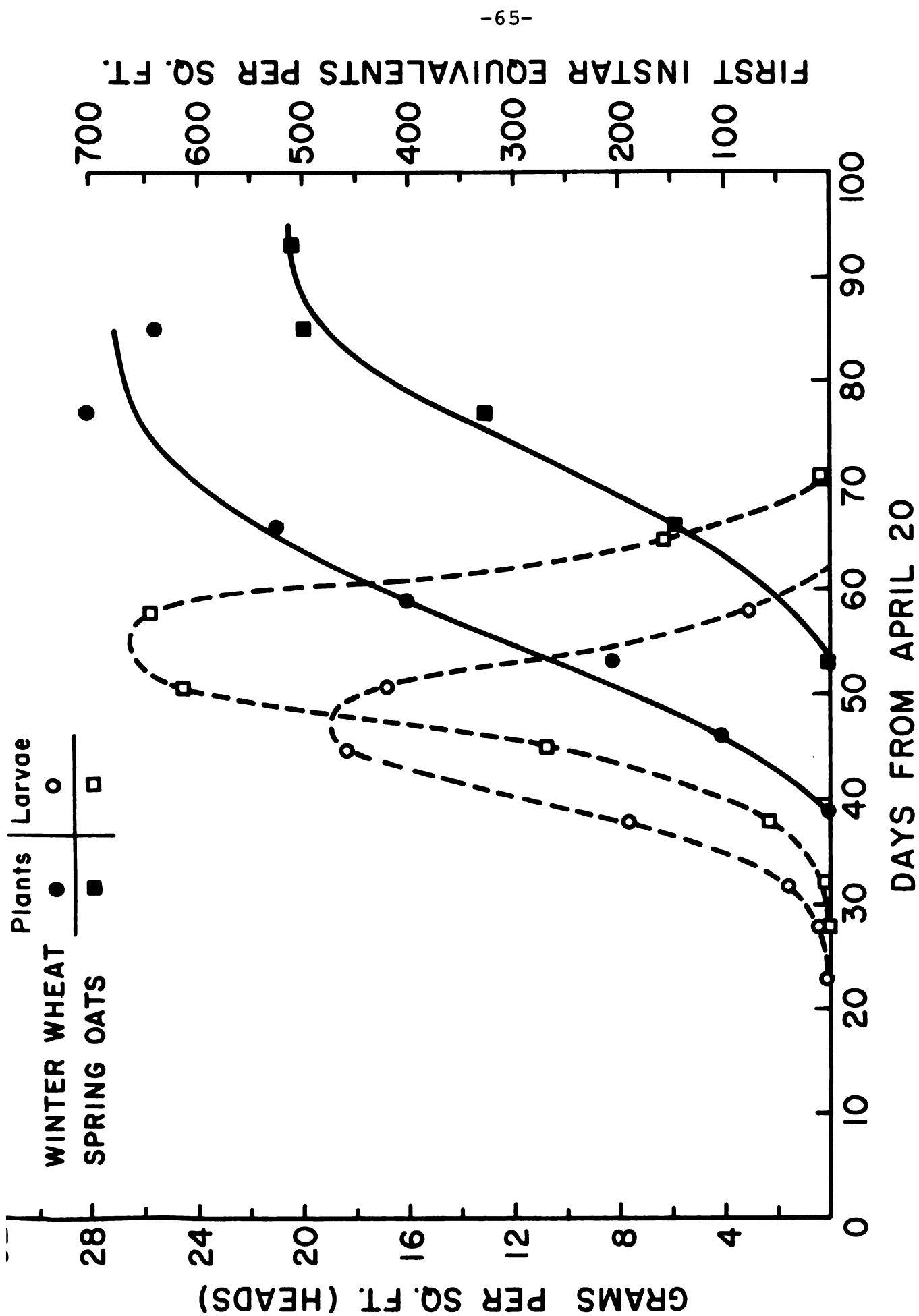


Figure 14d.--Relationship between accumulated days from April 20, first instar feeding equivalents on winter wheat and spring oats and the number of heads.

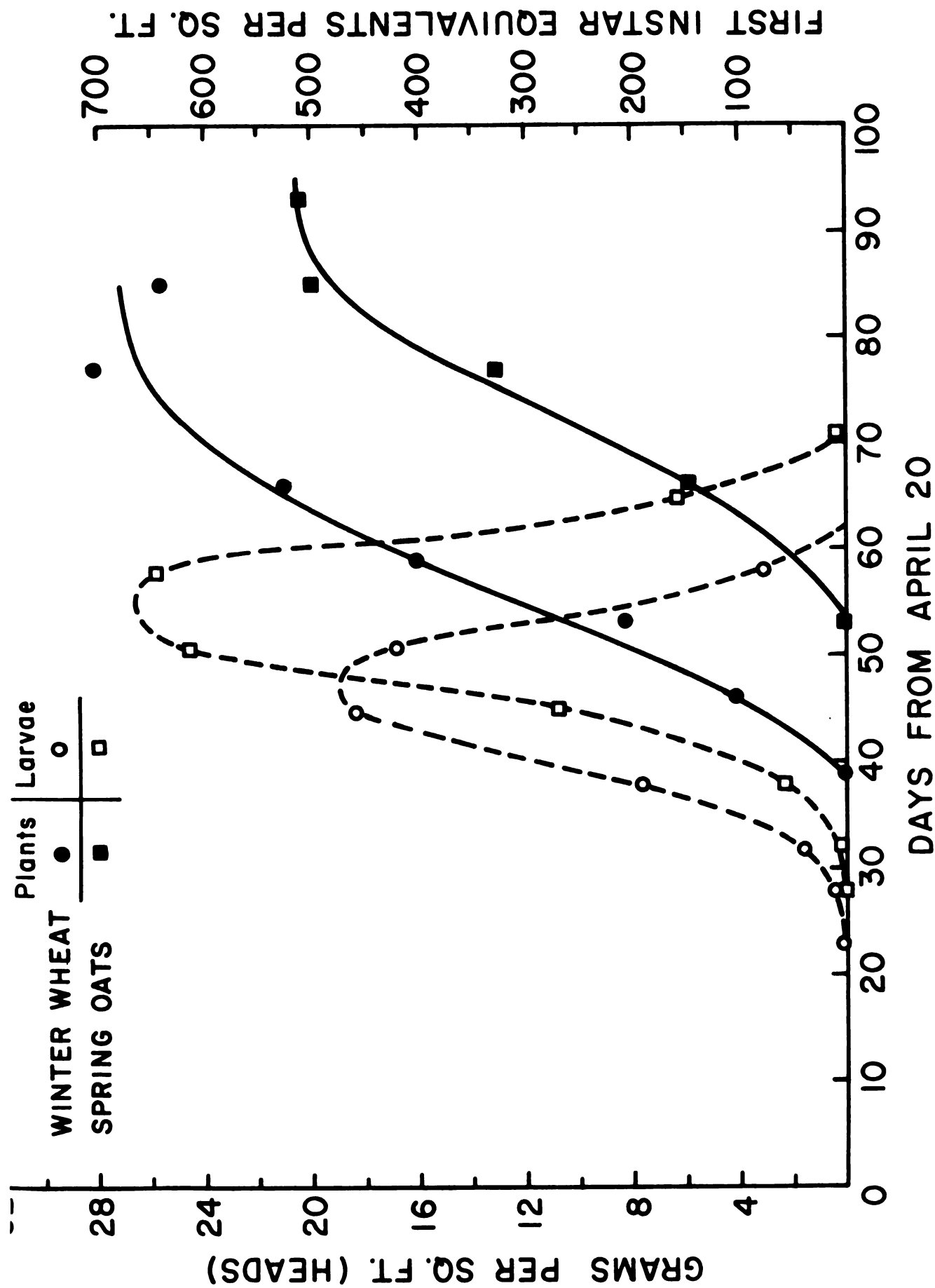


Figure 14d.--Relationship between accumulated days from April 20, first instar feeding equivalents on winter wheat and spring oats and the number of heads.

occurred prior to or at about peak larval feeding in wheat but near the end of larval feeding in oats (Figure 14 D).

In the 3 locations sampled (Gull Lake T and R and East Lansing - C) cereal leaf beetle population densities as well as the amount of foliage available for feeding were different. Figures 15 A - C illustrate these differences showing that cereal leaf beetle populations were highest at Gull Lake - T, slightly lower at Gull Lake - R and much lower at East Lansing - C. The total amount of foliage (oven dry weight per sq. ft.) on which the cereal leaf beetle fed (Figures 15 A - C) was greatest at East Lansing - C less at Gull Lake - R and lowest at Gull Lake T.

Table XXII shows the approximate amount of total foliage per sq. ft. available in each area at peak larval feeding. The differences between areas in the foliage available cannot be directly attributed to cereal leaf beetle densities but do indicate that damage caused by this feeding would be more intense when less foliage is available. A portion of the difference in crop growth may be related to the difference in total rainfall received during May, June and July (Table XXIII) and especially during June, Gull Lake received 2.35 inches less than East Lansing. Heat units, accumulated from January 1 do not seem to be appreciably different between the two areas (Table XXIV), although less heat was accumulated at East Lansing.

From larval populations in these 3 areas the amount of foliage consumed on each crop was calculated (Table XXV), also indicating the population levels attained in each area. Egg input by the cereal leaf beetle was also measured in each of these areas and was used to predict

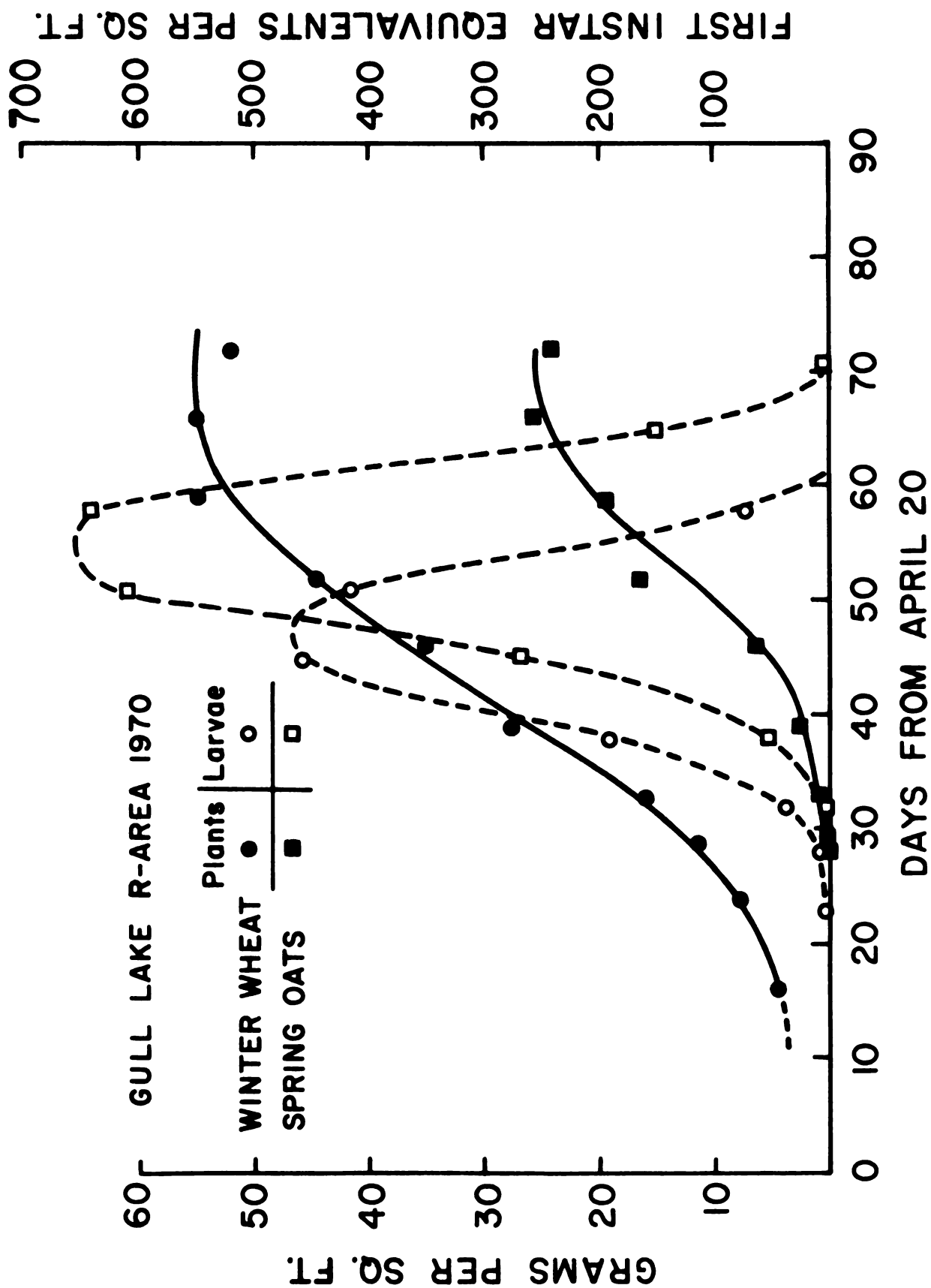


Figure 15a.--Relationship between accumulated days from April 20, first instar feeding equivalents and oven dry weight of foliage above ground for winter wheat and spring oats at Gull Lake - R area.

GULL LAKE T-AREA 1970

	Plants		Larvae
	WINTER WHEAT	SPRING OATS	
	●	■	○
			□

GRAMS PER SQ. FT.

40

30

20

10

0

DAYS FROM APRIL 20

10

20

30

40

50

60

70

80

90

100

FIRST INSTAR EQUIVALENTS PER SQ. FT.

700

600

500

400

300

200

100

-89-

Figure 15b.--Relationship between accumulated days from April 20, first instar feeding equivalents and oven dry weight of foliage above ground for winter wheat and spring oats at Gull Lake - T area.

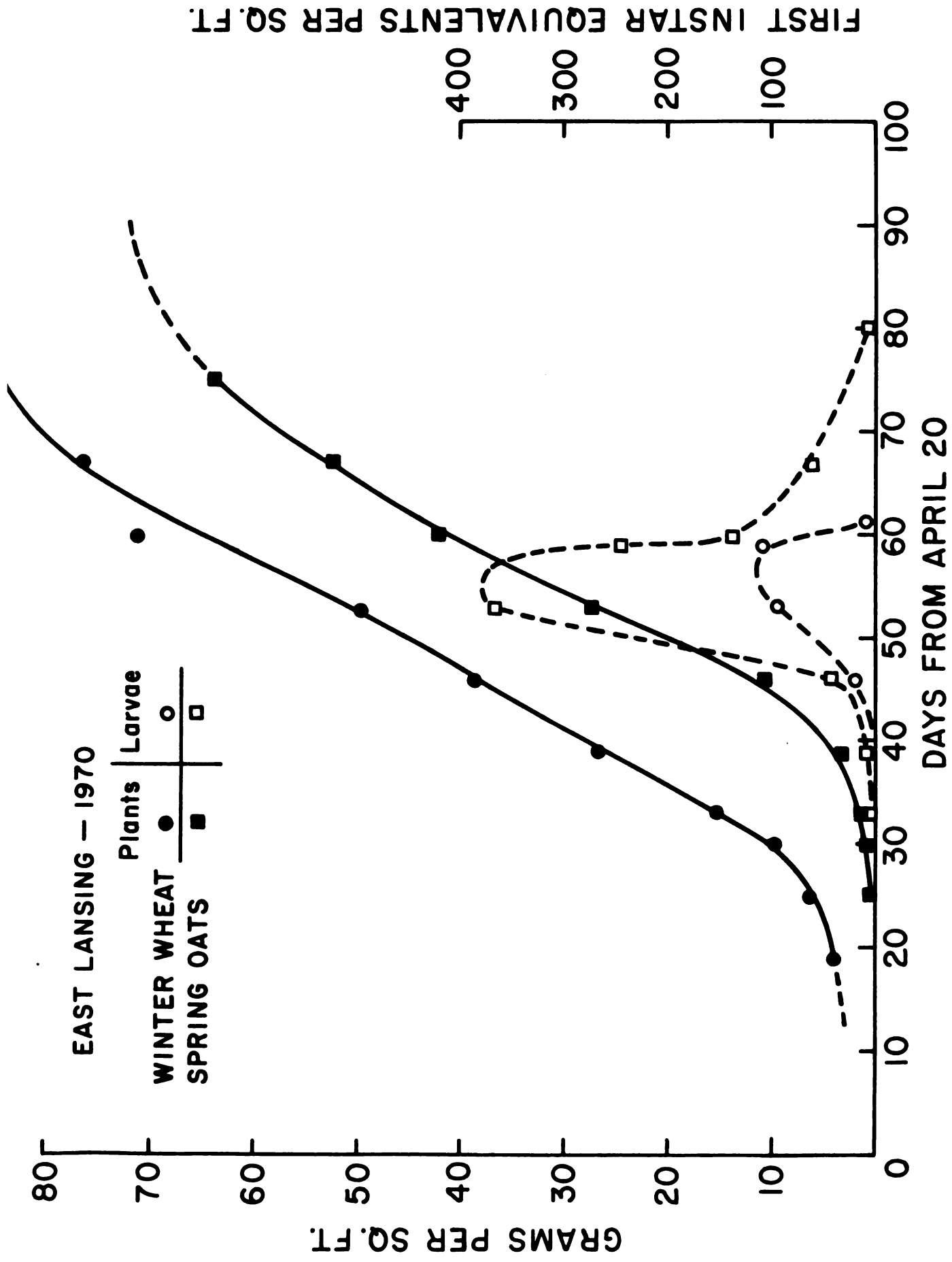


Figure 15c.--Relationship between accumulated days from April 20, first instar feeding equivalents and oven dry weight of foliage above ground for winter wheat and spring oats at East Lansing - C area.

survival (1 - mortality) of larvae and the total cereal leaf beetle generations (Table XXVI) using the model given by Helgesen and Haynes (in press).

TABLE XXII.--Total biomass of foliage (g. per sq. ft.) at peak cereal leaf beetle larval feeding

Area	Wheat	Oats
Gull Lake - R	35	16
Gull Lake - T	15	16
East Lansing - C	54	32

TABLE XXIII.--Total monthly rainfall (in.) for May, June and July at Gull Lake and East Lansing

Area	Monthly Rain		
	May	June	July
Gull Lake	4.09	3.62	4.85
East Lansing	2.40	5.97	6.98

TABLE XXIV.--Accumulated heat units from January 1 at base 42°F and 48°F for Gull Lake and East Lansing

Area	Accumulated heat units from January 1					
	May		June		July	
	42°	48°	42°	48°	42°	48°
Gull Lake	587	422	770	597	911	731
East Lansing	562	406	721	551	891	711

TABLE XXV.--Foliage consumed (sq. mm. per sq. ft.) calculated from
cereal leaf beetle population estimates converted to first
instar equivalents

Area	Wheat	Oats
Gull Lake - R	45,646.6	73,034.6
Gull Lake - T	61,259.8	90,356.1
East Lansing - C	7,883.1	28,982.2

TABLE XXVI.--Prediction of larval survival and mortality and generation survival and mortality from the within generation cereal leaf beetle model (Helgesen and Haynes in press)

	Winter wheat	Spring oats
	1970	
Gull Lake - R		
egg input (log)	2.40739	2.58535
larval survival	0.099	0.131
larval mortality	0.901	0.869
generation survival	0.069	0.091
generation mortality	0.931	0.909
Gull Lake - T		
egg input (log)	2.3541	2.8488
larval survival	0.103	0.089
larval mortality	0.898	0.911
generation survival	0.072	0.063
generation mortality	0.928	0.938
East Lansing - C		
egg input (log)	1.8319	2.1804
larval survival	0.138	0.209
larval mortality	0.862	0.791
generation survival	0.097	0.146
generation mortality	0.903	0.854

DISCUSSION

In cereal crops the production is the number of bushels of grain per acre that can be harvested by man. However, for insects that feed on portions of the plants, production is the useful food produced by the plant. In the case of the cereal leaf beetle, the production of leaves suitable for survival of the insects is most important because this species does not usually feed on any other plant part. Oviposition sites are specific to portions of the leaves (Table XXVII after Castro et al. 1965) and feeding occurs only on the upper leaf surface except under unusual circumstances (Merritt and Apple 1966).

The importance of local (within-field) conditions is illustrated by the differences in plant growth shown in Tables XIII and XIV from results obtained at the Gull Lake - T site. Between-field variation in growth indicates significant differences between Gull Lake - T and Gull Lake - R (Figures 15 A and 15 B) and even greater variation between the Gull Lake (T and R) sites and the East Lansing - C site (Figures 15 A and 15 C). Quantitative differences in growth of these areas is better expressed in terms of growth rate (g. per degree-day per sq. ft.) using:

$$C = \frac{W_2 - W_1}{d_2 - d_1}$$

where C (after Watson 1958) is defined as crop growth rate and W is the oven dry weight of foliage (g. per sq. ft.) and d is in degree-days

TABLE XXVII.--Observations on egg laying behavior of the cereal leaf beetle on oat seedlings in the laboratory (after Castro et al. 1965)

Place on leaves	Number of eggs	Per cent eggs
Upper surface	209	98.5
Lower surface	3	1.5
In whorl	7	3.35
Basal 1/3 of leaf	125	59.75
Central 1/3 of leaf	77	36.90
Apical 1/3 of leaf	0	0.00
Occur singly	87	41.70
Occur in twos	88	42.17
Occur in threes	24	11.50
Occur in fours	8	3.83
Occur in five or more	5	2.88

(base 42°F). Tables XXVIII and XXIX compare these 3 areas at their respective sampling times for wheat and oats. The variation exhibited between these areas makes it difficult to project the influence of the cereal leaf beetle on crops in different areas without having some measure of the amount of foliage available to that population in each area. The differences in growth and in the total amount of foliage produced per unit land area may bias an observer if attempts are made to extrapolate from the amount of damage caused by the cereal leaf beetle in a field to the cereal leaf beetle population. Under ideal plant growth conditions the damage by cereal leaf beetle larvae will be diluted as more foliage occurs through a high plant growth rate and increased tillering. In this case, estimates of cereal leaf beetle density would be underestimated and if environmental conditions the following year were poor or if the crop was planted late, damage caused by the cereal leaf beetle could be considerable. This problem is an important consideration when rating damage caused by the cereal leaf beetle because the ratings used in one particular year may not pertain to the same ratings used the next year if plant growth and production is altered by the environment.

Frequent sampling within a season appears unnecessary as damage and plant growth may be estimated by a few samples of plants and larvae collected at critical times (e.g. initial, peak and end) during a season.

An accurate estimate of feeding by each instar of the cereal leaf beetle is essential for proper calculation of first instar equivalent feeding and additional estimates to those of Wilson et al. (1969)

TABLE XXVIII.--Crop growth rate of winter wheat (g. per degree-day
(base 42°F) per sq. ft.) at Gull Lake (R and T) and
East Lansing - C

$\bar{X}$ degree-days between 2 samples	Crop growth rate		
	Gull Lake (R)	Gull Lake (T)	East Lansing (C)
412.5	0.023		
419.5		0.013	
471.5			0.017
520.5	0.049	0.011	
577.0			0.041
609	0.045	0.016	
660.5			0.066
732	0.086	0.046	
756			0.105
822	0.044	0.015	
894			0.71
1,044.5	0.061	0.027	
1,071			0.56
1,238	0.045	0.028	
1,263			0.105
1,435.5		0.017	
1,437			0.045
1,445	0.0		
1,599		0.0	0.050

TABLE XXIX.--Crop growth rate of spring oats (g. per degree-day) (base 42°F) per sq. ft. at Gull Lake (R and T) and East Lansing - C

$\bar{X}$ degree-days between 2 samples	Crop growth rate		
	Gull Lake (R)	Gull Lake (T)	East Lansing (C)
577			0.006
609	0.005	0.006	
660.5			0.008
732	0.011	0.015	
756			0.017
882	0.023	0.025	
894			0.051
1,044.5	0.032	0.034	
1,071			0.055
1,238	0.013	0.033	
1,263			0.083
1,437.5		0.034	0.090
1,445.5	0.061		
1,600		0.032	0.071
1,609	0.0		

should be made under field conditions and on different crops to provide a more concrete base for estimating damage.

Related to this is the problem of food quality and its impact on host preference. The preference for one crop over another when the plants are of similar age is complicated by plant variety, but when oat seedlings become available in the field, high densities of adult cereal leaf beetles appear in the fields of oat seedlings and begin feeding and ovipositing. In general, there is an increase in beetle density in spring planted oats. In some years however (ex. Gull Lake 1971) cereal leaf beetle populations in wheat are very low and higher densities of larvae appear in oats. This usually results when wheat is planted early and the foliage is more mature than usual when the beetles move out of their overwintering sites into the grains. A study designed to investigate this was initiated in 1972 where winter wheat was planted at several different dates throughout the fall.

To obtain an index of succulence, the ratio of oven dry weight to wet sample weight (in per cent) was calculated (Table XII) and the mean values for the top three leaves are shown in Figure 16. Some variation in the per cent moisture of the wet sample weight resulted in the length of time taken for the samples to be processed after they were brought from the field. The shape of the curves and their position with respect to the first instar equivalent feeding curves indicates that this measure is a realistic approach to succulence of leaves but a more exhaustive study of this mechanism is warranted. An additional observation in this regard is the amount of surface area removed from the top leaf of wheat (Table XVII). A much greater proportion was removed from this top leaf (the flag leaf) than from lower leaves of

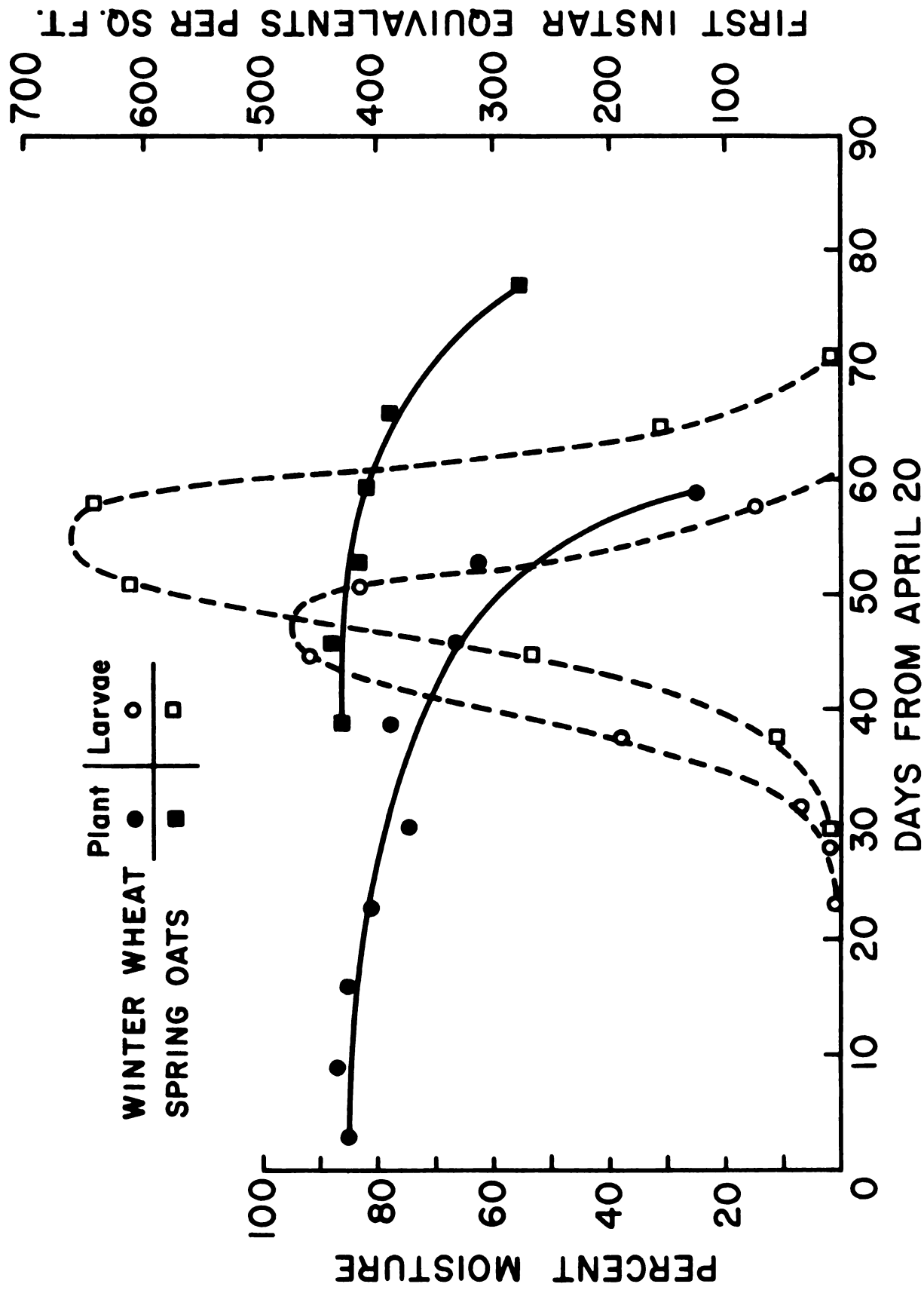


Figure 16. Relationship between accumulated days from April 20, first instar feeding equivalents and per cent moisture in the top 3 leaves of winter wheat and spring oats.

wheat. This did not seem to be the case with oats where the lower leaves were fed on to a greater extent than the top leaf, likely because the flag leaf was in the process of forming as the cereal leaf beetle population was entering the prepupal stage.

The actual mechanism causing the movement of beetles to less and less mature foliage has not been fully investigated and at present succulence seems to be the best word to describe a phenomenon which may be biochemical in nature.

The importance of leaf removal to grain yield was studied by Womack and Thurman (1962) who removed different amounts of leaves from winter wheat and winter oats. Their results (Table XXX) show that in wheat, leaf removal 1 week before the boot stage caused significant reduction in yield where as in winter oats, this effect is not evident.

It is not readily apparent that feeding damage caused by the cereal leaf beetle is directly comparable to the actual removal of whole leaves. In some cases larvae may intersect the energy transfer from the leaf to the developing head by feeding. Often, this feeding causes increased desiccation of the leaves contributing to rapid leaf senescence which is important to final yield (Watson 1956) and undoubtedly interrupts photosynthetic activity of the leaf surface by reducing the photosynthetic efficiency of the plant leaves. Because other portions of the plant are capable of photosynthetic activity (i.e. leaf sheaths, stems) more pressure is probably placed on these components to provide the necessary assimilates that are eventually translated into yield. However, Allison and Watson (1966) found that the parts above the highest node in wheat and barley supply most of the dry matter that fills the grain. Earlier, Watson (1956) stated that a

TABLE XXX.--Grain yields of Chancellor wheat and Arkwin oats for 5 levels of leaf area removal at 4 stages of plant development (after Womock and Thurmon 1962)

Stage of development	Grain yield, bu. per acre					Average
	% leaf removal					
	0	10	20	30	40	
Chancellor wheat						
	3 - year average, 1958 - 1961					
One week before boot	26	25	23	23	23	23.7
Boot	27	25	24	22	23	24.2
One week after boot	29	28	26	25	24	26.3
Average	27.4	25.7	24.4	23.7	22.5	
	2 - year average 1958 - 1961					
One week before boot	30	29	28	27	25	27.5
Boot	31	28	29	27	26	27.9
One week after boot	34	31	30	29	20	29.8
Two weeks after boot	31	32	28	28	28	29.3
Average	31.2	30.0	27.3	27.5	26.2	
Arkwin oats						
	3 - year average 1958 - 1961					
One week before boot	46	43	45	39	40	42.3
Boot	49	41	44	37	40	42.2
One week after boot	42	41	44	42	39	42.0
Average	46.3	42.1	43.6	39.9	39.6	
	2 - year average 1959 - 1961					
One week before boot	63	59	59	52	53	57.1
Boot	64	56	58	46	50	54.8
One week after boot	58	56	53	56	51	54.7
Two weeks after boot	63	60	60	57	51	58.2
Average	61.8	57.9	57.4	52.9	51.1	

7

high leaf area index at ear emergence and slow senescence of the leaves was the most important determiner of yield. This was challenged by Gregory (1966) who argued that yield depended on the number of ears produced thereby emphasizing the importance of tillering which would increase leaf area and the number of ears. There is, therefore, a definite need to examine the physiological effect on plants fed on by the cereal leaf beetles and although this must be conducted carefully it should be a field study rather than an environmental chamber type investigation.

One of the problems encountered during this investigation was the quantitative measure of surface area removed from leaves by the cereal leaf beetle. Variability in leaf size, feeding scar size and the number of feeding scars per leaf seems to indicate that some electronic method of quantifying damage would be most valuable and would standardize the present methods of visual estimates. Such techniques are being contemplated and initial investigations are under way (Fisher, Electrical Engineering, M.S.U.).

Because of the variation found in plant growth there is a definite need for a specific model of growth throughout the range of the cereal leaf beetle under variable environmental conditions. Yield was not a primary concern of this study because of such variability and reduction in yield could not be attributed to cereal leaf beetle feeding. The effect that the cereal leaf beetle will have in the prairie regions of North America is unknown. In northern areas, winter grains will not survive and the damage caused to a spring grain monoculture by the cereal leaf beetle can only be fearfully anticipated.

This study has attempted to bring together the plant and the insect and to place an insect's plant hosts in the proper perspective. Data from this investigation are limited to 1 year and principally 1 area. Much of the information is descriptive and awaits a more extensive analyses. Integrating plant growth with dynamic models of the cereal leaf beetle over a much wider range of conditions is suggested. The importance of the plant in the dynamics of a host specific insect must not be underestimated as it seems to have been in the past. Perhaps this is due to the entomologist's unwillingness to attempt to quantitatively relate the two or the botanist's unwillingness to consider the insect in relation to the plant he is studying. These remarks are not intended for the few of each profession who have tried but for those who have considered the interaction unimportant.

Until I attempted to bring the two together I felt that it was a plant physiologist's job to define plant growth and the entomologist's duty to define what the insect does to its host. Perhaps this is true but because the two are intertwined, it seems impossible to separate the insect from its host.

SUMMARY AND CONCLUSIONS

This investigation cannot be considered definitive on the relationship between the cereal leaf beetle and its primary hosts. The principle value of this study is that it describes basic relationships between an insect and its hosts and points out the complexities of the interaction. The dynamics of the cereal grains within a season are complex and working models of field plant growth and potential yield are essential.

To measure the impact of the cereal leaf beetle on small grains over a large geographical area, many of the factors measured in this study need further investigation under a range of environmental conditions to provide predictive models of damage. It is essential to be able to determine the magnitude of the insect population and to obtain an accurate fix on important crop growth parameters such as leaf surface per unit area. This can be accomplished within the present framework of the 'Cereal Leaf Beetle Population Dynamics Survey'.

This study has provided the appropriate techniques to convert conventional population density estimates into a realistic feeding entity called first instar feeding equivalents. From this information an accurate estimate of the amount of foliage removed by the population is available. Unfortunately, the transition from the amount of foliage removed by the cereal leaf beetle to the reduction of yield is not simple. By removing leaf tissue, this insect causes reduction in the

photosynthetic capacity of the crop. Further studies are suggested which will allow the translation of this subtle reduction of the plant's capacity to photosynthesize into a reduction of yield, which lies within the realm of a field plant physiologist.

There are several points that summarize the concepts and findings of this paper: (1) a technique has been developed from data in the literature to translate cereal leaf beetle larval populations into feeding equivalents which enable estimates of leaf surface area removed, (2) a significant interaction between cereal leaf beetle density and plant damage relates to the synchronization between the plant growth rate and the feeding rate of the insect population, (3) the most significant density dependent factor determined by Helgesen and Haynes (in press) was competition for food and this study points out that this competition occurs on the last or flag leaf of winter wheat and on several or all leaves of spring oats, (4) the growth pattern of the plant is a highly correlated system and this study offers a series of regression equations for converting various plant growth measurements, (5) only a few parameters are required to describe the principle total plant growth products, and (6) the model will be incomplete without the ability to translate leaf damage caused by cereal leaf beetle feeding into grain yield.

LITERATURE CITED

LITERATURE CITED

- Alcock, M. B., J. V. Lovett and D. Machin. 1968. Techniques used in the study of the influence of environment on primary pasture production in hill and lowland habitats. In The measurement of environmental factors in terrestrial ecology. R. M. Wadsworth, ed. Blackwell Scientific Pub., Oxford. p. 191-203.
- Allison, J. C. S. and D. J. Watson. 1966. The production and distribution of dry matter of maize after flowering. *Ann. of Bot. (N.S.)* 30:366-381.
- Baskerville, G. L. and P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology* 50:514-517.
- Blackman, V. H. 1919. The compound interest law and plant growth. *Ann. Bot.* 33:353.
- Blackman, G. E. 1959. Responses to environmental factors by plants in the vegetative phase. In Growth in living systems. p. 525-556.
- Borrill, M. 1959. Inflorescence initiation and leaf size in some Graminae. *Ann. Bot. (N.S.)* 23:217-227.
- Bunting, A. H. and D. S. H. Drennan. 1966. Some aspects of the morphology and physiology of cereals in the vegetative phase. In The growth of cereals and grasses. F. L. Milthorpe and J. D. Ivins, eds. Butterworths, London. p. 20-38.
- Castro, T. R., R. F. Ruppel and M. S. Gomalinski. 1965. Natural history of the cereal leaf beetle in Michigan. *Mich. State Univ. Agr. Sta. Quart. Bull.* 47:623-653.
- Crossley, D. A. 1963. Consumption of vegetation by insects. In Radioecology. V. Schultz and A. W. Klement, eds. p. 431-440.
- Evans, G. C. and A. P. Hughes. 1962. Plant growth and the aerial environment. III. On the computation of unit leaf rate. *New Phytol.* 61:322-327.
- Friend, D. J. C. 1965. Tillering and leaf production in wheat as affected by temperature and light. *Can. J. Bot.* 43:1063-1075.

- Friend, D. J. C. 1966. The effect of light and temperature on the growth of cereals. In The growth of cereals and grasses. F. L. Milthorpe and J. D. Ivins, eds. Butterworths, London. p. 181-199.
- Gallum, R. L., R. F. Ruppel and E. H. Everson. 1966. Resistance of small grains to the cereal leaf beetle. J. Econ. Entomol. 59:827.
- Gallum, R. L., R. T. Everly and W. T. Yamazaki. 1967. Yield and milling quality of Monon wheat damaged by feeding of cereal leaf beetle. J. Econ. Entomol. 60:356-359.
- Gregory, F. G. 1956. General aspects of leaf growth. In The growth of leaves. F. L. Milthrope, ed. Butterworths, London. p. 3-17.
- Helgesen, R. G. 1969. The within-generation dynamics of the cereal leaf beetle, Oulema melanopus (L.) Ph.D. Thesis, Michigan State Univ. 96 p.
- Helgesen, R. G. and D. L. Haynes. In press. Population dynamics of the cereal leaf beetle, Oulema melanopus (L.): A model for age specific mortality. Can. Entomol.
- Hogg, W. H. 1965. Climatic factors and choice of site, with special reference to Horticulture. In Biological significance of climatic changes in Britain. Symp. Inst. Biol. 14:141-155.
- Jewiss, O. R. 1966. Morphology and physiology aspects of growth of grasses during the vegetative phase. In The growth of cereals and grasses. F. L. Milthorpe and J. D. Ivins, eds. Butterworths, London. p. 39-54.
- McCloud, D. E., R. J. Bula and R. H. Shaw. 1964. Field plant physiology. Advan. Agron. 16:1-58.
- Merritt, D. L. and J. W. Apple. 1969. Yield reduction of oats caused by the cereal leaf beetle. J. Econ. Entomol. 62:296-299.
- Miczulski, B. 1971. Studies regarding the bionomics, economic importance and natural control affecting Oulema species in Poland. Agr. Univ. of Lublin, Project No. E21-ENT-14. 51 p.
- Pedigo, L. P., J. D. Stone and R. B. Clemen. 1970. Photometric device for measuring foliage loss caused by insects. Ann. Entomol. Soc. Amer. 63:815-818.
- Ruesink, W. G. 1972. The integration of adult survival and dispersal into a mathematical model for the abundance of the cereal leaf beetle, Oulema melanopus (L.). Ph.D. Thesis, Michigan State Univ. 80 p.

- Ryle, G. J. A. 1966. Physiological aspects of seed yield in grasses. In The growth of cereals and grasses. F. L. Milthorpe and J. D. Ivins, eds. Butterworths, London. p. 88-105.
- Schillinger, J. A. 1969. Three laboratory techniques for screening small grains for resistance to the cereal leaf beetle. J. Econ. Entomol. 62:360-363.
- Shade, R. E. and M. C. Wilson. 1967. Leaf vein spacing as a factor affecting larval feeding behavior of the cereal leaf beetle, Oulema melanopus (Coleoptera:Chrysomelidae). Ann. Entomol. Soc. Amer. 60:493-496.
- Thorne, G. N. 1966. Physiological aspects of grain yield in cereals. In The growth of cereals and grasses. F. L. Milthorpe and J. D. Ivins, eds. Butterworths, London. p. 88-105.
- U.S.D.A.--APHS--PPD. 1971. Cereal leaf beetle quaranteen map. 1 p.
- Van Der Brink, C., N. D. Stroman and A. L. Kenworthy. 1971. Growing degree-days in Michigan. Res. Rpt. 131:1-49. Michigan State Agr. Expt. Stn., East Lansing, Michigan.
- Wang, J. Y. 1960. A critique of the heat unit approach to plant response studies. Ecology 41:785-790.
- Watson, D. J. 1947. Comparative physiological studies on the growth of field crops. I. Variations in net assimilation rate and leaf area between species and varieties, and within and between years. Ann. Bot. (N.S.) 11:41-89.
- Watson, D. J. 1956. Leaf growth in relation to crop yield. In The growth of leaves. F. L. Milthorpe, ed. Butterworths, London. p. 178-191.
- Watson, D. J. 1958. The dependence of net assimilation rate on leaf area. Ann. Bot. (N.S.) 22:37-54.
- Webster, J. A. and D. H. Smith, Jr. 1971. Seedlings used to evaluate resistance to the cereal leaf beetle. J. Econ. Entomol. 64:925-928.
- Wellso, S. G., J. A. Webster and R. F. Ruppel. 1970. A selected bibliography of the cereal leaf beetle, Oulema melanopus (Coleoptera:Chrysomelidae). Bull. Entomol. Soc. Amer. 16:85-88.
- Whitehead, F. H. and P. J. Meyerscough. 1962. Growth analysis of plants. The ratio of mean relative growth rate to the mean relative rate of leaf area increase. New Phytol. 61:314-321.

- Williams, W. A., R. S. Loomis and C. R. Lepley. 1965. Vegetative growth of corn as affected by population density. II. Components of growth, net assimilation rate and leaf area index. *Crop Science* 5:215-219.
- Wilson, M. C. and R. E. Shade. 1964. The influence of various Graminae on weight gains of post diapause adults of the cereal leaf beetle, Oulema melanopa (Coleoptera:Chrysomelidae) *Ann. Entomol. Soc. Amer.* 57:659-661.
- Wilson, M. C., R. E. Treece, R. E. Shade, K. M. Day and R. K. Stivers. 1969. Impact of cereal leaf beetle larvae on yield of oats. *J. Econ. Entomol.* 62:699-702.
- Womack, D. and R. L. Thurman. 1962. Effect of leaf removal on grain yield. *Crop Science* 2:423-426.
- Yun, Y. M. 1967. Effect of some physical and biological factors on the reproduction, development, survival and behavior of the cereal leaf beetle, Oulema melanopus (L.) under laboratory conditions. Ph.D. Thesis, Michigan State Univ. 153 p.

1

APPENDICES



Appendix Ia. Accumulation of heat units (degree-days) from January 1 to August 31, 1970 at East Lansing, Michigan.

Day	Threshold 42°F							
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
1	0	3	7	22	331	923	1685	2612
2	0	3	7	22	343	947	1723	2639
3	0	3	7	22	352	961	1759	2671
4	0	3	9	22	363	975	1785	2691
5	0	3	9	23	372	993	1807	2714
6	0	3	9	25	375	1017	1832	2743
7	0	3	10	27	385	1041	1861	2772
8	0	3	10	40	411	1069	1891	2802
9	0	3	10	49	440	1101	1915	2831
10	0	3	10	51	470	1134	1937	2861
11	0	3	10	51	494	1168	1968	2891
12	0	3	10	55	510	1200	2001	2923
13	0	3	10	59	524	1222	2035	2953
14	0	3	10	66	532	1247	2073	2985
15	0	3	10	75	554	1274	2107	3019
16	0	3	10	85	572	1306	2135	3051
17	0	3	10	96	580	1344	2165	3078
18	0	5	10	102	594	1375	2196	3104
19	0	5	12	102	622	1395	2220	3134
20	0	5	14	108	645	1409	2234	3164
21	0	5	17	114	671	1425	2254	3186
22	0	6	19	122	699	1445	2276	3214
23	0	6	20	135	722	1471	2300	3240
24	0	7	20	151	745	1501	2330	3264
25	0	7	21	171	768	1517	2364	3292
26	0	7	22	191	787	1535	2398	3324
27	0	7	22	215	799	1553	2435	3354
28	1	7	22	239	913	1574	2471	3388
29	2	7	22	269	835	1606	2506	3414
30	2	7	22	299	863	1644	2540	3445
31	2	7	22	299	893	1644	2576	3470

1

Appendix Ib. Accumulation of heat units (degree-days) from January
1 to August 31, 1970 at East Lansing, Michigan

<u>Threshold 48°F</u>								
Day	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
1	0	0	0	0	206	636	1222	1963
2	0	0	0	0	214	654	1254	1984
3	0	0	0	0	220	662	1284	2010
4	0	0	0	0	227	671	1304	2024
5	0	0	0	0	232	683	1320	2041
6	0	0	0	0	233	701	1339	2064
7	0	0	0	0	239	719	1362	2087
8	0	0	0	8	259	741	1386	2111
9	0	0	0	15	282	767	1404	2134
10	0	0	0	15	306	794	1420	2158
11	0	0	0	15	324	822	1445	2182
12	0	0	0	17	335	848	1472	2208
13	0	0	0	18	344	864	1500	2232
14	0	0	0	21	347	883	1532	2258
15	0	0	0	27	363	904	1560	2286
16	0	0	0	33	375	930	1582	2312
17	0	0	0	39	379	962	1606	2333
18	0	0	0	41	389	987	1631	2353
19	0	0	0	41	411	1001	1649	2377
20	0	0	0	43	428	1010	1657	2401
21	0	0	0	45	448	1021	1671	2417
22	0	0	0	50	470	1036	1687	2439
23	0	0	0	58	487	1056	1705	2459
24	0	0	0	68	504	1080	1729	2477
25	0	0	0	82	521	1090	1757	2499
26	0	0	0	96	534	1102	1785	2525
27	0	0	0	114	540	1114	1816	2549
28	0	0	0	132	550	1129	1846	2577
29	0	0	0	156	566	1155	1875	2597
30	0	0	0	180	588	1187	1903	2622
31	0	0	0	180	612	1187	1933	2641

Appendix IIa. Accumulation of heat units (degree-days) from January 1 to August 31, 1970 at Gull Lake Biological Station, Michigan.

<u>Threshold 42°F</u>								
Day	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
1	0	1	3	17	294	909	1718	2665
2	0	1	3	17	302	932	1756	2695
3	0	1	3	17	311	948	1794	2725
4	0	1	5	17	327	964	1820	2744
5	0	1	5	17	338	986	1845	2766
6	0	1	6	18	342	1006	1869	2792
7	0	1	6	19	352	1032	1901	2820
8	0	1	6	29	376	1062	1929	2852
9	0	1	6	40	402	1093	1954	2884
10	0	1	6	42	427	1125	1980	2914
11	0	1	6	42	450	1159	2012	2945
12	0	1	6	46	470	1193	2046	2977
13	0	1	6	51	487	1221	2081	3009
14	0	1	6	59	495	1250	2119	3043
15	0	1	6	68	516	1280	2155	3071
16	0	1	6	78	530	1312	2184	3105
17	0	1	6	87	540	1351	2214	3132
18	0	2	6	90	554	1383	2246	3158
19	0	2	8	90	582	1406	2272	3192
20	0	2	9	96	608	1421	2292	3224
21	0	2	13	100	634	1440	2313	3246
22	0	2	16	109	664	1462	2336	3271
23	0	2	17	121	692	1490	2356	3295
24	0	3	17	132	720	1520	2385	3319
25	0	3	17	147	746	1540	2420	3350
26	0	3	17	165	764	1562	2456	3383
27	0	3	17	187	776	1580	2490	3415
28	0	3	17	209	800	1603	2528	3451
29	0	3	17	239	825	1637	2560	3479
30	0	3	17	268	853	1679	2596	3510
31	0	3	17	268	881	1679	2629	3534

Appendix IIb. Accumulation of heat units (degree-days) from January 1
to August 31, 1970 at Gull Lake Biological Station, Michigan

<u>Threshold 48°F</u>								
Day	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
1	0	0	0	3	187	631	1261	2022
2	0	0	0	3	191	648	1293	2046
3	0	0	0	3	197	658	1325	2070
4	0	0	0	3	207	668	1345	2083
5	0	0	0	3	213	684	1364	2099
6	0	0	0	3	215	698	1382	2119
7	0	0	0	3	221	718	1408	2141
8	0	0	0	10	239	742	1430	2167
9	0	0	0	17	259	767	1449	2193
10	0	0	0	17	278	793	1469	2217
11	0	0	0	17	295	821	1495	2242
12	0	0	0	18	309	849	1523	2268
13	0	0	0	20	320	871	1552	2294
14	0	0	0	25	323	894	1584	2322
15	0	0	0	31	338	918	1614	2344
16	0	0	0	37	346	944	1637	2372
17	0	0	0	42	351	977	1661	2393
18	0	0	0	43	360	1003	1687	2413
19	0	0	0	43	382	1020	1707	2441
20	0	0	0	45	402	1030	1721	2467
21	0	0	2	46	422	1043	1736	2483
22	0	0	3	52	446	1059	1753	2502
23	0	0	3	59	468	1081	1767	2520
24	0	0	3	65	490	1105	1790	2538
25	0	0	3	75	510	1119	1819	2563
26	0	0	3	88	522	1135	1849	2590
27	0	0	3	104	528	1147	1877	2616
28	0	0	3	120	546	1164	1909	2646
29	0	0	3	144	565	1192	1935	2668
30	0	0	3	167	587	1228	1965	2693
31	0	0	3	167	609	1228	1992	2711

APPENDIX III Date, degree-days from bases 42°F and 48°F and accumulated days from April 20 and at each sampling time for wheat and oats at Gull Lake (1970).

Date <u>Gull Lake 1970</u>	Degree - days		Days from <u>April 20</u>
	<u>base 42°F</u>	<u>base 48°F</u>	
April 23	121	59	3
April 29	239	144	9
May 6	342	215	16
May 13	437	320	23
May 20	608	402	30
May 29	825	565	39
June 5	986	684	46
June 12	1,193	849	53
June 18	1,383	1,003	59
June 25	1,540	1,119	66
July 6	1,869	1,382	77
July 14	2,119	1,584	85
July 22	2,336	1,753	93

APPENDIX IV Date, degree days from bases 42°F and 48°F and accumulated days from April 20 at each sampling date for wheat and oats at East Lansing (1970).

Date	Degree - days		Days from <u>April 20</u>
	<u>base 42°F</u>	<u>base 48°F</u>	
May 8	411	259	19
May 14	532	347	25
May 19	622	411	30
May 22	699	470	33
May 28	813	550	39
June 4	975	671	46
June 11	1,168	822	53
June 18	1,375	987	60
June 25	1,517	1,090	67
July 1	1,685	1,222	73

Appendix V. Total biomass of foliage (g. per sq. ft) of winter wheat and spring oats collected for cereal leaf beetle population density estimates ($n=30 \pm \text{S.E.}$).

Date	Degree-days (base 42°F)	Wheat Gull Lake (R-Area)	Oats
5/5	338	4.35 $\pm$ 0.18	
5/13	487	7.82 $\pm$ 0.37	
5/18	554	11.07 $\pm$ 0.63	0.36 $\pm$ 0.03
5/22	664	16.01 $\pm$ 0.62	0.87 $\pm$ 0.08
5/28	800	27.75 $\pm$ 1.32	2.43 $\pm$ 0.19
6/4	964	34.99 $\pm$ 2.01	6.26 $\pm$ 0.39
6/10	1125	44.82 $\pm$ 1.83	11.44 $\pm$ 0.56
6/17	1351	54.98 $\pm$ 2.90	14.35 $\pm$ 1.04
6/24	1540	54.97 $\pm$ 2.14	25.83 $\pm$ 1.05
6/30	1679	52.30 $\pm$ 2.80	24.08 $\pm$ 1.25

Appendix VI. Total biomass of foliage (g. per sq. ft.) of winter wheat and spring oats collected for cereal leaf beetle population density estimates (n=30; +S.E.)

Date	Degree-days (base 42°F)	Wheat Gull Lake (T-Area)	Oats
5/7	352	2.10 <u>+0.15</u>	
5/13	487	3.92 <u>+0.38</u>	
5/18	554	4.65 <u>+0.32</u>	0.83 <u>+0.10</u>
5/22	664	6.45 <u>+0.57</u>	1.52 <u>+0.19</u>
5/28	800	12.68 <u>+0.81</u>	3.57 <u>+0.24</u>
6/4	964	15.17 <u>+0.94</u>	7.63 <u>+0.43</u>
6/10	1125	19.51 <u>+1.14</u>	3.18 <u>+0.75</u>
6/17	1351	25.85 <u>+1.77</u>	20.72 <u>+0.99</u>
6/24	1520	28.70 <u>+1.99</u>	26.55 <u>+2.01</u>
6/30	16.79	20.18 <u>+2.12</u>	31.61 <u>+2.76</u>

Appendix VII. Total biomass of foliage (g. per sq. ft.) of winter wheat and spring oats collected for cereal leaf beetle population density estimates (n=30; $\pm$ S.E.)

Date	Degree-days (base 42°F)	Wheat East Lansing (C-Area)	Oats
5/8	411	4.05 $\pm$ 0.24	
5/14	532	6.15 $\pm$ 0.51	0.33 $\pm$ 0.05
5/19	622	9.87 $\pm$ 0.65	0.86 $\pm$ 0.07
5/22	699	14.96 $\pm$ 1.22	1.49 $\pm$ 0.14
5/28	813	26.96 $\pm$ 1.44	3.39 $\pm$ 0.27
6/4	975	38.46 $\pm$ 1.63	11.60 $\pm$ 0.75
6/11	1167	49.14 $\pm$ 2.43	22.08 $\pm$ 1.20
6/18	1374	71.53 $\pm$ 4.44	42.27 $\pm$ 2.14
6/25	1516	76.27 $\pm$ 3.29	52.04 $\pm$ 2.07
7/1	1684	84.72 $\pm$ 3.94	63.93 $\pm$ 3.00

Appendix VIII. Cereal leaf beetle egg and larval densities per sq. ft.
in winter wheat and spring oats (n=30; $\pm$ S.E.)

		Gull Lake (R-area)-1970				
	Degree- days (base 48°F)	Eggs	I	II	III	IV
Date		WHEAT				
5/7	213	29.17+1.90	0	0	0	0
5/13	320	118.80+7.24	0.40+0.11	0.17+0.08	0	0
5/8	360	95.20+5.71	2.73+0.37	0.60+0.22	0.03+0.03	0
5/22	446	82.66+6.24	17.62+1.87	7.21+1.20	0.17+0.09	0
5/28	546	36.03+3.10	4.10+0.71	12.27+1.30	12.40+2.12	3.17+1.07
6/4	668	9.87+1.71	4.80+0.56	8.80+0.93	11.10+0.91	14.93+1.65
6/10	767	0.63+0.31	0.79+0.22	3.97+0.68	8.83+1.04	14.60+1.56
6/17	977			0.03+0.03	0.73+0.18	2.90+0.48

OATS						
5/18	360	25.77 $\pm$ 3.01	0.03 $\pm$ 0.03	0	0	0
5/22	446	70.10 $\pm$ 5.89	1.69 $\pm$ 0.42	0.34 $\pm$ 0.12	0	0
5/28	546	91.71 $\pm$ 9.87	10.71 $\pm$ 1.30	7.79 $\pm$ 1.43	3.36 $\pm$ 0.93	0.07 $\pm$ 0.05
6/4	668	86.47 $\pm$ 5.96	23.27 $\pm$ 2.09	25.00 $\pm$ 2.18	12.90 $\pm$ 2.08	3.93 $\pm$ 1.25
6/10	767	12.40 $\pm$ 2.05	9.87 $\pm$ 1.77	18.87 $\pm$ 1.87	18.33 $\pm$ 1.92	18.13 $\pm$ 1.69
6/17	977	0.48 $\pm$ 0.14	1.13 $\pm$ 0.43	6.70 $\pm$ 1.21	11.87 $\pm$ 1.26	22.93 $\pm$ 2.90
6/24	1105	0	0.37 $\pm$ 0.10	0.90 $\pm$ 0.19	3.00 $\pm$ 0.49	5.40 $\pm$ 0.60
6/30	1228	0.23 $\pm$ 0.18	0.03 $\pm$ 0.03	0.17 $\pm$ 0.08	0.20 $\pm$ 0.09	0.20 $\pm$ 0.07

Appendix X. Cereal leaf beetle egg and larval density per sq. ft. in winter wheat and spring oats (n=30; $\pm$ S.E.)

		East Lansing (C-area)-1970				
Degree-days (base 48°F)		Eggs	I	II	III	IV
Date		WHEAT				
5/8	259	2.43+0.38	0	0	0	0
5/14	347	8.17+0.91	0	0	0	0
5/19	411	15.47+1.38	0.13+0.06	0	0	0
5/22	470	12.63+1.69	0.43+0.20	0.27+0.13	0.03+0.03	0
5/28	550	6.47+0.98	1.33+0.23	0.53+0.16	0.10+0.06	0.03+0.03
6/4	671	3.43+0.66	1.27+0.19	1.80+0.37	1.10+0.23	0.27+0.03
6/11	822	0.40+0.25	0.40+0.14	1.10+0.30	1.73+0.64	3.37+0.81
6/17	962	0.07+0.07	0	0.07+0.05	0.43+0.13	4.13+2.53
6/18		0	0	0.13+0.06	0.20+0.10	0.37+0.11
OATS						
5/14	347	1.90+0.33	0	0	0	0
5/19	411	4.90+0.91	0	0	0	0
5/22	470	38.33+2.44	0.23+0.14	0	0	0
5/28	550	36.30+3.92	1.03+0.30	0.40+0.15	0	0
6/4	671	34.07+3.89	8.03+0.94	7.18+1.42	1.73+0.40	0.13+0.06
6/11	822	8.37+1.16	3.03+0.56	5.40+0.77	10.00+1.17	11.83+1.47
6/17	962	2.17+0.37	1.00+0.22	1.83+0.31	3.97+0.53	8.93+0.91
6/18		0.13+0.08	1.37+0.39	2.87+0.52	3.17+0.47	4.60+0.84
6/25	1090	0.50+0.18	0.53+0.16	1.13+0.22	2.30+0.48	1.73+0.32

Appendix IX. Cereal leaf beetle egg and larval densities per sq. ft. in winter wheat and spring oats (n=30; ±S.E.)

Date	Degree-days (base 48°F)	Gull Lake (T-area)-1970				
		Eggs	I	II	III	IV
WHEAT						
5/1	187	32.20+2.58				
5/13	320	81.70+6.88				
5/18	360	103.27+8.45	7.67+1.05	0.90+0.29		
5/22	446	115.63+8.46	17.10+2.05	24.47+2.17	2.67+0.59	
5/28	546	48.60+5.04	13.27+1.70	23.30+2.25	26.90+3.48	7.47+1.67
6/4	668	9.86+3.10	6.45+1.73	10.10+1.37	19.76+1.92	17.45+1.92
6/10	793	0.77+0.30	0.53+0.15	5.13+1.22	9.43+1.08	15.90+1.84
6/17	977	0.07+0.05	0.03+0.03	0.07+0.07	0.57+0.19	1.93+0.44
OATS						
5/18	360	35.17+2.77	0.07+0.05			
5/22	446	150.07+10.74	3.50+0.46	1.07+0.22		
5/28	546	176.55+12.36	23.14+2.30	13.45+1.98	2.62+0.73	2.17+1.17
6/4	668	139.97+11.68	27.03+2.70	44.43+3.61	17.47+2.33	4.57+0.86
6/10	793	33.37+5.17	26.23+3.96	37.70+3.67	23.47+2.16	18.63+2.30
6/17	977	1.63+0.74	4.50+0.98	10.27+1.50	15.47+1.38	23.23+2.30
6/24	1105	0.67+0.41	0.13+0.06	1.73+0.40	4.90+0.73	5.50+0.80
6/30	1228	0.20+0.12	0.03+0.03	0.10+0.07	0.27+0.10	0.83+0.20

1

Appendix XIa. Date, accumulated degree-days (base 42°F) and the number of eggs per 2 linear feet of row in winter wheat at 2 sites at Gull Lake (n=10; +S.D.)

Date	Degree-days (base 48°F)	Number of eggs in wheat	
		Gull Lake R	Gull Lake T
5/5	213	22.2 $\pm$ 10.0	27.8 $\pm$ 12.7
5/7	221	11.1 $\pm$ 6.7	10.8 $\pm$ 6.1
5/13	320	66.5 $\pm$ 15.8	47.0 $\pm$ 18.4
5/18	360	34.6 $\pm$ 12.4	43.2 $\pm$ 13.2
5/21	422	41.8 $\pm$ 8.6	38.7 $\pm$ 14.2
5/26	522	41.4 $\pm$ 12.8	35.5 $\pm$ 13.1
5/28	546	22.6 $\pm$ 9.7	12.9 $\pm$ 7.6
6/2*	648		8.5 $\pm$ 5.0
6/8	742	7.5 $\pm$ 6.5	1.6 $\pm$ 1.6
6/18	1003		0.0
6/3	658	7.5 $\pm$ 3.8	
6/15	918	0.6 $\pm$ 1.1	
6/19	1020	0.0	

*Samples taken on different days

Appendix XIb. Date, accumulated degree-days (base 48°F) and the number of eggs per 2 linear feet of row in spring oats at 2 sites at Gull Lake (n=10; $\pm$ S.D.)

Date	Degree-days (base 48°F)	Number of eggs in oats	
		Gull Lake-R	Gull Lake-T
5/13	320	21.9 $\pm$ 10.6	27.0 $\pm$ 13.2
5/18	360	29.7 $\pm$ 21.5	22.3 $\pm$ 9.3
5/21	422	53.5 $\pm$ 35.5	111.1 $\pm$ 24.5
5/26	522	74.4 $\pm$ 20.1	137.5 $\pm$ 25.4
5/28	546	27.3 $\pm$ 13.6	45.3 $\pm$ 16.4
6/2*	648		207.3 $\pm$ 63.6
6/5	684	36.9 $\pm$ 16.3	85.4 $\pm$ 37.7
6/9	767	25.3 $\pm$ 11.4	47.8 $\pm$ 16.7
6/12	849	16.8 $\pm$ 5.8	16.9 $\pm$ 6.2
6/15	918	7.5 $\pm$ 4.0	5.1 $\pm$ 4.8
6/19	1020	1.5 $\pm$ 1.5	0.2 $\pm$ 0.6
6/3	658	90.1 $\pm$ 46.1	

*Samples taken on different days

Appendix XIc. Date, accumulated degree-days (base 48°F) and the number of eggs per 2 linear feet of row in winter wheat and spring oats at Collin's Road, East Lansing, Michigan (n=10; $\pm$ S.D.)

Date	Degree-days (base 48°F)	Number of eggs	
		Wheat-C	Oats-C
5/8	259	2.6 $\pm$ 2.5	-
5/14	347	11.5 $\pm$ 6.1	2.6 $\pm$ 2.8
5/19	411	10.8 $\pm$ 7.5	4.5 $\pm$ 5.1
5/22	470	12.4 $\pm$ 5.9	32.8 $\pm$ 16.4
5/26	534	18.5 $\pm$ 9.3	34.3 $\pm$ 15.0
6/3	662	9.7 $\pm$ 5.5	46.5 $\pm$ 23.2
6/10	794	2.4 $\pm$ 1.5	20.2 $\pm$ 8.9
6/15	904	0.0	9.6 $\pm$ 9.2
6/18	987	0.1 $\pm$ 0.3	1.0 $\pm$ 1.5

MICHIGAN STATE UNIV. LIBRARIES



31293103501031