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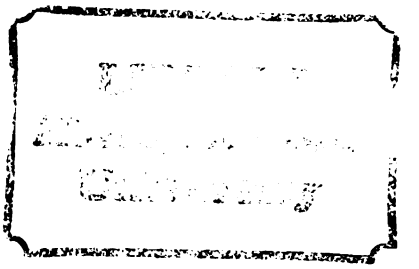

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presented by

Michael Edmund Mispagel

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Ph.D. degree in Entomology

Stuart H Gage
Major professor

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BIOTIC AND ABIOTIC STRESS INTERACTIONS BETWEEN THE CEREAL LEAF BEETLE (*Oulema melanopus* (L.)) AND OATS (*Avena sativa* (L.))

by

Michael Edmund Mispagel

A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Entomology

1982

ABSTRACT

BIOTIC AND ABIOTIC STRESS INTERACTIONS BETWEEN THE CEREAL LEAF BEETLE (Oulema melanopus (L.)) AND OATS (Avena sativa (L.))

by

Michael Edmund Mispagel

The effects of defoliation by the cereal leaf beetle, Oulema melanopus (L.), on the growth and physiology of oats were investigated under various levels of water stress in the field. Though induced insect defoliation was severe, loss of yield could not be attributed solely to defoliation. Soil water availability was shown to greatly affect plant growth and yield. Rewatering drought and defoliation stressed plants at heading caused significant recovery without yield loss. Water available at anthesis allowed grain filling to proceed with assimilates from sources other than the flag leaf blade. Upon rewatering, plants prestressed by drought and defoliation had a greater individual kernel weight.

Although leaf water potential was reduced by CLB defoliation, it was further correlated with leaf position, soil moisture, time of day, date and maximum air temperature. Leaf water potential of lower leaf blades did not increase to compensate for the decreased potential of

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defoliated upper blades. However, in dry plots particularly, a greater percentage of assimilates were translocated to the head of plants which had more than 60% blade defoliation than in those with less.

In contrast to CLB defoliation, radical artificial defoliation including flag leaf excision did significantly decrease yield by reducing the photosynthetically active basal portions of the blades which contain soluble carbohydrates for regrowth.

The contributiin of various organs to grain filling is reviewed and evidence is presented which suggests an important role of the flag leaf sheath in this process. In contrast, the contribution of the leaf blades in oats may not be as great as previously believed.

Oat plants measured 2-3 times a week were particularly susceptible to thigmomorphogenesis, i.e. morphological changes caused by physical manipulation. Both height and leaf area were reduced while tillering was increased.

A high incidence of Barley Yellow Dwarf Virus masked treatment effects during one season. Symptom expression of the disease was greatest in water stressed plants. However, plants which were prestressed and then rewatered withstood the disease as well as well watered control plants.

The oat plant is well adapted to withstand

perturbations as long as water is available. Compensation does occur in response to the gradual defoliation of the cereal leaf beetle.

ACKNOWLEDGMENTS

I would like to express my appreciation to Dr. Stuart H. Gage, my major advisor, for his guidance, encouragement and the financial freedom to accomplish this task. I thank my committee members, Drs. George Bird, Dean Haynes, James Miller, Gene Safir and Stanley Wellso for keeping me on track when I faltered. Dr. James Bath, department chairman, is thanked for his personal exhortations and encouragement, and for maintaining an excellent departmental climate in which to conduct research.

The following individuals are acknowledged for logistical support and the use of their laboratories and equipment: Dr. Michael Klug and Debbie Bartel for conducting plant tissue nitrogen analyses, Dr. Werner Bergen and Liz Rimpau for micro-Kjeldahl, Dr. Alan Putnam and Michael Willis for biological oxidation, and Dr. Robert Wetzel and Jay Sonnad for scintillation counting.

Student labor is invaluable in large scale field research. I greatly appreciate the efforts of Elizabeth Lake, John Klepsteen, Randall Cooper, Mark Lehman, Darren Reynolds, Kellie Dorin, Mark Willbur, James Deyo, Kevin Rice, Gloria Potter and Jeff Waldeck all of whom toiled without complaint many long hours.

Greatest appreciation is extended to my wife, Dr. Karen L. Jacobsen D.V.M., for her understanding and patience throughout this process.

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I. INTRODUCTION

Most investigations assessing crop losses have been concerned with the development of sampling methods or the relating of particular levels of pest density with loss of yield (Chiarappa 1967). Appraisal of losses is best accomplished in two phases (Large 1966). Field experiments should be conducted initially to describe the relationship between a pest and loss of yield which will permit methods to be developed to estimate the loss of yield associated with any given pest organism. This normally involves studying the pest or organism and the growth of infested and noninfested host crops throughout the season noting phenological relationships and damage symptoms indicative of particular population levels. The second phase involves applying the loss assessment methods developed in the first phase to a number of fields sampled in a regional survey. Once the relationship between pest abundance and loss of yield has been established and verified under a range of conditions, one can determine the population level of the pest at which control recommendations would be warranted.

From the widespread and indiscriminant use of pesticides over the last three decades and the unforeseen consequences of that use (Chant 1966, Kennedy 1968) has evolved the integrated control approach (Stern et al. 1959, Geier 1966, Smith and Van den Bosch 1967). Inherent is the

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concept of the "economic threshold" defined as "the density at which control measures should be determined to prevent an increasing pest population from reaching the economic injury level" (Stern et al. 1959). This latter term was defined as "the lowest population density that will cause economic damage" (Headley 1971).

Stern (1973) reviewed the status of developing economic threshold levels for agricultural pests and concluded by restating the belief and hope that pest control can be raised to higher competency levels in the form of applied population ecology (Geier 1966, Smith and Van den Bosch 1967).

These suggestions have been readily taken to heart by crop protection specialists and the ecological community. A linking of the basic sciences such as entomology, plant pathology, nematology, soil science, meteorology and economics has taken place through the technological advancements of electrical engineering and systems science (Koenig 1974, Koenig et al. 1976). Sophisticated methods have been developed to monitor the environment (Haynes et al. 1972), to track the progress of pests and crops through computer mapping (Fulton and Haynes 1975) and to survey pest populations through such monitoring programs as the Cooperative Crop Monitoring System (Gage and Mispagel 1981). And finally, rapid communications and information delivery systems have been developed (Croft et al. 1976,

Tummala and Haynes 1977), modified and implemented (Gage et al. 1981).

Although the technology and theory of pest management have evolved to a high level of sophistication, an immense amount of basic biology and understanding of the relationships between pest organisms and their hosts is lacking. A great deal more work in the first phase of crop loss appraisal (Large 1966) needs to be undertaken.

Towards this end, I have conducted preliminary investigations into the interactions of a single pest/host system, that of the Cereal Leaf Beetle (CLB), Oulema melanopus (L.), and its preferred host plant, oats, Avena sativa (L).

Many investigations have been conducted on the biology, population dynamics behavior and biological control of the CLB in small grains over the past two decades (see reviews by Battenfield et al., in prep., Haynes and Gage 1981). Though some have found significant correlation of loss of yield with population densities (Wilson et al. 1969, Merritt and Apple 1969, Gutierrez et al. 1974), few studies (Gage 1972, Jackman 1976) have examined the relationship between the CLB and its host plant from the plant's physiological or growth perspective. Certainly a plant cannot be solely affected by a single factor such as CLB defoliation without many other variables including climate, nutrients and the

plant's own biochemical changes through phenological time influencing the effects of that factor. It is easy to overlook the influence of other factors when judging a foreign variable's effect when the only concern is the integrated effect of that treatment over all variables, i.e. yield.

My intent in this thesis is to examine in detail the interactions of CLB defoliation and the abiotic environment, mostly water stress, which impinge on the growth and development of the oat plant. For the purposes of this investigation, the single plant perspective will be employed rather than whole field analysis.

The way in which the plant itself influences the insect's behavior and survival will affect the impact of that insect population on the plant's growth and survival. The same abiotic conditions affecting the plant, affect the insect through the plant either directly or indirectly, e.g. the plant's attractiveness and/or nutritional quality. Therefore an examination of the plant from the insect's perspective was undertaken and will be considered here.

II. MAJOR OBJECTIVES AND HYPOTHESES

The interaction between the imported pest, the Cereal Leaf Beetle (Oulema melanopus) and its preferred host plant, oats (Avena sativa) was to be investigated. Not only was plant fitness a concern, but more importantly was the determination of the effect of the CLB on the physiology of the oat plant and its eventual yield. This aspect of the investigation required monitoring the plant's water relations and growth parameters under the constraints of manipulated treatments of soil moisture and timing of CLB defoliation. Comparisons of insect vs. artificial defoliation treatments under similar regimes of soil moisture conditions as well as perturbations on a phenological schedule provided information regarding the changing source:sink relationships in the growing plant.

Major Objectives

1. To determine the effect of water deficits in conjunction with cereal leaf beetle defoliation on the growth, development and yield of the oat plant.
2. To determine the effect of these same stresses on the chemical composition of plant tissues as potential food resources for a defoliator.
3. To determine the effect of leaf surface area reduction on the optimization of the

transpiration:photosynthesis ratio for maximum crop productivity.

4. To determine whole plant growth and yield compensations to biotic and abiotic stresses.

General Hypotheses

A. That the timing and length of moisture deficits and the consequent degree of vegetative growth of the plant have a major influence on the effect that defoliation might have on eventual yield.

B. That, under moisture stress conditions, defoliation by the CLB can play an impotant role in changing the oat plant's ratio of minimum transpiration to maximum photosynthesis expressed in terms of growth.

C. That within and between plant growth compensation will occur under various biotic and abiotic stress levels to minimize yield loss at the field level.

D. That loss of grain yield in oats under moderate CLB defoliation pressures is related more to the seasonal soil moisture conditions than to CLB defoliation per se.

E. That soil moisture affects the total nitrogen and water content of the plant tissues and thus affects the nutritional value of foliage for a defoliator.

III. MATERIALS AND METHODS

A. Study Area and Plot Descriptions

Investigations of CLB defoliation on oat plant physiology were conducted at the W.K. Kellogg Biological Station (KBS) in Ross Township, Kalamazoo County, Michigan, from 1979-1981. This site was chosen because of its long history of CLB investigations (Haynes and Gage 1981), the endemic populations present and the technical and logistical support provided at KBS.

The majority of the research was conducted in Section 9, fields 9-11 (Table 1) though comparative data were collected in Section 5. Field numbering in this thesis follows that of Casagrande (1975) though a new field numbering scheme was instituted in 1981 for the Kellogg Biological Station (Appendix 1). Acreages for the Casagrande numbered fields are given in Lampert (1980) and for the new KBS field numbers in Figure A2 (Appendix 1).

Plots were laid out in a randomized complete block design with three replications. The following treatments were manipulated during the years specified:

Simulated Drought Conditions

1. No Defoliation (Dry Control) (1979-1981)
2. Defoliation through boot stage; water and insect stress relieved after heading (Dry Boot)

Table 1. Oat crop planting variables in the fields investigated at the Kellogg Biological Station from 1979-1981.

	Year		
Variable	1979	1980	1981
Field (Sec./Num.)	9-9	9-11	9-10
Variety	Korwood	Korwood/Mariner	Mariner
Planting Date	May 6	April 22	March 25
Planting Rate	2.5 bu/acre	3 bu/acre	2.5 bu/acre
Harvest	Aug 9	Aug 5	July 20

(1979-1981)

3. Defoliation and water stress during heading only (Dry Heading) (1979-1980)
4. Defoliation and water stress continuous throughout the boot and heading stages (Dry B & H) (1979-1981)

Irrigated Conditions

5. No defoliation (Wet Control) (1979-1981)
6. Defoliation through boot stage only (Wet Boot) (1979-1981)
7. Defoliation during heading stage only (Wet Heading) (1979-1980)
8. Defoliation throughout boot and heading (Wet B & H) (1979-1981)

Rain shelters in the 1979 season consisted of 1.0x1.7 m frames covered with clear plastic and sloped to intercept westerly storms. The following two years, the rain shelters were more elaborate and considerable larger. Sloped frames 3x4 m were constructed consisting of portable tops covered with 8 mil Visqueen plastic, roll down sides and plastic sheeting buried 30 cm around the plot's perimeter (Figures 1 and 2). Rain shelters were put in place only when rain was imminent and on nights when precipitation was forecast. Every attempt was made to keep

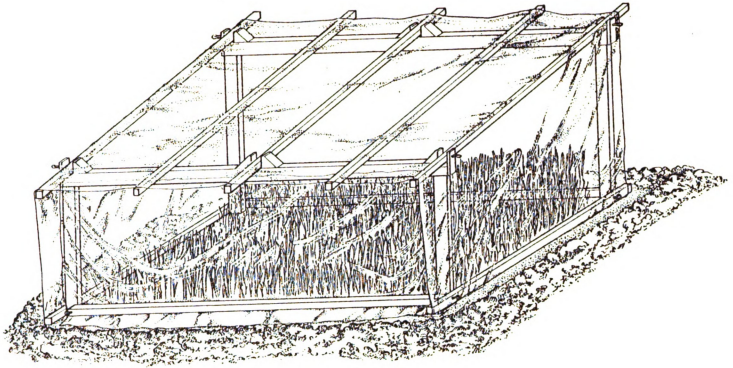


Figure 1. Construction of 3x4 m portable rain shelter with shelter in place over an oat crop.

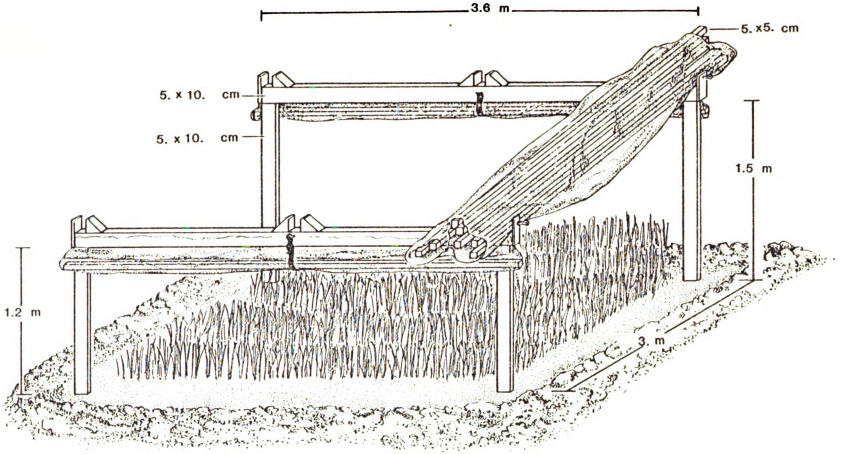
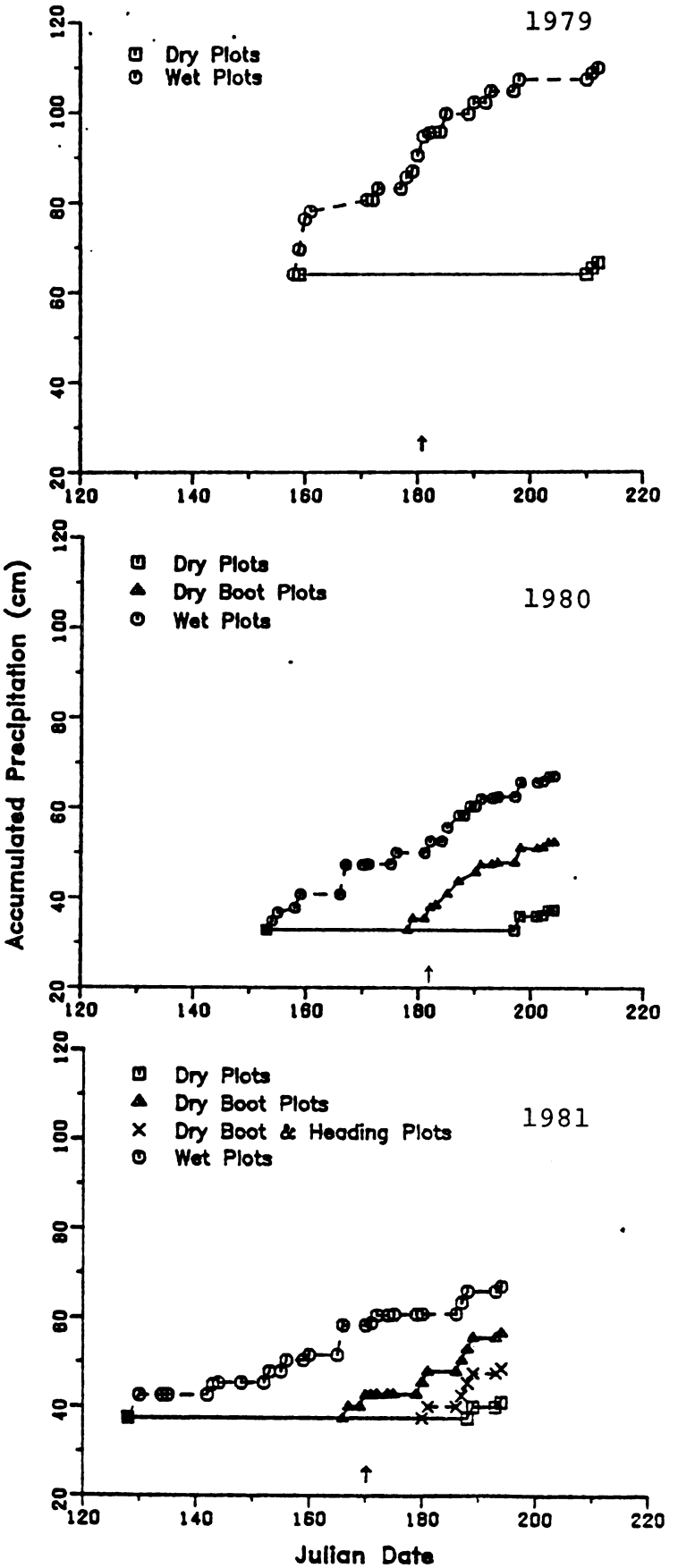


Figure 2. Construction and dimensions of 3x4 m portable rain shelter with shelter removed from an oat crop.

Figure 3. Accumulation of natural precipitation and irrigation water from January 1 by moisture treatment for 1979-1981. Vertical arrows indicate date of anthesis.


1979
Dry Plots
Wet Plots
1980
Dry Plots
Dry Boot Plots
Wet Plots
1981
Dry Plots
Dry Boot Plots
Dry Boot & Heading Plots
Wet Plots
Accumulated Precipitation (cm)
Julian Date
20
40
60
80
100
120
140
160
180
200
220

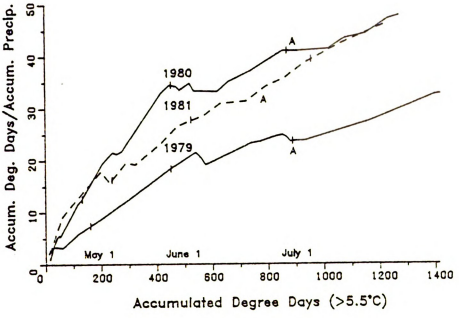


Figure 4. Ratio of accumulated degree days (>5.5C) to accumulated precipitation as a function of accumulated degree days. The vertical arrows indicate oat crop anthesis and the vertical lines mark the first day of the month listed on the horizontal axis.

the plots open to the ambient environment for as long a period as possible.

The wet plots were watered with 2.54 cm flood irrigation when the percent soil moisture fell below 50% available moisture according to a Buoyocos Moisture Meter.

B. Abiotic Monitoring

Maximum-minimum temperatures were recorded daily at the KBS weather station located adjacent to Gull Lake. Although temperatures recorded at this site were slightly different from those recorded in the field, heat unit accumulations derived from sinusoidal curves are nearly identical. However, maximum-minimum temperatures in the open at canopy height were used to compute degree day (DD) accumulation base 5.5C (Appendix 2).

Precipitation was monitored by a rain gauge at canopy height in the field. Accumulated precipitation included both natural precipitation and water added by irrigation (Figure 3).

Percent available soil moisture was monitored by a Boyoucos Moisture Meter (BN-2B) attached to gypsum resistance blocks buried at 15 and 30 cm in each plot. Soil moisture was manipulated by flood irrigation in the wet treatment plots with 2.5 cm of water across the plot whenever available soil moisture dropped below 50% at the 15 cm depth. Soil water potential was related to the

percent available soil moisture by means of a pressure plate and is described by the following equation:

SWP (-bars) = 3.21-0.031(PSM) (r^2= .97)

where SWP = soil water potential and PSM = percent soil moisture available.

An index of the ratio of accumulated degree days (>5.5 C) and accumulated precipitation including that added by irrigation is plotted against degree days in Figure 4. This index contrasts the interaction of abiotic relationships among the three years. The lower index values for 1979 indicate greater moisture levels early in the season, primarily in the form of snow, which contributed to plentiful soil reserves. However, the smaller indices of 1981 compared with 1980 are related to the higher temperatures of that spring and consequently a greater accumulation of growing degree days. The position of the first day of May, June and July, indicated by the short vertical lines in Figure 4, confirm this degree day accumulation in 1981. The early anthesis in 1981, Day 170, was due to early planting and degree day accumulation more than moisture availability since similar or greater soil moisure reserves were available the previous two years.

Soil analysis of several fields was conducted in 1979 and included particle size distribution (Figure A3), pH, nitrate-nitrogen, P, K, Ca and Mg in the top 15 cm and from 15-30 cm (Table A5, Appendix 3).

IV. CEREAL LEAF BEETLE DEFOLIATION

A. Historical Introduction

A simplified life history of the cereal leaf beetle is shown diagramatically in Figure 5. Detailed accounts can be found in Castro et al. (1965), and in many references cited by Haynes and Gage (1981) and Battenfield et al. (in prep.).

Briefly, the overwintering adult CLB population emerges from small grain stubble and roadside refugia about April 1 in southern Michigan. These adult beetles feed in the winter grains and grasses until spring planted grains emerge in May. Eggs are oviposited on small grains and field grasses. As the winter wheat matures the adult beetles are more commonly found in the preferred spring oats (Sawyer 1978).

Eggs are parasitized by the mymarid, Anaphes flavipes (Foerster) while larvae are attacked primarily by a eulophid, Tetrastichus julis (Walker), and less by two ichneumon wasps (Gage 1974). Parasitism continues through the egg stage and the four larval instars. The degree of parasitism is greatly dependent on the synchrony of planting date, beetle and parasitoid populations (Lampert 1980). Competition between A. flavipes and T. julis for hosts may adversely affect the population structure of the

CEREAL LEAF BEETLE LIFE HISTORY

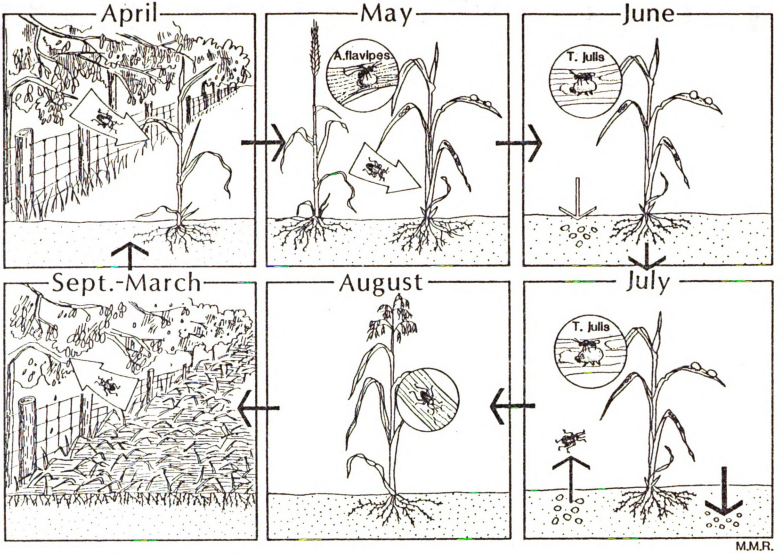


Figure 5. Cereal leaf beetle life history (see text for explanation).

latter.

Larvae pupate in the soil from mid-June through July when summer adults emerge. These adult beetles feed on grasses and on senescing small grain crops through August before dispersing to diapause sites for the winter (Wellso 1974).

The impact of CLB defoliation on grain yield in central Europe was reported as high as 70% (Knetchtel and Manolache 1936) while Balachowsky (1963) reported losses in the Balkan, Ukraine and the Caucasus regions of Europe. Wilson et al. (1964, 1969) reported 20% consumption of a stem's surface area for every CLB larva completing development to pupation regardless of the vigor of the plant. Loss of yield under favorable growing conditions was estimated at 2-4 bushels per acre for each increase of 1 larva per average stem infestation. These authors point out, however, that loss in grain yield will be dependent upon crop and soil conditions at the time of defoliation.

In contrast, Gutierrez et al. (1974) found that no significant loss of yield occurred where fewer than 1.5 larvae per plant complete development. Their model based in part on the findings of Wilson et al. (1969) was adjusted for this observation. With a high population, 1.4 larvae per stem, Merritt and Apple (1969) also found a substantial reduction in yield of oats amounting to 3.1 bu

per larva per stem or a 4.7% yield reduction per larva. These authors mention that nutrients from the carbamate insecticide used may have contributed to yield gains in plots kept free of larvae. Koval (1966) found that two and four larvae per stem reduced yield in oats by 34 and 72% respectively.

Steidl et al. (1969) noted that different strains of small grains offered to CLB resulted in significantly different weight gains of the larvae as well as some variable mortality. These results are attributed to varying degrees of antibiosis due, in part, to trichomes on the leaf surface (Wellso 1973). Lyon and Ray (unpubl. 1968) investigated larval feeding and yield of 2 varieties of oats in Ohio and found no correlation between these two parameters that season.

Webster et al. (1972) found variable yield losses among different varieties of spring wheat dependent, at least in part, upon the degree of leaf pubescence (Gallun et al. 1966). Losses of at least 25% from CLB damage could be expected based upon number of kernels per head, the weight of 1000 kernels, and straw length. Gallun et al. (1967) also found yield losses ranging from 0-23% in Monon winter wheat due to reductions in kernel number and kernel weight. Losses were dependent upon the amount of flag leaf surface consumed by the larvae. Nevertheless, no

significant losses were noted in protein content, pearling index, mill yield or alkaline water retention capacity.

Although substantial yield reductions have been related to CLB defoliation, none of these authors have examined consumption rates in terms of the plant's physiological or biochemical condition, although Gage (1972) stressed the latter's importance. On the other hand, Lyubenov (1956) noted a preference for succulent plants especially those given heavy applications of nitrogenous fertilizers. Castro et al. (1965) also noted higher adult feeding damage and increased egg laying on fertilized plants. The water content and/or total N in the plant tissues was not noted quantitatively in either of these papers.

Castro et al. (1965) and Wilson et al. (1969) were the first to determine the amount of leaf material consumed by the various life stages of this beetle (Table 2). Gage (1972), using the values of leaf area consumed provided by Wilson et al. (1969), developed an index of feeding quantities based on the composition of the larval population. This index, first instar feeding equivalent (FIFE), was based on the proportion of leaf surface area consumed by later instars related to that consumed by the first instar which was indexed as 1.0 (Table 3). The purpose of these conversions was to weight consumption by

Table 2. Amount of feeding (mg) on oat seedlings by larvae and adults of the cereal leaf beetle within 24 hours (Castro et al. 1965).

Stage	Number	Ave. wt (mg)	mg leaf consumed	
			Per Day	Per Life (est)
1st instar	10	0.22	2.14	5.35
2nd instar	25	2.68	7.80	19.50
3rd instar	10	7.80	12.90	41.70
4th instar	15	20.80	26.40	52.80
Adults	41	7.35	25.90	1040.00

Table 3. Amount of oat foliage consumed by each instar of the cereal leaf beetle and the corresponding first instar feeding equivalent (FIFE) conversion (Gage 1972).

Instar	Area Consumed (mm)	Percent	FIFE
1st	18.6	2.9	1.00
2nd	53.4	8.3	2.87
3rd	111.0	17.3	5.97
4th	459.5	71.5	24.23
Total	642.5	100.0	

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the population to the amount of feeding by each respective instar. The integral of the area under the curve of FIFE graphed against degree days greater than 9C on the abscissa, all divided by the length of 1st instar larval development, 30.6 DD, estimated the amount of foliage consumed by the larval populations. Multiplying this value by 18.6 mm^2, the average amount consumed by first instar larvae, converted the estimate to annual surface area consumed by the population.

Castro et al. (1965) estimated that a single spring adult may consume up to 1040 mg dry weight of leaf tissue, equivalent to 8.6 oat seedlings. These authors found that one larva will consume from 1.27 to 9.73 times its body weight per day or up to 119 mg in its lifetime.

CLB larvae generally feed on the epidermis between leaf veins on the adaxial surface of the leaf blades leaving the abaxial epidermal surface intact. Very high densities may force consumption of leaf sheaths though this is unusual (Merritt and Apple 1969). Major leaf veins may be damaged during such heavy feeding. Shade and Wilson (1967) found that feeding was deterred in host plants with interveinal widths that were too narrow to accomodate the CLB mouthparts. Wellso (1973) reported that the higher silica content or greater propensity of trichomes to be on or along the veins also deterred vein feeding. This type

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of defoliation which leaves intact the leaf's major vascular system is certain to have a different impact on leaf function than cross vein feeding.

B. Methods

Defoliation was induced by innoculative release. In 1979 cheese cloth cages were placed over 1.0x1.3 m plots for the containment of adult beetles collected the previous year and retained in a state of diapause. The limited number of adult beetles available dictated the size of the plots in 1979. It was believed that the larvae were sensitive to capture techniques and that oviposition by caged adults would offer the best chances to obtain large larval numbers.

It was found that if defoliation is the prime objective, handling CLB larvae does not decrease their effectiveness appreciably. The following two years, then, plot size was increased to 3x4 m, the size dictated now by the manageability and portability of the rain shelters. Larvae were collected by sweep net from infested fields and spread throughout the plots by hand in a sowing motion. The sticky fecal coat of the larvae helped them to stick to the plants when spread, but also caused an undesired clumping of larvae into a mass which resulted in mortality if the larvae were unable to extricate themselves.

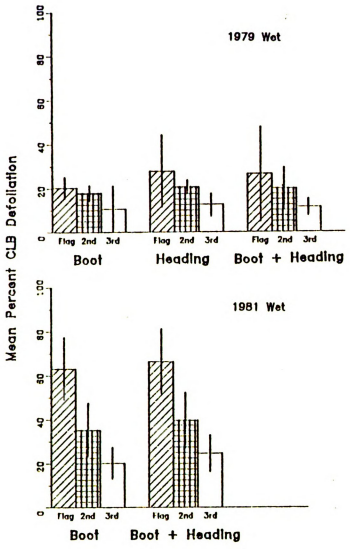
The actual number of larvae per stem was not determined because new releases of larvae into the plots were made every couple days which artificially altered the population responsible for the defoliation, and because the intent was to attain major defoliation by the CLB regardless of instars available or densities required. Moreover, it was assumed that the amount consumed per unit time by an individual larva was ot a constant but rather a function of food quality. The validity of this assumption would make any association between CLB density and defoliation questionable.

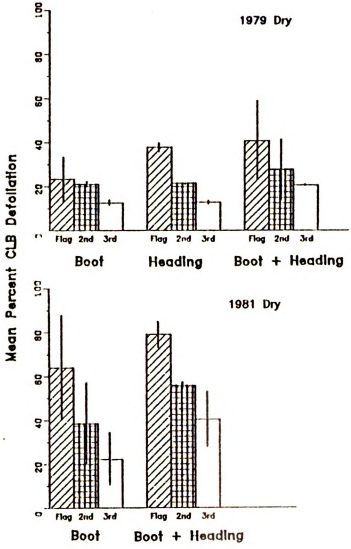
CLB defoliation of each of the top three leaf blades was estimated by eye on 20 plants per plot in 1979 and 50 plants per plot in 1981.

C. Results and Discussion

Green leaf surface area was dramatically reduced by defoliation caused by the CLB. Figure 6 shows the final level of CLB defoliation in 1979 and 1981 for the top three leaf blades in each treatment plot. In the dry plots, the mean CLB defoliation ranged from 23-41% on the flag leaves in 1979 and 64-79% in 1981. The wet plots exhibited less defoliation than the dry plots: 20-28% in 1979 and 63-66% in 1981. Because of destructive climate which lodged the entire field, these data were not collected in 1980, though

Figure 6. Mean percent defoliation (±SE) of oats by the cereal leaf beetle in 1979 (n=20) and 1981 (n=50) for dry and irrigated plots by leaf position.


Mean Percent CLB Defoliation
1979 Wet
1981 Wet
Flag 2nd 3rd
Boot
Heading
Boot + Heading


Mean Percent CLB Defoliation
1979 Dry
1981 Dry
Flag 2nd 3rd
Boot
Heading
Boot + Heading

the effects can indirectly be estimated from the reduced leaf area in the defoliation treatments shown in Figures 7 and 9. Being positively phototropic, larvae feed preferentially on the flag leaf and less on sequentially lower leaf blades (Wellso 1973). Defoliation is more intense in the dry plots despite the fact that the same relative number of larvae were distributed in both wet and dry plots. More defoliation occurred in the boot & heading plots due to the longer innoculation period of this treatment.

The effect of selective CLB defoliation on the flag leaf decreases the effectiveness of this organ more than others because the surface area of a non defoliated flag leaf was during the years of this study is often the smallest of the top five leaf blades (Figure 8). Nevertheless, with adequate water, the flag leaf persists longer than the lower blades thus making leaf loss even more impotant. During the period of this study, the 2nd and 3rd leaf blades had the greatest amount of surface area. If dry conditions are severe, senescence of all leaves is rapid (Figure 8). Persistence of leaves is apparent in the wet control plots and the dry defoliated (boot) plots which received water at heading. Maximum leaf area was attained 2-3 days after anthesis in the non defoliated control plots.

Total Main Stem Blade Area (cm^2)

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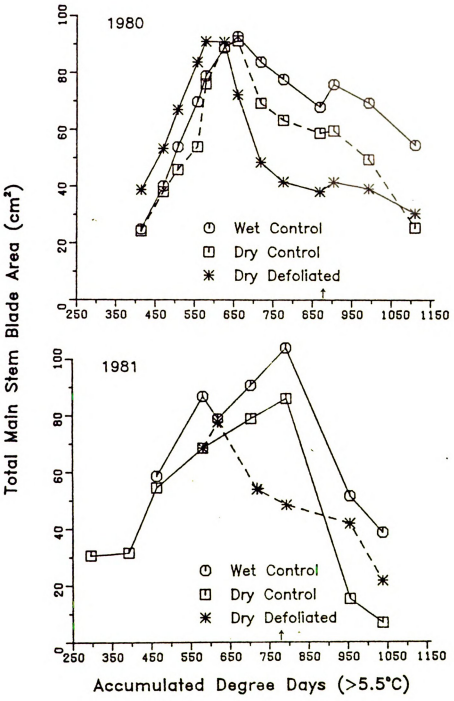
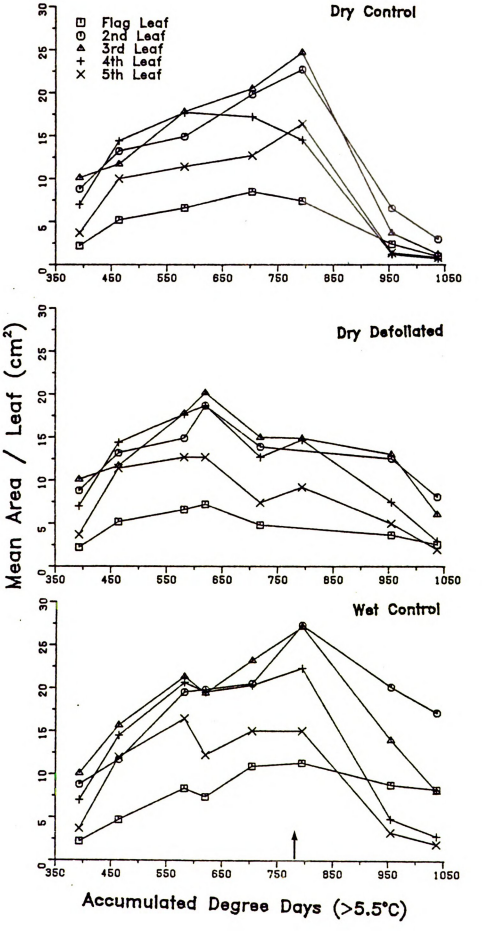


Figure 7. Influence of water and CLB defoliation stress on total main stem leaf blade area (cm^2) of oats as a function of accumulated degree days in 1980 and 1981.

Figure 8. Mean area (cm^2) per leaf by position for the dry control, dry defoliated (boot) and wet control plots. Vertical arrow indicates anthesis.


Dry Control
Flag Leaf
2nd Leaf
3rd Leaf
4th Leaf
5th Leaf
Dry Defoliated
Wet Control
Mean Area / Leaf (cm²)
Accumulated Degree Days (>5.5°C)
0
5
10
15
20
25
30
350
450
550
650
750
850
950
1050

V. ARTIFICIAL DEFOLIATION

A. Introduction

Radical defoliation by artificial means is often used to simulate pest, climatic or mechanical damage. This simulated damage can take many forms such as leaf blade excision by blade or hole punches, or sandpapering leaves (Wellso, pers. comm.). It is difficult to compare results of artificial defoliation studies because of differences in the timing of defoliation, the length of time defoliation continues, the leaf or leaves defoliated, the portion of leaf defoliated and the method(s) used. Artificial defoliation studies are conducted to measure the impact of leaf removal on growth and yield under relatively controlled conditions and manipulated treatments. These studies are often used to estimate the impact of similar levels of insect defoliation (Brown et al. 1972) or disease incidence (Hendrix et al. 1965).

Most of the literature on artificial defoliation of small grains is concerned specifically with wheat. In general, the greatest losses in yield result when defoliation occurs between heading and dough stage (Kiesselbach 1925, White 1946, Miller et al. 1948, Pauli and Laude 1959). However, Womack and Thurman (1962) found the greatest yield reductions of wheat occurred when at

least 10% defoliation was incurred one week before boot stage. In contrast, artificial defoliation of oat plants at four different life stage and five levels of clipping showed that removal at varying life stages had little effect on yield. Indeed, only defoliation treatments of 30% and 40%, the highest levels used, reduced yields significantly below check. It was concluded that the major reduction in grain yield due to leaf removal in oats was due to a reduction in seed size though significantly lower seed weights did not always result in lower grain yields (Womack and Thurman 1962).

Yield estimates are normally derived from the total yield per plot rather than from single plants. This is done because of the large variance from plant to plant but most importantly because of the variance among tillers on the same plant. The interrelationship between tillers and main stems in oats has been investigated by Labanauskas and Dungan (1956). Through various treatment combinations of defoliation, defloration and detillering just prior to anthesis, they investigated the translocation of nutrients between tillers and the main stem. They found that when the main stem alone was defoliated, part of the assimilates produced by adjoining tillers was translocated to the panicle of the defoliated main stem. Although the yield was greatest on main stems and declined on tillers from the

first formed to the last, nutrients moved from foliated stems to defoliated stems. However, the amount of yield reduction per defoliated stem was less with the older tillers. It was concluded that the whole plant is the appropriate field unit rather than individual stems and that because of translocations among stems, the loss of particular stems or heads may not be as serious a loss of yield as the number of dead panicles might indicate.

I employed this method to determine the amount of leaf removal possible in oats without loss of yield and the critical time of defoliation to ellicit this loss. It was anticipated that this information would shed some light on the consequences of a similar level of defoliation initiated by the CLB.

B. Materials and Methods

Effects of artificial defoliation were determined in a factorial experiment ($2x3^2$) as a completely randomized design. These defoliation levels were used: 0, 25 and 50% in 1979; 0, 50, 100% in 1980 and 1981. In 1981, 50% defoliation was conducted on May 27 and in an addiitonal plot June 5. Two foot rows in 3 replications were used in 1979 and 1981 while 3 foot rows were used in 1980. Defoliation was conducted at three phenological stages: preboot, boot, and heading. Half the plots were irrigated

while the others remained subject to ambient conditions (1979) or were drought stressed under the rain shelters (1980, 1981).

All leaves within the treatment rows were hand defoliated. Defoliation was conducted by slitting the leaf at the ligule and stripping the cut portion of the blade from the base to the leaf tip. The "25% defoliation" treatment had only one side of the leaf blade removed while the "50% defoliation" had both sides removed leaving the midrib and a portion of leaf blade on either side.

In 1979, total flag leaf excision at the ligule was conducted in irrigated vs. non-irrigated plots each consisting of 5 two foot rows with 5 replications. In 1980 and 1981 a single two foot row was designated for this purpose in each main treatment plot. All yield components were measured and expressed on a per stem basis.

C. Results and Discussion

In 1979, artificial defoliation of 25%, 50% and flag leaf excision conducted at preboot, boot and heading in general field micro plots had a significant effect on grain weight per stem, and the weight per kernel ($P<.05$) (Table 4) but not on the number of florets per panicle. Supplementation of ambient precipitation by irrigation also significantly increased plant height both on July 3 and

Table 4. Effect of artificial defoliation of all blades of Korwood oats on kernel weight (mg) per stem at preboot, boot and heading phenological stages in 1979 (n=80).

Defoliation	Preboot*	Boot	Heading
Check	1.41 a	1.41 a	1.41 a
25%	1.28 a b	1.21 b	1.14 b
50%	1.23 b	1.15 b	1.18 b

* Means followed by same letter are not significantly different by Duncan's Multiple Range Test (P=.05).

July 11, straw weight, head weight, number of florets per panicle and weight per kernel ($P<.05$) though only with weight per kernel was there a significant interaction of defoliation and water stress. Total grain weight was affected by defoliation from pre-boot through heading but by water at the pre-boot stage only. The number of florets was not affected by defoliation but water was a significant factor during the pre-boot and boot stages.

In 1980, artificial defoliation micro plots were situated under rain shelters and subjected to the controlled water treatments. In this season as well, defoliation of 50% and 100% in addition to dry water treatments effectively decreased the kernel weight per stem at the boot and the heading stages and decreased the weight per kernel at the heading stage (Table 5). Straw weight was affected by water stress only at the preboot stage. The number of stems was affected by water but not by defoliation.

Variation of grain yield per stem was so great in all these treatments that no differences due to defoliation or even to water were found. The field-wide spread of BYDV affected yield results in 1981 and effectively masked all treatment effects.

Loss of grain weight per stem as a percent of control is shown from 1979-1980 in Table 6. Flag leaf excision

Table 5. Influence of various levels of artificial defoliation on mean grain weight per stem (mg) for 1979-1981. ND = no data.

		Level of Artificial Defoliation					
Year		Check	Flag	25%	50%		100%
1979	$\bar{x}$	1.070	0.798	0.826	0.868		ND
	SE	0.023	0.026	0.042	0.042		
	n	4	50	12	12		
1980	$\bar{x}$	0.792	0.678	ND	0.509		0.383
	SE	0.102	0.360		0.035		0.050
	n	22	23		20		20
					May 27	June 5	
1981	$\bar{x}$	ND	0.723	ND	0.722	0.755	0.698
	SE		0.070		0.039	0.047	0.084
	n		9		9	9	9

Table 6. Percent loss of oat kernel weight per stem by artificial defoliation of the flag blade, a percent of all blades (25-100%) and by reduced water in 1979 and 1980.

	Level of Defoliation				
Year	Flag	25%	50%	100%	Dry
1979	18	7	16	ND	16
1980	14	ND	37	53	18

decreased kernel weight per stem 14-18%, a range similar to that found when water was witheld. Major defoliation of 100%reduced kernel weight per stem by 53%. This is greater than most reported values for this level of defoliation (Table 7).

Wardlaw et al. (1965) reported a loss of grain dry weight of 14-25% due to flag leaf excision, but only 6-16% when all lower leaves below the flag leaf were removed 6 days after anthesis. Compensation by adjoining organs was observed in response to these excisions. Thirty percent of assimilates which would have moved to the ear from the flag leaf were replaced by material from the second leaf when the flag leaf blade was removed. Moreover, a transfer of carbon from tillers to the main stem was noted only when the main stem was defoliated. Similar results of defoliated stems benefitting from blade-bearing members is reported by Labanauskas and Dungan (1956) and Ryle and Powell (1975). Despite these compensatory mechanisms, major losses are incurred by radical artificial defoliation. Keeping things in perspective, however, a maximum 50% decrease in grain weight is remarkably low considering that to ellicit this loss, total plant defoliation at its most vulnerable stage is required (Hendrix et al. 1965).

A partial explanation for this modest loss is

Table 7. Literature citations of critical phenological periods for defoliation of wheat and oats to incur loss of yield, the amount of defoliaton necessary to incur a loss and the maximum percent loss reported.

Crop	Stage	% Defoliation	Max. % Loss	Reference
Oats	Boot	30-40	22	Womack & Thurman (1962)
Oats	Preanthesis	100*	48	Labanauskas & Dungan (1956)
Wheat	Flowering	50-100	48	Roebuck & Brown (1923)
Wheat	3 days after Heading	100*	ND	Kiesselback (1925)
Wheat	Heading to Dough	100*	28	White (1946)
Wheat	Early Boot Flowering	41,50,100	20	Miller et al. (1948)
Wheat	Before Heading	100*	32	Pauli & Laude (1959)
Wheat	1 wk before Boot	>10	17	Womack & Thurman (1962)
Wheat	6 dy postanthesis	Flag	14-25	Wardlaw et al. (1965)
		Lower lvs	6-16	" "
Wheat	Variable	100	20-34	Hendrix et al. (1965)

* Only level of defoliation used

discussed by Davidson and Milthorpe (1966a). They have documented that expanding leaf cells of Dactylis glomerata are confined to a basal area below the ligule of the enclosing fully expanded leaf. Wellso (pers. comm.) has also found that in oats, leaf expansion is restricted to the basal cells of the blade closest to the ligule.

Removal of laminae of exposed and expanding leaves reduces the rate of leaf expansion because expansion is dependent on the leaf's own photosynthetic ability. If defoliation occurs, photosynthate from older, fully expanded leaves is drawn upon to maintain cell enlargement of expanding leaves (Davidson and Milthorpe 1966). However, leaf laminae attain their maximum photosynthetic rate at the time of full expansion and maintain this maximum rate for only a few days before the rate slowly declines (Friend 1966). Davidson and Milthorpe (1966b) suggested that following severe defoliation regrowth during the first week is limited by the soluble carbohydrate content of the bases of expanding leaves. Subsequently, the rate of photosynthesis and then, in later stages the rate of nutrient uptake by the roots will limit regrowth.

Few authors have investigated the effects of artificial defoliation on the yield of oats and only a few more have looked closely at this problem in wheat (Table 7). Womack and Thurman (1962), Wardlaw et al. (1965),

Hendrix et al. (1965) and Wellso (pers. comm.) are the only authors found to have investigated relatively low levels of artificial defoliation on oat or wheat grain yield. Estimated losses from these studies is extremely variable ranging from negligible to major loss. The general consensus appears to be that maximum loss would be attained by mechanical defoliation on or about anthesis. However, even with 100% defoliation, other environmental variables being kept favorable, the maximum loss would be 17-48% (Table 7).

VI. OAT PLANT GROWTH UNDER BIOTIC AND ABIOTIC STRESSES

A. Introduction to Oat Plant Development - A Background

Two leaves are present in the embryo of an oat plant. Initiation of additional leaves begins soon after germination. The plastochron, the time interval between new leaf initiation, is 2-3 days at spring temperatures so that the initiation of the flag leaf takes place 15-20 days after germination. However, in field crops, the phylochron, the time interval between the appearance of successive leaves, is considerably longer than the plastochron, often from 5-7 days (Bunting and Drennan 1966).

The leaf matures from the tip downwards, the sheath being the last to develop. Sharman (1942) and Begg and Wright (1962) have shown that lamina elongation ceases about the time of ligule exposure from the encircling leaf sheaths. Our data confirm this finding in oats. Borrill (1961) found that leaf laminae become successively longer until inflorescence formation when laminae up the flowering stem become progressively smaller. In oats, this smaller blade may be only the flag leaf. Pukridge (1968) found that nitrogen can have a major effect on the sequence of leaf sizes. His results suggested that the needs of the

ear and stem have precedence over those of the leaves and when nitrogen is in short supply the growth of late-forming leaves is restricted. Leaf sheaths, on the other hand, will increase in length and area after inflorescence formation and after the blade has ceased elongation. As a fully expanded leaf ages, it contributes progressively less to the rest of the plant, so that before final senescence it may be unessential (Jewiss 1966). A young elongating leaf retains all its assimilates if fed labelled CO_2. The young leaf receives assimilates from lower leaves while it expands. The fully expanded leaf becomes a source for assimilates and begins to export to other sinks such as younger leaves or to developing tillers (Wardlaw 1968, Williams 1964). Wheat laminae, even when fully emerged, continue to import one-quarter of their dry weight increase from lower leaves. About half of the dry weight of the sheath comes from sources other than its attached blade. Successive leaves have slower rates of cell division and expansion and therefore lower relative rates of growth. However, the rate of cell division in these leaves is maintained for a longer time so that the number of cells increases with successive leaf formation. The area and length of the leaf is dependent on the expansion of these cells and thus the nutrient supply available.

In general, the maximum photosynthetic capacity for a

leaf occurs for a few days after full expansion, which is when the leaf ligule appears from the enveloping sheaths. However, the distal parts of the leaves of cereals are less active on an area basis than are the basal portions (Milthorpe and Moorby 1974). Thus the mean growth rate of a leaf is a consequence of the ageing of fully expanded cells and emergence of tissue of inherently greater growth and photosynthetic activity.

Once flowering is initiated, the internodes which have previously been very short, begin to elongate. New cells are produced in the intercalary meristems of the lower part of each internode and growth occurs by elongation of these cells. The lower internodes elongate much less than the upper ones. Elongating stems during the postanthesis period are major sinks for substrates. The internode at this time is actually competing with the ear for available photosynthates and may actually draw from the photosynthesizing panicle (Wardlaw 1968).

Tillering of small grains is highly variable and is dependent upon the cultivar and the available water and nutrients. Tiller production ceases when heading occurs on the main stem. Assimilates for tiller growth come from the older leaves of the main stem until the tiller has leaves of its own and becomes independent. An insufficient supply of substrates to the apex and primordial leaves will cause

tiller death. An appreciable portion of tillers die without grain formation. If, however, the tiller survives to flowering, grain filling will continue as normal. Successive tillers are smaller and produce less grain, a function of decreasing assimilate supply. However, Labanauskas and Dungan (1956) found that the total yield of five tillers was more than twice that of the main stem. Even after tiller "independence" has been attained, defloration or defoliation of the tiller can shift sink strengths so that assimilates flow to the main stem from the tiller with the former, and vice versa with the latter. Rawson and Hofstra (1969) found that the ears of tillers provided a stronger sink for the lower leaves of the main stem and that movement of translocates continued in this direction during grain filling. The growth rate of the inflorescence slows towards anthesis with peduncle and rachis internodes elongating until the end of anthesis.

The panicle of oats is a determinate branched inflorescence, meaning that the main axis terminates in a spikelet. Panicle development occurs from the tip downward. Branching increases downward from the tip, the basal node having one-third or more of the total number of spikelets in the panicle. Although five or more florets are initiated in each spikelet, normally only two florets are fertile, the remainder aborting (Bonnett 1966).

Yield of a given plant is dependent not only on the number of grain producing tillers which develop, but on the number of spikelets which form per panicle. Environmental conditions influence in opposing ways the growth and development of spikelets as well as the number of spikelets formed. In wheat, spikelet differentiation appears to cease about the time of stamen differentiation in the most advanced floret. Therefore, the greatest number of spikelets will be formed when unfavorable conditions slow floret maturity.

B. Materials and Methods

Plots and treatments were as described in Section III. In 1980 and 1981, each stem of up to five plants per plot in two replications were labelled for growth rate measurements. Each tiller was labelled as it appeared. The length and width of each blade, and the height to each ligule and node was recorded twice weekly in 1980 and thrice weekly in 1981. When thigmomorphogenesis was observed, a new plant more characteristic of the plants in the plot was chosen as a substitute.

Each week, selected plants were harvested and dissected for biomass determination of component parts. Surface area of blades, sheaths and stems, percent water content and nitrogen content of leaf blades were measured.

Leaf area was measured by a Li-Cor leaf Area Meter (Lambda Corporation Model 3000A). Regression analysis of leaf area and dry weight on length and width measurements were conducted.

At the end of the season, plots were hand harvested, mechanically threshed and yield determined. In 1979, because few insects were available for innoculation, plot sizes were relatively small, 1.2x1.5 m. Two 1 m rows were harvested from each plot and total yields projected to the larger plot size harvested in 1981, 3.0x3.7 m. Total grain weights, 1000 kernel weights and straw weights were recorded. Each stem of the plants used for growth rate measurements was harvested separately. For each of these stems, panicle weight, floret number, kernel number, kernel weight, and straw weight were recorded.

in 1981, percent chlorosis caused by Barley Yellow Dwarf Virus (BYDV) was estimated by eye for the top four leaf blades, sheaths and heads of 30 randomly selected stems in each plot on July 3 and again on July 7.

C. Results and Discussion

Leaf Blade Production : The relationships of blade length and length x width on measured leaf area and dry weight were determined by least squares linear regression from the 1981 harvested plants ($n = 693$, $P<.001$).

The following equations were used to calculate leaf blade surface area and dry weight of the 1980 and 1981 data:

Area (cm^2) = ((L)(0.1138)-6.33)-%DEF (r^2 = .85)
Area (cm^2) = ((LxW) (0.0067)+0.098)-%DEF (r^2 = .92)
Dry Wt. (mg) = ((L)(0.422)-21.69)-%DEF (r^2 = .67)
Dry Wt. (mg) = ((LxW)(0.026)+0.321)-%DEF (r^2 = .78)

where L = leaf length (mm), LxW = length times width and %DEF = percent defoliation. Total main stem leaf blade areas for 1980 and 1981 are shown in Figure 7. Early in the season the plants were growing on soil saturated with moisture from the spring precipitation. Treatment effects were negligible at this time and growth among the plots was similar. Leaf expansion in irrigated plots exceeded that in dry plots which was expected since this variable is very susceptible to water deficits (Hsiao 1973). The decline in leaf area in the dry defoliated plots was due to CLB defoliation. Larval defoliation was curtailed at heading, DD 796, June 27, in 1980 and DD 782, June 19, in 1981 though most larvae had pupated by this time.

By DD 600 in 1980 and DD 800 in 1981 the rate of lower leaf senescence was greater than new leaf production. As a result, total main stem leaf area declined. The senescence rate was much greater in dry plots than irrigated plots as

expected. The mean blade area stabilized at the time of heading in 1980, DD 734, and anthesis in 1981, DD 782, indicating a decrease in the senescence rate. Blade expansion was complete by this time so new blade production did not result in the senescence rate decline. The 1981 data were not as distinct in this regard, though the dry defoliated plots showed this trend (Figure 7). The effects of irrigation on blade surface area is apparent from the figure.

Mean leaf area of individual blades over time is shown in Figure 8 for plants grown in 1981. The second and third leaf blades had the largest surface area while the flag leaf blade had the least. Natural senescence beginning from the lower leaf blades is apparent in Figure 8 as is the persistence of the flag leaf blade. Defoliation by the CLB decreased the effective blade area available for photosynthesis while the imposed drought treatment further reduced this area. Nevertheless, because the plants were growing on stored soil moisture at field capacity early in the season, most of the plants' vegetative growth was attained before the soil moisture had been depleted by either evaporation or transpiration. Thus the differences in individual leaf areas among these treatments were not as great as one would experience in greenhouse experiments. The primary effect of the moisture treatments was early

blade senescence during and after anthesis.

In 1980, plants commonly had 2-5 tillers or secondary stems, whereas, in 1981 tillering of Mariner oats was uncommon so in this year most measurements were taken from main stems. In general, the whole plant blade area (Figure 9) was 4x that of the main stem alone (Figure 7) in 1980.

Leaf Sheath Production : Leaves of monocots consist of a blade portion which in this system is subject to CLB defoliation, and a leaf sheath wrapped around the stem and not normally defoliated by the CLB. Thorne (1959) stated that at the time of ear emergence, leaf sheaths of small grains accounted for about half the total assimilating surface area. Estimation of the surface area of the sheaths was done using the following relationships:

$$\text{Area } (cm^2) = (pi(L)(D)/\ 100.)(0.66))-1.36 \quad (r^2 = .68)$$

$$\text{Area } (cm^2) = (0.100)(L)-2.17 \quad (r^2 = .56)$$

where L is length of sheath (mm) from the node of insertion to the ligule, and D is the maximum diameter (mm) of the stem plus sheath. The leaf emerges from the center of the developing plant and thus is overlapped by other leaf sheaths down to the node of insertion. As the penultimate and flag leaves emerge, the proportion of stem area comprised of lower leaf sheaths decreases (Figure 10). The general proportion of exposed to overlapped effective

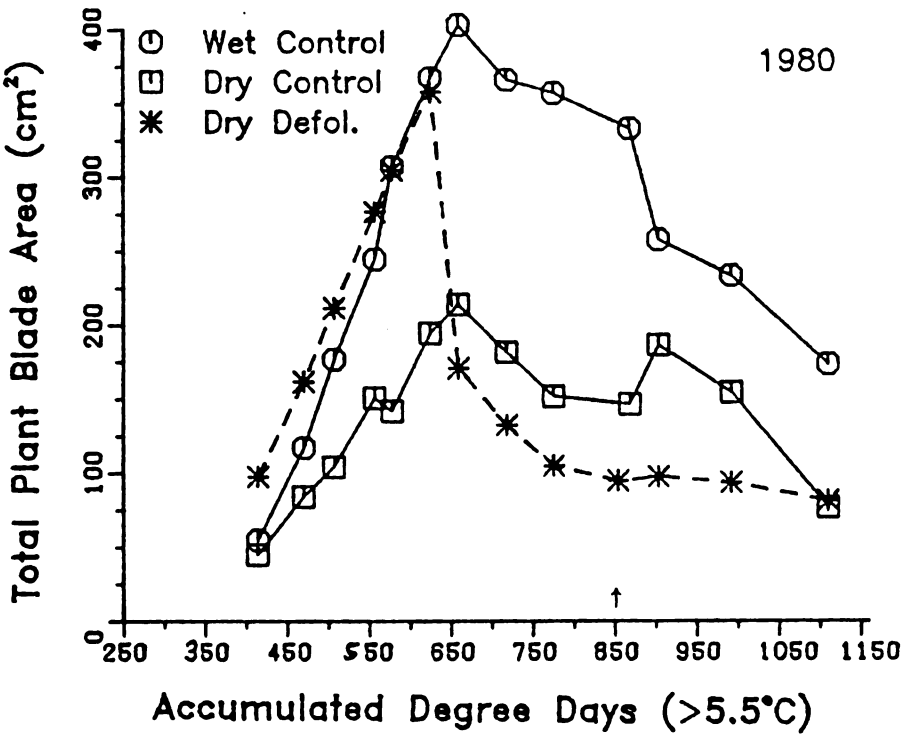


Figure 9. Influence of water and CLB defoliation stress on total oat plant blade area (cm^2) including tillers as a function of accumulated degree days in 1980.

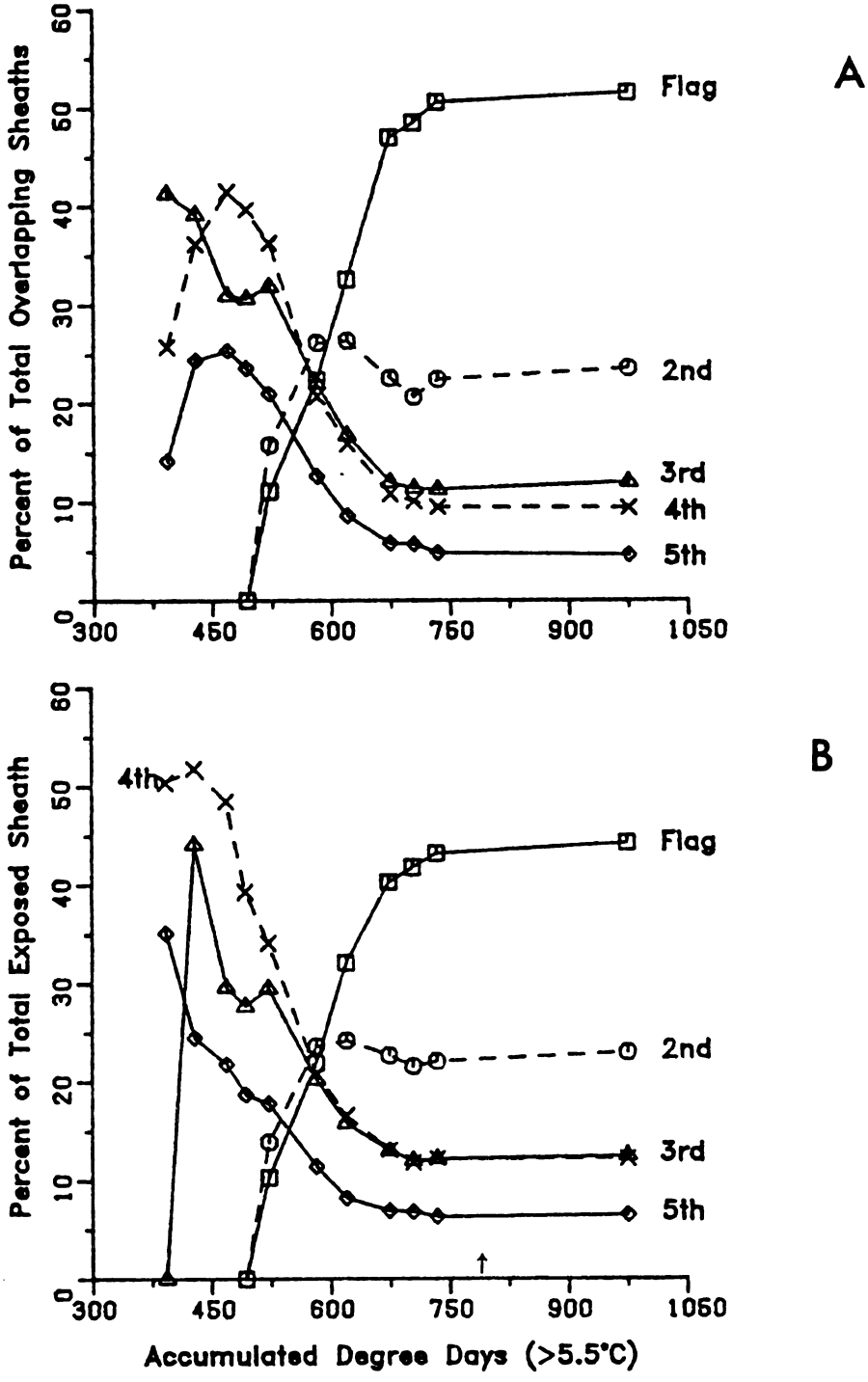


Figure 10. Influence of oat leaf position on percent of whole plant leaf sheath area for A) overlapped sheaths and B) exposed sheaths.

sheath area is 1:1. The area of the overlapped sheaths was computed as above and, because of the lower amount of chlorophyll in the overlapped sheaths, arbitrarily divided by 2.0 to estimate the area as photosynthetically active as the exposed sheaths. Sheath area generally increased with time and reached an asymptote by anthesis (Figure 11). The irrigated plots normally had the greatest sheath area but the plants measured from the dry defoliated (boot) plots in 1981 were unusually large and had a sheath area exceeding that of the irrigated plots. This may have been because of an extended root system grown under the prestressed conditions of this treatment.

Of major significance is the fact that by anthesis the flag leaf sheath comprised nearly 50% of the exposed sheath, i.e. stem, area (Figure 10). The availability of water in both the wet control and the dry defoliated (boot) plots after anthesis significantly increased the exposed and overlapped flag sheath area in contrast to that in the dry control plot (Figures 12 and 13). In addition, by prestressing the dry defoliated plot and forcing root penetration to greater depths, upon rewatering more growth of the 2nd leaf sheath occurred than in the wet control plots.

Thorne (1965) reported that flag leaf laminae were only 18-37% of the area of the flag leaf sheath in four

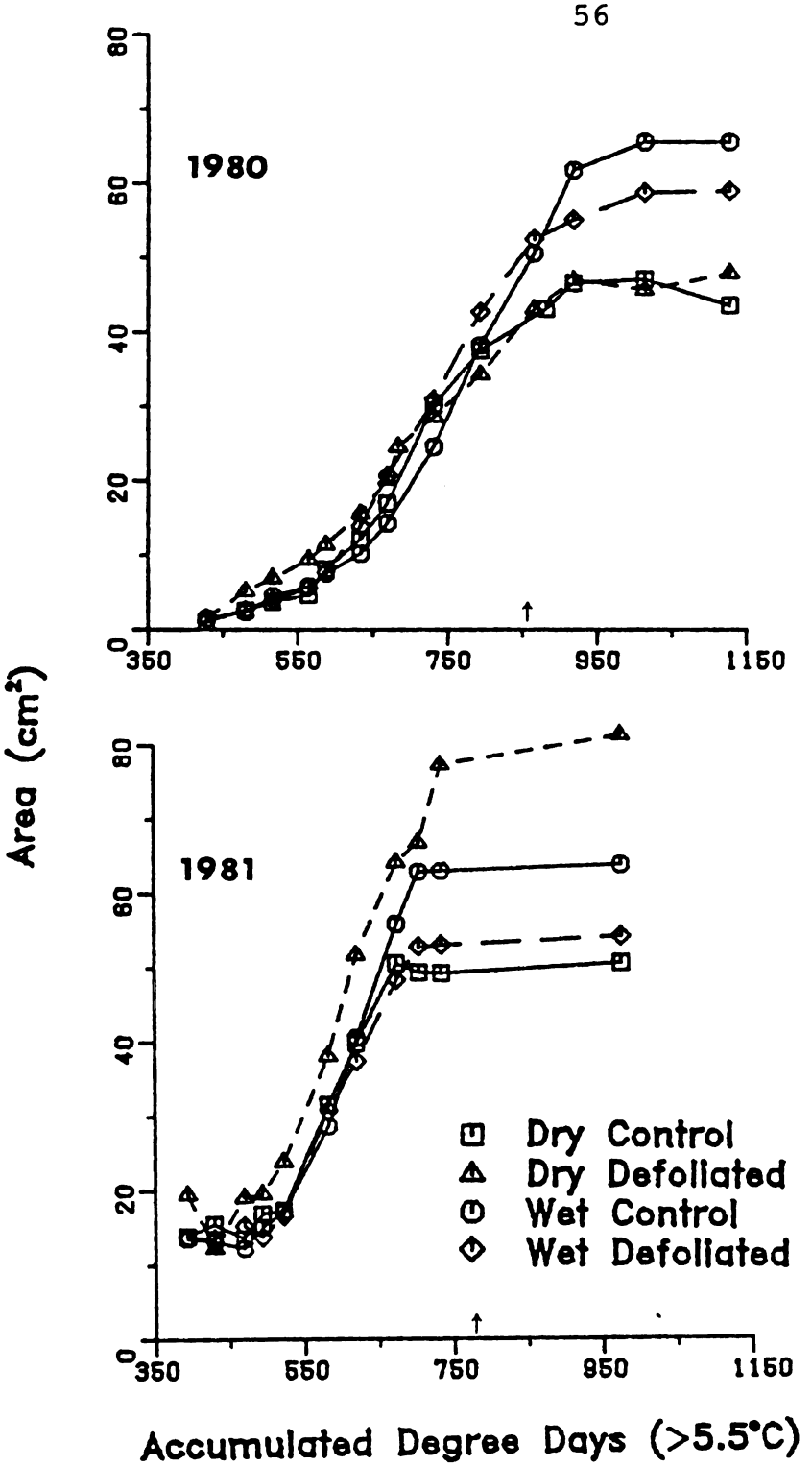


Figure 11. Influence of water and CLB defoliation stress on main stem sheath area (cm^2) as a function of accumulated degree days for 1980 and 1981.

Figure 12. Mean exposed sheath area (cm^2) by leaf position for wet control, dry control and dry defoliated treatments.

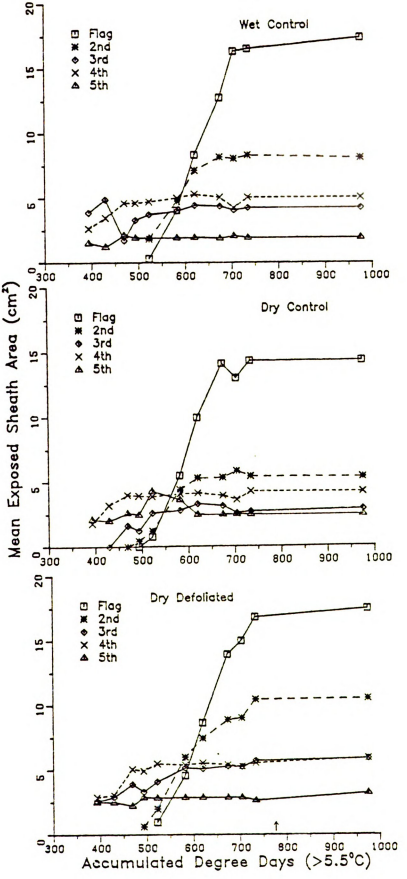
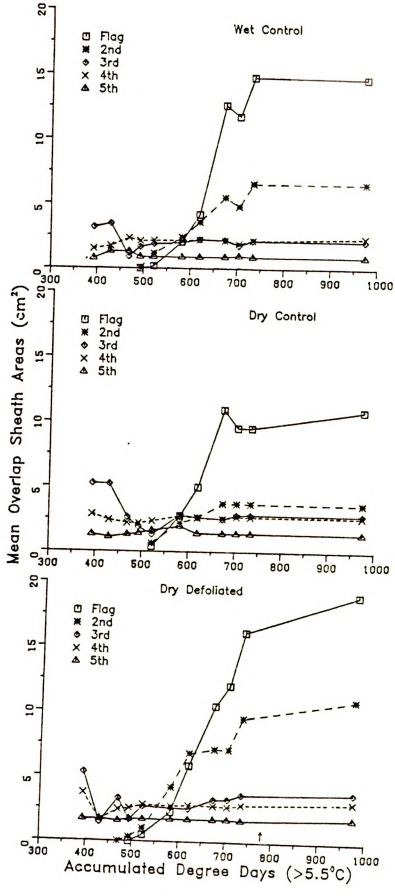

Wet Control
Dry Control
Dry Defoliated
Flag
2nd
3rd
4th
5th
Mean Exposed Sheath Area (cm²)
Accumulated Degree Days (>5.5°C)
0
5
10
15
20
300
400
500
600
700
800
900
1000

Figure 13. Mean overlap sheath area (cm^2) by leaf position for wet control, dry control and dry defoliated treatments.


Wet Control
Dry Control
Dry Defoliated
Flag
2nd
3rd
4th
5th
Mean Overlap Sheath Areas (cm²)
Accumulated Degree Days (>5.5°C)
0
5
10
15
20
300
400
500
600
700
800
900
1000

varieties of barley. In this study, the oat blades generally attained a slightly greater area than their sheaths (Figures 8 and 12).

Photosynthetic capacity of sheaths is often overlooked in favor of that of the blades which presumably intercept sunlight better than the vertical sheaths. However, Thorne (1959) estimates that the actual photosynthetic rate of barley sheaths per unit area was of the same order as that of the laminae. The persistence of all the sheaths beyond the life of their associated leaf blades ensures photosynthetically active surface area during the late grain filling period.

Panicle Surface Area : In addition to the photosynthetically active blade and sheath surface area, the inflorescence, i.e. the rachis, the rachis branches and the spikelets, contain chlorophyll and are able to photosynthesize (Carr and Wardlaw 1965). The average surface area of these rachis branches and the rachis itself was 7-11 mm^2.

The two glumes of the floret were also capable of carbon fixation. Each of the two glumes had eight veins containing chlorophyll with an area of about 30 mm^2. Each of the kernels also had 3-4 mm^2 of green surface area. The importance of the head in carbon fixation and grain filling will be examined in Section VIII regarding assimilate

translocation.

Thigmomorphogenesis : This term refers to the effects of mechanical stimulation on the growth and development of plants. The reader is referred to a discussion of this phenomenon by Jaffe (1980). The primary thigmomorphogenetic response of plants is retardation of stem growth accompanied by increased radial growth. A common expression of thigmomorphogenesis is the elongation of plants grown in the greenhouse in contrast to field grown plants. The continuous jostling of plants in the field by the wind is responsible for reduced stem elongation. A word of caution is in order to those undertaking "controlled" investigations in the greenhouse or growth chamber. The lack of wind in these units of and by itself may modify growth such that results may be invalid in the field situation.

On the other hand, the present field studies resulted in too much physical manipulation. As described previously in the Methods section, the growth of individual plants was followed through time by either bi-weekly or thrice weekly measurements of blades and stems of tagged plants. Plant handling was limited to simply stretching each blade along a ruler to observe its length and width, and standing the ruler vertically along the stem to observe the height to each node and leaf ligule.

Figure 14 shows differences in mean height of unhandled plants measured on June 30 (shaded) and the height on July 2 of plants measured 2-3 times a week. These latter plants were initially chosen as representative plants of the treatment plot. By late season, the differences between the handled and unhandled plants were striking.

Jaffe (1976) found that although mechanical stimulation may retard anthesis and fruiting in addition to stem elongation in kidney beans, no other aerial part of the plant appeared to be affected. With oats, there appeared to be an effect on blade growth (Figure 15). Maximum blade area was attained earlier and was substantially less among handled plants than among those merely harvested.

Jaffe and Biro (1979) reported that mechanical stimulation may induce ethylene production which in turn may inhibit basipetal auxin transport causing a decrease in elongation. The sequence of events leading to thigmomorphogenesis begins with an increase in cell permeability and a drop in the tissue electrical resistance either immediately following or simultaneous with stimulation. Recovery of pre-stimulus electrical resistance takes about 3 min and growth accelerates during this period but stops when the pre-stimulus resistance is


Mean Height (cm)
500
700

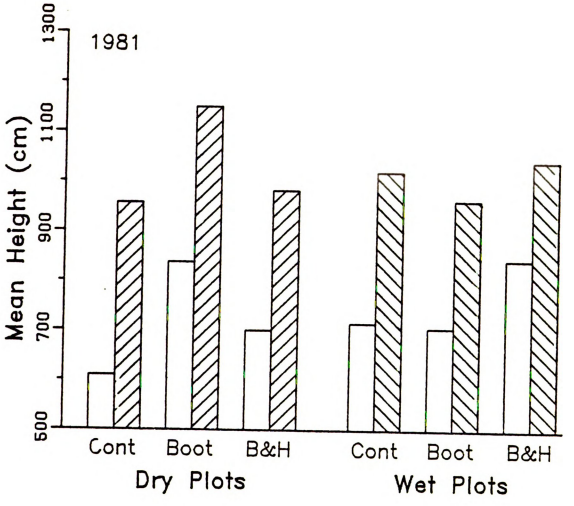


Figure 14. Influence of water and CLB defoliation stress on mean height (mm) of handled (open bars n=6) and non-handled (shaded bars n=27) oat plants.


Total Main Stem Blade Area (cm²)

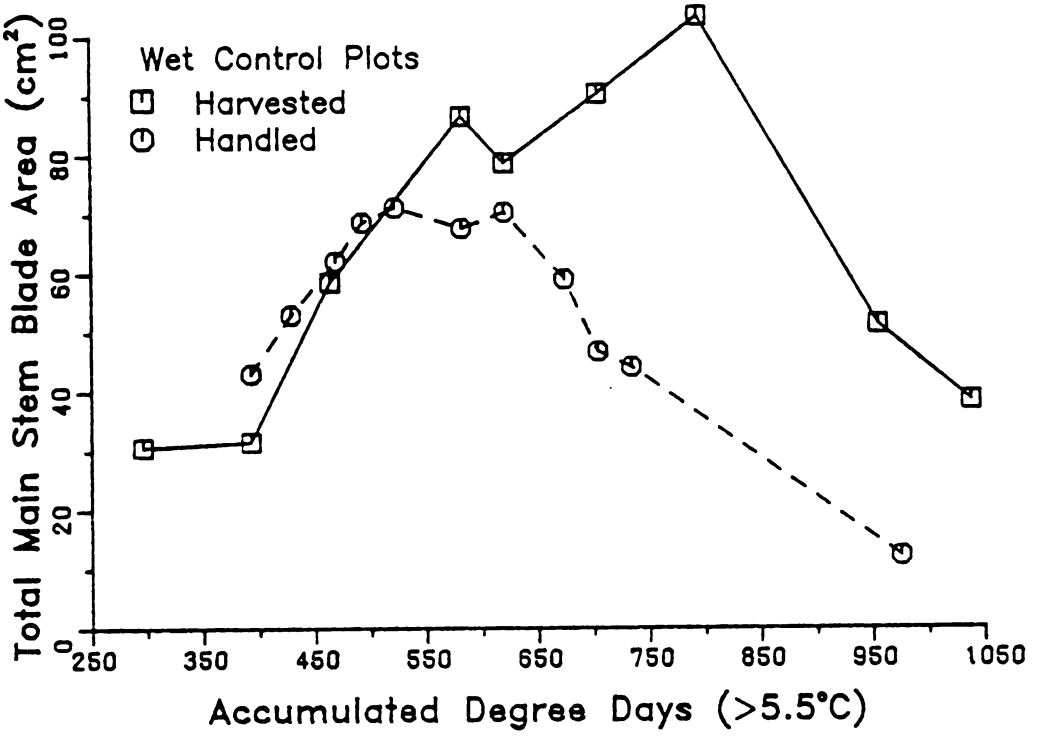


Figure 15. Total main stem blade area in wet control plots in 1981 for plants handled 2-3 time weekly and those harvested but not previously handled.

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Korwood

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reached. An increase in ethylene production begins about 30 min after stimulation and growth is about half its prestimulation rate. Ethylene production returns to normal 3 h after stimulation. Growth will continue at a retarded rate after 3 d. Obviously if oats respond similar to beans, physical measurements 2-3 times a week would cause substantial reduction in growth (Figure 15).

Curiously, prior physical manipulation which induces thigmomorphogenesis appears to precondition plants to withstand drought stress. Bean plants which had been rubbed, recovered completely from wilting upon rewatering, whereas control plants did not (Jaffe and Biro 1979).

Stress Effects on Yield of Oats 1979-1981 : In the final analysis, the effect of various perturbations on grain yield. Over the three years of this investigation results of grain yield were variable for reasons independent of the treatment conditions. In 1980 severe thunderstorms on July 16 and again on July 22 lodged the entire field and resulted in some grain loss. In 1981 a heavy area-wide infestation of Barley Yellow Dwarf Virus apparently had a major impact on grain production. Despite this infection, overall yieldof the Korwood oat cultivar in 1981 was substantially greater than that for 1980 with a mixed Korwood/Mariner cultivar.

Analysis of variance revealed no significant

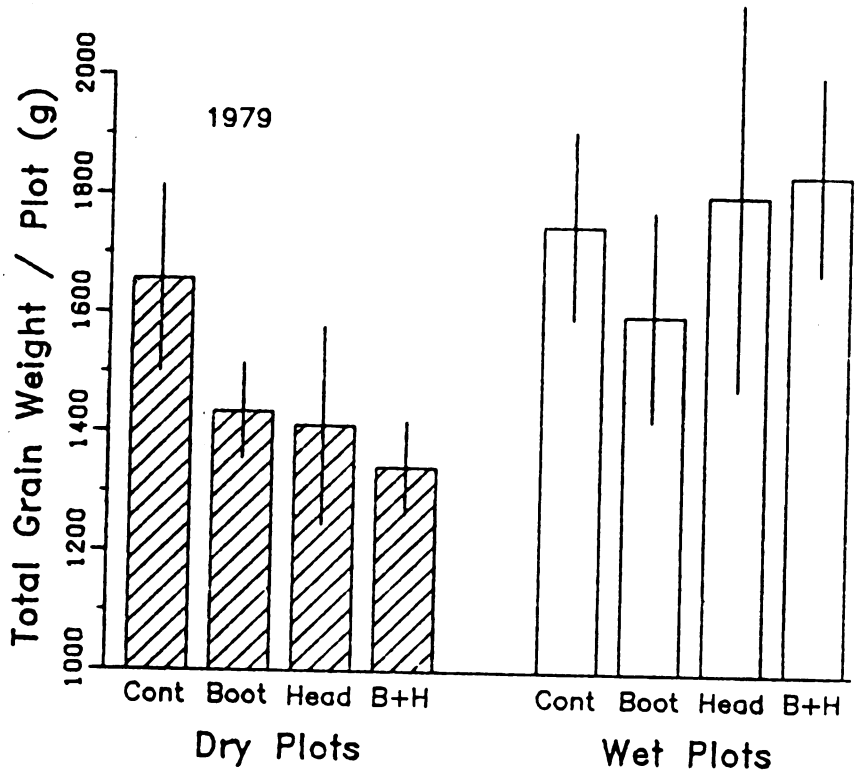


Figure 16. Influence of water and CLB defoliation stress on Korwood oat grain yield (g±SE) projected to 3.0x3.7 m plots in 1979 (n=3 Control; n=6 all others).

difference in total grain weight due to CLB defoliation but, as expected, a difference due to water treatment, even in these small plots, was found significant (P=.07). The mean grain weight in the irrigated plots was 1676.5 g (SE=84.8) while that in the dry plots was only 1434.4 g (SE=58.2) (Figure 16). Multiple correlation analysis showed that kernel weight was significantly related to the number of heads harvested and the stem weight by the following equation:

$$KWT\ (g) = 0.6625(HD) + 0.294(SWT) + 8.1442\ (r^2 = .57)$$

where KWT is kernel weight, HD is the number of heads and SWT is stem dry weight at harvest. The coefficient of determination indicates the relatively poor fit of this highly significant (P<.001) relationship. Other variables entered but not included in this stepwise multiple regression were water stress, defoliation and the number of stems and plants per harvested row.

Forty individual heads from each plot were harvested, hand threshed, and the number and weight of the florets from each panicle recorded. Again, an analysis of variance showed a difference due to water treatment (weight: P=.08; number: P=.025) (Table 8) but not to defoliation (Figure 7).

In 1979, the number of florets per panicle was related

Table 8. Influence of water and CLB defoliation treatments on mean number of florets and mean weight of kernels (mg) in Korwood oats in 1979 (n=40).

Plot	Number*	Weight
Water Treatments		
Dry Control	24.25 a	1.41 a b
Dry Boot & Heading	24.37 a	1.41 a
Dry Heading	25.84 a b	1.50 a b
Dry Boot	26.38 a b	1.52 a b
Wet Plots	26.88 b	1.58 b
Defoliation Treatments		
Control	26.88 a	1.570 a
Boot	26.01 a	1.503 a
Heading	26.65 a	1.551 a
Boot & Heading	25.29 a	1.499 a

* Means followed by same letter are not significantly different by Duncan's Multiple Range Test (P=.05)

to total panicle grain weight by the following equation:

$WT\ (g) = 0.06326(NUM) - 0.1268\ (r^2 = .65)$

where WT is grain weight and NUM is the number of florets per panicle.

In 1980 (Figure 17) significant differences in total grain weight were due to water treatments ($P<.001$) and to the interaction of water and the timing of stresses ($P<.01$). By comparing each treatment independently with the control plots, the effect of CLB defoliation under varying water regimes was compared. Grain weight between the dry control plots and the wet control plots was significantly different ($P<.02$) as expected. However, total grain weight in the dry boot plot which was severely water and beetle stressed through the boot stage, was significantly greater than the dry plot controls at the 10% level. What is most important however is that the yield from these same stressed boot plots was not different from the wet control plots which were well irrigated throughout the season but not defoliated.

As expected from these results then, comparison of the wet control plots with the irrigated and defoliated plots at boot stage showed no differences. Nor were there any differences between the wet boot treatment with the dry boot treatment. However, significant differences were

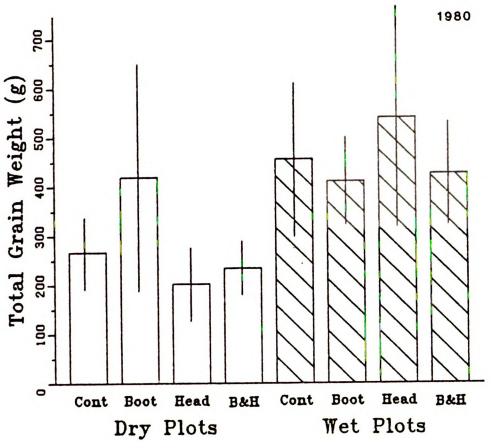


Figure 17. Influence of water and CLB defoliation stress on Korwood/Mariner oat grain yield (g±SE) from 3.0x3.7 m plots in 1980 (n=3).

obtained when the other defoliation treatments were compared across wet vs. dry plots. Within the two water treatments, however, there was no difference in grain weight from the non defoliated control plots.

In conclusion, CLB defoliation had very little, if any, affect on total grain weight in 1980. The only differences observed were directly attributed to the supply of water available. Indeed, even after major defoliation and severe water stress, irrigation at heading was sufficient for full recovery.

Individual stems which had been measured throughout the season were harvested and stepwise multiple regression techniques employed to determine associations of many variables with total kernel weight, number of kernels per panicle and number of florets per panicle. Variables tested included blade area, sheath area, 1000 kernel weight, percent defoliation, soil moisture at 15 and 30 cm integrated over the whole season, or only during the preanthesis period or the postanthesis period. Neither total kernel weight nor the number of florets per panicle showed any linear relationship with these variables on a single stem basis. However, the number of kernels per panicle was slightly associated with soil moisture (P=.075):

$$NKER = 71.8 - 0.0156(SM30) + 0.0121(SM15) \quad (r^2 = .15)$$

where NKER is total number of kernels per panicle, SM30 is the soil moisture at 30 cm integrated over the whole season, and SM15 is the integrated soil moisture at 15 cm over the season. With such a low coefficient of determination, little reliability can be ascribed to this equation.

Two way analysis of variance showed that kernel weight, number of kernels per panicle and number of florets per panicle were not related to either the water or defoliation treatments in 1980. However, blade and sheath area and 1000 kernel weight were significantly different among treatments ($P<.001$). The result of a Duncan's Multiple Range Test is shown in Table 9 for 1000 kernel weight.

Total plot yield in 1980 was described through stepwise multiple regression for the following variables: blade area, sheath area, and soil moisture at 15 and 30 cm for both the pre- and post-anthesis periods. All values were integrated over the season for each replication. The following equation describes the association of these variables with yield ($F=12.13$; $P<.001$; $r^2 = .82$):

$$YLD\ (g) = 170.0+0.235(Post15)+0.0125(SA) -0.2111(Pre15)-0.1223(Post30)$$

where YLD = total plot yield, Post15 and Post30 =

Table 9. Influence of water and CLB defoliation treatments on the mean 1000 kernel weight of Korwood/ Mariner oats in 1980.

Defoliation Treatments			Water Treatments		
Plot	Mean*		Plot	Mean	
Boot & Heading	23.6	a	Dry Control	23.68	a
Heading	24.7	b	Boot & Heading	23.33	a
Control	25.0	b c	Dry Boot	27.62	c
Boot	25.9	c	Dry Heading	25.13	b
			Wet Plots	24.86	b

*Means followed by the same letter are not significantly different by Duncan's Multiple Range Test (P=.05).

integrated soil moisture at 15 or 30 cm depth either pre- or post-anthesis, and SA = integrated sheath area. It is interesting to note that blade area was not significantly associated with yield in 1980.

In 1981, defoliation and water stress treatments were well maintained, cf. Figure 9, and plant growth for the most part expressed these treatment conditions. But total plot yield was extremely variable among replications (Figure 18), though greater than in 1980. Analysis of variance showed no significant differences among plots due either to CLB defoliation or water stress for kernel weight, number of kernels per panicle, number of florets per panicle, or even the total blade and sheath area. The primary reason for these results appears to be that a severe infestation of BYDV affected floral development and eventual yield.

Though total plot yields showed no significant associations with individual variables, individual plant yields did. The following stepwise multiple regression equations were found for kernel weight (KWT), number of kernels (NKER) and number of florets (NFL) ($P<.001$):

$$KWT\ (g) = 42.21(BA)-0.388(SM30)+0.372(SM15)\ (r^2 = .74)$$

$$NKER = 1.558(BA)+0.259(TV)-0.0162(SM30)+0.0165(SM15)-27.09\ (r^2 = .75)$$

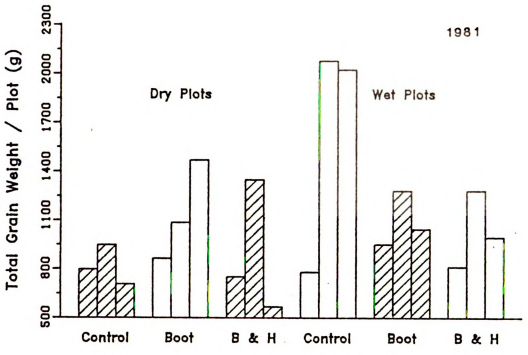


Figure 18. Influence of water and CLB defoliation stress on Mariner oat grain yield (g) from 3.0x3.7 m plots in 1981 for all three treatment replications.

$NFL = 0.636(BA)+0.098(BV)-6.261$ ($r^2 = .63$)

where BA = integrated blade area over time, SM15 and SM30 = soil moisture at 15 and 30 cm respectively, TV = percent chlorosis from BYDV over the whole plant, and BV = percent chlorosis from BYDV on blades alone.

Thousand kernel weight was influenced by water stress ($P<.05$) and not by defoliation effects ($P>.1$). In contrast to the 1980 data, the thousand kernel weight was greater in the irrigated plots ($\bar{x} = 25.56$) than in the dry boot plots ($\bar{x} = 24.7$), though not significantly different.

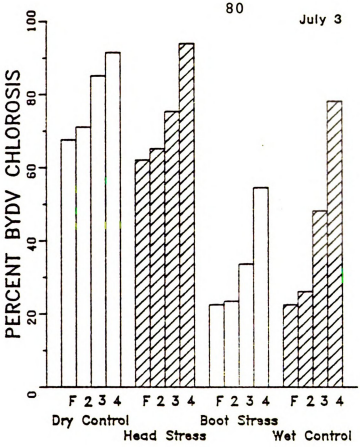
Effects of Barley Yellow Dwarf Virus (BYDV) : In 1981 the oat fields at KBS were subjected to an extreme epidemic of BYDV, red leaf. Although slightly red leaves were observed early in the season, the plants seemed to outgrow the virus. The population of aphids, the only known vector of BYDV, was relatively small compared with previous years so no control measures were deemed necessary. By July 3, however, leaf reddening and chlorosis suddenly became very intense despite the natural decline of the CLB population. Figure 19 shows the estimated percent leaf chlorosis on July 3 and July 7, 1981. Thirty plants per plot were harvested on both dates and the percent chlorosis estimated by eye for the top four leaf blades, leaf sheaths and the head.

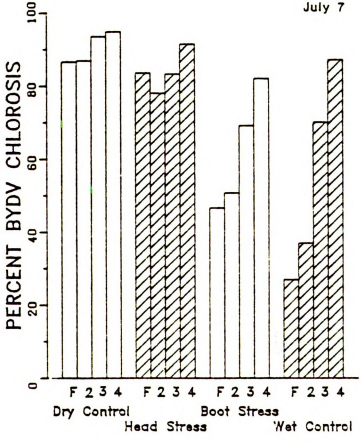
Under the variable conditions of our water and defoliation stress treatments, the symptoms of BYDV first appeared in the water deficient plots. The virus symptoms appear first on the bottom leaf blades and gradually move towards the head (Figure 19). It is difficult to determine what affect the virus had on the growth and yield of the oat plants in 1981 since there were no unaffected areas in this or adjoining fields. It is not known how or if the stress imposed by the systemic virus interacts with that caused by CLB defoliation.

Of interest is the apparent resistance to BYDV symptom expression in the boot stress plots which were previously defoliated by CLB and deprived of water until heading. As seen in Figure 19 the amount of chlorosis in these plots was substantially less than not only the dry plots but even less than that expressed in the wet control treatment. This would indicate that the previous stress caused the plants to be unresponsive to subsequent stresses.

This virus is known to cause blasting of florets rendering them sterile (Bruehl 1961). A 5-25% loss of grain can usually be attributed to the presence of this disease. Harper et al. (1976) have shown that viruliferous aphids carrying BYDV on oats reduced plant height, leaf width, yield of forage, yield of protein, percent and yield of total nonstructural carbohydrates and the yield of plant

Figure 19. Influence of water treatment and leaf position on percent leaf blade chlorosis caused by Barley Yellow Dwarf Virus on July 3 and July 7, 1981.


July 3
PERCENT BYDV CHLOROSIS
0
20
40
60
80
100
F 2 3 4 F 2 3 4 F 2 3 4 F 2 3 4
Dry Control
Head Stress
Boot Stress
Wet Control


July 7
PERCENT BYDV CHLOROSIS
0
20
40
60
80
100
F 2 3 4 F 2 3 4 F 2 3 4 F 2 3 4
Dry Control
Head Stress
Boot Stress
Wet Control

cell wall constituents.

Multiple correlation analysis of kernel weight from infected plants (KWTV) on ten different variables showed a definite relationship with the total plant virus and the soil moisture at 30 cm according to the following equation:

$$KWTV\ (g) = 2163. - 8.75(V) + 0.094(SM30)\ (r^2 = .22)$$

where V is the percent of total plant chlorosis and SM30 is the soil moisture at 30 cm. Kernel number (KNUM) was correlated again with virus infection levels on the blades and sheaths as well as soil moisture.

$$KNUM = 2178. - 7.92(VBL) + 0.23(E30) - 2.62(VSH)\ (r^2 = .24)$$

where VBL is the percent chlorosis on the leaf blades, VSH is the percent chlorosis on the leaf sheaths and E30 is the integrated soil moisture during the early part of the year, i.e. pre-anthesis, at 30 cm. There is little question that BYDV severely affected yield in all the plots in 1981 and thus, confounded the treatment effects.

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VII. WATER RELATIONS OF OATS

A. Introduction

Because most readers of this thesis are probably not familar with the terminology and concepts of plant water stress, a brief summary of water relations and its affect on small grains in particular will be presented.

General Principles : The general responses of vascular plants to water stress are documented in reviews by Slatyer (1967,1969), Hsiao (1973), Kramer (1969) and Kozlowski (1968,1972) and more specifically for wheat and barley crops by Frank and Harris (1973), Lawlor (1973), Nordin (1976), Simmelsgaard (1976), Kaul (1966), Asana and Basu (1963), Angus and Moneur (1976), Aspinall (1965), Aspinall et al. (1964), Biscoe et al. (1976), Johnson et al. (1974), Johnson and Moss (1976), Millar and Denmead (1976), Pandey (1972) and Wardlaw (1967). In contrast, relatively little work has been conducted on the response of oats to water stress (Salim et al. (1965), Sandhu and Horton (1977 a,b), Tetley and Thimann (1974) and van der Paauw (1949).

The process of evapotranspiration, i.e. the summed loss of water from the soil plus that lost by transpiration from a crop canopy, is an energy dependent process relying on the latent heat of solar radiation for the vaporization of water. Secondary sources of heat include the scattered

and reflected radiation from sky and clouds as well as the sensible heat of adjacent physical materials, e.g. crop, air, soil.

Potential evapotranspiration, the loss of free standing water from an open surface, which is dependent upon air temperature, relative humidity and vapor pressure, is a primary factor affecting the transpiration rate of a plant. However, the plant in contrast to the soil is able to regulate to some extent the amount of water lost from its surfaces through stomatal and cuticular resistances in the water pathway. The amount of water lost from a leaf is subject to Graham's Law of the diffusion of gases in air which requires that for every gram of CO_2 gained, approximately 100 grams of water must be lost. This is termed the transpiration or water use efficiency.

Water which moves through the soil-plant-atmosphere continuum does so along a gradient of decreasing water potential from the soil, through the plant and into the atmosphere (Weatherley 1965, Slatyer 1967, Kramer 1969). The driving force which causes the plant to absorb water from the soil against gravitational and frictional resistances is the evaporation of water from the leaf (Jarvis 1975). The rate of water lost through transpiration controls the rate of water uptake (Kramer 1956).

Plant water deficits develop as a result of the evaporation of water from leaf mesophyll cells causing a drop in the water potential of the cell wall matrix adjacent to the air-liquid interface. This drop in potential causes the movement of water along a gradient from an area of higher potential to an area of lower potential. The frictional resistances along which the water must flow cause the potential gradient throughout the plant. The driving force for movement of water from adjacent tissues is the lowered water potential caused by the transpirational loss. A water deficit, then, is the inevitable result of water flow against frictional resistances within the plant as well as gravitational pull. Water deficits will occur despite the fact that transpiration will exceed, be equal to, or be less than water uptake by the roots which is dependent on the state of internal equilibriums.

The water in the plant is seldom in equilibrium with that in the soil since the only way for the plant to extract soil water is if the water potential of the plant is lower than that of the soil. At night when transpiration has ceased and stomata are closed, water deficit recovery occurs. The water potential of the soil, then, merely sets a limit as to the amount of recovery from transpirational water loss that is feasible (Slatyer

1967).

Total leaf water potential (LWP) is composed of four parts:

1. The osmotic potential (OP) due to the presence of dissolved solutes;
2. The turgor potential (TP) due to pressure acting outward on cell walls and internal membranes resulting in growth;
3. The matric potential (MP) due to capillary forces and molecular imbibitional forces associated with cell walls and colloidal surfaces;
4. The gravitational potential (GP) due to gravitional forces on the plant water.

Therefore,

$$LWP = OP + TP + MP + GP$$

where the terms are defined as above and OP, MP, and GP are negative forces and TP is positive. Gravitational potential is normally considered insignificant and can be deleted from the equation.

Under a water deficit, TP approaches zero (incipient wilting) while the osmotic and matric forces decrease. In tissue which is fully turgid, MP approaches zero as the osmotic and pressure potentials interact as functions of

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It is intuitively apparent that at a low relative water content (RWC), i.e. the amount of water in the tissue compared with that at full turgor, the turgor potential will approach zero since the membrane of the cell shrinks away from the cell wall, i.e. incipient plasmolysis. In this case LWP will equal the OP. But under a high RWC, the turgor pressure necessary for growth may be maintained without any apparent change in the LWP by an alteration of the OP, the solute concentration of the cell.

In other words, at a given total water potential, a plant may be wilting or turgid depending on the osmotic potential. Goode and Higgs (1973) and Biscoe (1972) have reported compensation to water deficits by osmotic adjustment while Meyer and Boyer (1972) found osmotic compensation that caused tissue osmotic potential to change as much as the water potential in soybean hypocotyls. In wheat, LWP and OP were lower and TP higher in plants grown with a low root potential (Simmelsgaard 1976).

Osmotic adjustment can occur in two ways (McMichael 1980). Firstly, tissue dehydration can cause a concentration of a cell's solutes lowering OP. Secondly, tissues may accumulate solutes by absorption or synthesis to lower OP and maintain TP. This is termed osmoregulation. The primary compounds contributing to

osmotic adjustment seem to be soluble carbohydrates (Iljin 1957).

In many cases, however, solute accumulation and concentration are of insufficient magnitude to account for the adaptive responses observed. Maintenance of turgor in plant tissues may be due to changes in tissue elasticity through alterations in cell volume and cell wall thickness (Steudle et al. 1977, Cutler and Loomis 1977). Cutler and Rains (1978) have shown that in preconditioned cotton leaves there was less water per unit dry weight than in unconditioned controls. The low OP could not be accounted for by solute accumulation.

It has been demonstrated (McCree 1974, Thomas et al. 1976, Jones and Turner 1978) that stomatal closure occurs at lower water potentials in preconditioned plants than in non-conditioned plants. Brown et al. (1976) and Ludlow and Ng (1976) showed that this is due to osmoregulation by solute accumulation in the guard cells causing photosynthesis to continue at lower leaf water potentials in preconditioned plants (see also Ashton 1956, Blum and Sullivan 1974).

Effects of Water Deficits : The effects of water deficits on plant growth are discussed by Hsiao et al. (1976) who noted that the most sensitive process to water stress is cell growth. Any reduction in tissue water potential would

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cause a decrease in cell growth while a deficit of 3-4 bars would reduce turgor and stop cell growth completely (Boyer 1968, Acevedo et al. 1971).

It is generally believed that most annual determinate crops such as small grains are most sensitive to water stress at the time of floral initiation and flowering (Slatyer 1969, Boyer and McPherson 1975). Begg and Turner (1976) indicated that stress prior to heading can reduce tillering and the number of heads that emerge while Slatyer (1973) emphasized that water stress at flowering caused a reduction in the number of primordia and developing florets.

In wheat, Fischer (1975) showed that stress during the boot stage resulted in fewer grains per spikelet. A reduction of the photosynthetic surface area of leaves due to water stress could lead to decreased yield. Fischer and Kohn (1966) have shown an inverse correlation of wheat yield and the rate of senescence after anthesis induced by soil moisture deficits. Moreover, in maize a leaf water potential of -18 to -20 bars decreased the rate of photosynthesis to 15% or less of well watered control plants (Boyer and McPherson 1975). These authors emphasized that no symptoms of desiccation were apparent other than a slight gray cast to the leaves and therefore that visual symptoms, if they occur, may appear after a loss of

photosynthetic activity.

The decrease in net photosynthesis due to water stress is normally accompanied by a decrease in the transpiration rate due to stomatal closure. Though Hsiao (1973) has interpreted the decline of both processes to be due to stomatal closure, Boyer (1971b), Fry (1972) and Keck and Boyer (1974) have found that photosynthetic inhibition is at the chloroplast level rather than due to stomatal closure.

Recovery from water stress upon rewatering can be complete if the stress was of short duration and mild (Boyer 1971a). Under severe stress, however, two types of aftereffects are possible during recovery. First, an incomplete recovery of leaf water potential may result from a break in the water column causing increased resistance in the water transport system. If this resistance increases enough, leaf desiccation and death may continue despite rewatering. However, partial rehydration may lead to a decrease in water resistance over a number of days with gradual return to normal hydration.

The second aftereffect is reduced photosynthesis after full hydration following rewatering (Boyer 1971a). Chloroplast recovery may require 12-15 h while stomatal apertures may remain reduced for days. For sunflower plants, older leaves may never recover all oftheir prior

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photosynthetic activity and only new plant growth would return the plant to former levels (Boyer 1971a). Brown et al. (1976) found that prestressed cotton plants maintained a low stomatal resistance of the abaxial leaf surface through osmoregulation of the guard cells. However, a similar adjustment was not found on the adaxial leaf surface.

Boyer and McPherson (1975) related that a stress pretreatment dramatically improved the yield of desiccated maize plants over those without a pretreatment. Yield was 68% of control plants but photosynthesis during the grain filling period was only 37% of the control. They concluded that plants can adapt to desiccation to preserve grain formation and can mobilize photosynthates produced before the grain filling period and use them to fill the grain.

Historically, the majority of the yield was thought to be contributed by current assimilates during the grain filling period (Thorne 1966). Gallagher et al. (1975) found in barley grown under water stress that up to 70% of the final grain yield was translocated from the stem. Yoshida (1972) cited several studies with rice showing that up to 40% grain weight was translocated from the stem. Wardlaw (1967) also found that to compensate for the loss of flag leaf photosynthesis, wheat translocated assimilates from the stem and lower leaves to the grain. Finally,

Passioura (1976) has shown that in severely stressed wheat plants grown on stored water only one third of the final weight was from current assimilates fixed after anthesis but two-thirds was due to redistribution post anthesis of assimilates acquired earlier.

Yield of small grains growing predominantly on stored water is highly correlated with the amount of water available in the soil at anthesis (Nix and Fitzpatrick 1969). When water is limited, rapid growth due to application of a fertilizer or rotation after a leguminous crop can deplete the soil moisture reserves available during the grain filling period thus reducing yields (Passioura 1976). Fischer and Kohn (1966) showed that nitrogen application increased leaf area available for evapotranspiration during the vegetative phase and reduced the available soil water at heading. In contrast, plants grown on limited soil water rely mostly on deep seminal roots to provide water since the nodal roots at the soil surface develop little if at all under dry top soil conditions. The large hydraulic resistance in the vertical flow of water through a single xylem vessel restricts the amount of water available for growth and, as a result, the plant slows its growth rate. However, the leaf water potential and stomatal resistance in a plant forced to rely on even a single root are no different from those of a

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plant with a full complement of roots. Therefore, the plant's water use is controlled through size (Passioura 1976b).

B. Materials and Methods

Plant water stress was monitored by pressure chamber techniques using a PMS Instrument Company pressure chamber and a Soilmoisture plant water status console (Model 3005). Pressure of N was increased at a rate of 0.03 bars/sec to prevent cell damage and to allow pressure equilibration of plant tissues (Ritchie and Hinckley 1975). Leaf water potential (LWP) was measured by leaf position at the leaf ligule and at mid-blade under various CLB defoliation and soil moisture treatments.

In 1979, stomatal diffusive resistance was recorded in sito with a Lambda LI-65 autoporometer with a 3.5 x 20 mm aperture. Field measured Δt were not converted to standard conditions because of errors in measuring leaf surface temperatures. These temperatures were therefore assumed to be the same as ambient air temperatures.

Twenty plants were harvested weekly, transported in plastic bags to the laboratory and their leaves separated into groups by position. The wet and dry weights of these leaves were measured and the leaves subsequently ground in a Wiley mill. Nitrogen content of leaf material was

measured in 1979-1980 by a C-H-N gas analyzer and in 1981 by a micro-Kjeldahl procedure (Rimpau 1978) using a Technicon Autoanalyzer.

C. Results and Discussion

Leaf Water Potential : The LWP of oats followed a typical diurnal pattern in response to fluctuations in transpirational water loss with plants subjected to water stress treatments showing a 4-5 bar deficit compared with well watered control plants (Figure 20). Recovery was slower in the stressed plants but eventually attained the same turgor pressure as the control plants. In oats, LWP is heavily correlated with leaf position (Figure 21) emphasizing the potential gradients throughout the plant and increases basipetally. Thus LWP of a given organ is not directly proportional to the transpiration of that organ. The flag leaf has the lowest LWP providing through it the driving force for the upward mobility of water (Slatyer and Gardner 1965).

Millar et al. (1968) reported that for greenhouse grown barley the difference in LWP between top and bottom leaves of potted plants in soil near field capacity was 16.5 bars while that for plants grown near the permanent wilting point was only 5.6 bars. In contrast, our data for field grown oats sampled throughout the season show no such

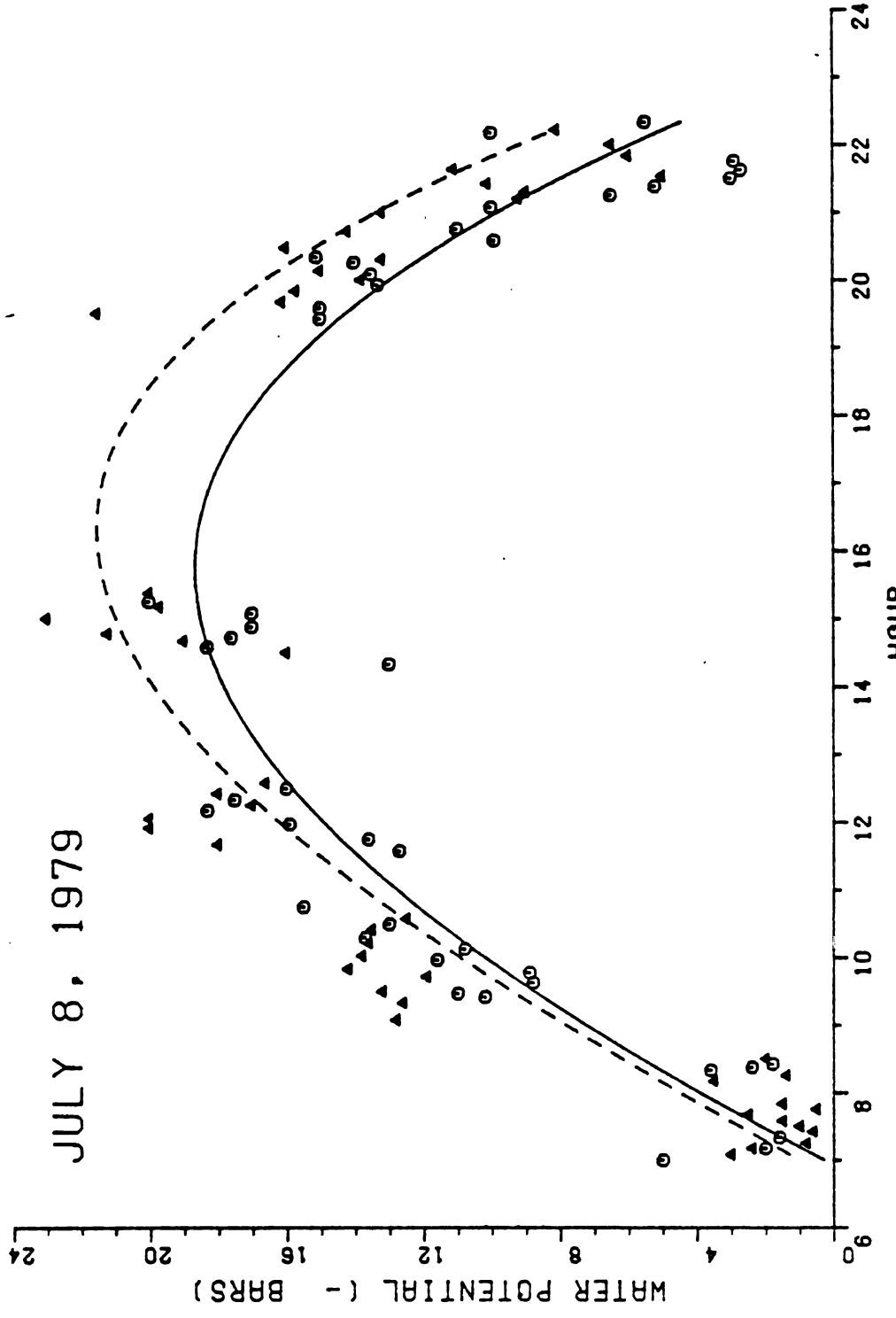

Figure 20. Leaf water potential (-bars) by hour of day for July 8, 1979. Triangles: dry plots; circles: wet plots.

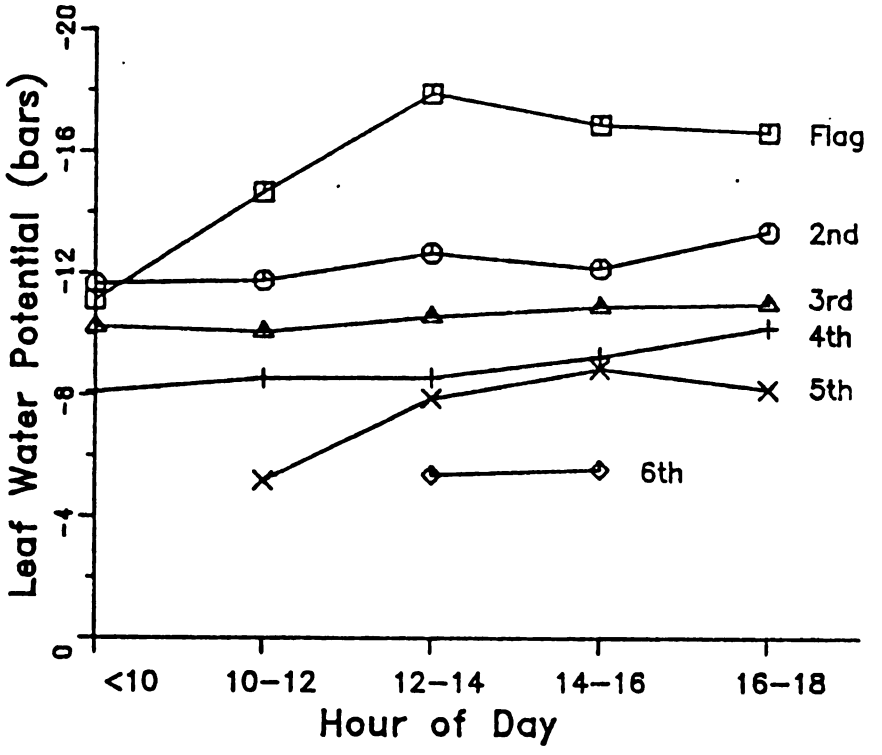

Figure 21. Mean leaf water potential (-bars) over the season by hour of day for each leaf position.

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disparity among water treatments (P>.05) permitting a pooling of treatment means (Figure 22). Never did the lowermost leaves of our field plants under the driest of treatments attain LWP approaching -25 bars as did the pot grown plants of Millar et al. (1968). Nor did the flag leaves in our experiments attain an average -33 bars. Perhaps the unnatural conditions of the pot experiments in which plants were subjected to relatively sudden drought after field capacity conditions effected the results reported (Begg and Turner 1976). Plants which experience a gradual drying were more hardened and acclimated to their growing conditions and had the time to compensate through root structure modifications, osmotic changes or stomatal control to attain internal water balance and turgor pressure integrity. Figure 22 shows the difference in LWP between the flag leaf and the three successively lower leaf blades of oats. The difference in LWP increased with time as the season warmed and transpirational water loss from the panicle increased. Denmead and Millar (1976a) showed how transpiration from the ear of wheat plants contributed to the low LWP of the upper leaf blades. The dramatic dip at DD 735 reflects an increase in LWP in response to cool climate (maximum of 22C vs. 31C the previous day) and precipitation on June 16, 1981. The dramatic decline in the differential after DD 930, June 29, was probably due to

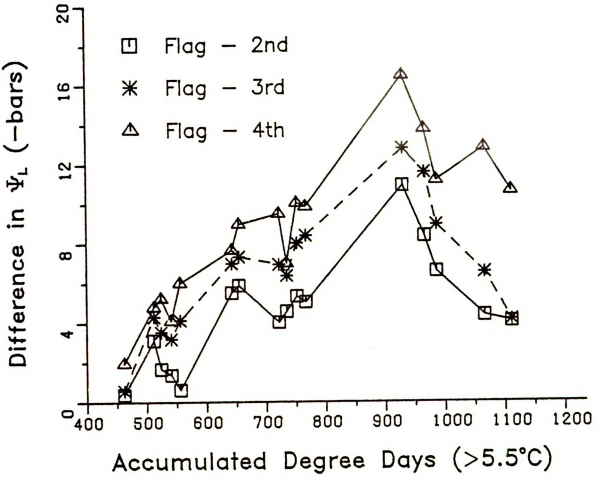


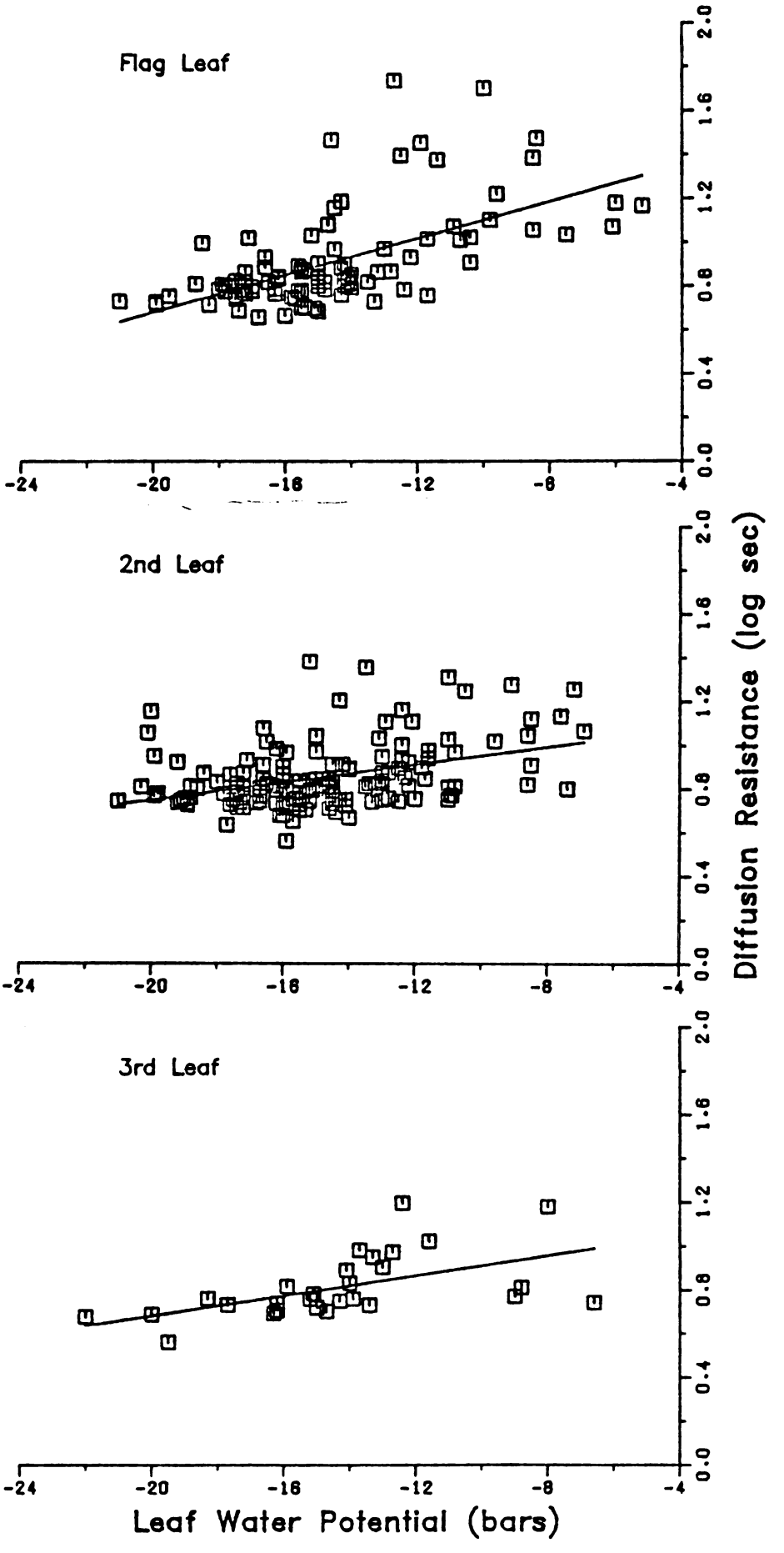
Figure 22. Difference of leaf water potential of the flag leaf blade of oats and the three successive leaves below it on accumulated degree days in 1981.

increased senescence and the manifestation of BYDV at this time (Figure 19).

It was hypothesized that flag blades defoliated by the CLB might show a decreas in LWP and TP, and that the lower leaf blades might compensate to this injury by an increase in their own LWP. One-tailed Students-t tests showed that the CLB decreased the LWP of leaves subjected to more than 40% feeding ($P<.05$). However, the lower leaves did not statistically show any compensation for this effect in their LWP. In fact there was significantly more stress ($P<.05$) among lower leaves which had greater than 70% flag leaf defoliation than those with less than 40% flag leaf defoliation. This may have been because plants with heavy flag leaf defoliation often have defoliation of the lower blades as well, albeit substantially less, which may cause a decrease in lower blade LWP. These results were the same regardless of water treatment or plant phenology.

As water is evaporated from the leaves through transpiration, the leaf water content and leaf water potential are lowered decreasing plant turgor (Figure 23). Small decreases in turgor have little effect on stomatal aperture or diffusive resistance. But a critical turgor potential of 8 bars exists for all leaf positions in wheat at which stomata begin to close and resistance rapidly increases (Millar and Denmead 1976). However, these

Figure 23. Leaf diffusion resistance on leaf water potential for the top three leaf blades. Line fitted by least squares regression analysis.


Flag Leaf
2nd Leaf
3rd Leaf
-24
-20
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-4
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Diffusion Resistance (log sec)
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authors found that the osmotic potential in response to higher irradiances at the top of the plant was 60% greater at that position than for turgid leaves at the bottom of the stem. Consequently, despite the similar critical TP at each leaf position at which stomata closed, the LWP at which closure occured decreased from bottom to top of the stem. In this way, stomata of upper blades required a lower LWP before closure and maintained a higher TP through osmotic adjustment when that closure occurred. If osmotic adjustment did not occur differentially with leaf position, the stomata of the flag leaf blade would be the first to close because of the high evaporative demand it must withstand. This is important for a small grain deriving photosynthates from that flag leaf blade.

In oats (Figure 23) diffusive resistance declined with LWP in response to decreased relative water content because of a high evaporative demand and transpirational water loss. However, a critical level was never attained since LDR never increased with decreasing LWP as for wheat (Millar and Denmead 1976). Our lowest LWP attained was -22 bars. Coincidentally, Millar et al. (1968) found that in barley stomates closed at a LWP of -22 bars. This would seem to indicate that a water deficit severe enough to close the stomata was never attained during the 1979 investigation.

Stomatal closure is also temperature dependent. Frank et al. (1973) found that in wheat grown under constant temperature conditions, stomata closed at -13 and -15 bars at tillering and -17 and -26 bars at heading for 18C and 27C, respectively. A general, non quantified observation made July 1, 1980, indicated that stomata were closed in mid afternoon of that day which was cool and cloudy. Mean LWP for flag leaves was -12.2 bars in a dry plot and -9.0 bars in an irrigated plot. The low temperature and cloudy conditions that day may have decreased vapor diffusivity and thus stomatal aperture (Sandhu and Horton 1977, Denmead and Millar 1976b).

Leaf water potential decreased from the ligule towards the blade tip (Figure 24). Measurements of LWP by the pressure chamber method are probably more representative of the whole leaf blade if taken at the mid-blade position. There is normally a 2-3 bar difference between measurements taken at the ligule and those taken at mid-blade. Ligule measurements though not absolutely representative of the whole leaf are adequate relative measurements to compare treatments or leaf position effects.

Defoliation by the CLB decreased leaf water potential. The magnitude of this effect was dependent on blade position and time of year (Figure 25). It is apparent from the decrease in LWP that the flag leaf blade

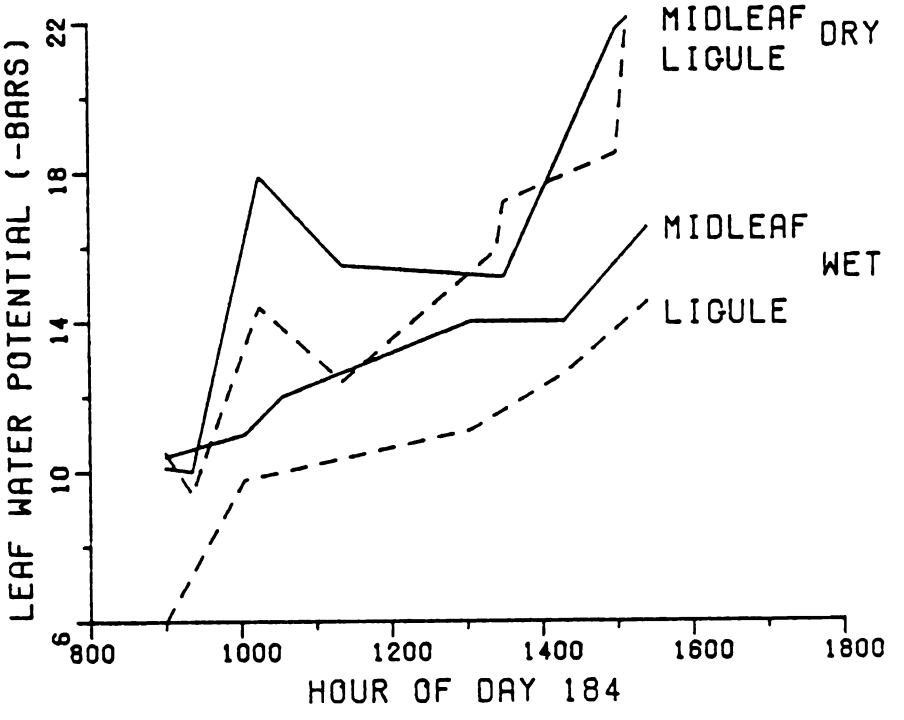
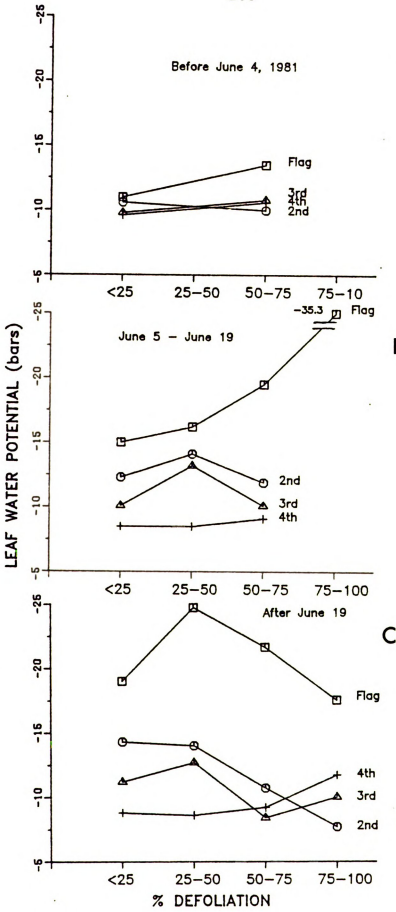


Figure 24. Measurements of leaf water potential by hour of day taken at the ligule and at the mid-blade position in wet and dry plots.

Figure 25. Leaf water potential as a function of percent defoliation by leaf position in 1981 before June 4, from June 4 to anthesis on June 19, and post-anthesis.


A
Before June 4, 1981
Flag
3rd
4th
2nd
B
June 5 – June 19
-35.3
Flag
2nd
3rd
4th
C
After June 19
Flag
4th
3rd
2nd
LEAF WATER POTENTIAL (bars)
-5
-10
-15
-20
-25
<25
25–50
50–75
75–100
% DEFOLIATION

responds more than do the other blades to defoliation pressure. Prior to anthesis on June 19, LWP decreased with increasing defoliation. But post-anthesis, defoliation between 25-49% resulted in the largest leaf water deficit. The diurnal affect of this defoliation in wet and dry plots is seen for four days in 1979 in Figure 26.

Infection by BYDV produced an apparent increase in leaf water potential compared with a non-infected plant (Figure 27). It cannot be assumed that this increase provided any benefit to the plant. On the contrary, it probably signified imminent death of the tissues.

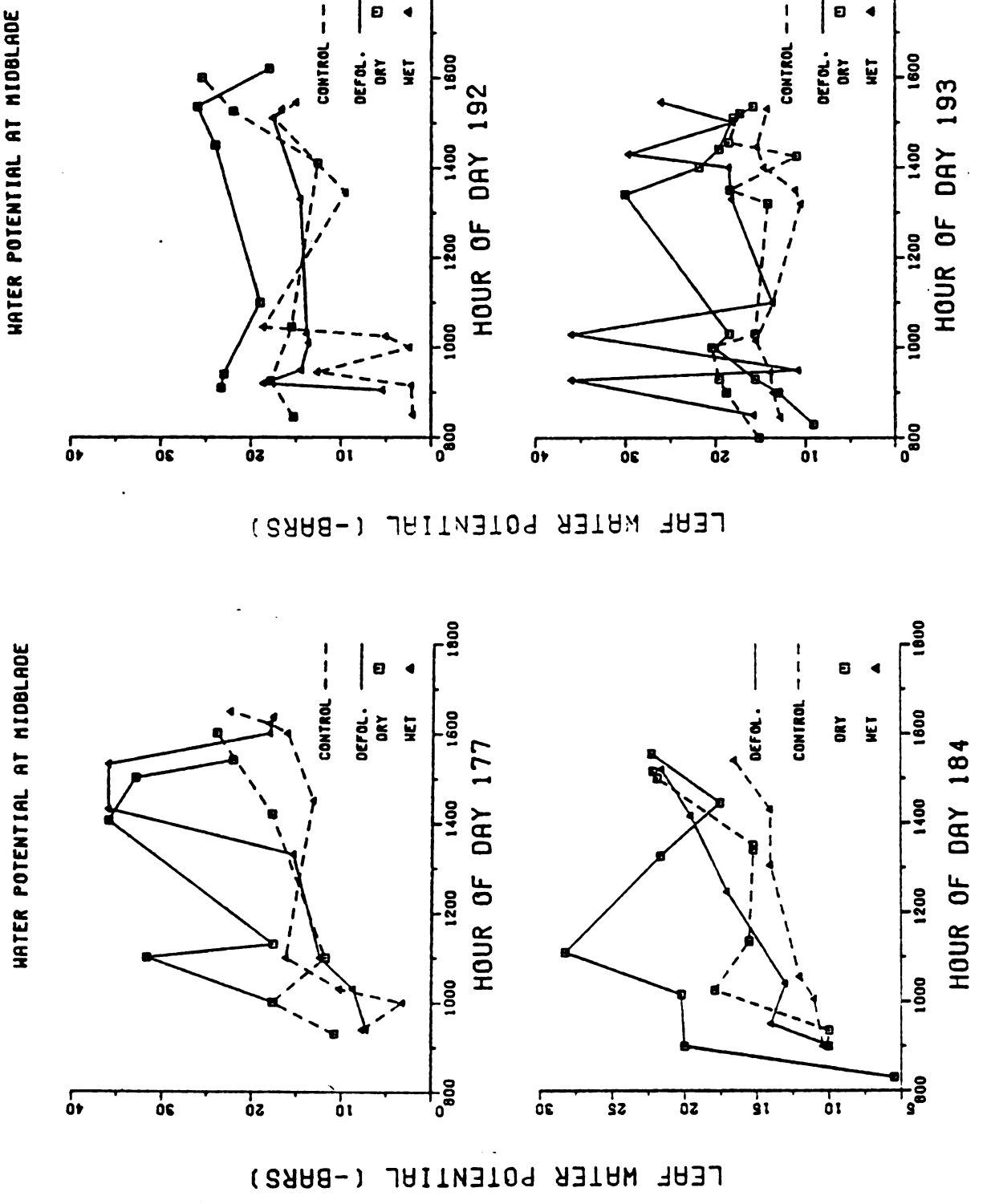
Over the season as the plants grew and matured, LWP decreased. Figure 28 shows that the mean LWP of flag leaves decreased with accumulated degree days. In this seasonal perspective, LWP decreased slightly in response to heavy defoliation in the boot and B&H plots.

Multiple reqression analysis was used to determine which variables best explained LWP during mid-afternoon periods in 1981.

$$\text{LWP (-bars)} = 2.72(\text{POS})-.038(\text{DEF})+.018(\text{SM30})-.0043(\text{T})-.078(\text{DAY}) +.071(\text{TMP})-6.56$$

where LWP is leaf water potential, POS is leaf position (1 = flag leaf, 2 = 2nd leaf, etc.), DEF is percent defoliation of the flag leaf, SM30 is percent soil moisture

Figure 26. Leaf water potential measured at mid-blade for four days in 1979 by hour of day. Defoliated plants are compared with controls in wet and dry plots.


WATER POTENTIAL AT MIDBLADE
LEAF WATER POTENTIAL (-BARS)
HOUR OF DAY 177
HOUR OF DAY 184
HOUR OF DAY 192
HOUR OF DAY 193
CONTROL
DEFOL.
DRY
WET

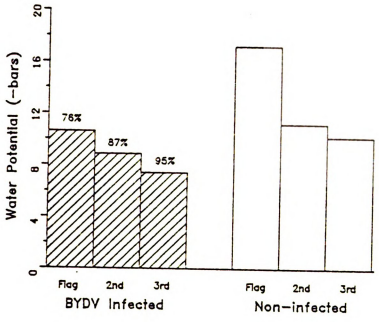


Figure 27. Leaf water potential by leaf position in plants infected (n=6) and non-infected (n=7) with Barley Yellow Dwarf Virus. Mean percent chlorosis is listed above infected bar graphs.

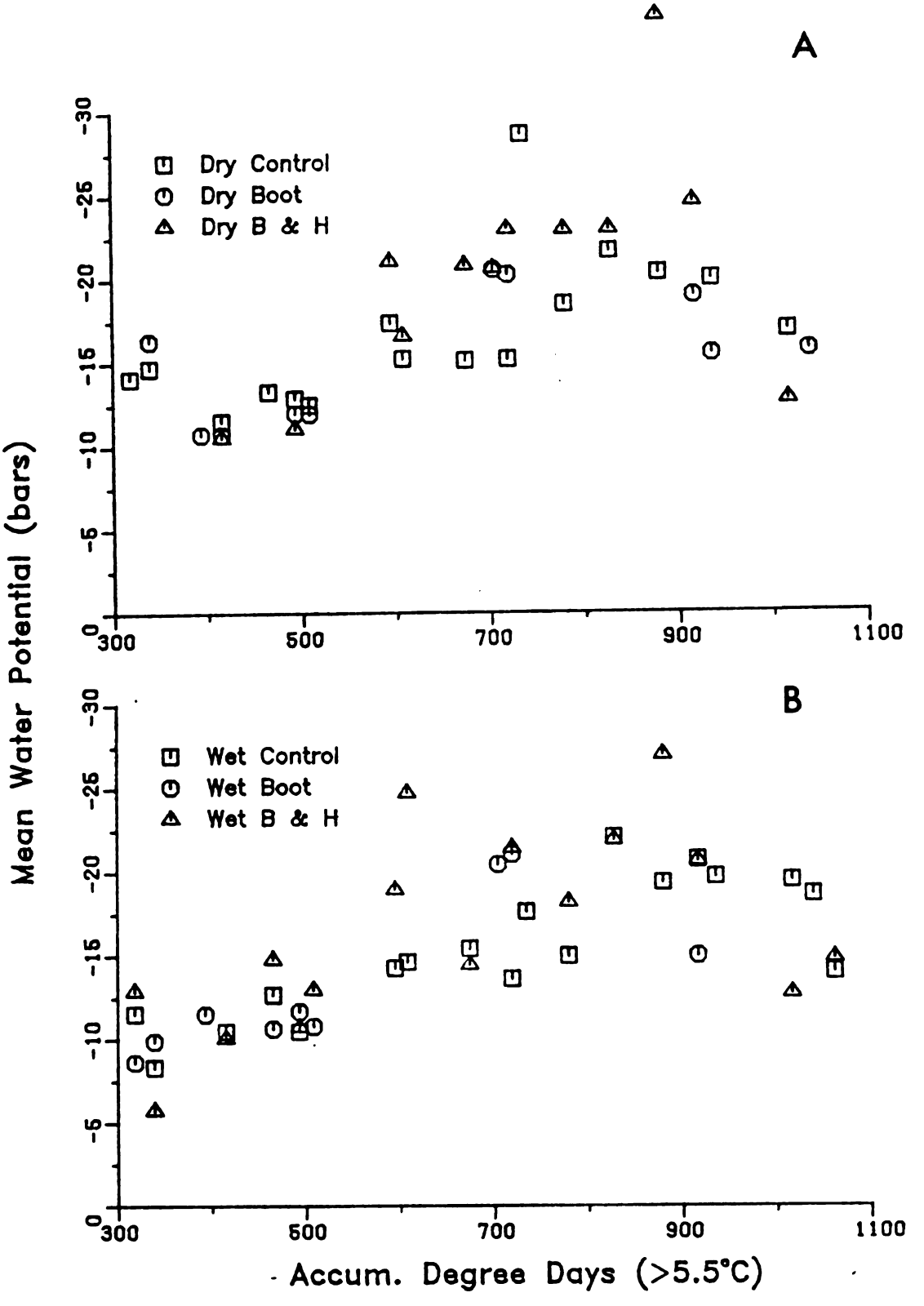


Figure 28. Mean leaf water potential by accumulated degree days in 1981 for A) dry treatment plots and B) wet treatment plots.

at 30 cm, T is hour of day, DAY is julian date and TMP is the maximum air temperature. These six variables explained 45% of the variation in leaf water potential ($F=80$; $P<.001$).

Leaf Water Content: Percent leaf water content was measured to determine whether there was any correlation between feeding preference sites of the CLB and water content. The wet fecal coat which covers the abdomen of CLB larvae might imply the importance of selecting food with a high water content. Examination of Figure 29 shows that in general lower leaf blades of oats had a greater percentage of water than the upper blades. Generally, the flag leaf blade had the lowest water content by weight until late in the season. However, as the lower leaves senesced, their water content declined quickly while the water content of the upper leaves remained great. However, dry conditions caused major declines in this variable even in the flag leaf blades (Figure 29). Since the CLB prefers the upper leaf blades which have a lower water content and since the larvae pupate before they can take advantage of the greater flag leaf water content late in the season, larvae are probably not selecting these leaves based solely on this variable.

The water content per unit area of the leaf blades was generally greatest in the lowest blade examined and least

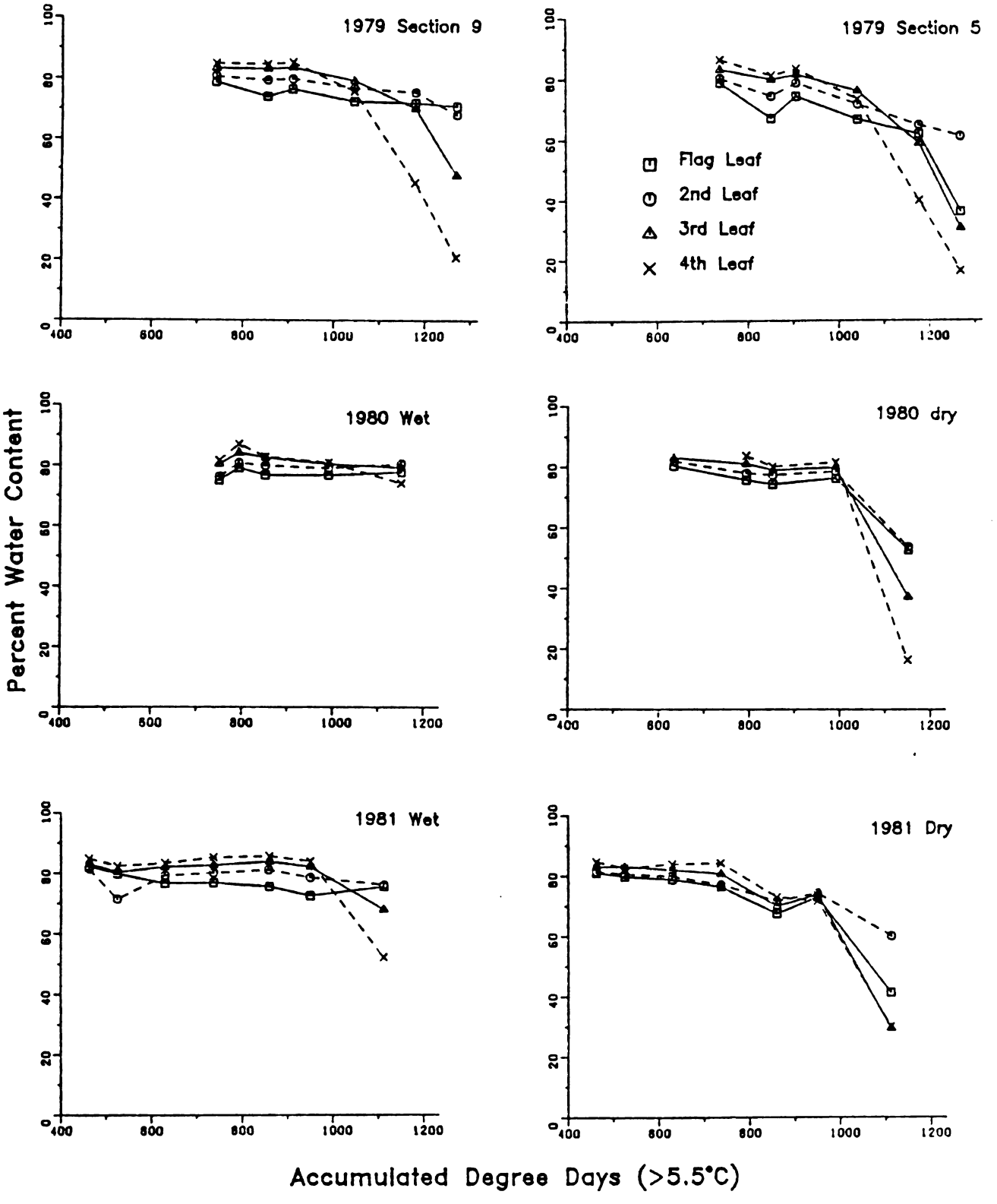


Figure 29. Percent water content of leaf blades by position as a function of accumulated degree days in wet and dry plots from 1979-1981. In 1971, Section 9 was more wet than Section 5.

in the flag leaf (Figure 30). Mean water content of blades in irrigated plots was significantly greater by leaf position than that of blades from dry plots. Data from 1980 (Figure 31 a-b) show this relationship between wet and dry plots. This figure also shows that the water content per unit area in older senescing blades decreased at a faster rate than in younger blades.

Water content per area also decreased with increasing defoliation. Figure 32 shows that 44% of the variation in flag leaf water content was explained by defoliation of these blades. The effect of defoliation on plant water relations was shown dramatically on June 15 and 16, 1981 (Figure 33). On June 15, the maximum air temperature reached 31C and rain had not fallen for five days. Both moderately defoliated and non-defoliated plants showed a fairly equal amount of water stress in response to evaporational demand and subsequent water deficits. That night 6.7 cm of rain fell and the next day, June 16, was cool and cloudy with maximum temperature of 22C. While the LWP for the non-defoliated plants rose due to a decrease in transpirational water loss and turgor potential maintenance, the stress in the flag leaf blades remained high with an average 63% defoliation.

Stomata may respond to water deficits rather suddenly once a certain threshold of water potential or relative

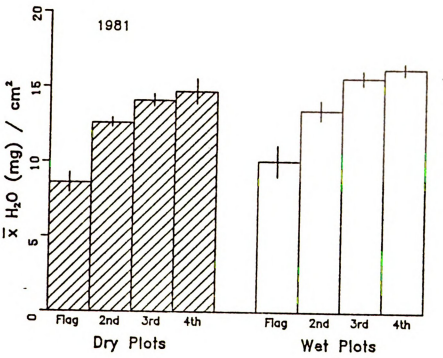


Figure 30. Mean weight of water (mg) per unit area of leaf blades by position in wet and dry plots in 1981.

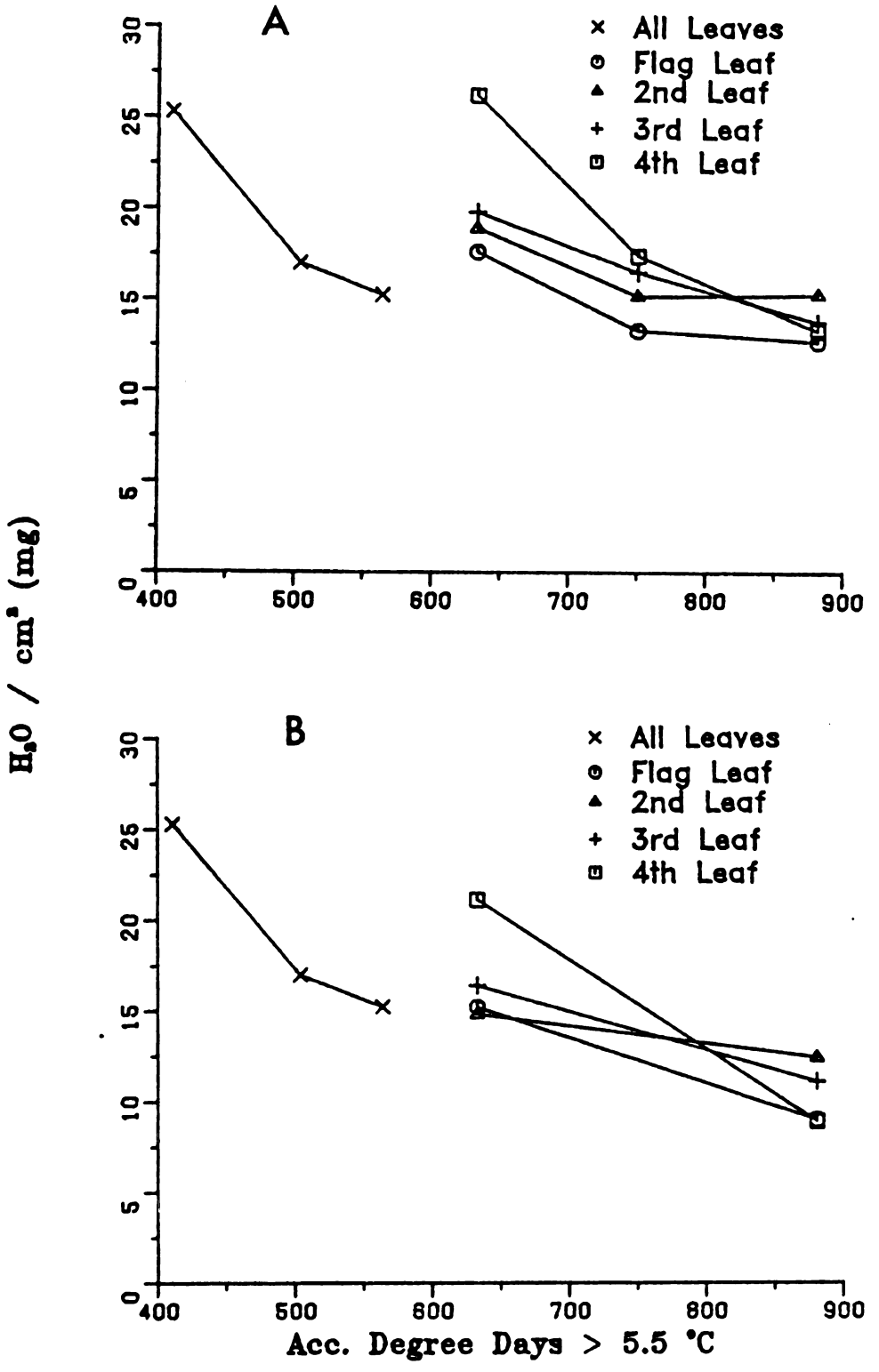


Figure 31. Mean weight of water (mg) per unit area of leaf blades by position in A) wet and B) dry plots in 1980.

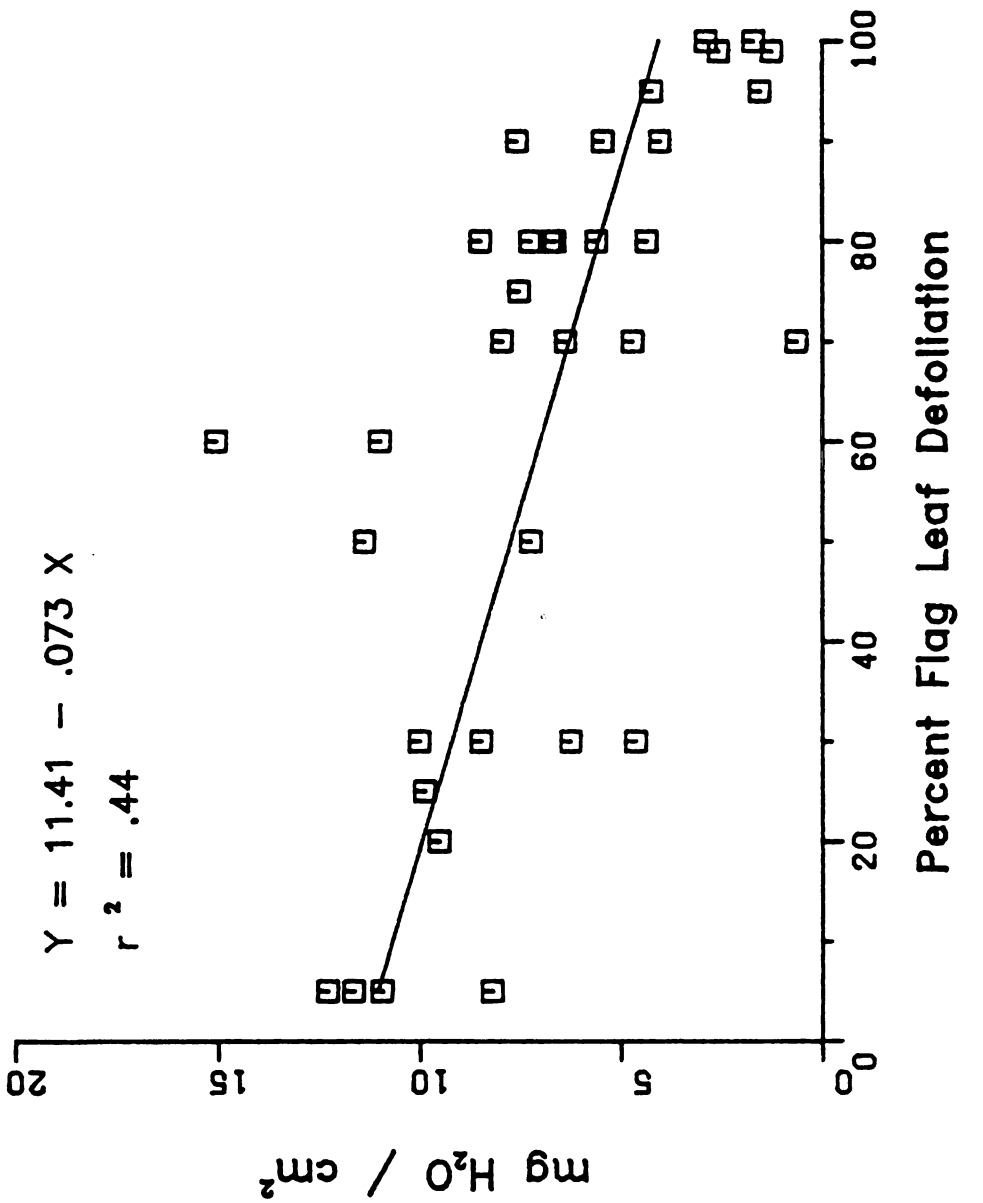
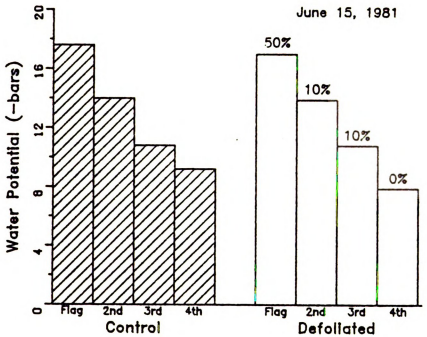


Figure 32. Weight of water per unit area as a function of blade defoliation in 1981.



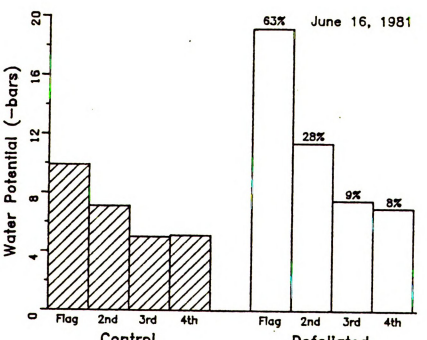


Figure 33. Mean leaf water potential in control and defoliated plants by leaf position for June 15 (n=3-4) and June 16, 1981 (n=3). Mean percent defoliation is listed above bar graphs.

water content has been attained (Begg and Turner 1975). As an example, on June 19, 1979, a warm and sunny day, mean stomatal conductance of upper leaf blades was a fairly low 0.0559 cm/sec indicating decreasing turgor and stomata which were nearly closed to conserve water. Air temperature was 26.7C, relative humidity was 48% and the mean LWP was -12.6 bars (n=28). The following day over 2.54 cm rain fell relieving soil and plant moisture deficits. On June 21, the maximum air temperature rose to 28.3C, relative humidity was 55% and LWP had decreased to a mean of -14.42 bars in response to evaporative demand, not significantly different than that on June 19. But because of available soil moisture and higher humidity, turgor pressure was maintained and stomatal conductance (0.159 cm/sec) was significantly greater than that on June 19 ($P<.001$). Although the plant water potential did not effectively change with precipitation, stomatal conductance did, allowing water loss for evaporative cooling. Despite the apparent leaf water deficit, the open stomata imply that turgor for growth was maintained since guard cell turgor is in part necessary for stomatal opening.

Leaf Nitrogen Content: The effect of soil moisture stress on N accumulation in leaves appears to be variable. Williams and Shapter (1955) noted that N tended to be excluded from the leaves and accumulated in the stems of

barley and rye as a result of wilting. And, McNeal et al. (1968) found lower, though not significantly so, levels of N in wheat leaves grown under dryland conditions compared with those in irrigated plots. However, Jackman (1976) found that leaves of oat plants grown under soil moisture stress had higher nitrogen contents than those grown under irrigation. This latter phenomenon is supported first by the work of McNeal et al. (1966) who suggested that at least 70% of the N from leaves and stems of wheat should, under normal unstressed conditions, be transferred to the developing grain. Secondly, Spratt and Gasser (1970) found that only 15% of the extra N taken up by wheat remained in the straw under no stress conditions, but with moisture stress imposed at the floret developmental stage, up to 75% of the extra N taken up remained in the straw.

An increased amount of N remaining in the leaves of stressed plants could conceivably make those leaves more nutritious to leaf feeding herbivores such as the CLB (White 1974, 1978, Slansky and Feeny 1977, Scriber 1978).

Not only are stressed oat plants higher in N content, but Jackman (1976) also noted greater N levels among the topmost leaves where the beetle prefers to feed. It was speculated that feeding at this site resulted from a positive phototrophic response rather than a specific choice of preferable diet at the uppermost leaves.

In contrast to the water content, leaf nitrogen as a percent of total weight was greatest in the flag leaf blade and declined with leaf position (Figure 34). Percent nitrogen declined with leaf age though the flag leaf still contained the greater amount (Philips et al. 1939). The range among leaf positions was widest in plants grown under irrigated conditions. Contrary to the studies cited above, these data show a higher N content in the foliage of irrigated plants indicating that water stress did not make the foliage more nutritious and consequently more attractive to the CLB.

The greater nitrogen contents found in the 1981 plants (Figure 34) may have been an anomaly of the micro-Kjeldahl procedures used that year, the BYDV or the different variety planted.

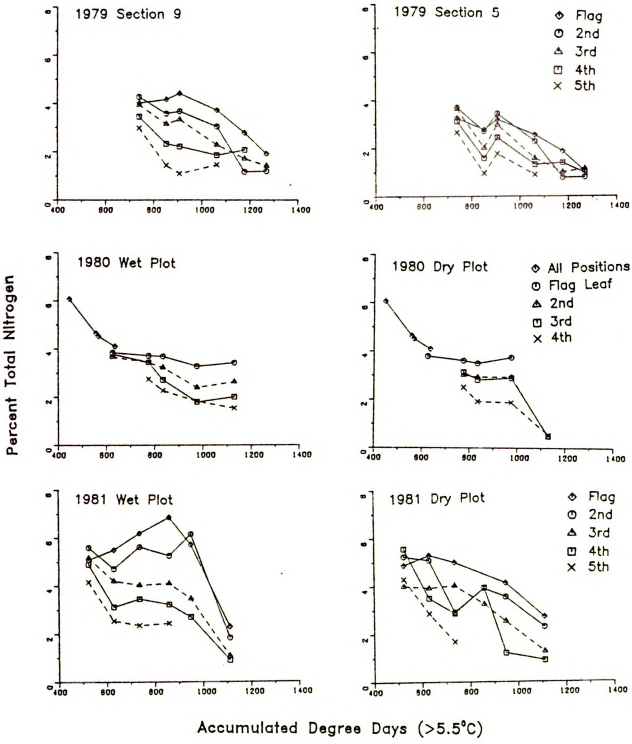


Figure 34. Influence of leaf position and water treatment on mean percent total nitrogen in oat leaves by weight from 1979-1981.

VIII. ASSIMILATE TRANSLOCATION

A. Introduction

It is generally accepted that the flag leaf is a crucial source of photosynthates for grain development (Williams 1964, Milthorpe and Moorby 1974, Wardlaw et al. 1965, Wardlaw 1968, Johnson and Moss 1976, Rawson and Hofstra 1969). There is little question that the flag leaf, flag leaf sheath, top two internodes, peduncle and panicle contribute most of the carbohydrates for grain filling in small grains. However, the amount of that contribution for each of these organs reported in the literature is highly variable. Table 10 summarizes reported values of the percent of grain filling contributed by various organs in small grains. Obviously, much of this variation is the result of the cultivars used and the experimental conditions employed. Some workers labelled whole plants with ^{14}C while others labelled individual organs. Shading and/or defoliation techniques were also employed to determine organ contribution to grain development. For these reasons, individual papers should be examined for specific details.

Jennings and Shibles (1968) are the only authors found to have examined assimilate translocation in oats. They found that the panicle contributed 38-63% of the

Table 10. Percent of total grain weight reported to be contributed by various plant organs.

Crop	Flag Blade	Flag Sheath	Other Blades	All Blades	Panicle	Stem & Sheaths	Notes	Reference
Oats	18		4	22	63	15	Large glume	Jennings & Shibles (1969)
Oats	10		26	36	38	26	Small glume	" "
Barley	12	35	35	47	18		Early fill	Biscoe et al. (1975)
	9	25	25	34	13	28	Final wt.	" "
Barley		15		15	30	40		Archbold (1942)
Barley		45		45	30		25% wt @ emg.	Porter et al. (1950)
Barley	40				60		Fl.=Bl.,Sh.,Ped.	Thorne (1965)
Barley					70		"	Thorne (1966)
Barley	40-50				40		"	Thorne (1963)
Barley					19-35	30-35		Thorne (1963a)
Barley					25-35			Watson & Norman (1939)
Barley	59				26	15	Fl.,Bl. & Sh.	Watson et al. (1958)
Barley					33-50			Birecka et al. (1964)
Barley		25			28-64	33	15-45d postanth.	Buttrose & May (1959,1965)
Wheat	66		21		13		Awnless,no stress	Evans et al. (1972)
	54		22		24		Awnless, stressed	" "
	47		19		34		Awned,no stress	" "
	42		15		43		Awned, stressed	" "
Wheat	55		12		67			Rawson & Hofstra (1969)
Wheat	83				17		Fl.=Bl.,Sh.,Ped.	Thorne (1965)
Wheat	50			50	50		Awned	Carr & Wardlaw (1965)
Wheat				25	30	25		Boonstra (1929)
Wheat				30	41	30		Smith (1933)
Wheat				23-45	18-46	28-44	6 cvs.	Asana & Mani (1950)
Wheat	29-36				25			Quinlan & Sagar (1965)
Wheat					26			de Silva (1961)
Wheat	19		13		21			Neales et al. (1963)
Wheat					20-33			Evans & Rawson (1970)
Wheat						10-11		Wardlaw & Porter (1967)
Wheat	35-41		20-23		21-24	15-21		Brenner & Rawson (1972)
Wheat					27-63			Buttrose (1962)
Grains			15		15	40		Thorne (1966)
Poa annua	45-48		33		60-80			Ong et al. (1978)
L. perenne					50			" "

photosynthates for grain filling while the flag leaf blade contributed only 10-18%, the larger percentage associated with a large glumed variety for both organs. In contrast, averaging the values reported for barley in Table 10, the inflorescence of this grain contributes about 36% and the flag leaf about 33%. Wheat shows a much higher dependence on the flag leaf, about 49%, while only about 30% of grain fill is contributed by the head. Based on the two values given by Jennings and Shibles (1968), the oat plant relies much more on the photosynthetic capacity of the panicle than on the flag leaf blade for grain filling. Nevertheless, the removal of the flag leaf blade by the CLB is cited as the major source of grain loss in oats (Wilson et al. 1969) though the actual effects of CLB defoliation on translocation and grain filling had not been previously examined. Defoliation by the CLB in excess of 70% has been shown to significantly decrease oat yields (Wilson et al. 1969; Merritt and Apple 1969). Since the CLB is positively phototropic, the flag leaf blade is selectively defoliated so that it incurrs the greatest damage of all the blades (cf. Figure 19). It is of interest, therefore, to delineate the importance of this blade to oat grain production and to determine what amount of defoliation affects translocation to the head.

In addition, if photosynthate production from the flag leaf is restricted by defoliation, do other organs

compensate for this deficiency by shifting the recipient sink of their assimilates, i.e. roots to head? An answer to this question is important to an understanding of the oat plant's adaptability not only to pest organisms but to climatic variability.

Environmental variables necessary for growth impact all portions of a plant (Figure 35). In the case of small grains, all the top organs may contribute to the translocation of assimilates for grain filling. This is not to imply that all organs are equally capable of photosynthesis and/or assimilate translocation. But, of interest in this context, is that defoliation by the CLB impacts directly on only a portion of one of these organ systems, the leaf blades, leaving other photosynthetically active organs untouched or indirectly affected.

B. Materials and Methods

The effects of defoliation and irrigation on assimilate transfer was determined by radiotracer techniques. Radiocarbon entering the leaf as $^{14}CO_2$ was used to quantify the partitioning of assimilates in single stem oat plants. Sodium ^{14}C bicarbonate (670 μCi/mg) at a concentration of 2.0 mCi/ml supplied by Amersham corporation was used to label individual leaves with 50 μCi of $^{14}CO_2$. Twenty-five microliters of NaH $^{14}CO_2$ was placed as a single drop in a horizontally held disposable

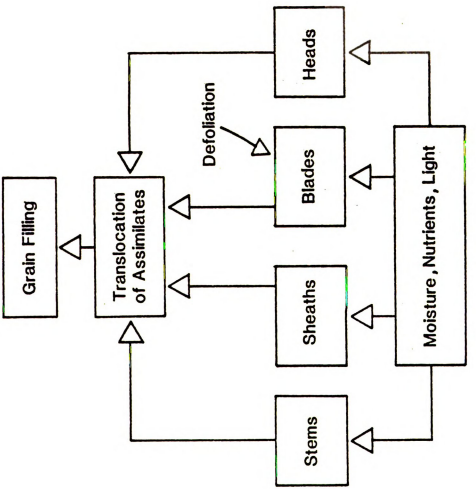


Figure 35. Flow diagram of organs and major processes influencing grain filling in small grains and the organ of CLB impact.

10 cc syringe with the plunger removed. Lactic acid was placed as a second drop in the syringe and the plunger was replaced to the 10 cc mark. Tilting the syringe and mixing the two drops liberated $^{14}CO_2$ within the chamber.

The plant organ selected for labelling was enclosed in a glass assimilation tube (Figure 36). A latex rubber glove with a piece of filter paper enclosed was attached to a side arm to allow for increased positive pressure and subsequent gas leaks upon injection of approximately 20 cc $^{14}CO_2$. The leaf blade was inserted into the assimilation tube through a slit foam plug sealed on both sides with a layer of silicone sealant. Subsequently parafilm was wrapped around the glass tube and the base of the plant organ. Injection of the labelled gas was through a disposable rubber septum.

A three minute exposure time was used for assimilation of the labelled $^{14}CO_2$. The reaction was halted and excess $^{14}CO_2$ was trapped by injection of NaOH onto filter paper inside the latex glove. By massaging this glove, air within the assimilation tube was drawn into the NaOH saturated side well.

Labelled plants were harvested approximately 24 hours after labelling and taken to the lab in plastic bags. The plant was dissected and the organs separated as depicted in Figure 37. The percent defoliation, the length, width, and diameter, wet weight and dry weight of each organ were

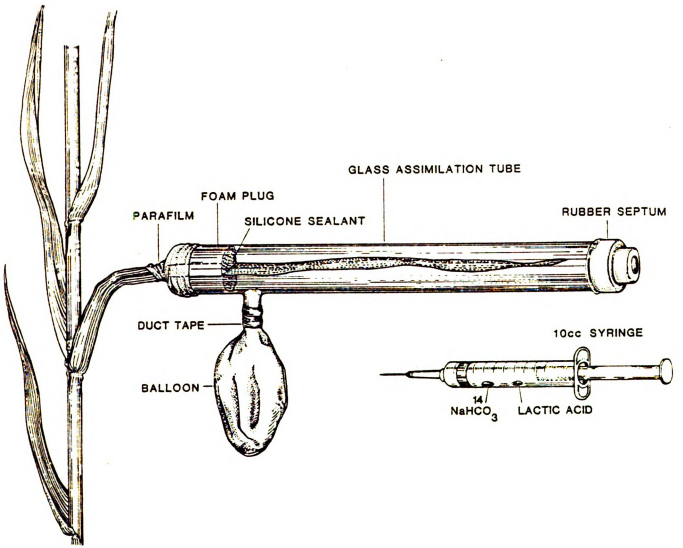
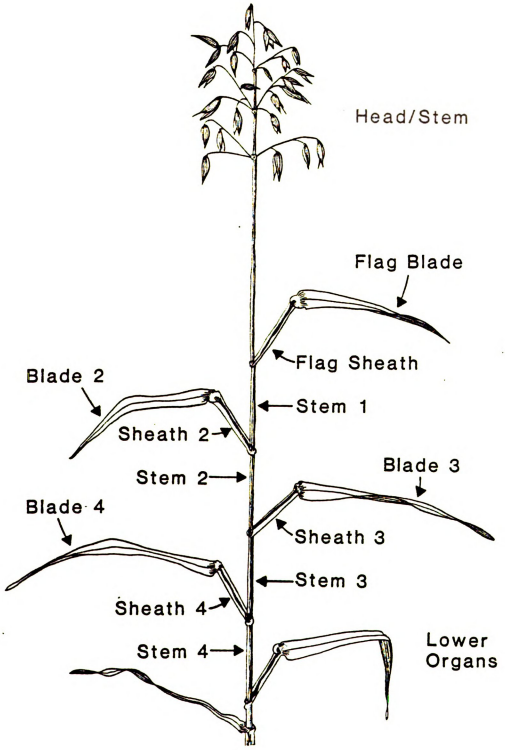


Figure 36. Assimilation chamber used for $^{14}CO_2$ generation and single blade labelling.

Figure 37. Plant organs dissected and in which radiotracer activity was determined after single organ labelling.


Head/Stem
Flag Blade
Flag Sheath
Blade 2
Stem 1
Sheath 2
Blade 3
Stem 2
Blade 4
Sheath 3
Stem 3
Sheath 4
Stem 4
Lower Organs

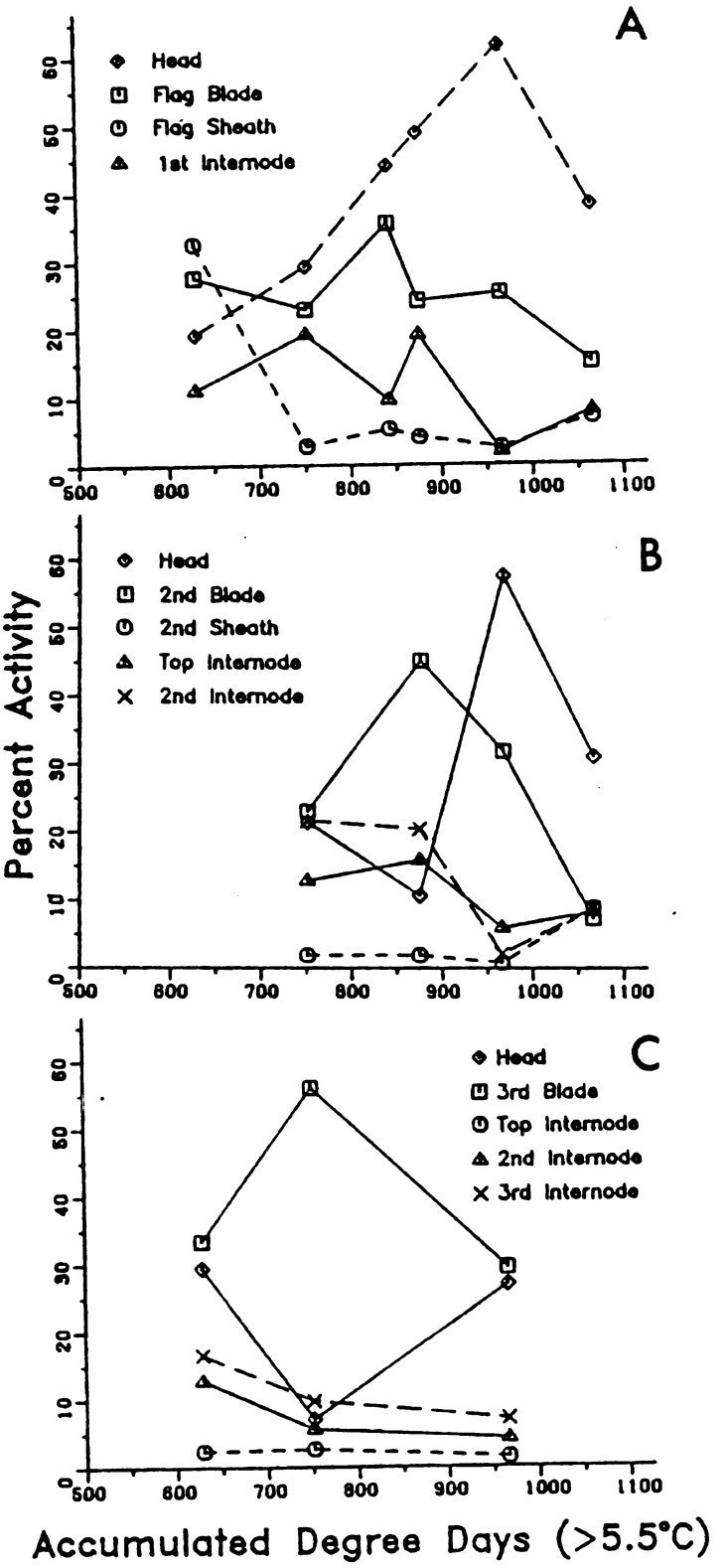
measured. Photosynthetic surface area was computed through regression equations from length, width and diameter data. Dry plant samples were processed in an OX-200 Packard Biological Oxidizer using Pemafluor 5 and Carbosorb 2 (2:1) as the scintillation cocktail. Activity of the samples was determined by scintillation counting.

Counts per minute (CPM) were used to compute the percent activity incorporated in each organ of the total CPM in the plant at harvest including the labelled organ, and the percent of the total in the plant excluding the remaining in the labelled organ. Counts per unit photosynthetic area (cm^2) and per unit dry weight (mg) were also computed correcting for the percent defoliation.

C. Results and Discussion

Contribution of Leaves to Grain Filling : A three way analysis of variance of the percent of activity translocated from a labelled flag leaf blade to the head shows significant differences ($P<.05$) due to date and the interaction of date and water stress. Less significance ($P<.10$) is associated with effects of defoliation and water stress as main effects. The percent activity found in various organs after the flag leaf was labelled is shown in Figure 38A. At heading (DD 629), the flag leaf blade, flag sheath and first internode retained ^{14}C from the labelled flag leaf. Soon after, the amount retained in the flag

Figure 38. Mean percent ^{14}C recovered after 24 h from various organs through the season when A) the flag leaf blade, B) the second blade, or C) the thrid blade was labelled.


A
Head
Flag Blade
Flag Sheath
1st Internode
B
Head
2nd Blade
2nd Sheath
Top Internode
2nd Internode
C
Head
3rd Blade
Top Internode
2nd Internode
3rd Internode
Percent Activity
0
10
20
30
40
50
60
500
600
700
800
900
1000
1100
Accumulated Degree Days (>5.5°C)

sheath and eventually, the internode, declined with time and senescence. However, the percent of ^{14}C assimilated by the flag leaf which was translocated to the head increased with time (Figure 39). The increase in the proportion translocated to the head was due to a decline in the proportion retained by the flag leaf sheath early in the season and the first internode later (Figure 38A). The amount retained by the flag leaf blade was relatively constant with a slight increase soon after anthesis and eventually declined later in the season. Specific activity in counts per minute translocated to the panicle from the flag leaf blade was not significantly associated with water stress or defoliation in a multiple regression analysis. However, the percent of that assimilated by the leaf blade and subsequently translocated to the head was significantly correlated with date (r^2= .70) (Figure 39).

The percent of assimilated ^{14}C retained by the labelled 2nd blade was at its maximum at about the same time as that from the flag leaf (Figure 38B). Regression analysis showed some association with date ($P<.10$) though none with defoliation or water stress. The sharp rise in the amount in the head by DD 966 was at the expense of that in the internodes and the blade. The large proportion in the head occured when the grain was milky ripe and carbohydrates were in demand. This finding is contrary to that of Patrick (1972) who found that before ear emergence

Figure

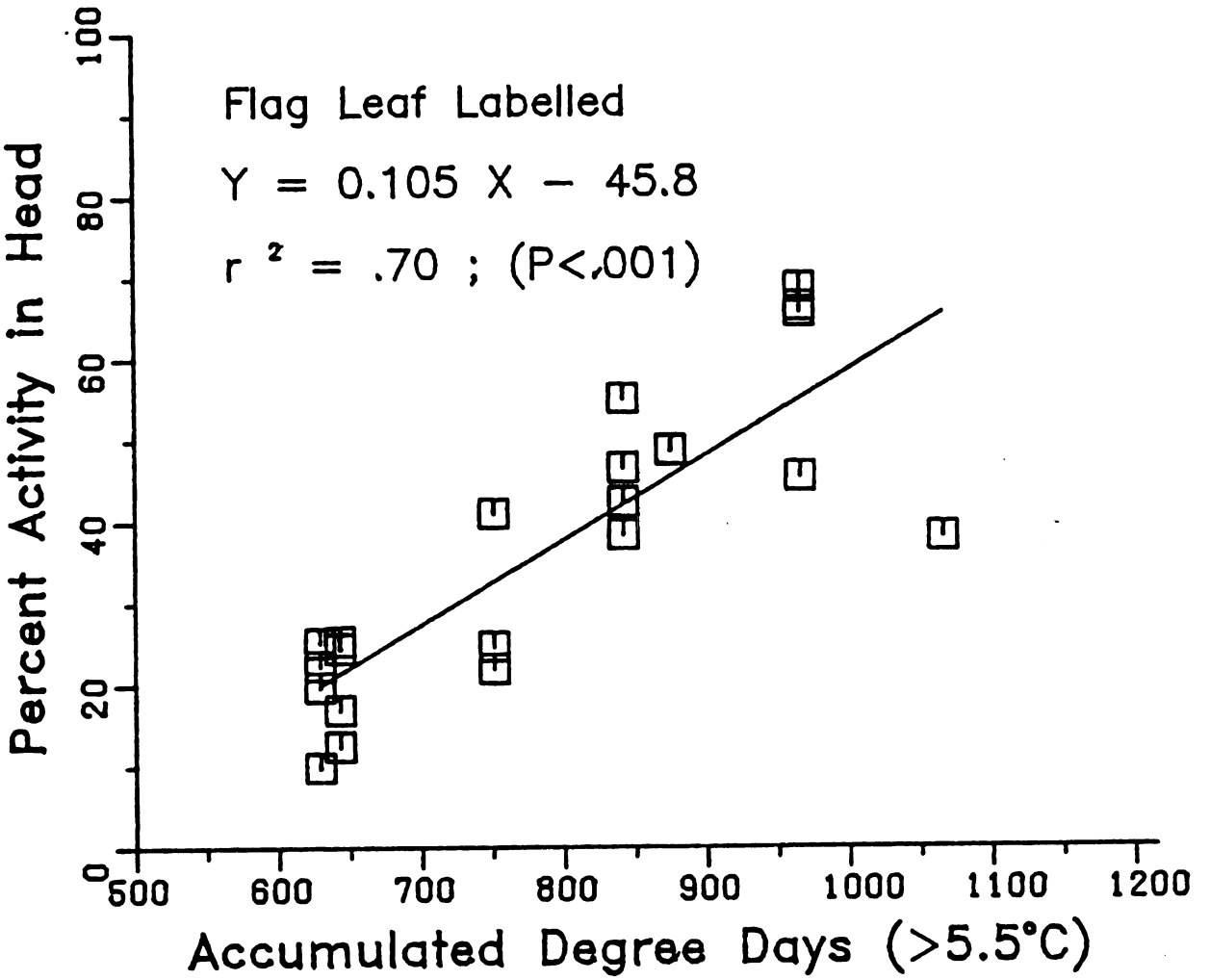


Figure 39. Percent of total ^{14}C assimilated by the flag leaf which was translocated to the head as a function of accumulated degree days.

in wheat the three leaf blades below the flag leaf supply photosynthates to the developing head while only the flag leaf blade performs this function by anthesis.

The proportion of translocates from the third blade (Figure 38C) to the head declined dramatically about DD 751. This was about the time of head emergence and anthesis. The decline in counts per minute was significantly correlated with date and water stress ($P<.05$; $r^2= .60$) as was the percent translocated from the third blade ($P<.06$; $r^2= .51$). Before heading, the third blade provided photosynthates to the expanding leaf blades above it (Doodson et al. 1964).

Porter et al. (1950) found that 25% of the dry weight of the ear of barley was present at emergence and that 30% of its final weight is contributed by its own assimilation. They suggested that the majority of the 45% remaining was contributed by the flag leaf sheath. On June 25, 1981, when the grain was milky ripe, a preliminary experiment was conducted in which two flag leaf sheaths were labelled with ^{14}C. On separate plants, flag leaf blades, second leaf blades and heads were also labelled. After 24 h, the activity in the heads of each of these plants was ascertained. Assuming that if each of these organs was on the same plant, its physiological processes would be similar to that recorded from each separate plant, the amount contributed to the head from each organ was

averaged, and the sum of these averages taken to estimate the number of CPM's the head would have received had all these organs been labelled on the same plant. Thus a composite plant was imagined with an amount of labelled carbon translocated to the head proportional to the assimilation rate of the five different organs exposed to the same amount of labelled material for the same length of time. Table 11 shows the percent contribution of each of these organs to the head in terms of total head activity. The amount of assimilate which was translocated to the head from each of these organs was a function of their photosynthetic capacity and assimilation efficiency at that particular time. The 55% contribution of the flag leaf sheath was surprisingly high relative to the ^{14}C translocated from other organs and higher than that previously reported (Table 10). The amount translocated from an organ is initially dependent upon the amount of CO_2 assimilated by the organ which in turn is a function of, among other things, the green surface area of the organ and the quantity of light incident upon it. It is reasonable to assume that the heads of each of the plants labelled on June 25 when the grain was milky ripe had similar demands for assimilates and that the physiology of the other organs was all similar. The sheath of the flag leaf a week after anthesis when this experiment was conducted can have a much larger green surface area than either the head or the flag

Table 11. Percent contribution of various plant organs to panicle on June 25, 1981 (n=2). CPM = mean counts of ^{14}C per min x 10^6, CPW = mean counts per g dry weight.

	CPM	CPW	Percent
Head	6.69	7.6	34
Flag Sheath	10.79	10.4	55
Flag Blade	1.45	1.5	7
2nd Blade	0.61	0.8	1
3rd Blade (est)	(0.10)	(0.5)	
Total Head CPM	19.24		

leaf blad

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leaf blade. Thus the ability of the sheath to assimilate more $^{14}CO_2$ than either of these organs would be expected. Total ^{14}C recovered from the plants with the flag sheath labelled averaged 21.3 x 10^6 counts per minute, a far greater assimilation by this organ than any other (Table 12).

Wardlaw and Porter (1967) found that carbohydrates are contributed directly to the ear from the flag leaf and indirectly by way of stored sugars in the second internode. This latter contribution from stored sugar was estimated as 5-10% of the final ear weight. No movement was found from the top internode so it was thought that it acts merely as a channel for assimilates to the ear. Archbold and Mukerjee (1942) also concluded that in barley no more than 10% of the final dry weight of the ear could be accounted for by stored stem sugar. At least 80% of the ear dry weight resulted from direct assimilation of leaves, stems and the ears themselves. However, Austin et al. (1977) concluded that of the 48% of whole plant assimilated carbon translocated to the grain over 18 days postanthesis, that about half was temporarily stored in stems and leaves. Other estimates of stem contribution to grain weight vary widely from 2.7% of grain weight in wheat (Rawson and Evans 1971) to 70% preanthesis contribution in barley (Gallagher et al. 1975).

A large proportion of assimilates remained in the stem

Table 12. Mean (SE) total 14C ($CPMx10^6$) recovered from plants labelled at different positions over time.

Stage		Flag	2nd	3rd	Sheath	Head
Boot	$\bar{x}$	ND	10.69	ND	ND	ND
	n		1			
Heading	$\bar{x}$	6.17	ND	10.42	ND	ND
	SE	(1.55)		(2.80)		
	n	8		8		
Anthesis	$\bar{x}$	4.54	10.30	5.48	ND	ND
	SE	(0.12)	(3.01)	(2.99)		
	n	3	3	2		
Milky Ripe	$\bar{x}$	2.22	11.33	ND	21.34	5.55
	SE	(0.93)	(0.20)		1.48)	(1.28)
	n	6	2		2	6
Mealy Ripe	$\bar{x}$	0.23	0.37	ND	ND	ND
	SE	(0.14)	(0.05)			
	n	5	2			

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24 h after labelling (Table 13). The internodal area just above and below the point of leaf insertion retained ^{14}C from that blade. The anastomosis of the leaf traces with the stem traces at the node below the node of insertion (Wardlaw 1965) explains the accumulation at that internode. Assimilate crossover to the stem traces at the node of insertion has been shown by Patrick (1972) and explains the accumulation above this point. The accumulation in these two internodes was most apparent among plants grown in dry plots which had less than 60% defoliation and in which the third blade was labelled. Twenty percent was moved to internode 4 while only 3% was found in this internode in the irrigated plants. At the same time, plants in the wet plots translocated 39% of the assimilates to the head from the third blade while only 19% was translocated in water stressed plants. It is probable that under water stress, the roots are a greater sink for assimilates from the third blade source than is the head. Although the roots were not collected in this investigation, the distribution of ^{14}C in the above ground organs below the node of labelled leaf trace anastomosis was very slight suggesting little directed movement toward the roots contrary to the report of Rawson and Hofstra (1969).

Among sheaths, only that of the flag leaf retained any substantial amount of ^{14}C irrespective of soil moisture.

Table 13. Mean percent counts per minute (CPM), CPM per sq. cm., and CPM per mg dry weight translocated to various organs of oats from the top three leaf blades after 24 h excluding that retained in the labelled blade.

	Labelled Organs								
	Flag	2nd	3rd	Flag	2nd	3rd	Flag	2nd	3rd
Organ	CPM			CPM per cm2			CPM per mg		
Head/Peduncle	26.0	20.7	26.6	(Area unestimated)			2,411	1,438	13,323
Peduncle	24.8	6.9	2.3	64,040	34,957	456	1,459	1,026	-
Flag Sheath	18.9	1.9	5.5	31,618	2,595	27,442	4,263	321	3,456
Flag Blade	-	1.2	0.4	870,235	2,936	2,950	56,567	255	542
Internode 1	14.2	16.9	5.9	133,989	174,606	87,398	13,420	6,961	15,530
Sheath 2	1.6	13.0	1.3	3,932	53,713	9,520	790	5,294	854
Blade 2	1.2	-	0.5	741	159,740	1,726	112	22,843	358
Internode 2	7.6	19.8	16.8	56,914	232,108	226,393	2,586	9,017	13,336
Sheath 3	0.5	1.2	4.5	691	1,123	25,131	96	162	2,914
Blade 3	1.1	1.3	-	338	655	134,419	79	137	31,130
Internode 3	1.7	8.2	20.4	16,006	90,769	298,197	1,634	2,679	12,355
Sheath 4	0.4	0.2	0.5	727	856	2,875	106	200	426
Blade 4	0.4	0.2	4.4	243	596	1,819	57	133	334
Internode 4	0.9	3.2	10.5	6,584	56,651	67,260	285	1,676	2,880
Sheath 5	0.3	0.1	0.2	1,632	743	2,386	213	103	340
Blade 5	0.3	0.3	0.2	1,371	2,438	1,556	117	171	186
Internode 5	0.9	2.0	2.9	4,122	29,377	23,899	233	966	1,228

At the time of labelling, the flag sheath may still have been expanding producing a sink effect, whereas the sheaths of the lower leaves were most likely fully expanded at labelling. Archbold (1942) reported that defoliation of barley leaves greatly reduced the sugar in the stem suggesting that leaf assimilation supplied those sugars rather than activity of the stems themselves.

Contribution of Panicle to Grain Filling : The head itself supplies a major portion of assimilates for grain filling. The glumes, rachis, rachis branches and kernel are all photosynthetically active (Carr and Wardlaw 1965). Prior to grain filling, the developing head is able to fulfill most of its needs. However, once grain filling commences, the head is no longer able to meet its demands for assimilates, and its sink increases requiring translocation of assimilates from other photosynthesizing organs. The ear and peduncle of oats retained an average of 93% of that assimilated. Carr and Wardlaw (1965) state that photosynthesis by the ear of wheat is equivalent to that of the two upper leaf blades in a non awned variety. Table 10 shows that various authors have found that the percent contribution to grain filling by the panicle of small grains is considerable. Awned varieties have much more head photosynthetic capacity than non awned varieties. The capacity of the head to produce its own assimilates explains partially why total artificial defoliation of leaf

blades decreases grain yield no more than about 50% (Buttrose 1962).

Although the percentage of assimilates translocated to the head increased with demand, the actual amount of ^{14}C translocated per unit weight, i.e. the specific activity, decreased with age and approaching senescence (Figure 40). The third blade translocated a large amount to the developing head before it emerged, but this function declined with the expansion of the second blade and the flag leaf (Figure 41).

The greatest specific activity in the head from the labelled flag leaf occured on DD 875 when the grain was milky ripe and blade expansion was complete (Figure 41). Demand for assimilates in the head after this time declined dramatically as the grain dehydrated and the leaves senesced. The remaining sink in the head while decreasing in strength, could be fulfilled by organs closer to, and more persistant than the leaf blades such as the sheaths, internodes of the stem and the head itself.

Effects of CLB Defoliation and Water Stress on Translocation : Water stress has been shown to inhibit assimilate translocation in a number of species (Brevedan and Hodges 1973, Hartt 1967, Johnson and Moss 1976, McPherson and Boyer 1977). Though velocity of translocation is unaffected (Wardlaw 1965, 1969), the major effect is to reduce and delay the rate of sugar transfer

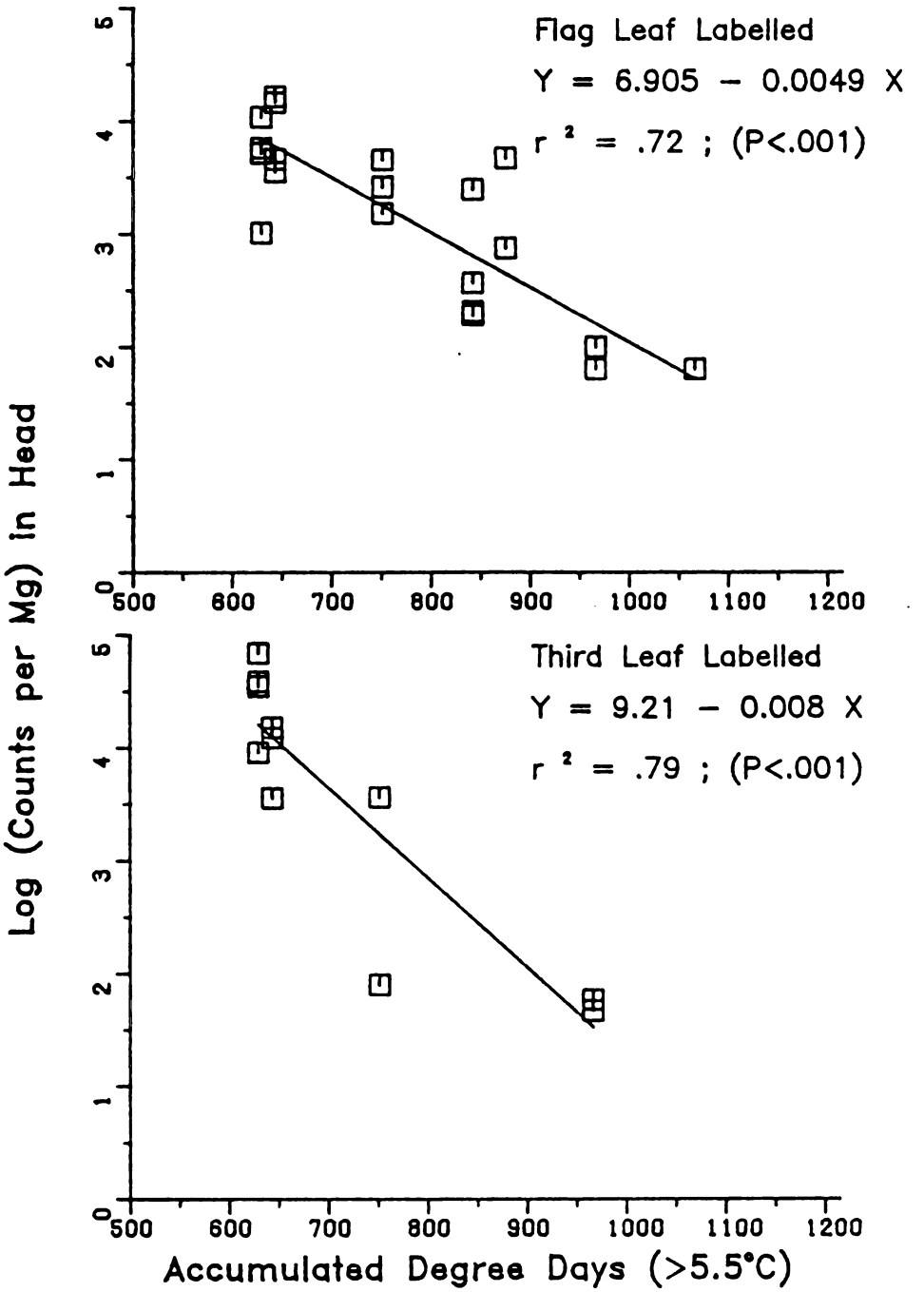

Figure 40. Specific ^{14}C activity in counts per unit head weight of oats translocated from the flag leaf blade and third leaf blade.

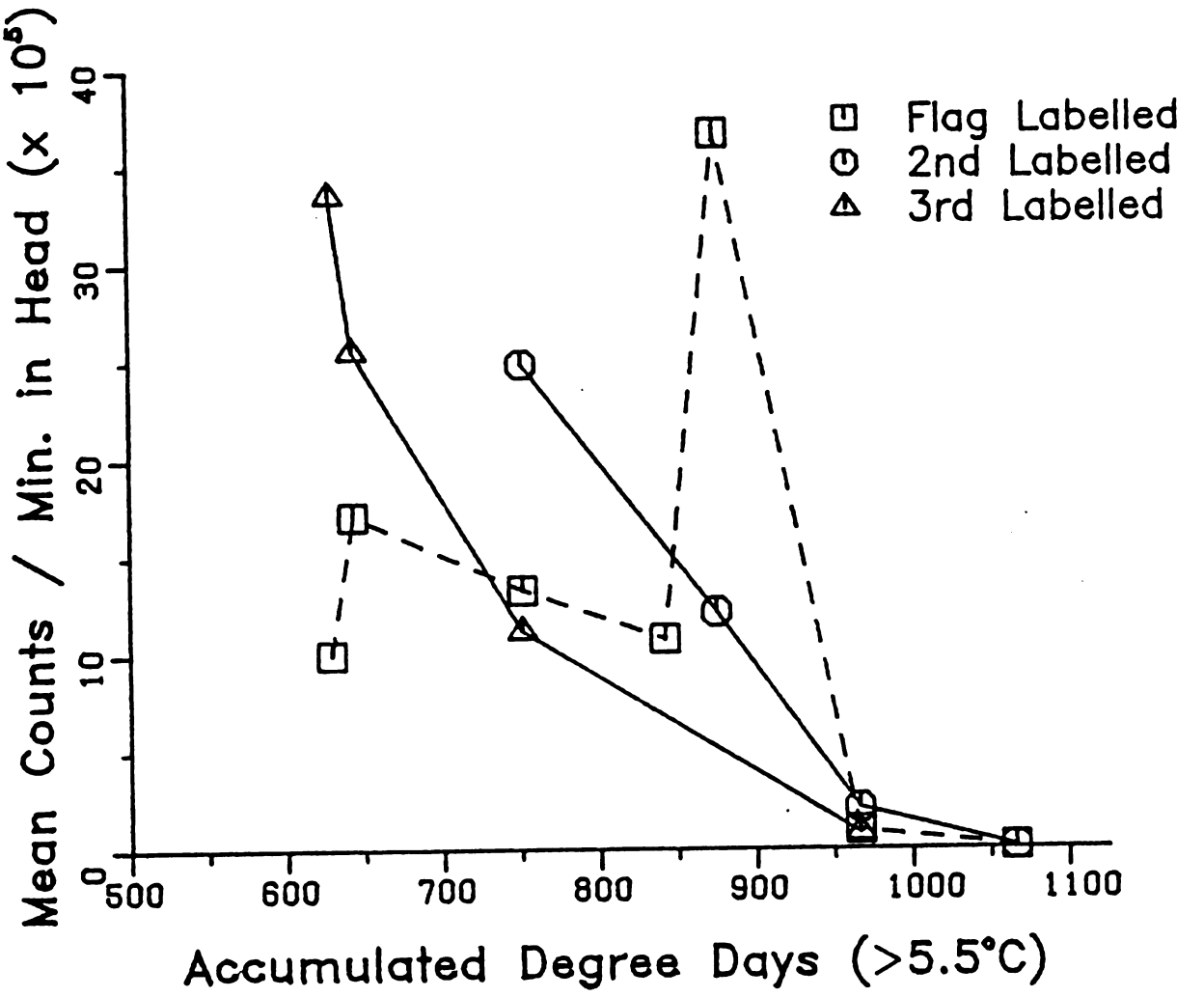

Figure 41. Mean ^{14}C activity recovered after 24 h from the head of oats contributed by the labelled flag leaf, second leaf or third leaf blades as a function of accumulated degree days.

from the assimilating tissue to the conducting tissue. Leaf photosynthesis may be affected by this accumulation of photosynthates in the assimilating tissue (Neales and Incoll 1968, Thorne and Koller 1974).

During wheat grain development, water stress which reduces photosynthetic activity of the leaves also results in an increased movement of assimilates from the lower leaves to the ear (Wardlaw 1967). A similar compensation occurs when low light intensities reduce assimilation.

Debate continues as to the sensitivity of photosynthesis and translocation to water stress. Many have suggested that photosynthesis is more sensitive to water stress than translocation (Johnson and Moss 1976, McPherson and Boyer 1977, Munns and Pearson 1974, Sung and Krieg 1979, Wardlaw 1967). However, Brevedan and Hodges (1973) and Hartt (1967) have suggested that translocation is more sensitive than the carbon dioxide assimilation process.

A strong correlation existed between the amount of soil moisture available and the specific activity of the head. Figure 42 shows both that more ^{14}C was translocated to the heads of plants in wet plots than to those in dry plots and that the contribution of each blade declined with position on the plant. The effect of moisture on translocation is a function of increased growth because of water availability and the accompanying increase in

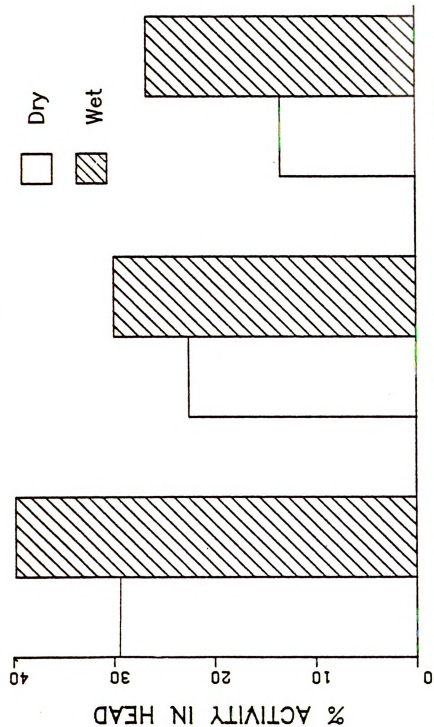

Figure 42. Influence of leaf blade position and water stress on ^{14}C recovered after 24 h from the head of oats.

assimilate demand, i.e. sink size.

Most of the assimilates translocated from the labelled organs was found in the developing head and stem structures (Figure 38, Table 10). The direction and intensity of flow either up or down the stem is of most interest in this study. Flow is regulated by the growth rates of individual organs which provide sinks for assimilates.

The emerging head, the elongating stem and the roots were the three primary sinks at labelling. Among the plants subjected to drought stress, growth of the blades and sheaths had generally ceased and most of the movement was toward these three sink areas.

Photosynthetic and respiration rates were not directly monitored in this investigation but total recovered ^{14}C after 24 h gives an indication of the assimilation abilities of the leaf blades under the treatment conditions. There was a decline in assimilation efficiency of the flag leaf with development as seen from recovered whole plant ^{14}C activity (counts per minute) after 24 h (Table 14). Stepwise multiple correlation analysis showed a negative correlation with date ($P<.05$; $r^2= .37$) but not with water treatment, insect treatment or defoliation amount of the labelled leaf. This analysis and the breakdown by defoliation pressure (Table 14) reflect the decreased photosynthetic capacity of the leaf blades with age and also indicate that even under moderate water stress

Table 14. Influence of CLB defoliation and plant phenology on the total 14C recovered (CPMx10^6) after 24 h from the labelled flag leaf blade of oats.

		Percent Defoliation		
		0-49	50-75	75-100
Heading	$\bar{x}$	5.69	7.62	ND
	n	6	2	
Anthesis	$\bar{x}$	4.30	4.69	4.62
	n	1	1	1
Milky Ripe	$\bar{x}$	1.31	2.60	3.40
	n	3	1	2
Mealy Ripe	$\bar{x}$	0.47	0.21	0.002
	n	2	1	2

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The effect of CLB defoliation on translocation is shown in Figures 43 and 44 for dry and wet plots, respectively. A higher percent of assimilates is translocated to the heads of plants in the wet plots. Of great interest, however, is the impact of defoliation on the sink strength in the developing head. A distinct trend is apparent, primarily in the dry plots (Figure 43) of increased assimilate translocation from the labelled organ, regardless of position, to the heads of plants with 60% or more CLB defoliation of the upper blades.

With the flag leaf labelled on dry plot plants with more than 60% defoliation of the upper two blades, 52% was translocated above the flag node with 44% in the upper two internodal areas (Figure 43). In the wet plots with greater than 60% defoliation of the upper leaves, 58% was above the flag node but only 17% in the upper two internodal areas. Only 2-3% was found in the lower organs of plants in both wet and dry plots when the flag blade was labelled.

In plots with less than 60% defoliation and the flag leaf labelled, plants in the dry plots translocated more to lower organs than those in wet plots (Figures 43 and 44). In the wet plots, about 60% was translocated above the flag node whereas in the dry plots, only 42% was above this

Figure 43. Mean percent of activity recovered after 24 hours in each organ of plants with less than or greater than 60% CLB defoliation with the A) flag leaf, B) second leaf or C) third leaf blade labelled in dry plots.

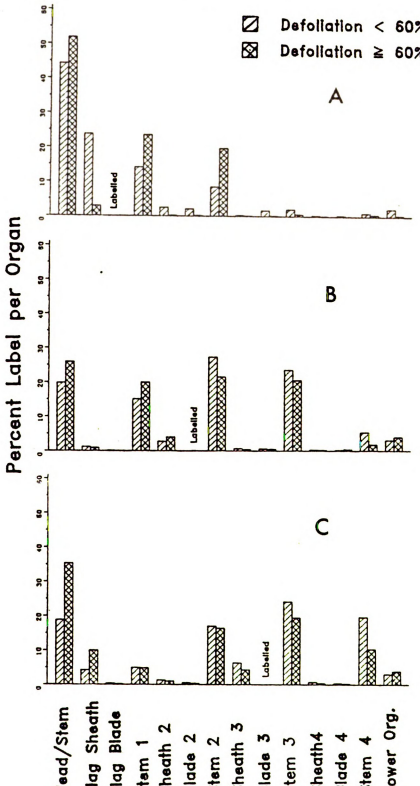
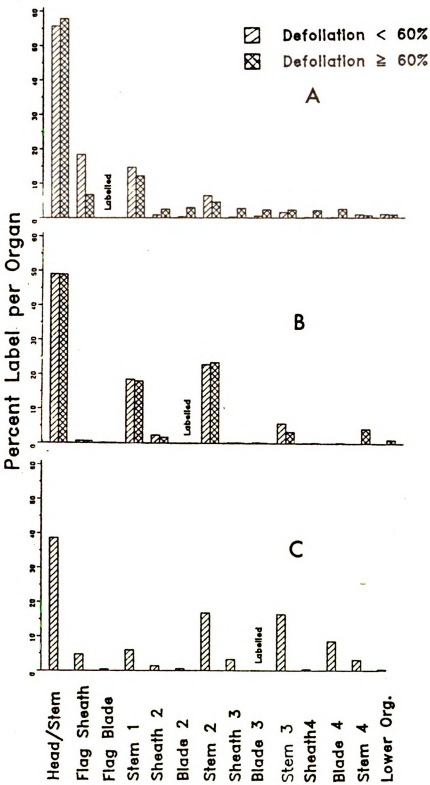

Defoliation < 60%
Defoliation ≥ 60%
A
B
C
Labelled
Percent Label per Organ
Head/Stem
Flag Sheath
Flag Blade
Stem 1
Sheath 2
Blade 2
Stem 2
Sheath 3
Blade 3
Stem 3
Sheath4
Blade 4
Stem 4
Lower Org.

Figure 44. Mean percent of activity recovered after 24 hours in each organ of plants with less than or greater than 60% CLB defoliation with the A) flag leaf, B) second leaf, or C) third leaf blade labelled in wet plots.


Defoliation < 60%
Defoliation ≥ 60%
A
B
C
Percent Label per Organ
Labelled
Head/Stem
Flag Sheath
Flag Blade
Stem 1
Sheath 2
Blade 2
Stem 2
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The only apparent trend in response to defoliation was during the last sampling period when the grain was mealy ripe (Table 14). Heavy defoliation did cause a substantial decrease in assimilation efficiency compared with lower levels. But even with no defoliation, the photosynthetic capacity of the flag leaf is about 10% of what it was at anthesis. Most assimilation at this late date is probably done by the panicle itself. During the milky ripe stage, the only period the head was labelled, the recovered assimilate from the plant after panicle labelling was 5.55 (SE 1.28) x 10^6 CPM, approximately twice as much as from the labelled flag blade. Continued blade senescence after this time would require more assimilation by the panicle or adjacent structures other than the leaf blades.

The close association of growth and translocation processes tend to confound the question of assimilate distribution under water stress. Where growth has been eliminated as a factor, it appears that translocation is relatively insensitive to water stress. The evidence presented by McWilliam (1968) that assimilate movement from stem to roots and buds is significant when Phalaris tuberosa is dormant due to a restricted water supply, suggests a resistance of the translocation mechanism to water deficits.

The specific activity (CPM) is presented in Table 15

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Table 15. Mean ^{14}C (CPMx10^3) translocated to the head and panicle of oats from the top three leaf blades under different defoliation and water stress treatments.

Flag Labelled	Percent Defoliation		
	<60%	>60%	Mean
Dry Plots	1445 8	1898 1	1495
Wet Plots	1316 10	76 2	1109
Mean	1373	683	1274

2nd Labelled	<60%	>60%	Mean
Dry Plots	566 2	1245 1	793
Wet Plots	425 3	2233 3	1329
Mean	481	1986	1150

3rd Labelled	<60%	>60%	Mean
Dry Plots	3881 4	1624 2	3128
Wet Plots	2270 6	ND	2270
Mean	2914	1624	2699

for the top three labelled leaf blades in defoliated and water stressed plots. Obviously, sample sizes were too small for the majority of these treatments and the opportunity for sampling error was great. Seasonal trends tend to mask some of these differences (Figure 38).

The amount of carbon assimilated and translocated from the 3rd leaf blade appears higher than previously reported values (Table 16). In fact, the total ^{14}C recovered from third blade labelling at heading was 10.42 (SE 2.8) x 10^6 CPM and at anthesis 5.48 x 10^6 CPM. Both of these amounts exceed that assimilated by the flag leaf blade during these periods (Table 14). The work of Austin et al. (1976) may explain these observations. They compared photosynthesis and yield in two wheat varieties with contrasting leaf postures, erect vs. lax, and found that the net CO_2 fixation was nearly always greater in genotypes with erect leaves than in those with lax leaves. This was due to greater light penetration to the lower canopy allowing a greater proportion of the fixation to take place in the lower leaves. Duncan (1971) also concluded that photosynthesis is maximized in dense canopies when the upper leaves are erect and the lower ones lax. The oat variety Mariner planted in 1981 definitely had this erect leaf posture in contrast to the Korwood variety planted in 1979. This fact may partially explain the relatively high abilities of the lower leaf blades to translocate to the

Table 16. Reported distribution of 14C-labelled assimilates in wheat after 24 h as a percent of total.

Labelled Organ	Sheaths	Flag Blade	Other Blades	Panicle	Top Internode	Lower Internode	Roots & Crown	Notes	Reference
Flag Blade		26.4		34.7	5.2	17.5	16.3	Control	Wardlaw (1967)
"		57.4		33.7	3.0	2.9	3.1	H20 stressed	" "
2nd Blade		28.9		6.0	3.7	12.4	49.1	Control	" "
"		46.5		15.1	5.8	9.8	22.4	H20 stressed	" "
Whole plant	5.7	3.2	4.3	49.1	8.4	29.3		Control	Johnson & Moss (1976)
"	6.0	4.1	5.2	63.8	6.0	14.7		H20 stressed	" "
"	6.5	3.5	6.4	41.0	10.1	32.4		12d posthead	" "
"	6.6	4.4	6.4	50.3	6.8	25.5		16d "	" "
"	4.5	2.9	1.5	78.2	4.7	8.1		23d "	" "

	Remaining	Young Blades	Older Blades	Panicle	Stem	Tillers	Roots & Crown		
Flag Blade	30.0		0.4	33.7	5.0	20.0	10.0	25d posthead	Rawson & Hofstra (1969
2nd Blade	25.0	0.7	0.3	2.7	4.0	48.0	20.0	"	" "
3rd Blade	43.0	1.5	0.2	2.1	4.0	32.0	17.0	"	" "
Flag Blade	26.0	0.5	34.3	32.0	4.0	3.0		15d posthead	" "
2nd Blade	14.0	3.4	0.5	4.3	44.0	13.0	21.0	"	" "
3rd Blade	15.0	1.9	0.1	1.2	7.0	23.0	51.0	"	" "
Flag Blade	3.7	15.2		17.9	61.9	1.4			Stoy (1963)
Flag Blade	14.0	8.0		13.0	60.0			48 hrs	Wardlaw & Porter (1967
2nd Blade	33.5	53.0	1.3	11.7				"	" "

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Heavy feeding by the CLB will often result in isolated patches of green leaf material separated from the ligule and the rest of the plant by a necrotic, scarified area. Nevertheless, these patches would remain green since the CLB feeding is interveinal. One of these isolated patches of a flag leaf that was approximately 75% defoliated was labelled to see how well this area could interact with the rest of the plant. Although 72% of the label remained in the flag blade, over 5% was actually translocated to the head within 5 h. Discounting the amount assimilated but not translocated from this green patch, 9.5% was found in the head. I think it is fair to assume that 3-4 times this amount would have reached the head given a full 24 h. It is important to remember that feeding by the CLB does minimal damage to the plant's vascular system under moderate population densities (Table 17).

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Table 17. Translocation from an isolated green tip of a flag leaf 75% defoliated in an irrigated plot five hours after labelling.

Organ	CPM	% Total	Percent Excl. Label
Flag Bl. Tip (Lab)	1,303,400	43.9	--
Flag Blade Base	859,383	28.9	51.5
Flag Sheath	202,552	6.8	12.1
Head Stem	448,345	15.1	26.9
Head	157,800	5.3	9.5

IX. SUMMARY OF BIOTIC AND ABIOTIC STRESSES ON OAT GROWTH AND YIELD

The growth and yield of a plant from germination to maturity are subject to an array of dynamic variables, both biotic and abiotic, many of which in the correct proportions, are essential for sustained growth. The presence of some of these variables, such as insects and disease, are generally considered detrimental if they become established while others, e.g. water and nitrogen, are essential and may limit growth if they are either too scarce or abundant. The interactions of these components are little understood. Within limits, a plant is able to avoid or tolerate many presumably detrimental conditions. Cereal leaf beetle defoliation has been shown to cause major losses of yield in oats and wheat at high population levels. These investigations, under regulated water treatments, have been unable to confirm those findings. One possible reason for this is that through the years of this investigation, the adult CLB population was low compared with reports from the 1960's and early 1970's. The majority of defoliation was caused by larvae released into the plots rather than by a large endemic adult population, and was attained well after stand establishment and vegetative development.

Although CLB larvae substantially and selectively reduced the leaf area of the topmost blades, this

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investigation has shown that with a suitable water supply during the anthesis stage, grain filling proceeded using assimilates from the panicle, leaf sheaths, leaf blades below the flag leaf and stored assimilates in the stem. Morever, carbon assimilation and translocation from patches of green leaf material isolated by severe defoliation were not reduced because the integrity of the vascular system under this form of defoliation is maintained. Defoliation of an organ which normally supplies a sink with assimilates shifts the strength of that sink relative to the remaining sources. Thus, a percentage of assimilate was provided to that sink from alternate sources such as lower leaves which was greater than that provided in control plants. Labanauskas and Dungan (1956) have shown a similar transference of assimilates from intact tillers as partial compensation for radical defoliation. Some authors (Archbold 1942, Porter et al. 1950) have concluded that the importance of the leaf blade is in providing assimilates for head initiation and spikelet differentiation. Severe defoliation during the plant's vegetative growth phase could decrease the number of spikelets differentiated and therefore decrease yield. If defoliation occurs after this period, leaf senescense will have already begun and, assuming water is not limiting blade area, defoliation may have only a small effect on grain filling.

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potential and water content. Undoubtedly osmotic potential was changed to maintain some turgor but the effects of defoliation on this variable were not measured. The leaf water potential of lower leaf blades was not increased as compensation for upper blade defoliation and lower leaf water potential, though the translocation from these blades to the panicle increased.

The conclusions of Lampert (1980) that CLB defoliation decreases both the weight per kernel and the number of kernels per panicle (termed "spikelet" by Lampert) must be taken with caution since it has been shown here that relief of prior stress including CLB defoliation results in an increase in kernel weight.

Bonnett (1966) indicated that oats may have many florets per spikelet and that two or more may be fertile. There is no definite phenological stage where this number is fixed. However, adverse growing conditions after spikelet and floret differentiation will cause a failure of seed development. Although water deficits and viral presence caused such a failure, this investigation showed no correlation of spikelet number with percent defoliation on individually monitored stems.

A second biotic factor which impinged on oat growth during the course of this study was Barley Yellow Dwarf Virus. This virus was shown to interact with water deficts to substantially reduce yield through floret blasting and a

reduction in spiklet differentiation. Water deficits increased susceptibility to the disease though total plot yields within treatments were extremely variable. Any effects of CLB defoliation other than blade area reduction were masked by this systemic disease.

The major abiotic stress investigated was that due to imposed water deficits. Though the effects of water deficits especially on small grains are fairly well understood (cf. references in section VII), the interaction of this variable with CLB defoliation had not been previously investigated. Though defoliation decreased leaf water potential, the magnitude of that decrease was dependent on leaf position and time of year since leaf water potential decreased naturally with height and plant age. Water potential of a given leaf blade under maximum stress was found to be correlated with leaf position, percent defoliation, soil moisture, time of day, date and maximum air temperature. The leaf water potential of lower leaf blades did compensate for decreased leaf water potential of upper blades subjected to defoliation.

Of greatest interest was the degree of oat plant recovery upon rewatering at heading after severe defoliation and water stress throughout the vegetative growth period. During this study, pupation of the CLB was usually completed by anthesis so defoliation during and after this period was minimal. Although defoliation

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decreased transpiratory leaf surface area, no conservation of soil moisture was apparent. However, it is probable that root growth in the dry plots was deeper and more dispersed than that in the irrigated plots. An extensive root system grown in response to soil water deficits would be able to take greater advantage of new moisture supplies than a root system grown under irrigated conditions which was less extensive because of the availability of water.

The accessability of water at anthesis is important for floral development and fertilization. Without it, these processes are hindered and loss of yield can be substantial. However, even if the number of florets per panicle is decreased due to defoliation early in the season, with adequate water, compensation in the form of heavier grain is possible as has been shown.

In contrast to the results of gradual CLB defoliation, radical artificial defoliation did cause substantial yield losses. Flag leaf excision reduced kernel weight per stem by 14-18% while 100% defoliation reduced yield 53%. It is obvious that the plant is unable to compensate as well to radical mechanical defoliation as to insect defoliation. The mechanical defoliation in this study removed portions of the leaf bases including veins which the CLB generally leaves intact. The basal portion of the leaf blade contains soluble carbohydrates used for regrowth. Moreover, the cells at the base of the leaf are younger and

more photosynthetically active than those at mid-blade or beyond. The sudden shift in source-sink relationships after mechanical defoliation has not been quantitatively compared to the gradual shift caused by insect defoliation and is suggested as an area of further investigation.

X. LITERATURE CITED

Angus, J.F. and M.W. Moneur. 1976. Water stress and phenology in wheat. Aust. J. Agric. Res. 28(2):177-181.

Archbold, H.K. 1942. Physiological studies in plant nutrition. XIII. Experiments with barley on defoliation and shading of the ear in relation to sugar metabolism. Ann. Bot. (N.S.) 6:487-531.

Archbold, H.K. and B.N. Mukerjee. 1942. Physiological studies in plant nutrition. XII. Carbohydrate changes in the several organs of the barley plant during growth with special reference to the development and ripening of the ear. Ann. Bot. (N.S.) 6:1-41.

Asana, R.D. and R.N. Basu. 1963. Studies in physiological analysis of yield. 6. Analysis of the effect of water stress on grain development in wheat. Indian J. Plant Physiol. 6:1-13.

Asana, R.D. and V.S. Mani. 1950. Studies in physiological analysis of yield. I. Varietal differences in photosynthesis in the leaf, stem, and ear of wheat. Physiol. Plant. 3:22-39.

Asana, R.D. and V.S. Mani. 1955. Studies in physiological analysis of yield. II. Further observations on varietal differences in photosynthesis in the leaf, stem and ear of wheat. Physiol. Plant. 8:8-19.

Ashton, F.M. 1956. Effects of a series of cycles of alternating low and high soil water contents on the rate of apparent photosynthesis in sugar cane. Plant Physiol. 31:266-274.

Aspinall, D. 1965. The effects of soil moisture stress on the growth of barley: II. Grain growth. Aust. J. Agr. Res. 16:265-275.

Aspinall, D., P.B. Nicholls and L.H. May. 1964. The effects of soil moisture stress on the growth of barley: I. Vegetative development and grain yield. Aust. J. Agr. Res. 15:729-745.

Austin, R.B., M.A. Ford, J.A. Edrich and B.E. Hooper. 1977. Some effects of leaf posture on photosynthesis and yield in wheat. Ann. Appl. Biol. 83:425-446.

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Balachowsky, A.S. 1963. The family Chrysomelidae. In "Entomologie applique al'agriculture". Tome 1, Vol.2. Masson et Cie, Paris. 1391 pp.

Barr, R.O., P.C. Cota, S.H. Gage, D.L. Haynes, A.N. Kharkar, H.E. Koenig, K.Y. Lee, W.G. Ruesink, and R.L. Tummala. 1973. Ecologically and economically compatible pest control. In "Insects: Studies in population management". Ecol. Soc. Aust., Memoirs 1, Canberra.

Battenfield, S.L., S.G. Wellso and D.L. Haynes. Bibliography of the cereal leaf beetle Oulema melanopus (L.) (Coleoptera: Chrysomelidae). Submitted to Bull. Ent. Soc. Amer.

Begg, J.E., and N.C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217.

Begg, J.E. and M.J. Wright. 1962. Growth and development of leaves from intercalary meristems in Phalaris arundinacea L. Nature 194:1097-1098.

Birecka, H. and J. Skupinska. 1963. Photosynthesis, translocation and accumulation of assimilates in cereals during grain development. II. Spring barley - photosynthesis and the daily accumulation of photosynthates in the grain. Acta Soc. Bot. Pol. 32:531-532.

Birecka, H., J. Skupinska and I. Bernstein. 1964. Photosynthesis, translocation and accumulation of assimilates in cereals during grain development. V. Contribution of products of current photosynthesis after heading to the accumulation of organic compounds in the grain of barley. Acta Soc. Bot. Pol. 33:601-617.

Birecka, H., and L. Dakic-Wlodkowska. 1964. Photosynthesis, translocation and accumulation of assimilates in cereals during grain development. IV. Contribution of products of current photosynthesis after heading to the accumulation of organic compounds in the grain of spring wheat. Acta Soc. Bot. Pol. 33:407-425.

Biscoe, P.V. 1972. The diffusion resistance and water status of leaves of Beta vulgaris. J. exp. Bot. 23:930-940.

Biscoe, P.V., Y. Cohen and J.S. Wallace. 1976. Daily and seasonal changes of water potential in cereals. Phil. Trans. Roy. Soc. Lond. 273:565-580.

Biscoe, P.V., J.N. Gallagher, E.J. Littleton, J.L. Monteith and R.K. Scott. 1975. Barley and its environment. IV. Sources of assimilate for the grain. J. Appl. Ecol. 12:295-318.

Blum, A. and C.Y. Sullivan. 1974. Leaf water potential and stomatal activity in sorghum as influenced by soil moisture stress. Israel J. Bot. 23:14-19.

Bonnett, O.T. 1966. Inflorescences of maize, wheat, rye, barley, and oats: their initiation and development. Illinois Agr. Exp. Sta. Bull. 721.

Boonstra, A.E.H.R. 1929. Invloed van de verschillende assimileererde deelen op de korrel-productie bij Wilhelminatarme. Meded. Landbhougesch. Wageningen. 33:3-21.

Borrill, M. 1961. The developmental anatomy of leaves in Lolium temulentum. Ann. Bot. (N.S.) 25:1-11.

Boyer, J.S. 1971a. Recovery of photosynthesis in sunflower after a period of low leaf water potential. Plant Physiol. 47:816-820.

Boyer, J.S. 1971b. Nonstomatal inhibition of photosynthesis at low leaf water potentials and high light intensities. Plant Physiol. 48:532-536.

Boyer, J.S. and G.H. McPherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-23.

Bremner, P.M. and H.M. Rawson. 1972. Fixation of $^{14}CO_2$ by flowering and non-flowering glumes of the wheat ear, and the pattern of transport of label to individual grains. Aust. J. Biol. Sci. 25:921-930.

Brenedan, E.R. and H.F. Hodges. 1973. Effect of moisture deficits on ^{14}C translocation in corn Zea mays L. Plant Physiol. 52:436-439.

Brown, K.W., W.R. Jordan and J.C. Thomas. 1976. Water stress induced alterations of the stomatal response to decreases in leaf water potential. Physiol. Plant. 37:1-5.

Bruehl, G.W. 1961. Barley yellow dwarf, a virus disease of cereals. Phytopath. Mono. No. 1. 52 pp.

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. Butterworth & Co., London. pp. 20-38.

Buttrose, M.S. 1962. Physiology of cereal grain. III. Photosynthesis in the wheat ear during grain development. Aust. J. Biol. Sci. 15:611-618.

Buttrose, M.S. and L.H. May. 1959. Physiology of cereal grain. I. The source of carbon for the developing barley kernel. Aust. J. Biol. Sci. 12:40-52.

Buttrose, M.S. and L.H. May. 1965. Seasonal variation in estimates of cereal-ear photosynthesis. Ann. Bot. (N.S.) 29:79-81.

Carr, D.J. and I.F. Wardlaw. 1965. The supply of photosynthetic assimilates to the grain from the flag leaf and ear of wheat. Aust. J. Biol. Sci. 18:711-719.

Casagrande, R.A. 1975. Behavior and survival of the adult cereal leaf beetle, Oulema melanopus L. Ph.D. dissertation, Michigan State University. 174 pp.

Castro, T.R., R.F. Ruppel and M.S. Gomulinski. 1965. Natural history of the cereal leaf beetle in Michigan. Quart. Bull. Mich. Ag. Exp. Sta. 47:623-653.

Chant, D.A. 1966. Integrated control systems. "Scientific Aspects of Pest Control". Nat. Acad. Sci., Nat. Res. Conc. Publ. 1402:194-218.

Chiarappa, L. (ed.) 1967. Crop loss assessment methods. FAO manual on the evaluation and prevention of losses by pests, disease and weeds. Commonwealth Agricultural Bureaux, England.

Croft, B.A., J.L. Howes and S.M. Welch. 1976. A computer-based, extension pest management delivery system. Environ. Entomol. 5(1):20-34.

Cutter, J.M. and R.S. Loomis. 1977. On the importance of cell size in the water relations of plants. Physiol. Plant. 40:255-260.

Cutter, J.M. and D.W. Rains. 1978. Effects of water stress and hardening on the internal water relations and osmotic constituents of cotton leaves. Physiol. Plant. 42:261-268.

Davidson, J.L. and F.L. Milthorpe. 1966a. Leaf growth in Dactylis glomerata following defoliation. Ann. Bot. (N.S.) 30:173-184.

Davidson, J.L. and F.L. Milthorpe. 1966b. The effect of defoliation on the carbon balance in Dactylis glomerata. Ann. Bot. (N.S.) 30(118):185-198.

Denmead, O.T. and B.D. Millar. 1976a. Water transport in wheat plants in the field. Agron. J. 68:297-303.

Denmead, O.T. and B.D. Millar. 1976b. Field studies of the conductance of wheat leaves and transpiration. Agron. J. 68:307-311.

de Silva, W.H. 1961. Studies in the crop physiology of wheat. Ph.D. Thesis, Univ. Reading.

Doodson, J.K., J.G. Manners and A. Myers. 1963. The distribution pattern of 14 carbon assimilated by the third leaf of wheat. J. Exp. Bot. 15:96-103.

Duncan, W.G. 1971. Leaf angles, leaf area and canopy photosynthesis. Crop Science 11:482-485.

Evans, L.T. and H.M. Rawson. 1970. Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. Aust. J. Biol. Sci. 23:245-254.

Evans, L.T., J. Bingham, P. Jackson, and J. Sutherland. 1972. Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears. Ann. Appl. Biol. 70:67-76.

Fisher, R.A. 1975. Yield potential in a dwarf spring wheat and the effect of shading. Crop Sci. 15:607-613.

Fisher, R.A. and G.D. Kohn. 1966. The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. Aust. J. Agr. Res. 17:281-295.

Frank, A.B. and Harris, D.G. 1973. Measurement of leaf

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water potential in wheat with a pressure chamber. Agron. J. 65:334-335.

Frank, A.B., J.F. Power, and W.O. Willis. 1973. Effect of temperature and plant water stress on photosynthesis, diffusion resistance, and leaf water potential in spring wheat. Agron. J. 65:777-780.

Friend, D.J.C. 1966. The effects of light and temperature on the growth of cereals. In "The Growth o Cereals and Grasses". F.L. Milthorpe and J.D. Ivins, eds. Butterworth & Co., London. pp. 181-199.

Fry, K.E. 1972. Inhibition of ferricyanide reduction in chloroplasts prepared from water stressed cotton leaves. Crop Science 12:698-701.

Fulton, W. C. and D. L. Haynes. 1975. Computer mapping in pest management. Environ. Entomol. 4:357-360.

Gage, S. H. 1972. The cereal leaf beetle, Oulema melanopus (L.), and its interaction with two primary hosts: winter wheat and spring oats. M.S. Thesis, Michigan State Univ., E. Lansing. 105 pp.

Gage, S. H. 1974. Ecological investigations on the cereal leaf beetle Oulema melanopus (L.), and the principle larval parasite, Tetrastichus julis (Walker). Ph.D. Thesis, Michigan State Univ., E. Lansing. 172 pp.

Gage, S. H. and M. E. Mispagel. 1981. Design and development of a cooperative crop monitoring system. A conference on automated data processing in IPM programs. Washington, D.C. 1979.

Gage, S. H. and J. V. Pieronek. 1980. A microcomputer application for integrated pest management. Mich. State Univ. Agric. Coop. Bull. 1(1):29-36.

Gage, S. H., M. E. Whalon and D. J. Miller. 1981. A pest event scheduling system for biological monitoring and pest management. Mich. Agr. Exp. Sta. Jour. Art. #10031.

Gallagher, J. N., P. V. Biscoe and R. K. Scott. 1975. Barley and its environment. V. Stability of grain weight. J. appl. Ecol. 12:319-336.

Gallun, R. L., R. Ruppel, and E. H. Everson. 1966. Resistance of small grains to the cereal leaf beetle.

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J. Econ. Entomol. 59:827-829.

Gallun, 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.

Geier, P. W. 1966. Management of insect pests. Ann. Rev. Entomol. 11:471-490.

Goode, J. E. and K. H. Higgs. 1973. Water, osmotic and pressure potential relationships in apple leaves. J. Hort. Science 48:203-215.

Gutierrez, A. P., W. H. Denton, R. Shade, H. Maltby, T. Burger and G. Moorehead. 1974. The within-field dynamics of the cereal leaf beetle (Oulema melanopus (L.)) in wheat and oats. J. Anim. Ecol. 43:627-640.

Harper, A. M., T. G. Atkinson, and A. D. Smith. 1976. Effect of Rhopalosiphum padi and barley yellow dwarf virus on forage yield and quality of barley and oats. J. Econ. Entomol. 69:383-385.

Hartt, C. E. 1967. Effect of moisture supply on translocation and storage of 14C translocation in sugarcane. Plant Physiol. 42:338-346.

Haynes, D. L., R. K. Brandenburg, and P. D. Fisher. 1972. Environmental monitoring network for pest management systems. Environ. Entomol. 2:889-899.

Haynes, D.L. and S.H. Gage. 1981. The cereal leaf beetle in North America. Ann. Rev. Entomol. 26:259-287.

Headley, J.C. 1971. Defining the economic threshold. Pest Control Strategies for the Future. National Acadamy of Sciences. pp. 100-108.

Helgesen, R.G. and D.L. Haynes. 1972. Population dynamics of the cereal leaf beetle, Oulema melanopus (Coleoptera: Chrysomelidae); A model for age specific mortality. Can. Entomol. 104:797-814.

Hendrix, J.W., M.W. Jones and C.G. Schmitt. 1965. Influence of stripe rust and mechanical defoliation at various stages of host development on growth and wheat yield. Washington Ag. Exp. Sta. Tech. Bull. 47. 18 pp.

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Hsiao. T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570.

Iljun, W.S. 1957. Drought resistance in plants and physiological processes. Ann. Rev. Plant Physiol. 8:257-274.

Jackman, J.A. 1976. A quantitative description of oat growth with cereal leaf beetle populations. PhD. Thesis, Mich. State Univ., E.Lansing, MI. 172 pp.

Jackman, J.A. and D.L. Haynes. 1975. An inverse relationship between individual size and population density in the cereal leaf beetle, Oulema melanopus. Environ. Entomol. 4:235-237.

Jaffe, M.J. 1976. Thigmomorphogenesis: A detailed characterization of the response of beans Phaseolus vulgaris L. to mechanical stimulation. Z. Pflanzenphysiol. 77:437-453.

Jaffe, M. J. 1980. Morphogenetic responses of plants to mechanical stimuli or stress. Bioscience 30:239-243.

Jaffe, M.J. and R. Biro. 1979. Thigmomorphogenesis: The effect of mechanical perturbation on the growth of plants, with special reference to anatomical changes, the role of ethylene, and interaction with other environmental stresses. In "Stress Physiology in Crop Plants". John Wiley & Sons, New York. pp. 25-69.

Jennings, V.M. and R. M. Shibles. 1968. Genotypic differences in photosynthetic contributions of plant parts to grain yield in oats. Crop Science 8:173-175.

Jewiss, O.R. 1966. Morphological and physiological aspects of growth of grasses during the vegetative phase. In "The growth of cereals and grasses". F. L. Milthorpe and J. D. Ivins, eds. Butterworth & Co., London. pp. 39-54.

Johnson, R.R., N.M. Frey and D.N. Moss. 1974. Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. Crop Science 14:728-731.

Johnson, R.R. and D.N. Moss. 1976. Effect of water stress on $^{14}CO_2$ fixation and translocation in wheat during grain filling. Crop Science 16:697-701.

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Jones, M.M. and N.C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61:122-126.

Kaul, R. 1966. Effect of water stress on respiration of wheat. Can. J. Bot. 44:623-632.

Keck, R.W. and J.S. Boyer. 1974. Chloroplast response to low leaf water potentials. Plant Physiol. 53:474-479.

Kennedy, J.S. 1968. The motivation of integrated control. J. Appl. Ecol. 5:482-499.

Kiesselbach, T.A. 1925. Winter wheat investigations. Nebraska Agric. Exp. Sta. Res. Bul. 31.

Knechtel, W.K. and C.I. Manolache. 1936. Biological observations on L. melanopa in Rumania. Anal. Inst. Cerc. Agron. Roman. 7:186-208.

Koenig, H.E. 1974. Ecology, economics and techonological development; A sociocybernetic perspective. Quaestiones Entomologicae. 10:155-164.

Koenig, H.E., D.L. Haynes and R.L. Tummala. 1976. Systems engineering - Prospects for technological development of an approach to systems in biometeorology. Int. J. Biomet. 20:73-81.

Koval, C.F. 1966. The cereal leaf bettle in relation to oat culture. Ph.D. Thesis. Univ. of Wisconsin. Madison, Wisconson. 120 pp.

Kozlowski, T.T. (Ed.). 1968a. Water deficits and plant growth. Academic Press, London and New York. Vol. 1.

Kramer, P.J. 1969. Plant and soil water relationships - A Modern Synthesis. McGraw-Hill, New York.

Labanauskas, C.K. and G.H. Dungan. 1956. Inter-relationship of tillers and main stems in oats. Agron. J. 48:265-268.

Lampert, E.P. 1980. Endemic ecology of the cereal leaf beetle Oulema Melanopus (L.). Ph.D. Thesis, Michigan State Univ., E. Lansing. 528 pp.

Large, E.C. 1966. Measuring plant disease. Ann. Rev. Phytopathol. 4:9-28.

Lawlor, D.W. 1973. Growth and water absorption of wheat with parts of the roots at different water potentials. New Phytol. 72:297-305.

Ludlow, M.M. and T.T. Ng. 1976. Effect of water deficit on carbon dioxide exchange and leaf elongation rate of Panicum maximum var. Trichoglume. Aust. J. Plant Physiol. 3:401-413.

Lyon, W.F. and D.A. Ray. 1968. Cereal leaf beetle infestation on 20 varieties of drill-seeded spring oats in Franklin County, Columbus, Ohio 1968. Cooperative Extension Service, Ohio State University. 5 pp.

Lyubenov, Y. 1956. The effects of fertilizers and sowing date on the degree of attack by Lema melanopa L. Rev. Appl. Ent. Ser. A 46(4):117-118.

Mayer, A. and H.K. Porter. 1960. Translocation from leaves of rye. Nature 188:921.

McCall, K.J. 1974. Changes in stomatal response characteristics of grain sorghum produced by water stress during growth. Crop Science 14:273-278.

McMichael, B.L. 1980. Water stress adaptation. In "Predicting Photosynthesis for Ecosystem Models." CRC Press, Inc. pp. 183-202.

McNeal, F.H., M.A. Berg and C.A. Watson. 1966. Nitrogen and dry matter in five spring wheat varieties at successive stages of development. Agron. J. 58:605-608.

McNeal, F.H., G.O. Boatwright, M.A. Berg and C.A. Watson. 1968. Nitrogen in plant parts of seven spring wheat varieties at successive stages of development. Crop Science. 8:535-537.

McPherson, H.G. and J.S. Boyer. 1977. Regulations of grain yield by photosynthesis in maize subjected to a water deficiency. Agron. J. 69:714-718.

McWilliam, J.R. 1968. The nature of the perennial response in Mediterranean grasses. II. Senescence, Summer dormancy, and survival in Phalaris. Aust. J. Agric. Res. 19:397-409.

Merritt, D.L. and J.W. Apple. 1969. Yield reduction of oats caused by the cereal leaf beetle. J. Econ.

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Entomol. 62:298-301.

Meyer, R.F. and J.S. Boyer. 1972. Sensitivity of cell division and cell elongation to low water potentials in soybean hypocotyls. Planta 108:77-87.

Millar, B.D. and O.T. Denmead. 1976. Water relations of wheat leaves in the field. Agron. J. 68:303-307.

Millar, A.A., M.E. Duysen and G.E. Wilkinson. 1968. Internal water balance of barley under soil moisture stress. Plant Physiol. 43:968-972.

Miller, E.C., G.A. Gries, W.A. Lunsford and J.C. Frazier. 1948. Effect of defoliation on the functions of red winter wheat. Kansas Agric. Exp. Tech. Bull. 62:1-95.

Milthorpe, F.L. and J. Moorby. 1974. An introduction to crop physiology. Cambridge Univ. Press, London. 202 pp.

Munns, R. and C.J. Pearson. 1974. Effect of water deficit on translocation of carbohydrate in Solanum tuberosum. Aust. J. Plant Physiol. 1:529-537.

Neales, T.F., M.J. Anderson and I.F. Wardlaw. 1963. The role of the leaves in the accumulation of nitrogen by wheat during ear development. Aust. J. Agric. Res. 14:725-736.

Neales, T.F. and L.D. Incoll. 1968. The control of leaf photosynthetic rate by the level of assimilate concentration in the leaf. A review of the hypothesis. Bot. Rev. 34:107-125.

Nix, H.A. and E.A. Fitzpatrick. 1969. An index of crop water stress related to wheat and grain sorghum yields. Agr. Meteorol. 6:321-337.

Nordin, A. 1976. Water flow in wheat seedlings after small water deficits. Physiol. Plant. 37:157-162.

Ong, C.K., K.E. Colvill and C. Marshall. 1978. Assimilation of $^{14}CO_2$ by the inflorescence of Poa annua L. and Lolium perenne L. Ann. Bot. 42:855-862.

Pandey, R.N. 1972. Effect of soil moisture stress on yield and seasonal water requirement of wheat. J. Agric. Eng. 9(3):19-23.

Passioura, J.B. 1976a. Physiology of grain yield in wheat growing on stored water. Aust. J. Plant. Physiol. 3:559-565.

Passioura, J.B. 1976b. The control of water flow through plants. In "Transport and Transfer Processes in Plants". I.F. Wardlaw and J. B. Passioura,eds. pp. 373-380.

Patrick, J. W. 1972. Distribution of assimilate during stem elongation in wheat. Aust. J. Biol. Sci. 25:455-467.

Pauli, A.W. and H.H. Laude. 1959. Protein and carbohydrate relationships in winter wheat as influenced by mechanical injury. Agron. J. 51(1):55-57.

Philips, M., M.J. Goss, B.L. Davis and P.H. Stevens. 1939. Composition of various parts of the oat plant at successive stages of growth, with special reference to formation of lignin. J. Agric. Res. 59:319-366.

Porter, H.K., N. Pal and R.V. Martin. 1950. Physiological studies in plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in the grain. Ann. Bot. (N.S.) 14:55-68.

Puckridge, D.W. 1968. Competition for light and its effect on leaf and spikelet development of wheat plants. Aust. J. Agric. Res. 19:191-201.

Quinlan, J.D. and G.R. Sagar. 1965. Grain yield in two contrasting varieties of spring wheat. Ann. Bot. (N.S.) 29:683-697.

Rawson, H.M. and L.T. Evans. 1971. The contribution of stem to grain development in a range of wheat cultivars of different height. Aust. J. Agric. Res. 22:851-863.

Rawson, H.M. and G.H. Hofstra. 1969. Translocation and remobilization of ^{14}C assimilated at different stages by each leaf of the wheat plant. Aust. J. Biol. Sci. 22:321-331.

Rimpau, L. 1978. Protein fractionation - Adapted for small amounts of tissue. Dept. of Animal Husbandry, Michigan State Univ., E. Lansing, MI 48824.

Ritchie, G.A. and T.M. Hinckley. 1975. The pressure chamber as an instrument for ecological research. In "Advances in Ecological Research". A. MacFadyen, ed. 9:165-254.

Roebuck, A. and P.S. Brown. 1923. Correlation between loss of leaf and damage to crop in late attacks on wheat. Ann. Biol. 22:326-334.

Ryle, G.J.A. and C.E. Powell. 1975. Defoliation and regrowth in the graminaceous plant: the role of current assimilate. Ann. Bot.(N.S.) 39:297-310.

Salim, M.H.. G.W. Todd and S.M. Schlehuber. 1965. Root development of wheat, oats, and barley under conditions of soil moisture stress. Agron. J. 57:603-607.

Sandhu, B.S. and M.L. Horton. 1977. Response of oats to water deficit. II. Growth and yield characteristics. Agron. J. 69:361-364.

Sandhu, B.S. and M.L. Horton. 1977. Response of oats to water deficit. I. Physiological characteristics. Agron. J. 69:357-360.

Sawyer, A.J. 1978. A model for the distribution and abundance of the cereal leaf beetle in a regional crop system. Ph.D. Thesis Mich. State Univ., E. Lansing. 279 pp.

Scriber, J.M. 1978. The effects of larval feeding specialization and plant growth form on the consumption and utilization of plant biomass and nitrogen: An ecological consideration. Ent. exp. & Appl. 24:494-510.

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. Ent. Soc. Amer. 60:493-496.

Sharman, B.C. 1942. Developmental anatomy of the shoot of Zea mays L. Ann. Bot., (N.S.) 2:245-282.

Simmelsgaard, S.E. 1976. Adaptation to water stress in wheat. Physiol. Plant. 37:167-174.

Slansky, F., Jr. and P. Feeny. 1977. Stabilization of the rate of nitrogen acculmulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecol.

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Mono. 47:209-228.

Slatyer, R.O. 1967. Plant-water relationships. Academic Press, London and New York.

Slayter, R.O. 1969. Physiological significance of internal water relations to crop yield. In "Physiological Aspects of Crop Yield". Eastin, J.D., F.A. Hoskins, C.Y. Sullivan and C.H. Van Bavel, eds. pp. 53-83.

Slayter, R.O. and W.R. Gardner. 1965. Overall aspects of water movements in plants and soils. Soc. Exptl. Biol. 29:113-129.

Smith, R.F. and R. van den Bosch. 1967. Integrated control. In "Pest Control: Biological, Physical and Selected Methods". W.W. Kilgore and R.L. Doutt, eds. Academic Press, New York. 470 pp.

Spratt, E.D. and J.K.R. Gasser. 1970. Effects of fertilizer and water supply on distribution of dry matter and nitrogen between the different parts of wheat. Can. J. Plant Sci. 50:613-625.

Steidl, R.P., J.A. Webster and D.H. Smith, Jr. 1979. Cereal leaf beetle plant resistance: antibiosis in an Avena sterilis introduction. Environ. Entomol. 8:448-450.

Stern, V.M. 1973. Economic thresholds. Ann. Rev. Entomol. 18:259-280.

Stern, V.M., R.F. Smith, R. van den Bosch and K.S. Hagen. 1959. The integration of chemical and biological control of the spotted alfalfa aphid. Part 1. The integrated control concept. Hilgardia 29:81-101.

Steudle, E., U. Zimmerman and U. Luttge. 1977. Effect of turgor pressure and cell size on the wall elasticity of plant cells. Plant Physiol. 59:285-289.

Stoy, V. 1963. The translocation of 14C-labelled photosynthetic products from the leaf to the ear in wheat. Physiol. Plant. 16:851-866.

Stubbs, L.L. and W.I. Walbran. 1963. Accumulation of nitrate in oats infected with Barley Yellow Dwarf Virus. Aust. J. Agric. Res. 14:737-741.

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of carbohydrates in plants. Bot. Rev. 34:79-105.

Wardlaw, I.F. 1969. The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in Lolium temulentum L. Aust. J. Biol. Sci. 22:1-16.

Wardlaw, I.F., D.J. Carr and M.J. Anderson. 1965. The relative supply of carbohydrate and nitrogen to wheat grains and an assessment of the shading and defoliation techniques used for the determinations. Aust. J. Agr. Res. 16:893-901.

Wardlaw, I.F. and H.K. Porter. 1967. The redistribution of stem sugars in wheat during grain development. Aust. J. Biol. Sci. 20:309-318.

Watson, D.J. and A.G. Norman. 1939. Photosynthesis in the ear of barley, and the movement of nitrogen into the ear. J. Agric. Sci. 29:321-346.

Watson, D.J., G.N. Thorne and S.A.W. French. 1958. Physiological causes of differences in grain yield between varieties of barley. Ann. Bot. (N.S.) 22:321-352.

Webster, J.A., D.H. Smith, Jr. and C. Lee. 1972. Reduction in yield of spring wheat caused by cereal leaf beetles. J. Econ. Entomol. 65:832-835.

Wellso, S.G. 1973. Cereal leaf beetle: larval feeding, orientation, development, and survival on four small grain cultivars in the laboratory. Ann. Ent. Soc. of Amer. 66(6):1201-1208.

Wellso, S.G. 1974. Aestivation in relation to oviposition initiation in the cereal leaf beetle. In "Chronobiology". L.E. Scheuing, F. Halberg and J.E. Pauly, eds. Igaku Shoin Ltd., Tokyo. pp. 597-601.

White, R.M. 1946. Preliminary observations on some effects of artificial defoliation of wheat plants. Sci. Agr. 26:225-229.

White, T.C.R. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of Selidosema suavis in a plantation of Pinus radiata in New Zealand. Oecologia 16(4):279-301.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oceologia 33:71-86.

Williams, R.D. 1964. Assimilation and translocation in perennial grasses. Ann. Bot. (N.S.) 28:419-426.

Williams, R.F. and R.E. Shapter. 1955. A comparative study of growth and nutrition in barley and rye as affected by low-water treatment. Aust. J. Biol. Sci. 8:435-466.

Wilson, M.C., H.H. Toba, H.F. Hodges and R.K. Stives. 1964. Seed treatments, granular applications and foliar sprays to control the cereal leaf beetle. Agr. Exp. Sta. Res. Prog. Rep. 96. Purdue Univ. 8 pp.

Wilson, M.C., R.E. Treece, R.E. Shade, K.M. Day and R.K. Stivers. 1969. Impact of cereal leaf beetle larvae on yields of oats. J. Econ. Entomol. 62:699-702.

Womack, D. and R.L. Thurman. 1962. Effects of leaf removal on the grain yield of wheat and oats. Crop Science 2:423-426.

Yoshida, S. 1972. Physiological aspects of grain yield. Ann. Rev. Plant Physiol. 23:437-464.

XI. APPENDICES

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Appendix 1. Field numbers at the Kellogg Biological Station.

Table A1. Relationship of numbered fields at the Kellogg Biological Station as delineated by Casagrande (1975), Figure A1, and the revised field numbers (1981), Figure A2.

Section 4		Section 5		Section 8		Section 9	
1975	1981	1975	1981	1975	1981	1975	1981
30-32	55	11	42	1-2	62	1-2	75
33-52	54	12	44	3-5	63	3-6	76
55-56	52	13	48	6-14	80W	7-13	77
57	68	14	49	15	80E	14	78
54,58,59	53	15	45	16	81	15-25	79
		17-22	51	17	68	26-36	79
		23-28	50	18	69	37-42	84
		29-32	46	19-24	82	43-44	85
		33-35	39	25	70	59-61	100
		36-37	38	26	71	62-63	99
		38	36	27-30	72	64-68	98
		39-41	35	31-34	74A	69-70	97
		42	34	35-38	74B		
		44-46	40	41-49	83		
		47	41	50	89		
		48	31	51	90		
		49	32	3,54-57	91		
		50-63	30	58-62	94		
				64	95		
				65-72	93		
				73-75	86		
				78	87		
				79-83	88		

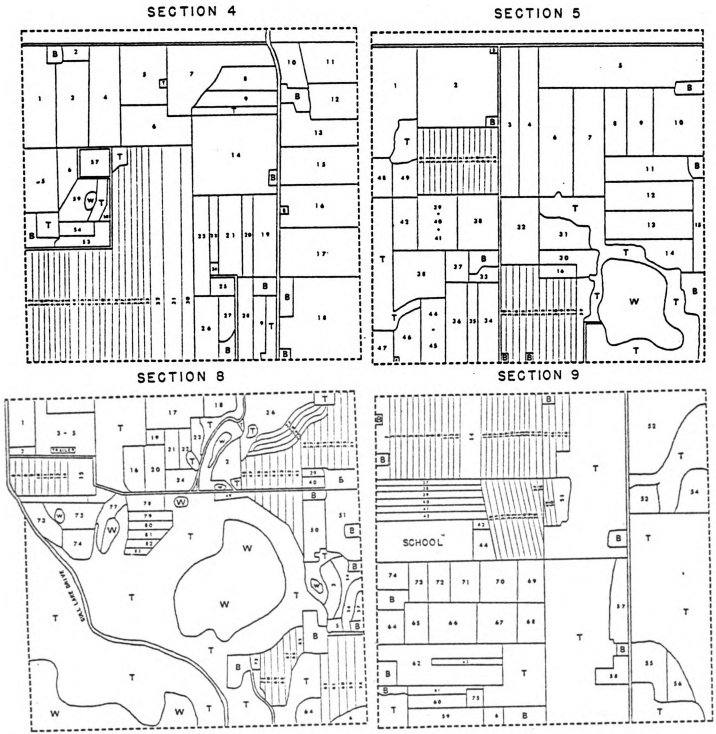

Figure A1. Numbered fields at the Kellogg Biological Station according to the scheme of Casagrande (1975).

Figure A2. Numbered fields at the Kellogg Biological Station revised in 1981.


Kellogg
Biological
Station
property boundary
field boundary
temporary boundary
fence row
road
45 Field number
6.0 acreage
Scale 1" = 600'
Kellogg
School

Appendix 2. Accumulated degree days (>5.5C) from 1979-1981.

Tab
Apr
the

Table A2. Accumulated degree days (>5.5C) from April-August 1979 at canopy height in the open at the Kellogg Biological Station.

Day	April	May	June	July	August
1	58	169	456	892	1434
2	58	177	466	907	1452
3	59	187	478	922	1468
4	60	190	492	935	1486
5	61	192	510	945	1503
6	61	202	525	959	1519
7	61	215	540	974	1539
8	61	231	560	990	1559
9	61	247	575	1007	1575
10	62	265	589	1024	1594
11	63	280	600	1042	1605
12	71	286	610	1062	1615
13	81	291	621	1082	1628
14	84	298	636	1105	1638
15	86	305	655	1129	1647
16	88	311	673	1147	1656
17	91	320	692	1163	1669
18	95	335	708	1177	1681
19	100	349	721	1192	1695
20	107	358	739	1209	1710
21	117	367	758	1229	1724
22	124	372	773	1247	1739
23	132	382	784	1268	1757
24	143	388	794	1289	1774
25	152	394	804	1309	1787
26	159	412	819	1324	1799
27	162	406	885	1342	1813
28	164	413	852	1362	1829
29	166	423	868	1380	1844
30	166	433	880	1398	1861
31		444		1418	

Table A3. Accumulated degree days (>5.5C) from April-August 1980 at canopy height in the open at the Kellogg Biological Station.

Day	April	May	June	July	August
1	23	140	456	868	1433
2	26	150	470	884	1452
3	28	161	483	903	1468
4	29	173	497	921	1485
5	31	185	508	939	1504
6	35	196	519	959	1520
7	42	202	533	976	1539
8	48	204	549	993	1560
9	49	207	557	1016	1580
10	49	214	567	1033	1598
11	50	222	572	1055	1614
12	51	231	579	1075	1632
13	52	241	590	1092	1649
14	52	248	604	1111	1665
15	52	253	618	1130	1680
16	53	260	625	1154	1691
17	56	267	636	1172	1703
18	61	274	645	1189	1719
19	68	284	659	1209	1734
20	78	294	672	1231	1752
21	85	305	686	1251	1773
22	99	319	701	1271	1789
23	112	333	718	1285	1804
24	114	348	734	1300	1819
25	116	361	753	1317	1836
26	119	370	775	1335	1854
27	122	381	796	1351	1874
28	126	393	816	1367	1894
29	131	414	834	1382	1913
30	135	431	854	1396	1933
31		446		1414	

Table A4. Accumulated degree days (>5.5C) from April-August 1981 at canopy height in the open at the Kellogg Biological Station.

Day	April	May	June	July	August
1	69	237	512	966	1542
2	74	242	524	986	1560
3	85	249	541	1006	1577
4	91	260	556	1026	1596
5	96	274	570	1046	1612
6	98	281	587	1067	1630
7	106	284	602	1088	1647
8	112	289	617	1112	1663
9	119	299	629	1135	1679
10	124	306	648	1158	1695
11	135	306	656	1181	1711
12	142	310	668	1204	1726
13	148	316	683	1227	1744
14	153	317	703	1244	1763
15	154	322	722	1261	1779
16	158	331	736	1278	1792
17	170	340	752	1295	1802
18	179	344	767	1313	1814
19	183	354	782	1334	1826
20	184	366	797	1352	1840
21	186	376	812	1376	1856
22	190	387	827	1389	1870
23	195	399	842	1402	1885
24	197	413	859	1418	1902
25	198	426	875	1436	1919
26	202	441	885	1456	1937
27	208	452	900	1472	1953
28	220	462	915	1483	1971
29	226	476	930	1499	1987
30	231	490	949	1512	2004
31		504		1527	

Appendix 3. Soil physical properties at the Kellogg Biological Station.

Table A5. Soil test conditions at the Kellogg Biological Station 1979 and 1980.

Year	Sec.	Field # (1975)	Depth (cm)	pH	P	K	Ca	Mg	NO3 (mg/kg)
					(lbs/acre)				
1979	5	51	15	5.4	94	76	600	56	6.70
			30	5.2	94	84	600	28	5.60
		54	15	5.4	82	160	1400	104	5.45
			30	5.3	78	190	1300	122	5.30
	8	9	15	5.6	200	145	900	75	5.25
			30	5.9	295	183	1000	94	5.05
		11	15	5.6	200	91	800	47	4.70
			30	5.6	94	61	800	38	4.90
	9	6	15	5.6	182	267	1300	85	4.80
			30	5.7	160	282	1200	94	5.05
		13	15	5.6	152	206	1400	94	4.85
			30	5.5	149	312	1400	104	4.80
1980	9	11	15	6.6	240	280	1813	128	ND


Percent
0
15
30
45
60

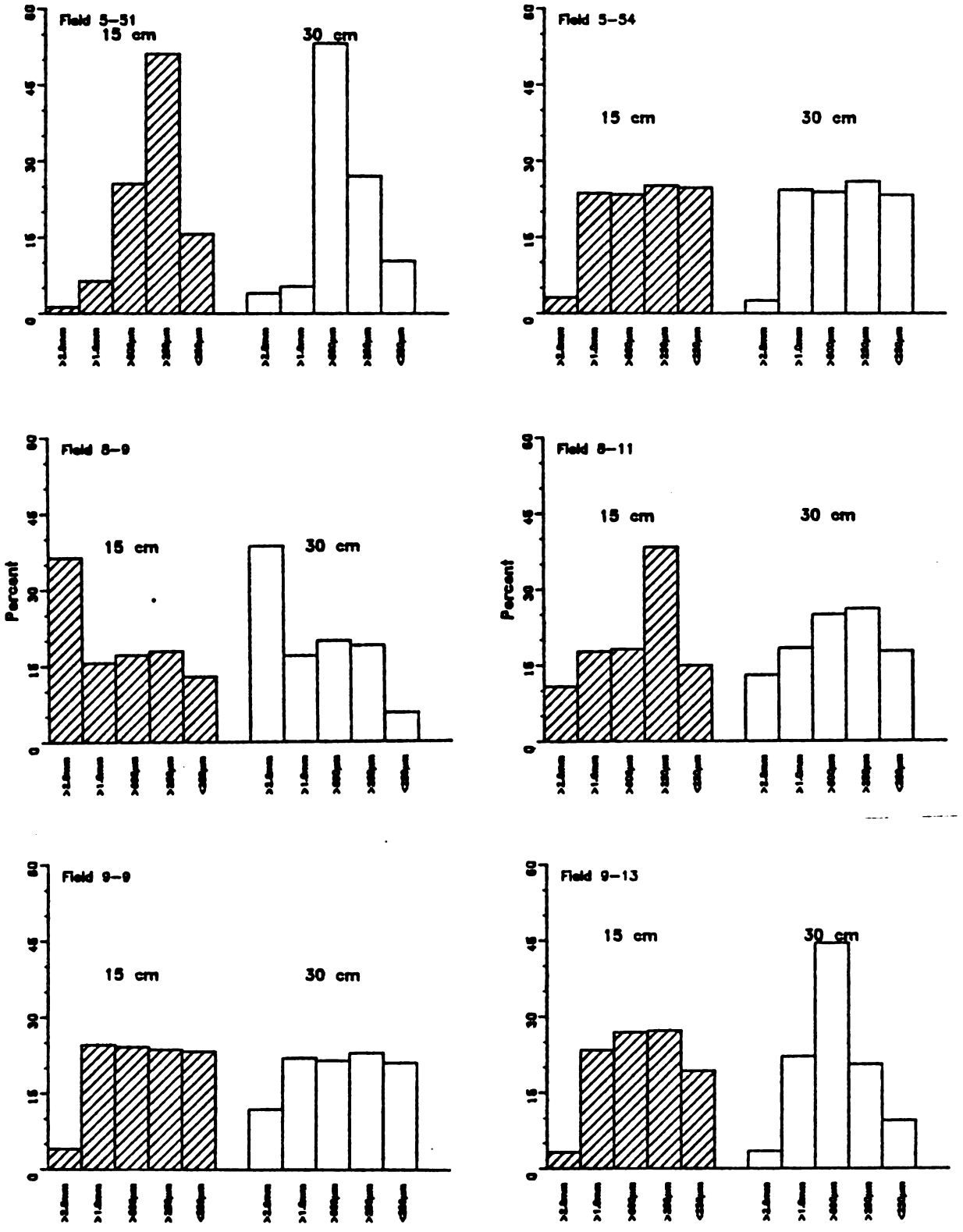

Figure A3. Soil particle size for six fields at the Kellogg Biological Station.

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APPENDIX 4. Computer Data Files

The following primary data files are stored at the MSU computer center on tapes UP1851 and UP1852. Complete documentation for these files and others can be obtained from the Department of Entomology, Michigan State University.

Abiotic Data

CDDA1979TEMPERATURES
CDDA79DEGREEDAY42
CDDADEGREEDAY48
CDDASOILMOISTURE79
CDDA1980TEMPERATURES
CDDA1980DEGREEDAYS42
CDDA80SOILMOISTUREBARS
CDDA80SOILMOISTURES
CDDAGULLLAKEDEGDAYS81
CDDA1981TEMPERATURES
CDDA1981DEGREEDAYS
CDDA1981SIXINCHMOISTURE
CDDA1981TWELVEINCHMOISTURE
CDDA81SOILMOISTUREDATA
CDDASOILPARTICLESIZE

Water Relations Data

CDDATOTWATREL79
CDDAWATREL79
CDDA1981PRESSUREBOMBDATA
CDDA1981WATERPOTENTIALSOILMOIST
CDDA1981WATERCONTENT

Artificial Defoliation Data

CDDA1979ARTDEFOL
CDDA1979ARTDEFOLHEADWT
CDDA79FLAGDEFOL
CDDA1980ARTDEFOL
CDDA1981ARTDEFYIELD

1981 BYDV Data

CDDAAVEGREENBYDVPLANTS
CDDABYDVDAY188YIELD
CDDABYDVYIELD
CDDABYDV1981

1981 Translocation Data

CDDATRANSLOCATIONDATA
CDDA1981TOTALCPM
CDDATRANSLOCATIONNOCONTROLS
CDDATRANSLOCATIONBYPOSITION
CDDATRANSFLAGTOHEAD

Growth Data

For 1979: CDDATOTALBIOMASS613
CDDATOTALBIOMASS620
CDDATOTALBIOMASS625
CDDATOTALBIOMASS701
CDDALEAFAREAPERDAY
CDDALEAFAREAPERDAY2
CDDALEAFWEIGHTPERDAY
CDDALEAFWEIGHTPERDAY2
CDDASHEATHWEIGHTSPERDAY
CDDASHEATHWEIGHTSPERDAY2
CDDATOTALSHEATHAREAPERDAY
CDDATOTALSHEATHAREAPERDAY2
For 1980: CDDA80LEAFDATA
CDDA80SHEATHDATA
CDDA1980BLADEAREASPERPLOT
CDDA1980MAINSTEMLEAFAREA
CDDA1980MAINSTEMLEAFWEIGHT
CDDA80SENESCING AREAS
CDDA1980EXPOSEDSHEATHAREA
CDDA19800VERLAPSHEATHAREA
CDDA1980SHEATHAREAWEIGHTS
CDDA1980SHEATHWEIGHTS
CDDA1980STEMSHEATHSUMMARY
For 1981: CDDA1981PLANTMEASURES
CDDA1981BLADEAREAS
CDDA1981BLADEGROWTHDATA
CDDA1981BLADEWEIGHTS
CDDA1981MAINSTEMLEAFAREA
CDDA1981EXPOSEDSTEMAREA
CDDA1981MAINSTEMLEAFWEIGHT
CDDA19810VERLAPSHEATHAREA
CDDA1981PERCENTEXPOSED
CDDA1981PERCENTOVERLAP

CDDA1981SHEATHAREAWEIGHTS
CDDA1981SHEATHDATA
CDDA1981SHEATHGROWTHRATES
CDDA1981SHEATHWEIGHTS
CDDA1981STEMSHEATHSUMMARY
CDDA1981DEFOLIATION

Yield Data

CDDA79HEADS
CDDA79HEADWT
CDDA79YIELD
CDDA80YIELDMULTREGVAR
CDDA1980INDIVIDUALYIELDMULTREGVAR
CDDA1981YIELD
CDDA1981THOUSANDKERWT
CDDA1981YIELDMULTREGVAR
CDDA1981INDIVIDUALYIELDMULTREGVAR

Appendix 5. Food quality preference by the Cereal Leaf Beetle

Introduction

Certain behavior by the cereal leaf beetle (CLB) has never been satisfactorily explained. It is known that the adult beetles migrate from winter wheat to spring oats as soon as the oat seedlings are available. The cause of this has usually been linked to some aspect of food quality which causes this attractancy to oats. But, the cause and effect relationship between some variable of the oats and beetle movement has not been shown.

Ruesink (1972) concluded that different beetle populations infest either roadside grasses, winter grains or spring oats, that movement between locations was minimal and that population reductions in each habitat were due to mortality, not emigration. Fulton (1978) assumed sequential movement of beetles from winter wheat to a more attractive spring oats in response to a fixed preference for each of these crops. In contrast, Sawyer (1978) hypothesized that movement occurs continuously from field to field in a random fashion. The rate of leaving a field was suggested to be a function of a field's attractiveness or "quality".

I investigated the hypothesis that through inductive

learning the cereal leaf beetle would "prefer" to feed on plant material of the same quality as that on which it had first fed. Verification of such a hypothesis would provide partial explanation for the insect's migration from wheat to oats and its positive phototactic behavioural response.

Materials and Methods

Summer CLB adults were collected in mid-July 1980 at the Kellogg Biological Station soon after they emerged. They were immediately placed on four different food types for a period of 9 days as a preconditioning treatment: new oats, old oats, new wheat and old wheat. Seedlings of the greenhouse grown plant material were designated as "new", and late vegetative plant material prior to heading was designated as "old".

Each of five beetles selected from the preconditioning treatments was placed individually in feeding choice arenas consisting of petri dishes 15x100 mm. A moist filter paper was placed inside the lid to prevent desiccation of the plant material. A fresh 2 cm length of each of the four food types was presented to the beetles every twelve h and the old pieces removed. Feeding scars were measured on each piece and the surface area consumed was calculated. The dry weight of the consumed material was calculated from control aliquots of each piece presented from which leaf

area and leaf dry weight relationships were determined. The feeding choice experiment began at 1:30 PM July 20 and ended at 8:15 AM July 28 after 187 hours. Feeding arenas were kept in an environmental chamber under constant temperature and regulated light.

Results and Discussion

It was hypothesized that once the insect was preconditioned to a particular food or food quality, it would maintain its preference for that food over other choices regardless of their nutritional value. The results of this experiment do not substantiate that hypothesis (Table A6). It is clear that new oats was clearly the preferred food item. In contrast, new wheat was the least preferred food implying that simple succulence was not the variable of most concern to the beetles. Preconditioning to the young plants ellicited a definite feeding preference whereas preconditioning to old wheat resulted in no significant preference for the four food items. Significantly, preconditioning to old oats resulted in the complete cessation of feeding.

Though pubescent cultivars were not used, these data seem to indicate that the physical makeup of the leaf was not as important to the summer adult CLB as was its chemical composition. The higher nitrogen content of the

Table A6. Dry weight (mg x 10^{-2}) of leaf material consumed by the cereal leaf beetle after 187 hours preconditioned to four food types. NF = No Feeding.

Choice	Preconditioned Food Type			
	New Wheat	Old Wheat	New Oats	Old Oats
New Wheat	1.844 a	1.665 a	1.7300 a	NF
Old Wheat	5.550 a b	8.830 a	11.575 b	NF
New Oats	15.232 b	9.388 a	23.815 c	NF
Old Oats	13.279 b	8.643 a	11.334 b	NF

* Means followed by the same letter are not significantly different by Duncan's Multiple Range Test ($P<.05$).

younger plant material (cf. Figure 34) may be a partial explanation for these results but it cannot be the only one since both new and old oats were preferred by beetles preconditioned to new wheat.

The cessation of feeding by beetles preconditioned to old oats is particularly interesting because it implies that there is a chemical component in this plant material which cues the insect to stop feeding. This is important to these beetles because as the spring oats senesce from late July to October, more and more summer adults seek refugia and begin diapause (Wellso 1974). It has been suggested by Wellso (1974) that the duration of diapause in the CLB is not solely dependent upon temperature or photoperiod but that perhaps some age-dependent metabolic factor within the insect governs the sensitivity of the insect to these variables. This investigation suggests that some age-dependent metabolic factor of the plant rather than of the insect signals the cessation of feeding and the onset of diapause. Whether spring adults act similarly is unknown.

More experimentation is required before it is known which factor(s) is responsible for new oat preference and the feeding cessation caused by old oats.

Literature Cited

Fulton, W. C. 1978. Development of a model for on-line control of the cereal leaf beetle (Oulema melanopus (L.)). Ph.D. Thesis, Dept. of Entomology, Michigan State Univ., East Lansing, MI. 130 pp.

Ruesink, W. G. 1972. The integration of adult survival and disperal into a mathematical model for the abundance of the cereal leaf beetle, Oulema melanopus (L.). Ph.D. Thesis, Dept. of Entomology, Michigan State Univ., East Lansing, MI. 80 pp.

Sawyer, A. J. 1978. A model for the distribution and abundance of the cereal leaf beetle in a regional crop system. Ph.D. Thesis, Dept. of Entomology, Michigan State Univ., East Lansing, MI. 279 pp.

Wellso, S. G. 1974. Aestivation in relation to oviposition initiation in the cereal leaf beetle. In "Chronobiology". L. E. Schevin, F. Holberg and J. E. Pauly, eds. Igaku Shoin Ltd., Tokyo. pp. 597-601.

Appendix 6. Oxygen Consumption by Larvae of the Cereal Leaf Beetle

Introduction

The minimal caloric food intake of animals is regulated by the energy required for production, excretion and respiration. The summation of these components would then equal ingestion (Mispagel 1978). The small size of early CLB larvae and the variable water content of leaves per unit area prevent an accurate dry weight estimation of food consumption. An indirect method of monitoring ingestion rates such as that proposed above could aid in determining the utilization efficiencies of these organisms with food of variable quality. Toward this end, I estimated the energy consumed by the immature stages of the CLB in respiratory maintenance. The oxygen consumption of CLB adults is given by Denton (1973).

Materials and Methods

A Gilson differential respirometer was used to monitor the amount (μl) of O_2 consumed per gram dry weight and per individual at 15, 25, and 35C for each of the four CLB immature life stages. The methods used were similar to those used before (Mispagel 1981) except for the temperatures as listed above and the fact that groups of

larvae, 40 for first instars down to 10 for fourth instars, were enclosed inside nylon mesh bags before being placed inside the reaction vessel. This was done to prevent their wandering into the KOH solution or into the micropippete tubing. The small size of the larvae necessitated grouping large numbers of individuals in each reaction vessel for accurate oxygen consumption readings. The increasing temperatures ellicited some wandering by the larvae so the values reported below are not due to simple maintenance metabolism, but, more realistically, include that due to limited movement.

Results and Discussion

The amount of oxygen consumed per individual per hour is given in Table A7 for the three temperatures and four instars tested. Oxygen consumption increased with temperature and larval size. Overall Q_{10} was based on the slope of the regression equations derived from the relationship of oxygen consumption per individual and increasing temperature from 15-35C. The equation used was $Q_{10} = e^{b(10)}$ where b = slope and e = base of the natural logarithm. The Q_{10} for each 10 degree interval was deterimined by $Q_{10} = O_{2(i+10)} / O_{2(i)}$ where O_2 = oxygen consumed per individual per hour and (i) = test temperature (C). Q_{10} decreased with age and with temperature (Table

Table A7. Mean (SE) µl oxygen per individual per hour for the four CLB instars at 15, 25, and 35 C.

	Temperature		
	15	25	35
1st Instar	0.403 (0.103)	1.397 (0.043)	2.097 (0.074)
2nd Instar	0.955 (0.186)	3.020 (0.331)	4.280 (0.364)
3rd Instar	2.060 (0.130)	5.455 (0.326)	7.650 (0.342)
4th Instar	5.371 (0.380)	12.570 (1.130)	17.150 (1.484)

Table A8. Q10's for the four CLB larval instars over the temperature range 15-35C, and from 15-25C and 25-35C.

	Temperature (C)		
	15-35	15-25	25-35
1st Instar	2.10	3.46	1.50
2nd Instar	2.20	3.16	1.42
3rd Instar	1.93	2.65	1.40
4th Instar	1.78	2.34	1.36

Table A9. Regression equations for the oxygen consumption per individual per hour of the form: $\ln Y = bX + a$ where Y is $\mu l\ O_2$ / ind. / hr and X is temperature (C). Nr is the number of points in the regression equation and Ni is the number of insects used.

	a	b	r^2	Nr	Ni
1st Instar	-1.875	.074	.88	6	80
2nd Instar	-1.169	.079	.87	12	120
3rd Instar	-0.170	.066	.94	21	140
4th Instar	0.890	.058	.89	21	90

A8) reflecting the decreasing surface area to volume ratio of the growing organism, the increasing complexity and efficiency of the developing tracheal system with each successive molt and the change in gas conductivity with increasing temperatures. Similar trends were found by Mispagel (1981) for 93 taxa of desert arthropods over a wider temperature range.

The regression equations listed in Table A9 for ul oxygen/ind/hr over temperature permit an estimation of the caloric expenditure attributable to this function by a field population. Hourly field temperatures can be used in these equations for each instar and the result multiplied by the density of each life stage during a given time interval. Using the oxy-caloric coefficient of 4.825 cal/ml (Brody 1945), the energy expended by a field population in respiratory maintenance as well as that due to activity can be estimated.

Literature Cited

Brody, A. 1945. Bioenergetics and Growth. Reinhold Publishing Co., New York.

Denton, W. H. 1973. Overwintering in the cereal leaf beetle, Oulema melanopus (L.) (Coleoptera: Chrysomelidae). Ph.D. Thesis, Purdue University. 140 pp.

Mispagel, M. E. 1978. The ecology and bioenergetics of the acridid grasshopper, Bootettix punctatus , on creosote bush, Larrea tridentata , in the northern Mojave Desert. Ecology 59:779-788.

Mispagel, M. E. 1981. Relation of oxygen consumption to size and temperature in desert arthropods. Ecol. Entomol. 6:423-431.

Appendix 7. Methods Attempted to Ascertain Energetics of the Cereal Leaf Beetle Reared on Food of Variable Quality

It was originally proposed the ecological efficiencies be determined for each larval instar of the CLB having been reared on food of varying quality. The two primary variables of quality to be tested were water and nitrogen content. Both these variables are functions at least of leaf age and leaf position as previously described. In a word, these attempts failed. This Appendix will set forth the methods used and the reasons why adequate data was unobtainable. Suggestions for further investigations will be offered.

The ecological efficiencies of both early and late instars of the CLB are of interest because the survival of the early, more susceptible instars is important to the overall population structure while the quantity of food consumption by the late instars affects plant stress and total defoliation levels.

The questions posed included the following: If the CLB larva is faced with food of "poor" quality, i.e. low nitrogen and/or water content, will its assimilation efficiency increase proportionately or will compensation for the poor quality occur by the larva consuming more than normal? Are water and/or nitrogen content important qualitative variables for the CLB and, if so, how important a role does this food quality play in the active selection

of feeding sites, e.g. uppermost leaf blades or oats in general? To answer these questions the consumption rate of newly molted CLB larvae must be measured and expressed in terms of dry weight of leaf material per unit time. Additionally, measurements of the growth rate of the larvae in dry weight terms as well as the dry weight of feces need to be taken. Furthermore, the nitrogen and water contents of the food material supplied to the insects must remain constant over the length of the experiment, i.e. 24-48 hours.

I initially attempted to maintain leaf material grown under various nitrogen regimes in the greenhouse at constant water contents in chambers of constant relative humidity as described by Scriber (1977). Different concentrations of KOH were used to attain a relative humidity of 100%, 70% and 40% in a 5 gallon sealed aquarium. In a chamber this size, maintaining a constant relative humidity was very difficult. Even attaining and maintaining 100% relative humidity with pure water in the container was difficult since it would vary with height above the water.

Leaf material was cut into 2.5 cm strips and placed in the open or in petri dishes with or without water supplementation by way of moistened filter paper. Leaf water content was assumed to be constant if the wet weight remained stable for 48 hours. Freshly cut leaves were used

as well as those which were allowed to lose 10% and 20% of their wet weight before being put into the chamber. In a closed petri dish, with moist filter paper, cut leaf blades continued to lose water if not touching the filter paper. However, if the cut edge was touching the moist filter paper, the leaf segment gained water until it was fully turgid. The humidity within the chamber had little affect on the water loss even if the blade was not inside a petri dish. These results were in contrast to the successful use of this method by Scriber (1977) who used whole tree leaves with petioles immersed in water rather than grass leaves with exposed xylem vessels. It was therefore assumed that the quality of an excised leaf blade was sufficiently altered as to make it an unacceptable object of investigation.

Since I knew that on a given plant the nitrogen and water contents varied with leaf position, the living plant in the field was deemed to be appropriate test material. This material would have a continuous range of water and nitrogen contents rather than a specified level. However, on any given leaf, the quality would be relatively constant over the time intervals to be used.

Four aliquots of leaf material were taken from one side of the midrib for measurements of wet weight, dry weight, area per unit dry weight and nitrogen content. Flag leaves and the third or fourth leaf from the top were

used to provide the range of qualities sought.

Freshly molted larvae without fecal coats were weighed and then placed on the leaves to feed for at least 24 hours. An aliquot of these larvae was weighed, frozen, dried and weighed again to estimate the water content and the initial dry weight of the experimental animals. The fecal coat was collected on a piece of dried, preweighed filter paper. Drying and reweighing this gave the excreted dry weight. Larvae were then removed and weighed live. They were then frozen, dried and the dry weight measured.

Dry weight of the leaf area consumed was estimated by measuring the length and width of all feeding scars with a micro-caliper and associating that area with the dry weight of leaf material per unit area measured from the leaf aliquots taken earlier. All dry weights were measured with a Cahn electrobalance.

Unfortunately, there were many problems with the application of this design. Field collected eggs did hatch at the same time but the hatch was on the weekend when no one was available to begin the experiment. The positive phototropic behavior of the larvae also caused some consternation since larvae placed on lower leaf blades refused to feed at that site and tended to move upward. Stopcock grease spread at the base of the leaf did not prevent them from getting through to the stem. Some larvae were even observed feeding on this material. Moreover,

mortality was high and many larvae were lost because they simply fell off the leaf blade. If more than one larva was placed on a leaf blade to increase the amount of area fed per unit time, invariably one or more would die or disappear leaving feeding scars representing an area of leaf blade consumed by an unknown number of larvae. Of the 56 larvae initially placed on leaves, only 27 remained alive and still on the leaf after 24 hours. Only 7 of these samples were usable since some were from multiple larvae leaves where one or more disappeared or where no feeding occurred.

Of the 10 samples placed on wheat and 28 samples on oats, only one on wheat and 6 on oats yielded valid data. None of the samples placed on lower leaf blades were usable. Spread across the four instars and two plant species, these data are of little value and will not be presented.

Nylon mesh cages were constructed to enclose an entire leaf blade and sealed with foam culture tube plugs on either end split for passage of the leaf blade. The bent wire that was used to support these cages was not satisfactory suggesting the need for a different design.

Enclosing CLB larvae in such cages is probably acceptable if they are not left in place for more than a few days. The efficiency of a cone-shaped structure to prevent the larva from reaching the stem for upward

movement might be tried. However, this would not prevent the larva from dropping to the ground if it desired.

I would recommend that an experiment to ascertain the ecological efficiencies of the CLB be conducted in an environmental chamber using a laboratory culture of CLB larvae whose life stages can be carefully monitored. Moreover, potted plants grown in the environmental chamber should be used for the relatively short term feeding trials to avoid the climatic variables which tend to dislodge the larvae or offer escape routes. One might attempt to keep the larvae on the lower leaves by manipulating the position of the light source, e.g. by placing it on the side or even below the plants. Since each sample requires at least eleven weight measurements, using a sensitive top loading balance would be more time efficient.

This is a very tedious experiment requiring a great deal of time and planning. However, having overcome the logistical problems involved in working with such small quantities, the results should be very enlightening as to the effects of variable food quality on the survival and behavior of the cereal leaf beetle.