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Effects of drought stress and defoliation on soybean physiology and yield

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Effects of drought stress and defoliation on soybean physiology and yield

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by

Thomas H. Klubertanz

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ABSTRACT
The effects of drought stress (R1 to R7) and insect defoliation (R2 to R4) on soybean physiology, growth, and yield were examined in a two-year study. Plots were protected from natural rainfall by a rainout shelter that remained away from the plots during dry conditions. Artificial defoliation was used to closely model injury caused by discrete populations of lepidopterous larvae. Both vegetative growth and seed yield were reduced by drought stress, while the effects of defoliation primarily were limited to reductions in yield components. Compensatory regrowth (leaf emergence) was observed in defoliated plants. This regrowth, however, did not significantly affect leaf area. Loss of latent leaf area potential in young, expanding leaves may result in an underestimation of the impact of defoliation on canopy size. Senescence of lower leaves was delayed and photosynthetic rates of remaining, intact leaves were greater in defoliated plants, as has been found in previous studies. The response of leaf photosynthesis to defoliation was similar in drought-stressed and well-irrigated plots. Leaf area removed did not predict yield as well as did remaining leaf area, especially when data were pooled over irrigation rate. However, data expressed as remaining leaf area has limited pest management applications unless these data can be coupled with addition information, such as initial canopy size, pest population density, or predictions of future injury. No statistical interactions were found between irrigation and defoliation rates.
Recovery from drought stress beginning at R5 resulted in significantly greater weight per seed, while recovery starting at R6 did not affect yield components relative to plots stressed until R7. This is the first study to experimentally examine the recovery potential of stressed and unstressed, defoliated plants.
GENERAL INTRODUCTION

Explanation of Dissertation Format

This thesis reports graduate research conducted at the Iowa State University Hinds Irrigation Farm near Ames from 1990 to 1992. The major sections include a dissertation abstract, literature review, three papers in manuscript form, a general summary, acknowledgements, and references cited. The three papers examine different effects of defoliation and drought stress in soybean and include their own abstract and literature cited sections. The first paper addresses plant physiological responses to defoliation and drought stress. The second paper concentrates on yield reductions caused by these two forms of stresses. Finally, the third paper presents a more theoretical discussion of the usefulness of various measures of defoliation to pest management. I have followed the writing style used by the Entomological Society of America (ESA 1992). Although at least one of the three papers will be submitted to the Agronomy Journal, the ESA style is used throughout for consistency.

Literature Review

Many factors, such as pest injury and abiotic stresses, may limit soybean yield. Plant responses to injury and stress can be complex, with multiple stresses frequently occurring in a single season. The ability to predict yield of stressed plants is important for pest management and crop assessment. In addition, the timing of stress
agents frequently is not predictable. Drought stress, for example, is highly unpredictable and, in the absence of irrigation, is mostly unavoidable. Defoliation, with the exception of hail damage, is more predictable and manageable. Insect defoliators have discrete phenologies, and sampling for these pests can alert growers to potential economic infestations. However, accurate assessment of pest status requires an understanding of plant tolerance and injury/yield relationships. The relationship between pest injury and yield may change in the presence of additional stresses, such as drought stress, thereby complicating pest management decisions. This review discusses the status of drought stress and defoliation research in soybean. Discussions involving specific soybean growth stages will follow the standard terminology of Fehr et al. (1971) and Ritchie et al. (1989).

**Drought Stress**

Water deficits in plants occur when roots cannot replace water lost to transpiration. Prolonged water deficits during drought conditions can reduce soybean growth and yield substantially. However, more transient water deficits in soybean can occur in response to midday heat, even in fields with adequate soil moisture (Mederski et al. 1973). Therefore, although "drought" technically relates to sub-normal precipitation, the term will be broadened in this review to include all plant water deficits related to soil moisture availability.

**Yield Responses to Drought Stress**

The factors affecting soybean responses to drought stress are well
known. Plant phenology has considerable impact on yield reductions caused by drought stress. Stress before flowering has less effect on yield than drought stress during reproductive stages (Matson 1964; Kpoghomou et al. 1990). For example, Matson (1964) found that soybean irrigated throughout the season in Missouri only slightly out-yielded plots irrigated just from flowering to one month before harvest. Soybean is most susceptible to water deficits during pod fill (R4-R5) (Doss et al. 1974; Kpoghomou et al. 1990). Westgate & Peterson (1993) found that the earliest stages of pod development, especially ovary expansion, were most susceptible to stress. Dornbos & Mullen (1991) and earlier studies have shown that germination and overall quality of seeds from drought-stressed plants can be lower than those from unstressed plants. More recently, Smiciklas et al. (1992) also found that drought stress reduced seed quality but not evenly on all nodes of the plant.

**Developmental and Physiological Responses to Drought Stress**

Several changes in plant development have been associated with drought stress. Constable & Hearn (1978) and Meckel et al. (1984) both found that drought stress during pod fill shorts the seed-filling period. In addition, Meckel et al. (1984) found that although the filling period was shortened, the rate of seed fill was unchanged, resulting in yield reductions. Although accelerated senescence of lower leaves is common for many crops, sufficient studies of leaf senescence patterns have not been conducted in soybean. Cortes & Sinclair (1986), however, did find that drought stress after mid-podfill resulted in earlier leaf senescence in upper nodes by 5-10 days.
Many components of soybean physiology and growth are affected by drought stress (Hsiao 1973; Mederski et al. 1973; Cortes & Sinclair 1986; Neyshabouri & Hatfield 1986; Raper & Kramer 1987). As transpiration exceeds water uptake, leaf water potential decreases (i.e. becomes increasingly negative). Low leaf water potentials can affect many important physiological systems and result in low turgor pressure and tissue dehydration (Hsiao 1973; Raper & Kramer 1987; Sinclair et al. 1987; Vu et al. 1987). Therefore, leaf water potentials are excellent measures of overall plant stress (Clark & Hiler 1973; Hsiao 1973). Plants may avoid severe stress and dehydration by partially or completely closing stomata and reducing transpiration. Because transpiration is the primary mechanism of heat loss in plants, leaf temperatures rise rapidly in response to increased stomatal resistance. Therefore, leaf temperatures (including stress-degree-day and delta T calculations and crop water stress indices) also are important indicators of plant stress (Carlson et al. 1972; Idso et al. 1981; Jackson et al. 1981)

differentiation from primordia. Drought stress during leaf expansion has been shown to reduce expansion rates (Neyshabouri & Hatfield 1986), especially for leaves near their full size (Randall & Sinclair 1989). These data suggest that leaf turgor is more easily maintained in smaller leaves. Because leaf expansion is possible only for a limited time, the effects of drought stress on leaf expansion rates permanently affect canopy size. Also, because soybean yield is strongly affected by plant biomass, one major cause of yield reductions during drought is reduced leaf area and limited photosynthate for seed production (Cortes & Sinclair 1986; Raper & Kramer 1987). In addition, changes in canopy size affect plant/pest interactions, possibly lowering plant tolerance to subsequent injuries such as defoliation.

Defoliation

The effects of soybean defoliation have been studied extensively. Defoliation can be caused by a variety of biotic and abiotic agents, including hail, drought, plant pathogens, and vertebrate and arthropod herbivores. Because crop assessments frequently are required for insurance claims, the effects of hail injury on yield have been studied closely. Defoliation is an important component of hail injury to soybean, although additional injury may occur from stem bruising, lodging, and stem cut-off (Kalton et al. 1949). Because of experimental difficulties, most hail-defoliation studies have been conducted by simulating defoliation using leaf picking and/or cutting techniques.
Reviews of defoliating arthropod pests of soybean have been made by several authors, including Turnipseed & Kogan (1976, 1987) and Zeiss & Klubertanz (1993). Pest species commonly causing economic damage to soybean include the velvetbean caterpillar \textit{Anticarsia gemmatalis} (Hubner), the soybean looper \textit{Pseudoplusia includens} (Walker), the green cloverworm \textit{Plathypena scabra} (F.), and the Mexican bean beetle \textit{Epilachna varivestis} (Mulsant) (Zeiss & Klubertanz 1993).

**General Effects of Defoliation**

By definition, defoliation reduces plant photosynthetic area. Several studies, however, have found little yield reduction in response to moderate defoliation before flowering (Camery & Weber 1953; Weber 1955; Weber & Caldwell 1966; Banks & Bernardi 1987; Turnipseed & Kogan 1987; Hammond 1989; Hintz & Fehr 1991; Hintz et al. 1991). Even as much as 50 to 100% defoliation during vegetative stages may not affect yield, unless that rate of injury occurs over an extended period of time (Banks & Bernardi 1987) or is combined with other forms of injury (Hintz et al. 1990). As reproductive structures develop in soybean, plant sensitivity to defoliation increases. Todd & Morgan (1972) found significant yield reductions from 66 and 100% simulated hail defoliation one week before flowering. Banks & Bernardi (1987) reported that 100% defoliation at R2 (full bloom) hastened maturity by 24 days and reduced seed yield more than 58%. Camery & Weber (1953) found greatest yield reductions from defoliation during seed fill. Vasilas \textit{et al.} (1989) simulated defoliation patterns caused by brown spot \textit{Septoria glycines} during R5, resulting in an 18% yield reduction. Similarly, Fehr \textit{et al.} (1977) and
Fehr et al. (1981) found maximum yield loss between stages R4 and R5. However, even during reproductive stages, low rates of defoliation (less than 33%) do not cause yield losses (Begum & Eden 1965; Turnipseed 1972). Complete defoliation may cause significant yield reductions as late as R7 (Thomas et al. 1974; Fehr et al. 1977), although Begum & Eden (1965) found no effect of complete defoliation on yield after "full seed" stage (R6).

In addition to affecting seed yield, defoliation also can reduce seed quality. Camery & Weber (1953) found that 50-100% defoliation beginning at late flowering significantly reduced seed quality. Towards the end of pod fill, however, seed quality is less affected by defoliation (Vieira et al. 1992). In a study using simulated hail damage, Weber (1955) found that, although percent seed protein was not affected, defoliation did reduce seed oil content. Turnipseed (1972) found no reduction in seed germination from plots defoliated up to 67% during flowering and/or pod fill.

Defoliation has been shown to affect several developmental and physiological processes in soybean. Late-season defoliation can shorten the seed filling period and accelerate maturity (Camery & Weber 1953; Lockwood et al. 1977; Ingram et al. 1981; Goli & Weaver 1986; Vieira et al. 1992). A shortened filling period may reflect altered source-sink relations due to less stored photosynthate and not a direct response to defoliation. Several authors have documented altered patterns of leaf senescence in defoliated plants. In plants with upper-canopy defoliation, Higley (1992) and Higgins et al. (1983) observed delayed
leaf senescence of lower leaves relative to similar leaves on undefoliated plants. Ostlie & Pedigo (1985) also observed this response but stated it was transient and most likely had little effect on yield. The physiological mechanism of lower leaf retention has not been determined. Additional responses to soybean defoliation include reduced lodging (Ostlie & Pedigo 1985; Goli & Weaver 1986) and reduction in plant nitrogen fixation rates (Layton & Boethel 1988).

**Effects of Crop Growth Form on Defoliation Response**

Determinate and indeterminate soybean cultivars differ in relative rates of vegetative and reproductive growth after flowering. Although light to moderate defoliation has not been shown to affect determinate and indeterminate soybeans differently (Turnipseed & Kogan 1987), the effects of complete defoliation can vary with crop growth form. Fehr et al. (1977) found that determinate cultivars suffered greater yield reductions from complete defoliation during reproductive stages than indeterminate cultivars. Fehr et al. (1985) compared the effects of complete defoliation of 10 isogenic lines at R2 and R5. These lines exhibited either a semideterminate or indeterminate growth form. Yield of the semideterminate lines was 10.2 to 10.9% greater from R2 defoliation and 7.9 to 10.4% greater from R5 defoliation than yield of indeterminate lines. However, Goli & Weaver (1986) found that yields from determinate and indeterminate late-planted (late June) soybean cultivars treated with complete defoliation did not differ. Based on these studies, the impact of crop growth form on the reliability of economic thresholds and crop assessment models should be considered.
Action of Other Stressors

Few studies have examined the effect of multiple stresses on soybean yield response to defoliation. Simmons & Yeargan (1990) found green cloverworm and stink bug injuries at R1 caused additive yield reductions (no statistical interactions). Two studies (Higgins et al. 1984; Helm et al. 1992) examined the interaction between velvetleaf competition and defoliation. Again, the effects were additive. The effects of drought stress and defoliation on seed quality were studied by Vieira et al. (1992). They found that although drought and severe defoliation from R5 to R7 caused significant yield losses, germination was unaffected unless seeds were shriveled. Hammond & Pedigo (1982) noted that insect defoliation simulated during two drought years reduced yields, whereas the same leaf area removed during a wet year did not.

Defoliation Research

Many different techniques have been used to study soybean defoliation, partly because of the diversity of defoliating agents. Some of these techniques have utility in pest management research, despite their non-entomological intent. In addition, data from hail, plant pathogen, and other research may provide clues to the effects of insect defoliation. Therefore, a brief review of the techniques used to study all causes of defoliation is justified. However, significant differences in plant response mechanisms, for example, may exist between insect and hail defoliation. Therefore, data transferred across disciplines should be interpreted with caution.

Caged insects have been used in many defoliation studies. Species
studied have included the Mexican bean beetle (Nolting & Edwards 1989), soybean looper (Layton & Boethel 1988; Helm et al. 1992), green cloverworm (Poston et al. 1976), and larvae of the painted lady butterfly (Poston et al. 1976). Simmons & Yeargan (1990) caged green stink bugs to examine potential interactions with simulated green cloverworm defoliation.

Most researchers have used simulation techniques to study the effects of hail, arthropod, or plant pathogen injury. The first simulated defoliation study was conducted by Gibson et al. (1943) in an attempt to quantify the utility of soybean as a forage crop for livestock. Simulations have been instantaneous (as in most hail studies) or have included a temporal component to more precisely mimic pest population growth (as in Hammond & Pedigo 1982 and Higley 1992). Several studies have compared the effects of various simulated defoliation techniques to natural defoliation. Poston et al. (1976) simulated insect defoliation both in the greenhouse and in the field and compared leaf physiological responses to those of naturally-defoliated plants. Cork borer, paper punch, and longitudinal leaflet-bisection techniques adequately simulated natural defoliation, while transverse leaflet-bisections did not. Leaflet picking is more rapid than leaf punching and has been used in a number of defoliation studies. In addition, removing 1, 2, or 3 leaflets/leaf has been used as a simple way to establish multiple defoliation treatments. Hammond and Pedigo (1981) determined that water loss caused by leaf punching was greater than for leaf picking, suggesting that edges of exposed mesophyll tissue
were an important site of water loss. However, Ostlie and Pedigo (1984) conducted a similar study and found that water loss was greater in hole-punched leaves for only 16 h after injury. They concluded, based on the transient nature of the effects on water loss, that both leaf picking and hole punching adequately simulated natural defoliation.

Almost a decade ago, Ostlie (1984) identified more than fifty papers concerning defoliation. These and more recent studies have been conducted using a variety of different cultivars, plant growth stages, and geographic locations. Methods and terminology also have varied considerably among researchers, making it difficult to summarize and interpret existing data (Goli & Weaver 1986). In addition, as mentioned previously, little is known about the mechanisms of plant response to defoliation (Higley 1992). Because of these factors, some existing thresholds for defoliating pests may be suspect (Higley 1992; Thomas et al. 1978). Recent studies, such as the multi-state study reported by Higley (1992) and other studies (Hammond & Pedigo 1982; Kogan & Turnipseed 1980; Browde 1993), have emphasized the importance of understanding plant-response mechanisms and quantifying plant growth characteristics. Additional studies using this approach will be required to improve our understanding plant responses to defoliation under various environmental and agronomic conditions, to develop more effective sampling programs, and to improve the utility of existing economic thresholds for defoliating pests.
PAPER 1: EFFECTS OF DROUGHT STRESS AND DEFOLIATION ON PHYSIOLOGY, REGROWTH, AND SENESCENCE OF REMAINING LEAVES IN SOYBEAN
Effects of drought stress and defoliation on physiology, regrowth, and senescence of remaining leaves in soybean

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ABSTRACT

Recent studies have shown that one component of soybean response to insect defoliation is delayed senescence and increased physiological activity of lower, remaining leaves. The ability of these and other mechanisms of defoliation tolerance to function in drought-stressed plants was investigated in a two-year study using controlled irrigation rates and artificial defoliation treatments. Defoliation significantly increased percent soil moisture in both years, showing that defoliated, stressed plants conserve more water than undefoliated, stressed plants. Compensatory regrowth was observed following defoliation, resulting in more leaves in defoliated plants than predicted. Removal of expanding leaves, however, reduced leaf area as well as reduced future growth relative to undefoliated plants. Senescence of lower leaves was delayed in defoliated plants, as has been found in previous studies. The responses of leaf physiological rates to defoliation were similar in drought-stressed and well-irrigated plots.
INTRODUCTION

Although the effects of defoliation on soybean yield have been studied closely, few studies have examined the impact of leaf loss on canopy growth, physiology, and senescence. Defoliation affects soybean dry matter accumulation primarily by reducing the effective leaf area for light interception and carbon fixation. Several studies have showed strong relationships between leaf area index (LAI), defoliation, percent light interception, and canopy CO₂ fixation rates (Shibles & Weber 1965; Rudd 1980; Boote et al. 1985; Higley 1992). Therefore, models of defoliated-plant productivity could be developed based upon LAI and light interception, providing that the effects of defoliation on the remaining canopy are known.

Several defoliation studies in other plants have found that defoliation increases photosynthetic rates of remaining leaves (Wareing et al. 1968; Welter 1989). Recently, Higley (1992) showed similar results for soybean. In addition, studies have found that defoliation delays senescence of lower leaves in soybean (Higgins et al. 1983; Ostlie & Pedigo 1985; Higley 1992). These responses may aid soybean in tolerating defoliation during vegetative and early reproductive stages. However, the ability of these mechanisms to function in the presence of additional stresses is not known. Therefore, the objective of this study was to determine if drought stress may impact the relationships between defoliation and canopy developmental and physiological responses.
MATERIALS AND METHODS

Plot Establishment

Soybean (c.v. 'Elgin') plots were established within an automatic rainout shelter at the Hinds Irrigation Farm, 1 km north of Ames, Iowa. This shelter automatically covered the research area when rainfall was detected by an electronic sensor. Planting dates were 6 June, 1990, and 2 June, 1992. Each plot consisted of 72 (1990) or 80 (1992) plants in four consecutive, 121-liter Rubbermaid® garbage cans (potometers) that had been buried and filled with Nicollet loam. Plots were assigned randomly within blocks to combinations of two irrigation and four defoliation treatments. Replications were blocked along rows of potometers to facilitate data collection.

Irrigation Treatments

Irrigation treatments were imposed beginning on 23 July in 1990 and 27 July in 1992 (plant stage R1). Plots either were provided ample water or were drought-stressed from these dates until plant physiological data were collected at R5 and R6. Visible leaf wilting at midday was used to guide relative irrigation rates of stressed and unstressed plots. In 1990, 75.70 l of water were applied to stressed plots between 23 July and 5 September (R6). During the same period, 302.82 l of water were applied to each well-irrigated plot. In 1992, 128.70 and 272.55 l of water/plot were applied to stressed and well-irrigated plots, respectively, from R1 to R6.

Gravimetric techniques were used to determine percent soil moisture in well-irrigated and stressed plots. In 1990, cores were
collected 2 d (12 August) and approximately one month (11 September) after the defoliation period. In 1992, soil cores were collected just before (6 August) and 3 d after (20 August) the defoliation period. Soil cores were extracted from the entire depth of two potometers in each plot. The two subsamples from each plot were combined and the mixture was weighed before and after drying.

Drought-stress levels were quantified by collecting leaf-temperature data. Leaf temperatures were determined with an Everest infrared thermometer (Everest Interscience, Inc., Fullerton, CA; emissivity = 0.98) from 1200 - 1400 h on days with full sunlight. Because of the sparse canopy in defoliated plots, thermometry data were collected from individual leaflets, not as an average over the entire canopy.

Leaf-temperature data were used to calculate crop water stress indices (CWSIs), as developed by Idso et al. (1981) and Jackson et al. (1981). However, the additional assumption that treatments did not affect equations used to calculate CWSIs (Jackson et al. 1981, Eq. 11) was made. CWSIs incorporate both leaf-air temperature differentials (delta T) and vapor pressure deficits (VPD) to adjust leaf temperature data for different atmospheric conditions. Air temperature and relative humidity, required for calculation of VPD, were collected with a hand-held, aspirated psychrometer and at a weather station next to the research area.

The upper limit of delta T (E0), approximating the delta T of non-transpiring leaves, was set at 5°C. Although this upper limit is
greater than reported for soybean in previous studies (Idso et al. 1981), it was required because of the number of plots with delta Ts up to 5°C. CWSI values, by definition, range from 0, representing maximum transpiration and no stress, to 1 for a non-transpiring leaf (Jackson et al. 1981). Therefore, CWSIs of plots less than 0 or greater than 1 were adjusted to fit within the theoretical minimum and maximum limits of evaporative cooling, respectively. The CWSIs for the defoliation and irrigation treatments, shown in Figure 1, illustrate that the two irrigation rates resulted in two distinct regimes of plant water status.

**Defoliation Treatments**

To more precisely control defoliation rates in plots, feeding by lepidopterous larvae was simulated by hand-picking randomly-selected leaflets from the upper two-thirds of the canopy beginning at R2 (full bloom). This leaf-picking technique has been shown to closely simulate actual larval feeding (Ostlie & Pedigo 1984). Treatment levels were set to result in target leaf area indices (LAIs) of 4.50, 3.50, 2.50, and 1.50 at plant stage R6. The prediction of LAI in undefoliated plots (4.50) at R6 was based upon leaf area at the research site in previous years. The daily intensity of defoliation was based upon a generic computer model of lepidopteran larval development and feeding discussed by Higley (1992). Defoliation was conducted over a 12-day period to closely simulate a developing cohort of larvae. Picked leaflets were returned to the laboratory, with removed leaf area and average cm²/leaflet determined using a LiCor™ LI-3100 Area Meter (LiCor, Inc., Lincoln, NE). Because these data subsequently were entered into the
computer model, defoliation rates were adjusted daily for changes in leaflet size due to plant growth and irrigation treatments. Therefore, defoliation treatments simulated injury from discrete pest-population levels.

**Plant Physiological Data**

Apparent photosynthesis, transpiration, and stomatal conductance were measured 1-2 d after the defoliation period for leaves on the sixth mainstem node using a LiCor 6200 Portable Photosynthesis System with a one liter chamber. Leaves used for these samples had been tagged previously to prevent their accidental picking during artificial defoliation. Because the surrounding canopy was gently moved aside, these data represent potential physiological rates in full sunlight, not rates in an undisturbed canopy. Sampling dates were 11 August in 1990 and 19 August in 1992.

**Plant Samples**

Plant samples were collected 1-3 d (R5) and one month (R6) after the defoliation period to determine developmental stage, remaining leaf area per plant, and lowest leaf-bearing node. Three plants per plot were randomly selected and returned to the laboratory. Leaf areas were determined using the Li-3100 Area Meter.

**Data Analysis**

Data were analyzed using ANOVA, GLM, CORR, REG, and STEPWISE procedures of SAS (SAS Institute, 1985a,b). Means averaged over subsamples were calculated for each plot before data were analyzed. Analysis of variance routines with target LAI and the presence/absence
of drought stress as independent variables were used to test treatment effects and interactions. Linear and quadratic contrast statements were tested to determine trends in response to target LAI. Regression analyses were used to determine observed and predicted rates of leaf number and area reduction with increasing defoliation. Regression analyses also were used to examine the effects of defoliation and drought-stress treatments on leaf physiology.
RESULTS

Soil-Moisture Data

The effects of irrigation and defoliation rates on percent soil moisture are shown in Table 1. Plots under the drought-stressed treatment had significantly lower percent soil moisture than well-irrigated plots on all sampling dates in 1990 and 1992. Soil moisture increased linearly with defoliation immediately after the defoliation period in 1992 (d.f.=1,21; F=6.46; p<0.025), but not until one month later in 1990 (d.f.=1,21; F=4.44; p<0.05). No statistical interactions were found between irrigation and defoliation rates in data from either year (d.f.=3,21; F<0.70; p>0.5616).

Leaf Production and Senescence

Mean number of picked leaves and leaf area removed for each treatment combination are listed in Table 2. As would be expected, leaf area per plant decreased linearly with target LAI in all plant samples (d.f.=1,21; F=53.00; p < 0.0001). Drought stress also consistently reduced leaf area (d.f.=1,21; F=25.2; p<0.0001). Number of leaves per plant decreased linearly with target LAI in all plant samples (d.f.=1,21; F=7.88; p<0.025). One month after the defoliation period in 1992 (R6), leaf-count data showed a significant quadratic interaction between target LAI and stress (d.f.=3,21; F=6.58; p<0.025). Slightly-defoliated, unstressed plants had produced more leaves than undefoliated plants, suggesting the presence of a regrowth response to defoliation.

The rate of apparent regrowth was examined more closely by developing predictive models of number and area of remaining leaves.
Predictions were based on the rates of defoliation already presented in Table 2. For a canopy with static leaf area, a unit increase in defoliation results in an equivalent decrease in numbers of leaves and leaf area. Therefore, defoliation data were regressed against target LAI to determine the relationship between 1) number of leaves and 2) leaf area removed per plant to the treatment levels. These regressions produced slopes ($\beta_p$) that could be used to predict remaining canopy size after defoliation. Similarly, remaining leaf counts and remaining leaf area taken from plant samples were regressed against target LAI to determine the observed rate of canopy change over treatment levels ($\beta_c$). Regressions to determine $\beta_p$ and $\beta_c$ were made for each plant sample, for each year, and for both leaf area and number of leaves (Tables 3 and 4). Because irrigation rate affected canopy growth and mean leaf size, more leaves were picked from stressed than well-irrigated plots. Therefore, separate regressions were made for each of the two irrigation treatments. Predicted canopy values were determined for each plot by subtracting defoliation data from leaf counts and leaf areas of undefoliated plants. To reduce possible bias, the leaf counts and areas of undefoliated plants were calculated from the $\beta_c$ regressions (target LAI = 4.5). With this analysis, regrowth after defoliation would result in greater leaf area or more leaves per plant than predicted, i.e., $\beta_p$ would be greater than $\beta_c$.

At R5 in both years, $\beta_p$ was not significantly different from $\beta_c$ for leaf counts of both stressed and unstressed plants (Table 3). One month after defoliation in 1992 (R6), significant rates of apparent
regrowth were detected. Results at R6 were similar in 1990, with leaf counts in excess of those predicted in both stressed and unstressed plots, although levels of significance were marginally acceptable.

Remaining leaf area per plant also differed significantly from predicted values (Table 4). However, the $B_C$ of unstressed plants in 1992 was significantly greater than $B_D$ one month after the defoliation period (R6), with data from R5 showing similar trends. With the exception of data from stressed plots at R6, data collected in 1990 were similar, but significance was not detected. These results are opposite of those needed to show apparent regrowth.

In addition to affecting leaf production, defoliation rate also affected leaf senescence. In 1990, the lowest leaf-bearing node (LLBN) decreased linearly with increasing defoliation one month after the defoliation period (d.f.=1,21; $F=10.42$; $P<0.005$) (Figure 2; 5 Sept.). Because defoliation treatments were imposed primarily in the upper two-thirds of the canopy, these differences are not the direct result of leaf picking. LLBN on 12 August was not affected by defoliation rate (d.f.=3,21; $F=1.21$; $P=0.3291$). In 1992, defoliation rate did not affect lower-canopy senescence 1 d (d.f.=3,21; $F=1.40$; $P=0.2702$) or one month after the defoliation period (d.f.=3,21; $F=0.77$; $P=0.5246$) (Figure 3). LLBN was not affected by irrigation rate on any of the sampling dates (d.f.=1,21; $F<1.87$; $P>0.1857$).

**Plant Physiological Data**

Forward stepwise regressions were used to develop models of leaf physiological rates relative to measures of defoliation and canopy size.
Leaf area removed was used in these regression because it, in contrast to remaining leaf area, was not correlated with irrigation rate. Physiological data collected 1-2 d after the end of the defoliation period are presented in Table 5. Stepwise regression models of transpiration, stomatal conductance, and transpiration versus leaf area removed show that both defoliation and irrigation rate affected leaf physiology. The general model, including all possible terms, tested by the stepwise regression procedure was:

$$\dot{Q} = \beta_0 + (\beta_1*\text{STRESS}) + (\beta_2*\text{AREA}) + (\beta_3*\text{AREA}^2) + (\beta_4*\text{AREA}*\text{STRESS})$$

where STRESS = the presence (1) or absence (0) of the drought-stress level tested, AREA = leaf area removed (m$^2$), $\beta_0$ is the regression intercept, and $\beta_1$ to $\beta_4$ are coefficients for respective terms. Final models from the stepwise regressions of photosynthesis, transpiration, and stomatal conductance rates are presented in Table 6. These models fit the data well, with $r$-square values of 0.30 to 0.83. The drought-stressed treatment consistently caused reductions in physiological rates. The AREA and/or AREA$^2$ term explained a significant amount of variation ($p<0.05$) in all physiological parameters measured except transpiration in 1992. Stomatal conductance in 1990 increased linearly with increasing defoliation in well-irrigated plants, but not for plants under the drought-stressed regime. These data show that defoliation of the upper and middle canopy significantly increased leaf physiological rates (per leaf area) of remaining leaves in the lower canopy.
DISCUSSION

In both years, defoliation resulted in significantly greater percent soil moisture. Although the differences were small in comparison to irrigation rates, they most likely reflect the effect of LAI on total canopy transpiration. Similarly, Fukushima et al. (1985) found that defoliated rice conserved soil moisture and subsequently maintained higher photosynthetic rates during drought. Although we were not able to show greater stress levels in undefoliated plants using the physiological parameters measured, the secondary impact of insect defoliation on plant-soil water balance needs further examination.

Previous studies have questioned whether defoliated soybean alter vegetative growth rates to compensate for leaf loss. Boote (1981) argued that apparent compensatory regrowth after defoliation is an artifact of the visual characteristics of a defoliated canopy. Higgins et al. (1983) corroborated this view in finding no increases in leaf area after defoliation at R2, above those found in undefoliated plants. The findings of our study support the conclusion that defoliated soybean plants do not rapidly compensate for lost leaf area. However, we did find that defoliated plants had more leaves than predicted one month after the defoliation period, based on leaf-picking rates. This evidence strongly suggests that the phenomenon of canopy regrowth after defoliation merits closer examination. Such research should document remaining leaf area after defoliation and changes in leaf area over time relative to undefoliated plants. In addition, based on our data, an analysis of leaf emergence rates and pattern of leaf-size distribution
would be essential.

With the exception of stressed plants at R6, remaining leaf areas were consistently less than predicted. This unexpected result likely reflects the impact of defoliation on total canopy growth. Whenever defoliation includes actively expanding leaflets, the penalty to the plant includes leaf area removed as well as potential area of leaves at full size. Leaf counts, therefore, were more useful in this analysis for determining rates of compensatory regrowth. In addition, these conclusions show that injury to developing leaves may reduce eventual leaf area considerably more than an equal amount of leaf area removed from mature leaves. Current pest management programs have not addressed this effect of defoliation on plant growth.

Higley (1992) reported that defoliation of the upper canopy resulted in increased apparent photosynthesis of lower, remaining leaves. Increases in physiological rates of remaining leaves following defoliation have been observed for several plant species (Welter 1989). Our data agree closely with those presented by Higley (1992), including delayed senescence of lower leaves after upper-canopy defoliation exposes them to increased sunlight. In addition, our data, with the exception of stomatal conductance in 1990, show that the presence of drought stress does not affect the nature of this response. Therefore, crop models of carbon fixation rates and biomass accumulation may be able to add or subtract the effects of stress as a constant or relatively simple function. Additional studies are required that examine physiological trends over a continuum of drought-stress levels.
REFERENCES CITED


Table 1. Mean percent soil moisture for defoliation and irrigation treatments in 1990 and 1992.

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R5</td>
<td>R5</td>
<td>R6</td>
</tr>
<tr>
<td><strong>Irrigation Treatments</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Irrigated</td>
<td>19.4</td>
<td>13.9</td>
<td>20.6</td>
</tr>
<tr>
<td>Sustained Stress</td>
<td>9.4</td>
<td>10.8</td>
<td>12.1</td>
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<tr>
<td>Prob.&gt;F</td>
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<td>.0002</td>
<td>.0001</td>
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<tr>
<td>df=1,21</td>
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<tr>
<td>Recovered¹</td>
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<td>20.5</td>
</tr>
<tr>
<td>Prob.&gt;F</td>
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<td>-</td>
<td>.0001</td>
</tr>
<tr>
<td>df=1,12</td>
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<td>15.4</td>
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<td>LAI 1.5</td>
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<td>14.0</td>
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<td>.0840</td>
<td>.0501</td>
</tr>
<tr>
<td>df=3,21</td>
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</table>

¹ recovery analysis conducted with data set including only recovered and sustained stress plots.
Table 2. Mean numbers of leaves picked, leaf area removed, R5 leaf area, and R6 leaf area per plant after a 12-day simulated defoliation period in soybean under defoliation and irrigation treatments.

<table>
<thead>
<tr>
<th>Irrigation Rate Lo</th>
<th>Target LAI</th>
<th>Leaves Picked Per Plant</th>
<th>Leaf Area Per Plant (cm^2)</th>
<th>Removed</th>
<th>R5</th>
<th>R6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>I</td>
<td>4.5</td>
<td>0.00</td>
<td>0.00</td>
<td>1472.82</td>
<td>1213.82</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>3.5</td>
<td>1.22</td>
<td>232.83</td>
<td>1130.19</td>
<td>812.69</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>2.5</td>
<td>2.75</td>
<td>463.36</td>
<td>888.17</td>
<td>718.06</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>1.5</td>
<td>4.70</td>
<td>690.01</td>
<td>536.60</td>
<td>462.05</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>4.5</td>
<td>0.00</td>
<td>0.00</td>
<td>1039.13</td>
<td>583.67</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>3.5</td>
<td>1.83</td>
<td>246.32</td>
<td>766.35</td>
<td>538.85</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>2.5</td>
<td>4.00</td>
<td>491.12</td>
<td>321.22</td>
<td>161.37</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>1.5</td>
<td>6.97</td>
<td>694.39</td>
<td>175.80</td>
<td>85.43</td>
</tr>
<tr>
<td>1992</td>
<td>I</td>
<td>4.5</td>
<td>0.00</td>
<td>0.00</td>
<td>1165.53</td>
<td>1083.30</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>3.5</td>
<td>1.36</td>
<td>205.52</td>
<td>841.10</td>
<td>1053.91</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>2.5</td>
<td>2.67</td>
<td>409.83</td>
<td>533.17</td>
<td>488.12</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>1.5</td>
<td>4.65</td>
<td>607.15</td>
<td>273.71</td>
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<td></td>
<td>S</td>
<td>4.5</td>
<td>0.00</td>
<td>0.00</td>
<td>678.20</td>
<td>721.58</td>
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<tr>
<td></td>
<td>S</td>
<td>3.5</td>
<td>1.73</td>
<td>205.71</td>
<td>451.82</td>
<td>405.00</td>
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<tr>
<td></td>
<td>S</td>
<td>2.5</td>
<td>3.87</td>
<td>409.50</td>
<td>188.68</td>
<td>138.01</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>1.5</td>
<td>6.68</td>
<td>592.99</td>
<td>64.70</td>
<td>96.12</td>
</tr>
</tbody>
</table>

\[a\] I = Well-irrigated; S = Drought-stressed

\[b\] Each leaf represents three leaflets that were picked independently
Table 3. Observed ($\beta_c$) and predicted ($\beta_p$) slopes of leaf counts per plant versus target LAI for stressed and well-irrigated treatments.

<table>
<thead>
<tr>
<th>Plant Stage</th>
<th>Irrigation Treatment</th>
<th>$\beta_c$</th>
<th>$\beta_p$</th>
<th>Prob &gt; F</th>
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</thead>
<tbody>
<tr>
<td>R5</td>
<td>Unstressed</td>
<td>0.87</td>
<td>1.56</td>
<td>0.12</td>
</tr>
<tr>
<td>R5</td>
<td>Stressed</td>
<td>2.35</td>
<td>2.31</td>
<td>0.21</td>
</tr>
<tr>
<td>R6</td>
<td>Unstressed</td>
<td>0.73</td>
<td>1.56</td>
<td>0.06</td>
</tr>
<tr>
<td>R6</td>
<td>Stressed</td>
<td>1.22</td>
<td>2.31</td>
<td>0.08</td>
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</tbody>
</table>

Table 4. Observed ($\beta_c$) and predicted ($\beta_p$) slopes of leaf area per plant versus target LAI for stressed and well-irrigated treatments.

<table>
<thead>
<tr>
<th>Plant Stage</th>
<th>Irrigation Treatment</th>
<th>$\beta_c$</th>
<th>$\beta_p$</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>R5</td>
<td>Unstressed</td>
<td>305.07</td>
<td>230.05</td>
<td>0.51</td>
</tr>
<tr>
<td>R5</td>
<td>Stressed</td>
<td>303.51</td>
<td>232.80</td>
<td>0.37</td>
</tr>
<tr>
<td>R6</td>
<td>Unstressed</td>
<td>235.00</td>
<td>230.05</td>
<td>0.14</td>
</tr>
<tr>
<td>R6</td>
<td>Stressed</td>
<td>187.22</td>
<td>232.80</td>
<td>0.06</td>
</tr>
</tbody>
</table>
Table 5. Leaf photosynthesis, transpiration, and stomatal conductance of leaves from the sixth mainstem node for defoliation and irrigation treatment combinations. Data were collected 1-2 d after the 12-day defoliation period.

<table>
<thead>
<tr>
<th>Irrigation Rate&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Target LAI</th>
<th>Photosynthesis Rate* LAI μmol m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</th>
<th>Transpiration Rate* LAI mmol m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</th>
<th>Stomatal Conductance Rate* LAI mol m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>11 August 1990</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>4.5</td>
<td>14.96</td>
<td>15.49</td>
<td>1.05</td>
</tr>
<tr>
<td>I</td>
<td>3.5</td>
<td>17.19</td>
<td>15.22</td>
<td>1.15</td>
</tr>
<tr>
<td>I</td>
<td>2.5</td>
<td>20.51</td>
<td>15.31</td>
<td>1.21</td>
</tr>
<tr>
<td>I</td>
<td>1.5</td>
<td>19.24</td>
<td>15.51</td>
<td>1.39</td>
</tr>
<tr>
<td>S</td>
<td>4.5</td>
<td>6.62</td>
<td>4.84</td>
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<tr>
<td>S</td>
<td>3.5</td>
<td>7.02</td>
<td>5.39</td>
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<td>S</td>
<td>2.5</td>
<td>7.39</td>
<td>5.41</td>
<td>0.24</td>
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<tr>
<td>S</td>
<td>1.5</td>
<td>11.26</td>
<td>7.15</td>
<td>0.35</td>
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<tr>
<td><strong>19 August 1992</strong></td>
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<td></td>
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<tr>
<td>I</td>
<td>4.5</td>
<td>8.61</td>
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<td>13.48</td>
<td>0.75</td>
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<tr>
<td>I</td>
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<td>13.47</td>
<td>13.53</td>
<td>0.63</td>
</tr>
<tr>
<td>S</td>
<td>4.5</td>
<td>7.77</td>
<td>6.98</td>
<td>0.26</td>
</tr>
<tr>
<td>S</td>
<td>3.5</td>
<td>8.76</td>
<td>8.73</td>
<td>0.31</td>
</tr>
<tr>
<td>S</td>
<td>2.5</td>
<td>12.74</td>
<td>11.60</td>
<td>0.54</td>
</tr>
<tr>
<td>S</td>
<td>1.5</td>
<td>10.96</td>
<td>10.79</td>
<td>0.51</td>
</tr>
</tbody>
</table>

<sup>a</sup> I = Well-irrigated; S = Drought-stressed
Table 6. Regression models relating leaf photosynthesis, transpiration, and stomatal conductance to leaf area removed and the presence/absence of drought stress.

General Model:
\[
\dot{\gamma} = \beta_0 + (\beta_1 \cdot \text{STRESS}) + (\beta_2 \cdot \text{AREA}) + (\beta_3 \cdot \text{AREA}^2) + (\beta_4 \cdot \text{AREA} \cdot \text{STRESS})
\]

<table>
<thead>
<tr>
<th></th>
<th>Parameter Coefficient</th>
<th>(r^2)</th>
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<tr>
<td></td>
<td>(\beta_0)</td>
<td>(\beta_1)</td>
</tr>
<tr>
<td>Photosynthesis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\mu\text{mol m}^{-2} \text{s}^{-1})</td>
<td>1990: 15.76</td>
<td>-9.98</td>
</tr>
<tr>
<td></td>
<td>1992: 9.30</td>
<td>-2.40</td>
</tr>
<tr>
<td>Transpiration</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\text{mmol m}^{-2} \text{s}^{-1})</td>
<td>1990: 9.60</td>
<td>-2.90</td>
</tr>
<tr>
<td></td>
<td>1992: 15.38</td>
<td>-9.69</td>
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<tr>
<td>Stomatal</td>
<td></td>
<td></td>
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<tr>
<td>Conductance</td>
<td>1990: 0.65</td>
<td>-0.40</td>
</tr>
<tr>
<td>(\text{mol m}^{-2} \text{s}^{-1})</td>
<td>1992: 1.11</td>
<td>-0.91</td>
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</table>

\(\text{AREA} = \text{leaf area removed (m}^2/\text{plt}); \ \text{STRESS} = \text{presence (1) or absence (0) of stress}\)
Figure 2: Lowest leaf-bearing node (LLBN) from plant samples collected 3 d (R5) and one month (R6) after the defoliation period in 1990
TARGET LAI

Unstressed

Stressed

12 Aug

5 Sept
Figure 3: Lowest leaf-bearing node (LLBN) from plant samples collected 1 d (R5) and one month (R6) after the defoliation period in 1992
PAPER 2: IMPACT OF DROUGHT STRESS AND DEFOLIATION ON YIELD OF SOYBEAN
Impact of Drought Stress and Defoliation on Yield of Soybean

T. H. Klubertanz*, L. P. Pedigo, and R. E. Carlson

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Carlson, Department of Agronomy, Iowa State University, Ames, IA 50011.

To: Agronomy Journal

* Corresponding author.
ABSTRACT

The effects of drought stress (R1 - R7) and insect defoliation (R2 - R4) on soybean yield were examined in a two-year study. Simulated defoliation was used to closely model feeding rates caused by discrete populations of lepidopterous larvae. Both vegetative and reproductive yield were reduced by drought stress, while defoliation primarily reduced reproductive yield. Drought stress also increased rates of apparent pod abortion. Interactions between defoliation and irrigation rates were not found in yield data from either year. Recovery from drought stress beginning at R5 resulted in significantly greater weight per seed, while recovery starting at R6 did not affect yield components relative to plots stressed until R7. This is the first study to experimentally examine the recovery potential of stressed and unstressed, defoliated plants.
INTRODUCTION

Soybean injury caused by defoliating pests such as the velvetbean caterpillar [*Anticarsia gemmatalis* (Hubner)], the soybean looper [*Pseudoplusia includens* (Walker)], the green cloverworm [*Plathypena scabra* (F.)], and the Mexican bean beetle [*Epilachna varivestis* (Mulsant)] often occurs simultaneously with other forms of plant injury and stress. Economic thresholds have been developed for most soybean defoliators (Zeiss & Klubertanz 1993). Yield reductions caused by defoliators may be different under adverse growing conditions, such as drought, thereby requiring thresholds that change with overall plant health.

Although the individual effects of drought stress on and defoliation to soybean are well-known, little data are available about yield potential under combinations of drought stress and defoliation. Few studies have examined interactions between multiple stress factors (Barfield *et al.* 1987). Simmons & Yeargan (1990) studied green cloverworm defoliation and stink bug pod injury at R1 (see Ritchie *et al.* 1989 or Fehr *et al.* 1971 for descriptions of soybean growth stages). Helm *et al.* (1992) and Higgins *et al.* (1984) examined the interactions between velvetleaf competition and defoliation. Although these studies found no statistical interactions between stress factors, Browde (1993) recently found some non-additive responses of soybean to defoliation, herbicide, and soybean cyst nematode (*Heterodera glycines*) injury.

Only two papers have addressed the combined effects of defoliation and drought stress on soybean. Turnipseed (1972) found that irrigated
and non-irrigated, determinate soybean yield responded similarly to defoliation. Vieira et al. (1992) examined yield and seed quality under similar treatment combinations in two indeterminate cultivars. However, their study included only two levels of R6 defoliation and one year of defoliation data.

In the Midwest, injury from several important arthropod pests is most likely from R2 to R4 (Poston & Pedigo 1976; Higley 1992; Zeiss & Klubertanz 1993). We were, therefore, more interested in the effects of defoliation and drought during these stages than at R6, as studied by Vieira et al. (1992). We conducted the following study to determine the individual and combined effects of R2 defoliation from lepidopterous larvae and drought stress on soybean pod growth and yield. Relief from drought in the Midwest frequently occurs in late August and early September. Despite the possible usefulness of recovery data in crop models, such data have not been published. Therefore, we also examined yield of stress-recovered plants relative to plants under a regime of continuing drought stress.
MATERIALS AND METHODS

Plot Establishment

Soybean plots were established in 1990 and 1992 within an automatic rainout shelter at the Hinds Irrigation Farm, 1 km north of Ames, Iowa. This shelter automatically covered the research area when rainfall was detected by an electronic sensor. The shelter contained 150, 121-liter Rubbermaid\textsuperscript{R} garbage cans (potometers) buried in the ground and then filled with Nicollet loam. Prior to planting, narrow spades were used to mix soil and make an adequate seed bed. Forty 'Elgin 87' soybean seeds were hand-planted in each potometer on 6 June and 2 June in 1990 and 1992, respectively. Plant stands were thinned to 18 plants/potometer on 6 July, 1990, and to 20 plants/potometer on 2 July, 1992.

As plants began to flower (R1), plots of four consecutive potometers (2.2 m of row and 80-88 plants) were assigned randomly to irrigation and defoliation treatments. The experimental design consisted of two irrigation rates and four artificial defoliation treatments. Replications were blocked along rows of potometers to facilitate data collection. Drought-recovery potential was tested by establishing two split-plots within each plot of drought-stressed plants. These were assigned randomly to recovery treatments as one of two pairs of adjacent potometers within the set four potometers in a plot. Split-plots were either stressed early in the season and subsequently recovered or maintained under the stress regime (sustained stress) until plant senescence. Split-plots were not established within
plots that were well-irrigated throughout the study because such plots would be redundant. All discussions of the effects of drought stress in this paper refer only to sustained-stressed plots, unless otherwise indicated.

Irrigation Treatments

Irrigation rates of drought-stressed plots were reduced from R1 (23 July, 1990, and 27 July, 1992) until late R7 (plant senescence). Stress-recovered plots were stressed similarly from R1 to R5 (1990) or R6 (1992) but were well-irrigated for the remainder of the season. Specific watering rates were adjusted to maintain distinctly stressed and unstressed plots over a wide range of weekly temperature and humidity conditions. Visible leaf wilting at midday two days after watering was used to guide timing of stressed-plot irrigation. Well-irrigated plots were provided ample water at all times. In 1990, a total of 22.7 and 83.3 liters of water/potometer were added to drought-stressed and well-irrigated plots, respectively, from R1 to late R7. In 1992, during the same period, stressed plots received 39.7 and well-irrigated plots received 75.7 liters/potometer.

Drought-stress levels were quantified by collecting leaf-temperature data. Leaf temperatures were collected with an EverestR infrared thermometer (Everest Interscience, Inc, Fullerton, CA; emissivity = 0.98) on 7 dates and times in 1990 and 2 dates in 1992. Because of the sparse canopy in defoliated plots, thermometry data were collected from individual leaflets, not as an average over the entire canopy.
Leaf-temperature data were used to calculate crop water stress indices (CWSIs), as developed by Idso et al. (1981) and Jackson et al. (1981). However, an assumption was made that treatments did not affect the nature of the equations for CWSI (Jackson et al. 1981, Eq. 11). CWSIs incorporate both leaf-air temperature differentials (delta T) and vapor pressure deficits (VPD) to adjust leaf temperature data for atmospheric conditions. CWSIs were calculated by treatment for data collected from 1200-1400 h and under full sunlight. A baseline of maximum evaporative potential (\(E_p\)) was established by regressing delta Ts of well-irrigated, undefoliated plots against VPD. Because of the limited data set any single year, data from 1990 and 1992 were combined to establish the baseline. Air temperature and relative humidity, required for calculation of VPD, were collected with a hand-held, aspirated psychrometer and at a weather station next to the research area. The upper limit of delta T (\(E_0\)), approximating the delta T of non-transpiring leaves, was set at 5°C. Although this upper limit is greater than reported for soybean in previous studies (Idso et al. 1981), it was required because of the number of plots with delta Ts up to 5°C. CWSI values, by definition, range from 0, representing maximum transpiration and no stress, to 1 for a non-transpiring leaf (Jackson et al. 1981). Therefore, CWSI of plots less than 0 or greater than 1 were adjusted to fit within the theoretical minimum and maximum limits of evaporative cooling.
**Defoliation Treatments**

Defoliation treatments were set to result in target leaf area indices (LAI) of 4.50, 3.50, 2.50, and 1.50 at plant stage R6. The prediction of LAI in undefoliated plots (4.50) was based upon leaf area at the research site in previous years. The timing and intensity of artificial defoliation was based upon a generic computer model of lepidopteran defoliators discussed by Higley (1992). Larval feeding was simulated by hand-picking randomly-selected leaflets from the upper two-thirds of the canopy beginning at late R2 (full bloom). This leaf-picking technique has been shown to closely simulate actual larval feeding (Ostlie & Pedigo 1984). In addition, defoliation was conducted over a 12-day period to more closely simulate a developing cohort of larvae. Defoliation rates for each day were determined by the computer model of larval development and feeding. Picked leaflets were returned to the laboratory, and removed leaf area and average cm per leaflet were determined using a LiCor® LI-3000 leaf area meter (LiCor, Inc., Lincoln, NE).

Figure 1 shows the timing of defoliation and irrigation treatments for each year relative to plant phenology. It is important to note that leaf area to be defoliated was determined before drought stress was imposed. Because the computer model was adjusted daily for deviations in leaf size, drought stress effects on canopy growth and LAI did not affect total leaf area removed by the end of the defoliation period. Therefore, defoliation treatments appropriately simulated injury from discrete pest population densities.
Plant Data

To monitor pod development, plant samples were collected shortly after the defoliation period and approximately one month after defoliation. In 1990, sample dates were 13 August (R5) and 5 September (R6). Dates in 1992 were 18 August (R5) and 1 September (early R6). On each date, three plants per plot were collected. Samples were processed in the laboratory, with pods, leaves, and stems oven-dried for determination of dry weights.

Plots were harvested on 5 October in 1990 and on 19 October in 1992. At harvest, six plants per plot or split-plot were randomly selected for analysis of vegetative and yield components. All harvest samples were taken from the middle potometers in each plot to reduce effects from adjacent plots.

Data Analysis

Data were analyzed using SAS ANOVA and GLM procedures appropriate for randomized complete block designs to examine main effects and treatment interactions (SAS Institute, 1985a,b). Linear contrast statements were used to identify significant trends in response to the four defoliation levels. Analysis of drought-recovery data were conducted using a restricted data set including only recovered and sustained-stress split plots. Apparent pod abortion was determined by calculating the percent change in pod counts between R5 and subsequent sampling dates in each plot.
RESULTS

Crop Water Stress Indices

Regression of the delta Ts from unstressed, undefoliated plants over VPD resulted in the equation:

\[ E_p (°C) = 5.00 - (0.42 \times VPD) \]

which represents the theoretical maximum of evaporative cooling \((r^2 = 0.68)\). Drought stress resulted in significantly greater delta Ts averaged over all dates, VPDs, and defoliation treatments \((d.f.=1,21; F=213.65; P<0.0001)\). CWSIs calculated by treatment are presented in Table 1. Drought stress caused almost a five-fold increase in CWSI, while defoliation level apparently did not affect the CWSI. These data show that the two irrigation rates resulted in two distinct levels of moisture-deficit stress.

Plant Samples

Plants in drought-stressed plots had significantly fewer pods and less pod weight (including developing seeds) at R5 and/or R6 (Table 2). On 5 September, 1990, 29 d after split-plots were established, stress-recovered plants had significantly greater number and weight of pods than plants under sustained drought stress. Defoliation rate also affected pod weight and number significantly during the season, although data from 13 August, 1990, showed no defoliation effects. A significant, linear reduction in pods per plant with increasing defoliation was found only on 5 September, 1990 \((d.f.=1,21; F=11.60; P<0.005)\). Pod weight per plant decreased linearly with increasing defoliation on 5 September, 1990 \((d.f.=1,21; F=17.40; P<0.005)\), and 1
September, 1992 (d.f.=1,21; $F=11.84; P<0.005$). Although significant differences in pod weights in response to defoliation were detected on 18 August, 1992, no linear trend was detectable (d.f.=1,21; $F=0.19; P > 0.10$).

Harvest Samples

All reproductive and vegetative components measured at harvest were reduced significantly by drought stress in both seasons, except for average weight per seed in 1990 (Tables 3 and 4). Drought stress reduced seed yield per plant 63.5% in 1990 (d.f.=1,21; $F=50.33; P=0.0001$) and 49.5% in 1992 (d.f.=1,21; $F=64.15; P=0.0001$). Although pods per plant and pod weight per plant at R6 were significantly greater in 1990 stress-recovered plots (Table 2), yield at harvest was unaffected by late-season recovery in both years. Stress-recovered plants in 1990 did have significantly greater weight per seed than both sustained-stress and well-irrigated plants. Stress recovery did not significantly affect weight per seed at harvest in 1992 (Table 4). For almost all other parameters measured at harvest, means for stress-recovered plots were consistently, but not significantly, greater than those for plots under sustained stress.

In 1990, many pods initially were set on plants, with apparent pod abortion reducing total pod numbers by 47.9% between R5 and harvest (Figure 2). In 1992, pod counts at harvest were only 18.6% of those at R5. The rate of pod abortion from R5 to harvest was increased significantly by drought stress in 1990 (d.f.=1,21; $F=26.52; P=0.0001$) and in 1992 (d.f.=1,21; $F=9.70; P=0.0052$). In 1992, drought stress
caused a 9-fold increase in apparent pod abortion between R5 and harvest. Apparent pod-abortion rates in stressed plots at R6 (1992), relative to R5 pod counts, already were significantly greater than in well-irrigated plots (d.f.=1,21; F=4.62; P=0.0434).

Defoliation did not affect most vegetative plant characteristics (Tables 3 and 4), although stem weight and plant height did decrease linearly with increasing defoliation in 1990 (d.f.=1,21; F>6.44; Ps<0.025). Yield components, in contrast, were more strongly affected by defoliation. Yield per plant decreased linearly with increasing defoliation in both years (d.f.=1,21; F>17.02; P<0.005). A curvilinear tolerance curve over increasing defoliation rate was expected but not observed (d.f.=1,21; F>0.22; P>0.30). Seed yield per plant from the most heavily-defoliated plots was 54.0% and 33.5% lower than that of undefoliated plots in 1990 and 1992, respectively. Defoliation reduced weight per seed linearly in both years (d.f.=1,21; F>20.49; Ps<0.005). In 1990, weight per seed decreased with increasing defoliation more rapidly in stressed plots than in unstressed plots (defoliation-by-stress linear), although the difference in slopes was slight (d.f.=1,21; F=5.44; P<0.05). However, the interaction sum of squares itself was not significant (d.f.=3,21; F=2.26; P=0.1114). Pod counts at harvest decreased linearly with increasing defoliation in 1990 (d.f.=1,21; F=12.91; P<0.005), but not in 1992 (d.f.=1,21; F=1.84; P>0.100). Defoliation rate did not affect apparent pod abortion between R5 and harvest in 1990 (d.f.=3,21; F=1.63; P=0.2134) or in 1992 (d.f.=3,21; F=1.23; P=0.3222). Weight of pod shells per plant at harvest decreased
linearly with increasing defoliation in 1990 (d.f.=1,21; F=17.82; p<0.005) and in 1992 (d.f.=1,21; F=8.22; p<0.01).
DISCUSSION

Several studies have shown that soybean is most susceptible to both drought stress and defoliation during pod fill (Camery & Weber 1953; Doss et al. 1974; Fehr et al. 1977; Fehr et al. 1981; Meckel et al. 1984; Kpoghomou et al. 1990). In this study, drought stress was imposed from late R1 to R7 with defoliation treatments superimposed for 12 d starting at late R2. While drought stress reduced both vegetative and reproductive growth and increased pod abortion, the effect of defoliation primarily was limited to reproductive components of growth and yield, including number and weight of pods and seeds. These results are similar to those found in the previous studies.

Recovery potential of drought-stressed soybean has not been documented previously. Stress recovery in 1990 increased weight per seed. This supports the hypothesis that limited stress recovery is possible during R5. Because pod and seed numbers were limited by stress prior to R5, recovered plants had fewer available sinks and produced seeds larger than those from both stressed and unstressed plants. No differences in yield were detected between sustained and stress-recovered plots. Recovery effects on yield may be detected with an earlier recovery date and/or increased sample sizes. Similarly, an earlier recovery date may increase the impact of mid-season defoliation on recovery potential. In 1992, stress recovery was not initiated until R6 and no changes in yield components were observed. These data suggest that after R5, relief from drought conditions may not result in appreciable yield increases. Additional research would be required to
further identify relationships between plant stage and stress recovery.

Defoliated plants had fewer pods one month after the defoliation period and at harvest in 1990. In 1992, no trend in the number of pods per plant was found in relation to defoliation rate. These differences in pod development may have been caused by changes in pod set, pod growth, pod abortion, or a combination of factors. Almost all previous defoliation studies have reported only yield data, with little or no data regarding pod development after defoliation. Higgins et al. (1984) followed pod development during the season, but their defoliation levels never caused significant changes in pod biomass. In our study, pod biomass one month after the defoliation period (including developing seeds) and at harvest (empty pods) consistently was reduced by defoliation. Apparent pod abortion, in contrast, was not affected by the defoliation levels used. In support of previous studies, these data show that soybean is most susceptible to defoliation during seed fill, not pod formation (Camery & Weber 1953; Doss et al. 1974; Fehr et al. 1977; Fehr et al. 1981; Meckel et al. 1984; Kpoghomou et al. 1990). These data also show the importance of intensive plant sampling throughout the season to developing accurate models of plant response to injury and stress.

Statistical interactions indicate the nature of combined treatment effects in multi-factor studies. In this study, weight per seed was significantly more affected by defoliation in stressed than in well-irrigated plots in 1990. However, the slope difference between irrigated and stressed-plot responses to increasing defoliation was only
0.0088 g/(seed*LAI unit). No other statistical interaction was significant in either year. Therefore, the effects of defoliation and drought stress on yield components primarily were additive. Although an additive model of defoliation and drought stress injury is simpler than one containing an interaction term, it is somewhat counter-intuitive for drought stress not to exascerbate yield losses to defoliation. Browde (1993) found significant herbicide-by-defoliation yield interactions in a study of Iowa soybean. However, many other studies have not found statistical interactions between injury and stress factors. Simmons & Yeargan (1990) found yield losses from green cloverworm and stink bug injuries at R1 were additive. Helm et al. (1992) and Higgins et al. (1984) found no interactions between velvetleaf competition and defoliation. If the interactive effects of drought stress and defoliation are negligible, then yield losses to defoliating pests can be estimated adequately without considerations of plant water status. Drought and other stresses significantly reduce leaf area index and plant biomass (Raper & Kramer 1987, Cortes & Sinclair 1986). The effect of defoliation on remaining canopy size is greater, in terms of percent defoliation, for stressed plants with relatively less initial leaf area than plants not under drought stress. Such considerations are important when selecting measures of pest impact during the development of pest management sampling programs.
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Raton, Florida (in press).
Table 1. Mean crop water stress indices for irrigation and defoliation treatments. Data collected from 1200 - 1400 h under clear skies. Calculations of CWSI incorporate both 1990 and 1992 leaf-temperature data.

<table>
<thead>
<tr>
<th>Irrigation Rate</th>
<th>Defoliation (Target LAI)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4.5</td>
</tr>
<tr>
<td>Well-irrigated</td>
<td>0.11</td>
</tr>
<tr>
<td>(n = 36)</td>
<td></td>
</tr>
<tr>
<td>Drought Stressed</td>
<td>0.45</td>
</tr>
<tr>
<td>(n = 32)</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Mean pod count and pod dry weight (g) per plant at R5 and R6 for irrigation and defoliation treatments. Developing seeds were not separated from pods before weighing.

<table>
<thead>
<tr>
<th></th>
<th>1990</th>
<th>1992</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>13 Aug</td>
<td>5 Sept</td>
</tr>
<tr>
<td></td>
<td>R5</td>
<td>R6</td>
</tr>
<tr>
<td>ct\wt</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Irrigated</td>
<td>29.33\1.22</td>
<td>21.73\6.71</td>
</tr>
<tr>
<td>Sustained</td>
<td>23.50\0.87</td>
<td>13.17\2.49</td>
</tr>
<tr>
<td>Stress</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prob.&gt;F</td>
<td>.0423\0.0271</td>
<td>.0003\0.0001</td>
</tr>
<tr>
<td>df=1,21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recovered</td>
<td>--</td>
<td>16.42\3.46</td>
</tr>
<tr>
<td>Prob.&gt;F</td>
<td>--</td>
<td>.0501\0.0312</td>
</tr>
<tr>
<td>df=1,12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TLAI 4.5</td>
<td>28.17\1.13</td>
<td>21.25\6.18</td>
</tr>
<tr>
<td>TLAI 3.5</td>
<td>29.58\1.19</td>
<td>20.96\5.55</td>
</tr>
<tr>
<td>TLAI 2.5</td>
<td>23.33\0.90</td>
<td>14.29\3.84</td>
</tr>
<tr>
<td>TLAI 1.5</td>
<td>24.54\0.96</td>
<td>13.29\2.82</td>
</tr>
<tr>
<td>Prob.&gt;F</td>
<td>.3395\0.4401</td>
<td>.0140\0.0042</td>
</tr>
<tr>
<td>df=3,21</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 recovery analysis conducted with data set including only recovered and sustained stress plots.
2 TLAI = target leaf area index determined at the beginning of the defoliation period.
Table 3. Mean values of plant parameters for irrigation and defoliation treatments at harvest, 5 October 1990.

<table>
<thead>
<tr>
<th></th>
<th>Ht. (g)</th>
<th>Dia. (mm)</th>
<th>No. Nodes</th>
<th>No. Pods</th>
<th>No. Seeds</th>
<th>Stem Pod Seed -Weight/plt (g)-</th>
<th>Wt. per Seed (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Irrigation Treatments</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Irrigated</td>
<td>59.09</td>
<td>4.89</td>
<td>11.76</td>
<td>20.05</td>
<td>48.88</td>
<td>3.02 2.38 5.34</td>
<td>0.108</td>
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<tr>
<td>Sustained Stress</td>
<td>39.14</td>
<td>4.10</td>
<td>9.42</td>
<td>8.10</td>
<td>17.16</td>
<td>1.73 0.82 1.96</td>
<td>0.103</td>
</tr>
<tr>
<td>Prob.&gt;F df=1,21</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001</td>
<td>.0001 .0001 .0001</td>
<td>.1846</td>
</tr>
<tr>
<td>Recovered(^1)</td>
<td>41.17</td>
<td>4.15</td>
<td>9.69</td>
<td>10.24</td>
<td>22.36</td>
<td>1.76 1.12 2.84</td>
<td>0.122</td>
</tr>
<tr>
<td>Prob.&gt;F df=1,12</td>
<td>.2158</td>
<td>.8010</td>
<td>.3725</td>
<td>.2096</td>
<td>.2165</td>
<td>.8842 .1820 .1428</td>
<td>.0075</td>
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<td><strong>Defoliation Treatments</strong></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>TLAI 4.5(^2)</td>
<td>52.13</td>
<td>4.50</td>
<td>10.73</td>
<td>16.92</td>
<td>40.31</td>
<td>2.82 2.03 4.85</td>
<td>0.120</td>
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<td>TLAI 3.5</td>
<td>50.29</td>
<td>4.75</td>
<td>10.74</td>
<td>17.18</td>
<td>40.74</td>
<td>2.58 2.02 4.66</td>
<td>0.112</td>
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<tr>
<td>TLAI 2.5</td>
<td>48.21</td>
<td>4.54</td>
<td>10.52</td>
<td>11.88</td>
<td>27.75</td>
<td>2.20 1.30 2.87</td>
<td>0.094</td>
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<tr>
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<td>45.83</td>
<td>4.18</td>
<td>10.38</td>
<td>10.33</td>
<td>23.27</td>
<td>1.91 1.06 2.23</td>
<td>0.096</td>
</tr>
</tbody>
</table>

\(^1\) recovery analysis conducted with data set including only recovered and sustained stress plots.

\(^2\) TLAI = target leaf area index determined at the beginning of the defoliation period.
Table 4. Mean values of plant parameters for irrigation and defoliation treatments at harvest, 19 October 1992.

<table>
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<tr>
<th></th>
<th>Ht. (g)</th>
<th>Dia. (mm)</th>
<th>Nodes</th>
<th>Pods</th>
<th>Seeds</th>
<th>Stem Weight/plt(g)</th>
<th>Pod Weight/plt(g)</th>
<th>Seed Weight/plt(g)</th>
<th>Wt.per seed(g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Irrigation Treatments</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Irrigated</td>
<td>58.30</td>
<td>4.50</td>
<td>10.30</td>
<td>19.18</td>
<td>41.47</td>
<td>2.66</td>
<td>2.55</td>
<td>5.52</td>
<td>0.134</td>
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<tr>
<td>Sustained Stress</td>
<td>43.66</td>
<td>3.94</td>
<td>8.90</td>
<td>11.85</td>
<td>23.19</td>
<td>1.56</td>
<td>1.48</td>
<td>2.79</td>
<td>0.115</td>
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<tr>
<td>Prob.&gt;F</td>
<td>.0001</td>
<td>.0002</td>
<td>.0001</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Recovered¹</td>
<td>44.59</td>
<td>2.89</td>
<td>8.85</td>
<td>11.87</td>
<td>23.36</td>
<td>1.55</td>
<td>1.46</td>
<td>2.87</td>
<td>0.121</td>
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<tr>
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<td>5295</td>
<td>.7253</td>
<td>9655</td>
<td>.8705</td>
<td>.8678</td>
<td>.8698</td>
<td>.5456</td>
<td>.0728</td>
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<td>df=1,12</td>
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<td></td>
</tr>
<tr>
<td><strong>Defoliation Treatments</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>TLAI 4.5²</td>
<td>52.12</td>
<td>4.17</td>
<td>9.66</td>
<td>16.62</td>
<td>36.25</td>
<td>2.23</td>
<td>2.32</td>
<td>5.19</td>
<td>0.143</td>
</tr>
<tr>
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<td>51.17</td>
<td>4.15</td>
<td>9.44</td>
<td>16.09</td>
<td>34.24</td>
<td>2.20</td>
<td>2.17</td>
<td>4.52</td>
<td>0.130</td>
</tr>
<tr>
<td>TLAI 2.5</td>
<td>49.35</td>
<td>4.23</td>
<td>9.42</td>
<td>14.27</td>
<td>28.44</td>
<td>1.83</td>
<td>1.78</td>
<td>3.46</td>
<td>0.117</td>
</tr>
<tr>
<td>TLAI 1.5</td>
<td>51.27</td>
<td>4.33</td>
<td>9.88</td>
<td>15.08</td>
<td>30.39</td>
<td>2.18</td>
<td>1.80</td>
<td>3.45</td>
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</table>

¹ recovery analysis conducted with data set including only recovered and sustained stress plots.
² TLAI = target leaf area index determined at the beginning of the defoliation period.
Figure 1. Timing of research activities relative to soybean phenology in 1990 and 1992 (S = drought stress; D = defoliation period; SUS = sustained drought stress; REC = stress-recovered).
Figure 2. Apparent pod abortion (%) in stressed (S) and unstressed (U) soybean plots in 1990 and 1992 based on changes in pod counts from R5 to harvest.
PAPER 3: RELATIVE RELIABILITY OF YIELD MODELS OF DEFOLIATED SOYBEAN
BASED ON LEAF AREA INDEX VERSUS LEAF AREA REMOVED
Relative reliability of yield models of defoliated soybean based on leaf area index versus leaf area removed

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To: Economic Entomology

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ABSTRACT

Several different measures of defoliation have been used in pest management to predict yield losses and potential yield, including leaf area removed, percent defoliation, and remaining leaf area. Plots were defoliated at four levels from R2 to R4, with the effects of drought stress also tested. Differences in precision of yield and yield-loss estimates based on remaining leaf area and leaf area removed were examined. Leaf area removed did not predict yield as well as did remaining leaf area, especially when data were pooled over irrigation rate. However, data expressed as remaining leaf area has limited pest management applications unless these data can be coupled with additional information, such as initial canopy size, pest population density, or predictions of future injury.
INTRODUCTION

Defoliation is the most common and obvious form of pest injury to soybean (Kogan & Turnipseed 1980) and many other row crops. The effects of defoliation on soybean have been studied in detail (Kogan & Turnipseed 1980; Ostlie 1984; Turnipseed & Kogan 1987). Defoliating pest populations easily can be evaluated either by direct population sampling or by the use of population indices (Kogan & Turnipseed 1980; Zeiss and Klubertanz 1993). However, these programs depend on the ability to accurately predict yield and yield loss in defoliated and undefoliated fields under a wide variety of agronomic and environmental conditions.

Many factors, in addition to pest injury, may reduce or limit leaf area index (LAI), including drought stress, nutrient deficiency, and herbicide injury. Because light interception, photosynthesis, and biomass accumulation depend strongly on LAI, canopy size predicts yield well over a variety of growing conditions (Shibles & Weber 1965; Kogan & Turnipseed 1980; Ingram et al. 1981; Herbert et al. 1992; Higley 1992).

Measurements and forecasts of leaf area removed and percent defoliation commonly are used in pest management to predict yield losses (Zeiss & Klubertanz 1993). However, predictions of potential yield based on leaf area removed and percent defoliation are affected by initial canopy size. Hammond & Pedigo (1982), for example, showed that defoliation rates causing low yields during drought failed to do so during a summer with normal rainfall.

The only study published comparing the relative value of using
LAI, leaf area removed, and percent defoliation in yield predictions is that of Herbert et al. (1992). Their study used determinate soybean defoliated during R5 to R6 and found that LAI was the best predictor of yield. In the Midwest, defoliation frequently occurs while plants are in stages R2 to R4 (Poston & Pedigo 1976; Higley 1992; Zeiss & Klubertanz 1993). In addition, comparable studies to Herbert et al. (1992) have not been conducted with indeterminate cultivars. Therefore, the objective of this study was to determine the relative value of yield predictions of indeterminate soybean made from absolute defoliation and LAI over a range of soil moistures. A second objective of this study was to evaluate the utility of these variables to pest management.
MATERIALS AND METHODS

Plot Establishment

Plots of indeterminate soybean (c.v. 'Elgin 87') were hand-planted on 6 June and 2 June in 1990 and 1992, respectively, at the Hinds Irrigation Farm, 1 km north of Ames, Iowa. Plots were protected from rainfall by a rainout shelter that automatically covered the research area when rainfall was detected by an electronic sensor. The shelter contained 150, 121-liter Rubbermaid® garbage cans (potometers) buried in the ground and then filled with Nicotlet loam. Plant stand was thinned to 18 plants/potometer on 6 July, 1990, and to 20 plants/potometer on 2 July, 1992.

As plants began to flower (R1), plots of four consecutive potometers (2.2 m of row and 72-80 plants) were assigned randomly to irrigation and defoliation treatments. The experimental design consisted of two irrigation rates and four artificial defoliation treatments. Replications were blocked along rows of potometers to facilitate data collection.

Irrigation Treatments

Irrigation rates of drought-stressed plots were reduced form R1 (23 July, 1990, and 27 July, 1992) until late R7 (plant senescence). Because of weekly changes in atmospheric demand, specific watering rates were adjusted to maintain distinctly stressed and unstressed plots. Visible leaf wilting during midday heat two days after watering was used to guide timing of stressed-plot irrigation. Well-irrigated plots were provided ample water at all times.
Defoliation Treatments

Defoliation treatments were initiated at R2 (full bloom) to simulate feeding by lepidopterous pests. Treatment-levels were set to result in target leaf area indices (LAI) of 4.50, 3.50, 2.50, and 1.50 at plant stage R6. The prediction of LAI in undefoliated plots (4.50) was based upon leaf area at the research site in previous years. Larval feeding was simulated by hand-picking randomly-selected leaflets from the upper two-thirds of the canopy. Picked leaflets were returned to the laboratory, and removed leaf area and average cm per leaflet were determined using a LiCor\textsuperscript{R} LI-3000 leaf area meter (LiCor, Inc., Lincoln, NE). This leaf-picking technique has been shown to closely simulate larval feeding (Ostlie & Pedigo 1984). The timing and intensity of defoliation in each plot was determined by computer model of lepidopteran defoliators outlined in Higley (1992). In addition, this program defoliates plants over a 12-day period to simulate a developing cohort of larvae.

Defoliation treatments were imposed while the effects of irrigation treatments were affecting crop growth. Because the computer model adjusted daily for deviations in leaf size, drought stress effects on canopy growth and LAI did not affect total leaf area removed by the end of the study. Therefore, defoliation treatments appropriately simulated injury from discrete pest population levels.

Plant Data

Plant samples were collected 1-3 d after and approximately one month after the defoliation period to monitor pod development. In 1990,
sample dates were 13 August (R5) and 5 September (early R6). Dates in 1992 were 18 August (R5) and 1 September (R6). On each date, three plants per plot were collected. Leaf areas were determined using a LiCor\textsuperscript{R} Li-3100 Area Meter (LiCor, Inc., Lincoln, NE).

Plots were harvested on 5 October in 1990 and on 19 October in 1992. At harvest, six plants per plot were randomly selected for determination of yield. All harvest samples were collected from the middle potometers in each plot to reduce effects from adjacent plots.

Data Analysis

Plot means of plant and harvest samples were calculated for the 3 to 6 plants collected from each plot. Data were analyzed using SAS ANOVA and GLM procedures appropriate for randomized complete block designs to examine main effects and treatment interactions (SAS Institute, 1985a,b). Linear and quadratic contrast statements were used to identify significant trends in response to increasing defoliation. The relationships between remaining leaf area, defoliated leaf area, and yield were investigated with regression analyses also using plot means.
RESULTS AND DISCUSSION

Irrigation Rates

In 1990, a total of 22.7 and 83.3 liters of water/potometer were added to drought-stressed and well-irrigated plots, respectively, from R1 to late R7. In 1992, during the same period, stressed plots received 39.7 and well-irrigated plots received 75.7 liters/potometer.

Drought Stress and Defoliation

Yields of stressed and unstressed plots defoliated to each of the four target LAIs are shown in Figures 1 and 2. Drought stress reduced seed yield per plant 63.5% in 1990 (d.f.=1,21; \(F=50.33; P=0.0001\)) and 49.5% in 1992 (d.f.=1,21; \(F=64.15; P=0.0001\)). Yield per plant decreased linearly with increasing defoliation in both years (d.f.=1,21; \(F>17.02; P<0.005\)). A curvilinear tolerance curve of yield relative to increasing defoliation (decreasing target LAI) was not observed in either year (quadratic contrast, d.f.=1,21; \(F>0.90; P>0.20\)). Seed yield per plant from the most heavily-defoliated plots was 54.0% and 33.5% lower than from undefoliated plots in 1990 and 1992, respectively.

No stress-by-defoliation interactions were found in seed yield per plant (d.f.=3,21; \(F>0.36; P>0.1752\)). Because we also found that a linear model best described the relationship between target LAI and yield, these data suggest that the incremental damage caused per insect is the same for drought-stressed and normal soybean. A similar, linear relationship between light interception and yield was found by Higley (1992). The damage or yield loss caused per unit of arthropod injury is a key component to economic injury levels (EILs). If each unit of
injury causes the same amount of damage regardless of canopy size and plant water status, then a single EIL is satisfactory for a wide variety of LAIs and stress levels. Although a linear relationship between defoliation and light interception usually exists for unclosed canopies, closed canopies often have leaf areas in excess of that required for nearly complete light interception (Shibles & Weber 1965). Under these conditions, some type of "tolerance" response of yield to defoliation would be expected. However, this tolerance response is not easily detected in small-plot research with limited degrees of freedom to test non-linear models. Future studies using several defoliation rates clustered near the critical LAI (95% light interception) are needed. In addition, further studies are needed to document the dates or stages at which critical LAIs are exceeded for a variety of cultivars, regions, and agronomic practices.

**Leaf Area-yield Relationships**

Seed yields per plant as a function of leaf area removed, R5 leaf area, and R6 leaf area are shown in Figures 3 and 4. Leaf areas in these graphs represent actual field measurements, not target LAIs, because drought stress significantly altered plant growth rates. Slopes, intercepts, and r-square values for each of the regression lines are shown in Table 1. Leaf area removed and remaining leaf area were associated with changes in yield. However, in 1992, no relationship between leaf area removed and yield was found in unstressed plots, as shown in a test of non-zero slope (d.f.=14; \( t = 1.8654; P > 0.05 \)).

In both years, regressions of leaf area removed resulted in very
low r-square values when data were pooled over irrigation treatments (0.14 - 0.22; n = 32). In contrast, regressions of the data either from unstressed or stressed plots resulted in better fit (0.20 - 0.52; n = 16), despite the smaller sample sizes. In both years, intercepts of regressions using leaf area removed (yield per plant in the absence of defoliation) were significantly greater in unstressed plants (d.f.=1; \( t < -3.610; P < 0.0012 \)).

Predicting yield using remaining leaf area substantially improved r-square values over the defoliation-rate models. For data pooled over irrigation treatments, plot-yield predictions made at R6 had slightly improved r-square values over predictions using R5 leaf area. In all regressions based on remaining leaf area, intercepts (yield per plant with complete defoliation) were significantly greater in unstressed than in stressed plots (d.f.=1; \( t < -2.382; P < 0.0242 \)). The R5 regression in 1992 also resulted in significantly different slopes for the unstressed and stressed-plot regression lines (d.f.=1; \( t = 2.457; P = 0.02 \)) (Fig 4B).

In this study, yield predictions based on remaining leaf area gave greater precision than predictions based on leaf area removed, as indicated by r-square values. These findings are in agreement with the Alabama study of Herbert et al. (1992) and are especially important to researchers attempting to quantify the responses of row crops to defoliation. Our study also shows that factors, in addition to remaining leaf area, must be taken into account when plants are stressed by drought. This is shown by significantly different intercepts in regressions with leaf area removed and yield. Theoretically, this
intercept could be subtracted as a constant from yield predictions at a given LAI.

In addition to predicting yield, data on leaf area remaining after defoliation could be useful in pest management under certain circumstances. Table 2 shows the theoretical, relative utility of percent defoliation, absolute defoliation, and remaining leaf area in pest management models. For each cell in Table 2, only one of the variables along the left margin is known. Based on this table, percent-defoliation data are most appropriate for predicting percent yield loss, assuming that a linear relationship between LAI and yield exists. For unclosed or early-season canopies, there is a linear relationship between defoliation and light interception (Shibles & Weber 1965; Rudd 1980; Boote et al. 1985). However, for canopies with leaf areas in excess of the critical LAI (greater than 95% light interception), low defoliation rates only expose other canopy layers to full sunlight and total light interception remains mostly unaffected (Shibles & Weber 1965; Boote et al. 1985; Higley 1992). If leaf area is in excess of the critical LAI, then percent defoliation cannot be translated accurately into percent yield loss without LAI data. Similarly, predictions of absolute yield loss and yield potential using percent defoliation data are confounded by canopy size. This confounding occurs regardless of the linearity of the LAI-yield relationship. Using the same logic, models using leaf area removed (including larval equivalents) are most appropriate for predicting absolute yield loss, assuming that the LAI-yield relationship is linear.
In contrast to percent defoliation and leaf area removed, remaining leaf area by itself provides little information about the impact of a specific pest. For example, pesticide treatment recommendations should not be based solely on LAI because other causes of reduced leaf area, such as drought, nutrient deficiencies, or foliar pathogens, cannot be accounted for. However, when coupled with data on percent defoliation or leaf area removed, status of pest populations relative to economic injury levels (EILs) can be determined as long as the LAI-yield relationship is known (linear or curvilinear). If treatment decisions are made based upon sampling of young, developing larvae or of a non-damaging stage, then predictions of future LAI by crop-development models could be coupled with estimates of feeding rates and population growth.

Many studies examining the effects of insect and hail defoliation have documented only percent defoliation. We have shown, in corroboration with Herbert et al. (1992), that the variables used to describe defoliation levels can impact the accuracy and precision of yield models and yield-loss estimates. Researchers, therefore, should document as many canopy characteristics as possible, including leaf area removed and remaining leaf area, as well as plant growth and development throughout the season.
REFERENCES CITED


Table 1. Regression equations for yield (Y; g/plant) predictions based on leaf area removed, leaf area at R5, and leaf area at R6. Slopes and intercepts are reported as ± SE. Regressions were made with graphs of individual plot means.

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1990</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf Area Removed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unstressed</td>
<td>-0.0045 ± .0011</td>
<td>6.92 ± 0.49</td>
<td>.53</td>
</tr>
<tr>
<td>Stressed</td>
<td>-0.0038 ± .0013</td>
<td>3.31 ± 0.60</td>
<td>.36</td>
</tr>
<tr>
<td>Pooled</td>
<td>-0.0043 ± .0015</td>
<td>5.16 ± 0.64</td>
<td>.22</td>
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<td>R5 Remaining Leaf Area</td>
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<tr>
<td>Unstressed</td>
<td>0.0030 ± .0007</td>
<td>2.28 ± 0.77</td>
<td>.56</td>
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<tr>
<td>Stressed</td>
<td>0.0032 ± .0007</td>
<td>0.10 ± 0.49</td>
<td>.60</td>
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<tr>
<td>Pooled</td>
<td>0.0042 ± .0006</td>
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<td>.65</td>
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<tr>
<td>R6 Remaining Leaf Area</td>
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<td>Unstressed</td>
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<td>2.47 ± 0.88</td>
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<tr>
<td>Stressed</td>
<td>0.0051 ± .0009</td>
<td>0.22 ± 0.38</td>
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<td>Pooled</td>
<td>0.0055 ± .0006</td>
<td>0.53 ± 0.40</td>
<td>.74</td>
</tr>
<tr>
<td></td>
<td>1992</td>
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<tr>
<td>Leaf Area Removed</td>
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<tr>
<td>Unstressed</td>
<td>-0.0021 ± .0011</td>
<td>6.17 ± 0.43</td>
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<td>Stressed</td>
<td>-0.0041 ± .0011</td>
<td>4.03 ± 0.40</td>
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<tr>
<td>Pooled</td>
<td>-0.0030 ± .0014</td>
<td>5.08 ± 0.51</td>
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<td>R5 Remaining Leaf Area</td>
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<td></td>
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<tr>
<td>Unstressed</td>
<td>0.0016 ± .0006</td>
<td>4.38 ± 0.49</td>
<td>.33</td>
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<tr>
<td>Stressed</td>
<td>0.0040 ± .0007</td>
<td>1.42 ± 0.29</td>
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<td>R6 Remaining Leaf Area</td>
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<td>0.0019 ± .0006</td>
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<td>0.0037 ± .0008</td>
<td>1.54 ± 0.34</td>
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<tr>
<td>Pooled</td>
<td>0.0037 ± .0005</td>
<td>2.12 ± 0.35</td>
<td>.62</td>
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\(^a\) cm\(^2\)/plant
Table 2. Utility of various canopy measurements to three important types of yield models.

<table>
<thead>
<tr>
<th>Canopy Measurement</th>
<th>Yield Potential</th>
<th>Yield Loss</th>
<th>Percent Yield Loss</th>
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<tr>
<td>Percent defoliation</td>
<td>C</td>
<td>C</td>
<td>+</td>
</tr>
<tr>
<td>Leaf Area Removed</td>
<td>C</td>
<td>+</td>
<td>C</td>
</tr>
<tr>
<td>Remaining Leaf Area</td>
<td>++</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

1 Each cell assumes that only the corresponding canopy measurement and yield component are known.

'C' = model confounded by canopy size

'+' = model will predict yield component if there is a linear LAI-yield relationship

'++' = model will predict yield regardless of nature of LAI-yield relationship

'-' = factor by itself cannot be used to predict yield component
Figure 1. Seed yield/plant ± SE from defoliation and irrigation treatments at harvest, 5 October, 1990.
1990

UNSTRESSED

STRESSED

TARGET LAI

SEED YIELD/PLT (g)
Figure 2. Seed yield/plant ± SE from defoliation and irrigation treatments at harvest, 19 October, 1992.
TARGET LAI

SEED YIELD/PLT (g)

UNSTRESSED

STRESSED

1992

0 1 2 3 4 5

TARGET LAI
Figure 3. Regression lines of soybean yield in 1990 versus leaf area removed, remaining leaf area at R5, and remaining leaf area at R6. Points represent individual plot means of subsamples.

(a) yield versus leaf area removed

(b) yield versus R5 leaf area

(c) yield versus R6 leaf area
Figure 4. Regression lines of soybean yield in 1992 versus leaf area removed, remaining leaf area at R5, and remaining leaf area at R6. Points represent individual plot means of subsamples.

(a) yield versus leaf area removed

(b) yield versus R5 leaf area

(c) yield versus R6 leaf area
GENERAL SUMMARY

This dissertation has discussed several of the important effects of drought stress on plant responses to insect defoliation. The three papers included have discussed the physiological, yield, and management consequences of drought stress and defoliation in soybean. In addition, Paper 2 discusses the potential of plants to recover from drought stress after pod fill. These papers are the first comprehensive report of these factors in soybean and will be useful in development of crop models and pest management strategies in the future.

Several counter-intuitive conclusions were reached in these papers. First, we consistently found no significant interactions between drought stress and defoliation in physiological, crop growth, and yield data. Secondly, a non-linear response of yield to increasing defoliation was not observed. In both cases, we have determined that a simpler model was acceptable, making these data easier to incorporate into existing crop models and pest management programs. Although the levels tested may have had some impact upon results, these conclusions are mostly in agreement with several previous studies (Higgins et al. 1984; Simmons & Yeargan 1990; Helm et al. 1992; Higley 1992; Vieira et al. 1992). Although future studies may show that more complicated defoliation/drought stress models provide estimates with greater precision, their acceptance by scouts and growers must be weighed relative to the economic benefits of more reliable pest management programs.
In all three of these studies, we found that the way in which data were expressed prior to analysis considerably affected results. Not only did percent defoliation, leaf area removed, and remaining leaf area predict yield with different levels of precision (Paper 3), they also affected results of analyses. For example, because irrigation rate and remaining leaf area were highly correlated, stepwise regression analyses of photosynthesis data using these variables differed substantially from analyses substituting leaf area removed for remaining leaf area. Conclusions from future studies and comparisons of past studies, therefore, should be made only after carefully considering how data were collected, expressed, and analyzed.
ACKNOWLEDGEMENTS

These studies were made possible by a coordinated, team effort of faculty, graduate students, and technicians. I would like to thank all of the technicians and hourly employees involved with this study, especially Jason Humble, Brian Buhman, Jason Strohman, and Cynthia Lidtke. Their enthusiasm despite continuous threats by Mother Nature to hamper research efforts always will be appreciated. I am grateful to Soil Fumigants, Inc. (Sanford, FL) and Great Lakes Chemical Corporation (West Lafayette, In) for providing technical assistance and applicator trays to fumigate soil infested with soybean cyst nematodes in 1992. I also thank Leon Higley, Richard Shibles, Joe Browde, Gordon Brown, and Mike Wallendorf for their help with analyzing and interpreting data.

While I conducted soybean research within the rainout shelter, woodchucks and rabbits showed greater persistence than any researcher should be allowed to bear. In 1990, winds were a bit too persistent and my study of the effects of canopy level on *Neozygites floridana* epizootics was turned upside down. However, I never faced true persistence until 1992, when She just wouldn’t leave me alone. Today, I am glad for my wife Theresa’s persistence and am grateful for the changes she has brought to my life. I just wish she could have been there by my side back when I was battling woodchucks.
REFERENCES CITED


