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**EFFECTS OF SIMULATED INSECT DEFOLIATION AND ANNUAL WEED
COMPETITION ON SOYBEAN AND VELVETLEAF DEVELOPMENT**

Iowa State University

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Effects of simulated insect defoliation and annual
weed competition on soybean and velvetleaf development

by

Randall Alan Higgins

A Dissertation Submitted to the
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Crop Production and Physiology

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INTRODUCTION

Much information has been generated on pest losses from single-species studies. Growers, however, are normally faced with a multiplicity of pest types (often several weeds, insects, plant diseases, and(or) nematodes). Without firm experimental evidence derived from interdisciplinary research efforts, pest management specialists are often left with unsupported 'guesstimates' as to whether pest combinations cause losses that are additive or synergistic. As a consequence, losses cannot be properly partitioned between causative factors, and the probability of making sub-optimal management decisions and employing untimely control procedures increases (Pedigo et al., 1981). Several review articles and policy statements have expressed concern over the continued dearth of published data on pest-stress interactions (Allen and Bath, 1980; Barfield and Jones, 1979; Chiarappi et al., 1972; Edens and Koenig, 1980; Pedigo et al., 1981). This concern is particularly apparent with annual field crops where strong discipline-oriented research efforts have continued for some time.

Firm commitments to interdisciplinary pest research probably have been approached with trepidation because of unclear monetary responsibilities and the fact that a single researcher's knowledge does not encompass all major aspects of the cooperative endeavor. Pilot studies should probably employ species combinations with large data bases to avoid many of the procedural uncertainties which may otherwise undermine the fledgling coalition. For 3 years, such a cooperative program has been underway at Iowa State University between the disciplines of entomology and weed science. Significant sources of biological, ecological, and managerial information

were available on the soybean defoliator *Plathypena scabra* (F.) or green cloverworm (GCW) and separately, on the annual weed competitor *Abutilon theophrasti* (Medic.) or velvetleaf (Carner et al., 1974; Eaton et al., 1976; Pareja, 1976; Pedigo, 1974; Pedigo et al., 1973, 1977; Staniforth and Lovely, 1974; Staniforth and Weber, 1956; Stone and Pedigo, 1972). Because of the above reasons, GCW and velvetleaf were considered prime candidates to combine in the present interdisciplinary study. Although a better understanding of separate GCW and velvetleaf stresses on soybeans, *Glycine max* (Merr.), has become available through information published since the inception of this project (Hagood et al., 1980; Hammond et al., 1979a; Hammond and Pedigo, 1982; Oliver, 1979), no published information on the effects of combinations of these pests is yet available.

Although natural or artificially established pest populations of known magnitude have proven satisfactory for studies of crop and weed competition (Buchanan, 1977), pest mobility and sampling difficulties often have hampered efforts to quantitatively assess insect-induced crop stresses. Natural insect populations are often unpredictable, and insecticidal modification of high-density populations may alter the damage-potential of surviving individuals. The artificial establishment of various densities of insects has merit, but questions often remain as to effective documentation of the proportion surviving in each experimental plot. Many materials used to restrain insects in cage experiments can also alter the micro-environment sufficiently to cause undesirable and unnatural plant developmental responses (Trang and Giddens, 1980), especially if the cages are left for an extended interval. For these and other reasons, labor-intensive, manually imposed damage simulations have recently been employed in

several studies (Coggin and Dively, 1980; Hammond and Pedigo, 1982; Kincade et al., 1971; Thomas et al., 1974, 1978; Turnipseed, 1972). Comparative simulation studies (Capinera and Roltsch, 1980; Hammond and Pedigo, 1981; Poston et al., 1976) have shown that caution should be employed in selecting an appropriate simulation methodology if the goal is to truly mimic a given insect damage pattern. Plant response to environmental stresses has been shown to be extremely dynamic, and plant development exhibits a high degree of plasticity in form and growth (Harper and Gajic, 1961). Therefore, to obtain typical plant responses, it seems logical that simulated-insect damage should be imposed piecemeal, following the normal phenology of insect attack as closely as possible. These restrictions are particularly germane if the observed effects on plant growth and yield are to be related to a specific insect density as required for economic-injury levels. A temperature-dependent hole-punching technique (Hammond and Pedigo, 1982; Hammond et al., 1979a, 1979b) was employed to create the defoliation expected from specific incremental densities of green cloverworm larvae, thereby circumventing many of the aforementioned technique criticisms.

A major deficiency of many past studies is the limited attention given crop responses to pest or simulated-pest damage. Invaluable managerial information on plant morphological plasticity, compensatory growth (or the lack thereof), and phenological variation in crop susceptibility to biological stressors is often overlooked when plant sampling is restricted to yield only or a few token growing season evaluations.

A shortage of interdisciplinary studies on interacting biological stresses is currently limiting the development of truly integrated programs of pest management. Therefore, studies (reported in this dissertation) were conducted with the following objectives in mind:

- 1) define the separate and combined effects of varying degrees of velvetleaf competition and simulated green cloverworm (SGCW) defoliation on soybean morphological development (Part I) and soybean dry weight accumulation and allocation (Part II);
- 2) detection of temporal and proximity limitations in the development of interspecific stress using soybeans as an indicator species (Parts I and II);
- 3) define differential effects of interspecific competition with defoliated and undefoliated soybeans on velvetleaf morphological development (Part III) and velvetleaf dry weight accumulation and allocation (Part IV);
- 4) detection of temporal limitations in the development of interspecific stress using velvetleaf as the indicator species (Parts III and IV);
- 5) detection of proximity interactions during the development of intraspecific velvetleaf competition (Parts III and IV); and
- 6) determination of the separate and combined effects of varying degrees of velvetleaf competition and SGCW defoliation on soybean yield and specific components of yield (Higgins et al., 1982).

REVIEW OF RELEVANT LITERATURE

Selected Studies on the Effects of
Defoliation on Soybeans

Artificial plant defoliation methodologies have varied widely depending on research goals (hail, insect, pathogen, frost, or other simulation desired), labor and pest availability, and the sophistication of the supportive data base. A vast amount of published data exists on the effects of specific defoliation treatments on yield. In contrast, relatively few data are available which describe the above-ground pre-harvest influences of insect or, at least, insect-like defoliation on soybeans. This shortcoming of published studies is especially unfortunate because environmental conditions prevailing between the imposition of defoliation and harvest maturity may effectively obscure treatment effects. The limited information available, albeit perhaps of questionable validity when considering insect defoliation *sensu stricto*, has helped in the formulation of theories on how natural insect defoliation may alter soybean development. Thus, the results of a few of the most notable physiological studies will be summarized before a brief review of defoliation effects on yield is presented.

Selected Studies of the Effects of Defoliation on Soybeans,
Leaf and Canopy Characteristics

Fehr et al. (1977; 1981) reported on the effects of 100% defoliation of indeterminate and determinate soybeans at various reproductive stages (leaflet-picking). Determinate varieties showed less ability than indeterminate varieties to compensate for defoliation through the production of new leaves once flowering had begun. For example, indeterminate plants

sustaining 100% defoliation during the reproductive stages, eventually produced 37 to 49% of the leaf area of undefoliated indeterminate control plants. Leaflet number increased up to 45% above undefoliated levels when indeterminate varieties were completely defoliated. Although leaf number increased, average leaflet size declined 63 to 67% on the indeterminate varieties. In contrast, 2 determinate soybeans compensated by producing only 21 to 22% of maximum leaf area of undefoliated plants with a 14 to 27% decrease in leaflet number after complete defoliation. However, neither determinate type produced any significant leaf area when 100% defoliation was imposed at the late bean-fill stages (approximately R6).

Soybeans severely defoliated (up to 80%) by the corn earworm, *Heliothis zea*, in the vegetative stages (V4 through V6) compensated by producing new leaves (Mueller and Engroff, 1980). These authors concluded that "the plants usually recuperated fully by the first reproductive stages," without adequately qualifying or substantiating the statement.

In contrast to the compensation (increase in leaf number) observed with early season defoliation of soybeans by Mueller and Engroff (1980) were the results of McAlister and Krober (1958). They showed that indeterminate soybeans (stages R5 to R6 or bean-fill) did not respond to 80% defoliation (leaflet-picking) by producing additional leaves. Leaf protein, leaf starch, and leaf sugar content also were not responsive to this level of defoliation (samples removed shortly before substantial leaf-drop began).

Ingram et al. (1981) reported some of the effects of natural velvet-bean caterpillar (VBC, *Anticarsia gemmatalis* Hubner) defoliation on 'Bragg' soybeans. In plots not receiving protective insecticidal sprays, this insect reduced the average Leaf Area Index (LAI) from 5.5 to 2.8. The

largest reduction in area occurred during the last 2 weeks of the pre-seed growth phase. Canopy light interception declined from 94% to 72% in the defoliated plots during this time. However, later in the season (during the linear seed-growth phase), midday light interception substantially improved without concomitant increases in LAI or leaf dry weight. The authors concluded that the plants partially compensated for defoliation by rearranging their surviving leaf displays within the canopy. In this study, specific leaf weight (SLW) eventually increased to levels which were 1.0 mg/cm² greater in defoliated plants than in the insecticide-treated and relatively-undefoliated control plants. In contrast, 66% defoliation by leaflet-picking during bloom did not significantly alter soybean SLW 17 to 18 days after defoliation terminated (Egli et al., 1976).

Defoliation of soybeans by VBC reduced canopy net photosynthesis (measured at a photosynthetic photon flux density of 1500 $\mu\text{E}/\text{m}^2\cdot\text{sec}$) by 6.8 mg CO₂/dm²·h in defoliated plots (Ingram et al., 1981). Defoliation (up to 50% by VBC) did not alter the canopy light compensation point significantly. However, dark respiration declined 3.3 mg CO₂/m²·h as a result of VBC defoliation. Canopy capacity, rather than canopy efficiency, seemed to be affected to a greater extent. Additionally, these authors speculated that VBC feeding behavior may enhance reductions in long-term canopy photosynthesis as a result of the selective removal of tissue from the more efficient upper canopy leaves. It should be noted, however, that Johnston and Pendleton (1968) have shown that lower canopy leaves do have some capacity for increasing their photosynthetic rates if they are adequately illuminated (assuming senescence of these leaves has not progressed beyond their point-of-no-return). Thaine et al. (1959) concluded from radioautography

experiments that defoliation (imposed during the vegetative stage) between source leaves and the apex sink often resulted in a significant increase in the amount of carbohydrate (produced by the source leaves) arriving at the apex. Turnipseed (1972) also concluded that soybeans could partially compensate for defoliation of the upper canopy through an increase in the photosynthetic production of the undamaged lower leaves. In contrast, if defoliation was restricted to the lower canopy, a greater proportion of carbohydrates produced by the surviving lower leaves moved to the root rather than the apex (Thrower, 1962).

The delayed effects of defoliation (which was imposed during the blooming stages) on short-term carbohydrate translocation were studied by Egli et al. (1976). Seventeen to 18 days after two-thirds of the leaf area was removed (leaflet-picking), the lower trifoliolates were exposed to $^{14}\text{CO}_2$. Seven hours after labeling, 55% of the radioactive carbon was still in the treated leaf (59% in the control plots). Even after 24 hours, approximately 50% of the radioactivity remained in the treated leaves, regardless of leaf area. Thus, it was concluded (somewhat surprisingly) that defoliation probably did not greatly influence the rate of ^{14}C movement out of the leaf for an extended period (at least at 3 weeks post-defoliation). In contrast, pod-removal treatments caused a greater percentage of radioactive carbon (72%) to remain within the treated leaf at 7 hours after treatment.

Boote et al. (1980) reported effects of artificial defoliation (leaflet-picking) on peanut (*Arachis hypogae* L.) photosynthesis. Data were collected on leaf area, canopy C exchange rates (CER), uptake of $^{14}\text{CO}_2$, and

light interception in 3 canopy layers. Defoliation (25%, primarily from the upper one-half of the canopy) reduced $^{14}\text{CO}_2$ uptake (30%) and canopy CER (35%). In undefoliated plants, the upper 40% fixed 63% of the total $^{14}\text{CO}_2$ taken up and intercepted 74% of the light. Because of the importance of maintaining 95% light interception (to minimize wastage of sunlight), these authors concluded that defoliation becomes extremely important when LAI of peanuts is reduced below a LAI of 3 or 4 (close similarities to peanuts and soybeans may exist in this regard). It was suggested that future studies should also quantify the location of defoliation by stratum. If precise modeling is attempted, the photosynthetic capacity of the remaining leaves should also be quantified. Several authors of defoliation studies on other crops also have stated that the upper leaves contribute substantially more of the photosynthate designated for yield (Johnston and Pendleton, 1968; Puckridge, 1969; Stickler and Pauli, 1961). Thus, insect defoliation (often concentrated in the upper canopy) could restrict yield to a greater extent than an equivalent foliage loss occurring lower in the canopy (e.g., leafspot on peanuts; see Boote et al., 1980).

At least one study (Poston et al., 1976) was specifically designed to quantify differential effects of defoliation techniques on soybean net photosynthesis. In this study, defoliation caused by caged insects (GCW and the painted lady, *Cynthia cardui* (L.)) did not always result in reduced net-carbon exchange rates of individual excised soybean leaves (even when 50% of the tissue was consumed). Paper punch, cork borer, and along-the-midrib defoliations had a similar effect on net photosynthesis with that of natural insect defoliation. In contrast, across-the-midrib defoliation was not determined equivalent in effect on net photosynthesis.

Net photosynthesis ($\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$, excised-leaf basis) actually increased when the distal portion of the leaf was removed, probably indicating differences in efficiency of proximal and distal regions. Lepidopterous defoliators of soybeans do not selectively consume the distal portion of attacked leaves. Therefore, across-the-midrib defoliations would probably not be an adequate simulation for studying the effects of feeding by these arthropods. Thus, the results of studies employing an across-the-midrib defoliation methodology (e.g., Weber, 1955) should probably not be accepted verbatim for use in insect pest management programs.

Hammond and Pedigo (1981) studied the effects of several types of defoliation methodologies on water lost through the soybean tissue remaining after the defoliations were terminated. Punch defoliation techniques resulted in foliage water-loss rates that more closely paralleled rates observed with actual green cloverworm defoliation than leaflet excision methods. These results indicate that the excision methods commonly employed in attempts to simulate hail damage and, reportedly, insects may not achieve an adequate level of realism for use in the insect simulation studies. Davidson (1973) reached similar conclusions when comparing the effects of punch and pick defoliation methods on cotton plants. A series of defoliation methodologies has recently been compared by Ostlie.¹ Significant technique differences in many developmental and yield characteristics have been confirmed.

Hinson et al. (1978) noted that studies employing leaflet-picking usually assume that each leaflet contributes 33% of the total area of a

¹K. R. Ostlie, Department of Entomology, Iowa State University, Ames, Iowa, personal communication, 1982.

trifoliolate leaf in soybeans. However, their observations showed that terminal trifoliolates often possessed 40% of the area. Therefore, the majority of leaflet-picking studies may not have achieved the stated levels of defoliation with precision.

In general, soybeans (both determinate and indeterminate) are less susceptible to lodging when defoliated (leaf-picking). Defoliation early in the reproductive stages (R2 to R3) resulted in lower lodging scores than late reproductive (R5 to R6) defoliation (Fehr et al., 1981). A pronounced degree of stunting also seems to commonly accompany severe defoliation by leaf-picking (Fehr et al., 1981). In another study (Enyi, 1975), 100% defoliation at 4, 8, and 12 weeks after planting also stunted the soybeans. The defoliation resulted in plants that were only 78%, 90%, and 90% of the control plant heights, respectively (Enyi, 1975). The reduction in wind and rain infiltration resistance caused by defoliation and the shorter plant height probably interact to reduce lodging susceptibility. Teigen and Vorst (1975) also noted a similar relationship between defoliation, soybean height, and lodging score. In contrast, when defoliation treatments were restricted to lower canopy levels (simulating many soybean-leaf pathogens), plant height was not affected (Lockwood et al., 1977).

Mueller and Engroff (1980) noted that, in addition to defoliation, the corn earworm damages the main-stem meristematic area. This injury commonly stimulates the development of numerous axillary buds, which results in a shorter, more densely-branched plant. In contrast, Enyi (1975) reported that 100% defoliation at 4, 8, and 12 weeks after planting resulted in plants with 1 or 2 fewer branches than the undefoliated control.

Harvest stem weight was reduced 14 to 17% by 80% defoliation (leaflet picking) late in the season (bean-filling stages; McAlister and Krober, 1958). However, 67% defoliation (leaflet-picking) at bloom also has been shown to reduce stem dry weight when this characteristic was quantified 8 days after defoliation (Egli et al., 1976). Additionally, the stem weights of completely defoliated soybeans (treated at 4, 8, and 12 weeks after planting) averaged only 58% of the undefoliated control plants at harvest (Enyi, 1975).

Determinate soybeans ('Bragg') in Florida terminated leaf area production within 17 days after flowering (Hinson et al., 1978). These authors presented evidence that defoliation (leaflet-picking) can potentially decrease nitrogen fixation and speculated that this effect also could add to the direct defoliation effect in limiting yield. The leaf-picking studies conducted by Lawn and Brun (1974) also support this concept. Late-bloom defoliation effectively reduced nitrogen fixation by lowering both specific and total nodule activity. A reduction in carbohydrate supply to the nodules is the most commonly accepted theory as to why the decline seemingly occurs. Other authors also have reported a decline in the root-to-shoot ratio after severe defoliation (Whittaker, 1979).

Fehr et al. (1977), found that developmental rates of determinate and indeterminate soybeans respond similarly to complete defoliation. Overall, severe defoliation in the blooming stages tended to delay maturity a few days, whereas defoliation at pod-filling tended to hasten maturity (shorten the pod-filling stages) 3 or more days (Fehr et al., 1977; 1981). Maturation of lima-bean plants similarly was delayed by pre-bloom defoliation

(Coggin and Dively, 1980). Leaf picking (50 to 100% defoliation) before full bloom delayed maturity 1 to 8 days (Weber, 1955). Hinson et al. (1978) showed that maturity of determinate soybeans may be hastened 1 to 5 days by defoliation (leaflet-picking). The higher the percentage leaf removal and the later in development defoliation began, the more rapidly that maturity was reached. Late-season Japanese beetle defoliation, when severe, has been shown to hasten maturity by inducing early leaf senescence (Gould, 1963). Thus, duration of photosynthesis, as well as quantity of available photosynthetically-active leaf tissue may be reduced.

Selected Studies on the Effects of Defoliation on Soybean Yield and Yield Components

A vast literature exists on the effects of defoliation on soybean yield. Hammond (1979) recently summarized a majority of relevant studies and should be consulted for a more complete listing of the early literature. In general, this review will examine several of the more recent studies or those of particular interest to entomologists. The overall organization is by developmental stage during which the defoliation was imposed.

Defoliation of soybeans during the vegetative stages, even if severe, often will not reduce yields substantially (particularly if favorable growing conditions follow). For example, studies conducted very early in development have shown the importance of cotyledons in compensating for complete defoliation (Weber and Caldwell, 1966). Persistence of at least one cotyledon for 12 days after emergence was required to obtain maximum

yields when the unifoliolate leaves were destroyed. Removal of both cotyledons and both unifoliolates before the first trifoliolate had expanded reduced yields 7.3%. Complete defoliation at V2 (first trifoliolate, V-stage corresponds to main-stem trifoliolate number plus 1) reduced yields approximately 21%.

Although level of defoliation was estimated at 70 to 80%, *Heliothis zea* (Boddie) populations up to 33 larvae/m of row did not consistently reduce yield during the early vegetative stages (V4 through V6; Mueller and Engroff, 1980). As vegetative growth continued, equivalent populations of larvae consumed less foliage on a percentage basis (only 30 to 50% at V8). In one year, nonirrigated plants lost 24.9% in yield from 39 larvae/m of row, whereas 65 larvae/m of row were required to cause a 23.3% yield loss under irrigated conditions. Obviously, plant compensation to defoliation can offset significant amounts of early-season defoliation.

Poston and Pedigo (1976) determined that 33% defoliation (cork borer, scheduled defoliation) at the 2-trifoliolate stage (V3) did not always significantly reduce grain yield. In comparison, 50% defoliation resulted in a 14 to 31% yield reduction. Pods/plant was the yield component most susceptible to damage at this stage. When combined with 66% leaf rolling (characteristic of some insects), 33% defoliation reduced yield 22% (again, largely by reducing pod number). The effects of sequential defoliation, occurring at V3 and R2 (full bloom), on yield were additive.

Significant yield reductions were reported from Iowa when soybeans (stages V3 through V4) were defoliated more than 41% with cork borers (Hammond and Pedigo, 1982). Defoliation intensity increased with time to

simulate development of a natural population of painted lady (*Cynthia cardui*, L.) larvae. Reductions in pod and bean number resulted from complete defoliation. In comparison, when defoliation was limited to 41.5% only pod numbers were significantly depressed.

Defoliating determinate 'Lee 74' soybeans (50% area reduction) during V3 or V5 resulted in a 0 to 9% yield reduction from the undefoliated control (Caviness and Thomas, 1980). In comparison, 100% defoliation in the same study reduced yields from 0 to 20%, depending on the year. Somewhat surprisingly, percentage reductions from the controls were similar regardless of whether or not the plots were irrigated (even under droughty conditions). In contrast, other studies have shown large differences in yield-loss from early season defoliation with varying soil-moisture conditions. For instance, Todd and Morgan (1972) reported that 100% defoliation (leaflet-picking) at the 5-to-6 leaf stage resulted in yields only 43.8% of the undefoliated controls (if the season was extremely droughty). However, equivalent defoliation (in temporal and intensity patterns) reduced yields only 26% when favorable growing conditions continued for the majority of the season. Sixty-six percent defoliation at this stage did not decrease yield under either soil moisture regimen. This study also showed that continuous progressive defoliation (repeated removal of a designated percentage every week) limited yield to a greater degree than single defoliations. Weight per seed (seed size) was more consistently reduced by continuous progressive defoliation beginning in the vegetative stages than by single defoliations at this time.

Up to 50% defoliation (across-the-midrib) at V7 also did not significantly reduce soybean yield (Teigen and Vorst, 1975). Fifty-percent defoliation (leaflet-picking and across-the-midrib excision) at V2 or V7 did not reduce yield significantly (Weber, 1955). Complete defoliation at either of these stages reduced yield 18 to 20%, with at least a portion of this loss attributed to smaller seeds (5% below control values). Lima beans exhibit a similar high tolerance to severe defoliation in the early prebloom stages. Sixty-six percent defoliation caused no significant yield loss. In contrast, 100% defoliation reduced yields 21% (at the normal harvest date), largely by delaying maturity (Coggin and Dively, 1980).

Complete defoliation (leaflet picking and across-the-midrib excision) at V2 or V7/R1 did not measurably affect protein content (Weber, 1955). Slight reductions in oil content were caused by complete foliage removal at this time, however.

The determinate variety 'Lee 74' suffered a 5 to 21% yield loss with 50% defoliation (scissors) at full bloom (R2; Caviness and Thomas, 1980). Seventy-five and 100% defoliation resulted in 7 to 24% and 26 to 50% yield losses, respectively. Increasing the frequency of irrigation did not alter the loss relationships significantly. Pod number was seemingly the primary component reduced with seed size reductions becoming more important with later defoliation treatments (e.g., R4 or R5).

A thermal-unit (= degree-day) based defoliation-developmental model was used in an Iowa study to ascertain defoliation damage predicted from specified populations of green cloverworm larvae (Hammond and Pedigo, 1982). Twenty-one percent defoliation (equivalent to ≥ 21.0 larvae/0.3 m of row under extreme drought conditions), imposed with cork borers, reduced yields

32.6%. Pod number was the yield component most susceptible to loss. Perhaps most importantly, the study showed that the effects of a specified level of larval-equivalent defoliation varied between seasons (viz, soybeans required more larval-equivalents to cause a comparable yield reduction when conditions were favorable for growth (e.g., large plants) than when conditions were less favorable (e.g., small plants)).

A 2-year mean of 17, 18, and 43% yield reductions were observed following single 33, 66, and 100% defoliations applied 2 weeks after first bloom (Todd and Morgan, 1972). Continuous defoliations beginning 1 to 2 weeks after first bloom in general, reduced yield 10 to 20% more than equivalent single-day defoliations. Continuous progressive defoliations (intensity gradually increasing over time until 100% defoliation was attained) reduced yields approximately 45%, when initiated 1 week after first bloom. Continuous defoliation and continuous progressive defoliation, beginning within 1 or 2 weeks of first bloom reduced seed size significantly. Seed size was reduced by a single 100% defoliation imposed at full bloom but not necessarily reduced by lesser amounts of defoliation at this time.

Hinson et al. (1978) reported on defoliation (33 and 67% removal by leaflet picking) beginning during the bloom stages, R1 through R2. Yield declined only 4% when 33% defoliation occurred, regardless of phenological stage. Begum and Eden (1965) also reported that 33% defoliation by leaflet picking during the blooming stages had no significant effect on yield. Both seed size and seed number were depressed by 67% defoliation beginning after flowering was completed (Hinson et al., 1978). Complete defoliation

at blooming always reduced yield (20 to 97%) in a study conducted in Alabama, but 67% defoliation had no consistent effect (+3.2 to -20.9%; Begum and Eden, 1965). In comparison, 67% removal at 3, 17, 31, and 42 days after flowering began (Florida) effectively lowered yield 8, 21, 31, and 30%, respectively (Hinson et al., 1978).

Defoliation at R2 (cork borer, scheduled defoliation over 7 days attaining 20 to 33% reduction in area) reduced yield less than 24% in Iowa (Poston and Pedigo, 1976). The yield-limiting effects of repeated defoliation applied initially at V3 and again at R2 were shown to be additive in this study. A reduction in bean weight (g/100 seeds) and numbers of beans/pod were not influenced by defoliation at R2. In another study of indeterminate soybeans (Teigen and Vorst, 1975), 25% defoliation (shears, across-the-midrib) did not significantly reduce yield. Fifty percent defoliation did reduce yield (8%, averaged across several stand reductions). In this study, seed weight (g/100 seeds) declined 4.5 to 6%, but the number of pods/plant was not significantly altered.

In a study of pathogen-simulated loss of lower leaflets, Lockwood et al. (1977) reported that severe early bloom defoliation (67%) reduced yield only approximately 20%. A greater reduction in numbers of pods than reductions in seed size was evident with earlier defoliation.

Stone and Pedigo (1972) developed regression equations from the hail-simulation data of Kaiton et al. (1949, leaves shredded with heavy wire) relating percentage defoliation to percentage yield loss. These regressions confirmed that the effects of defoliation vary with developmental stage. Maximum yields become less likely when significant defoliation occurs from R3 through R5 (pod-set through seed enlargement). As Kogan

(1976) has pointed out, this dynamic response requires that unique damage/loss relationships are often required for each developmental stage.

Removal of two-thirds of the leaf area (leaflet-picking at pod-set or R3 to R4) reduced yield (42%) by reducing seeds/plant (28%) and seed size (20%; Egli et al., 1976). Only a limited amount of carbohydrate transferred to the seed had previously been stored. Instead, the majority of the carbohydrate designated for grain was derived from photosynthesis occurring during grain filling. In addition, several studies have shown that, during reproductive growth (increasing sink demand), photosynthetic rates may increase (Dornhoff and Shibles, 1970).

At least 1 study (leaflet picking at R3 to R4) did not always confirm a close relationship between seed growth rates and photosynthetic production (Egli and Leggett, 1976). Additionally, severe defoliation resulted in a marked decrease in stem sugar concentration. Therefore, these authors concluded that it may be possible that storage carbohydrates can serve to maintain (e.g., buffer or stabilize) seed growth rates during brief periods unfavorable for normal rates of carbohydrate synthesis.

Defoliation during pod set and early bean filling has often resulted in substantial yield loss (relative to equivalent defoliation at other developmental stages). Significant yield losses were not always observed following 67% defoliation at mid-bloom, but were observed after either 50 or 67% defoliation at pod-set in South Carolina (Turnipseed, 1972).

Fehr et al. (1977) showed that indeterminate varieties can tolerate a higher level of defoliation than determinate varieties (on a yield loss basis). Complete defoliation at any reproductive stage resulted in an

average 59% yield reduction for determinate varieties. Indeterminate varieties lost only 39% when equivalent levels of defoliation were compared over comparable reproductive intervals. Determinate soybeans progress through the reproductive stages at a relatively uniform rate (little intra-plant stratum variability). In contrast, indeterminate varieties often transcend a broad range of reproductive development on the same plant (depending on the stratum under consideration). Thus, stage-specific stress effects would probably not affect the entire plant equally. Determinate cultivars were most susceptible to a defoliation-induced yield loss at R4 (pod set), whereas indeterminate varieties exhibited more loss at R5 (beginning bean development). Thus, it seems logical that the results of defoliation studies conducted on one determinate-type may not be applicable directly to the other type. Both varieties lost yield early in the reproductive stages by producing fewer numbers of seeds (probably through a reduction in pod numbers). Reduced seed size also contributed to lower yields, particularly from R5 through R7.

Pod number and seed weight (g/100 seeds) were reduced 32.2 and 16.8%, respectively, by 75 to 80% defoliation during the podding stages (Hamerton, 1972). If the level of defoliation (leaflet picking) was reduced to 40 to 50% at podding, seed weight was the only component reduced, approximately 16%). Enyi (1975) also concluded that, at the early podding stage, soybeans were relatively more sensitive to defoliation-induced yield loss. In this study, severe (complete) defoliation increased the number of barren pods (thus decreasing numbers of fertile pods), reduced the number of seeds/pod, and lowered individual seed weight. Caviness and Thomas (1980), after studying 4 levels of defoliation at 3 stages of

development, also concluded that the podding to early seed development stages (R4 and R5) were the most susceptible to defoliation. Although pod number was the component contributing most of the yield loss, a reduction in seed size also was important. The data of Todd and Morgan (1972) also concur in this regard. Severe defoliation beginning 4 weeks after first bloom and persisting for 3 or 4 weeks reduced yield 92%. The regression equations developed by Stone and Pedigo (1972) from the data of Kalton et al. (1949) also predict that the late pod-set, early bean-development stages are the most defoliation sensitive. During rapid pod-filling, pods in the axil of the source leaf receive the largest percentage of photosynthate (Blomquist and Kust, 1971). Next in line, due to phyllotactic connections, were pods in the axils of leaves 2 nodes below the source leaf. The lowest nodes become particularly dependent upon the downward translocation of adequate photosynthate after their own source leaves have abscised (which commonly occurs during development). It should be obvious that defoliation in the upper canopy could potentially have a very severe effect in affecting the reproductive success of lower plant stratum.

Eighty-percent defoliation (leaflet-picking?) at approximately R4 (late pod set) reduced both oil and protein content (McAlister and Krober, 1958). Yield declined 16 to 26% with 40% defoliation and 45 to 51% with 80% defoliation. Both pods/plant and seed weight were significantly reduced by either level of defoliation. Plants defoliated severely (80%) at R4 showed many unfilled pods containing aborted seeds.

Ingram et al. (1981) reported that time-distributed natural defoliation by velvetbean caterpillar (approximately a 49% area reduction) peaking

during seed set reduced yield (about 13%). Defoliation did not affect seed-growth duration or abortion rates (therefore, did not hasten maturity in this study), but, rather, reduced yield (12%) by depressing individual seed growth rates (19%), which, in turn, lowered 100-seed-weight. From a study of net carbon balance, the authors concluded that defoliation during the seed setting stages may reduce the number of pods and seeds set and maintained. Later defoliation would probably limit seed growth rates to a greater extent.

Research in South Carolina (Turnipseed, 1972) indicated that determinate soybeans (at pod-set) could tolerate 17% defoliation (scissors, some of which seemingly was an across-the-midrib defoliation) without realizing a significant loss in yield. However, 50 to 67% defoliation was usually and always, respectively, adequate to cause a significant yield loss. A wide range of sequential defoliation treatments also was reported. Sequential combinations of otherwise nonsignificant single defoliations could cause significant yield losses. In general, defoliation at pod-set was more important than a comparable foliage loss during bloom or pod-fill. The author concluded that insecticidal treatments should not be considered until 35% defoliation was achieved at the bloom stages or 20% defoliation occurred in the later stages (based on market values and control costs typical for the period).

In a recent study of indeterminate and determinate cultivars, Fehr et al. (1981) concluded that R5 (76% yield loss) or R5.5 (80% yield loss), beginning and mid seed-fill, respectively, may be the most susceptible stages to 100% defoliation (leaf picking). An examination of yield components

revealed that seed number continued to decrease even when defoliation was delayed until R5 or R5.5, whereas seed size declined through R6 defoliation, inclusively. The determinate variety characteristically showed a greater reduction, particularly in seed number. This study indicated that the one-half stages may not be adequately represented by extrapolating between R5 and R6. In fact, differences of only 1 week, in this study, in the time that the defoliation was imposed, could significantly alter the results.

Thomas et al. (1978) found no detectable yield loss with 40% defoliation (leaflet-picking) imposed at R3 (early pod-set) or 19% defoliation (leaflet picking) imposed at R4 (late pod set). Sequential defoliations of 40% at R3 and 19% at R4 also did not reduce yield significantly. However, when these levels were combined with low level defoliations (12%, during the bean-fill or R5-to-R6 stages) the combination resulted in significant yield reductions (largely a reduction in pods/plant). Multiple regression techniques were used to relate various combinations of defoliation (leaflet picking during the reproductive stages) and depodding in an earlier study (Thomas et al., 1974). This yield loss information then was combined with species-specific consumption data to generate economic injury-levels for 7 insect species at 5 stages of soybean reproductive development.

Begum and Eden (1965) also reported that the podding to early-bean growth stages were more susceptible to low levels of defoliation (approximately 33%) than either the blooming or full-grown bean stages. Quality (U.S. Grade) was not affected by 100% defoliation at any tested developmental stage. Enyi (1975) concurred by reporting that the most significant

yield reductions (averaging 86.4%) following complete defoliation (scissors) occurred during the podding stages. Early podding defoliation seemed slightly more stressful than late podding defoliation. Both pod number (largest effect at 8 weeks after planting) and bean size (largest effect at 12 weeks after planting) were adversely affected. In contrast, defoliation at R7 (beans fully developed, pods yellowing, 50% of leaves yellow) rarely resulted in a significant yield loss (Fehr et al., 1977; Thomas et al., 1978). Stage R7 (by definition) is physiological maturity, and, therefore, the yield should no longer be dependent on amount or duration of the foliage. In general, the plant parts that are most actively growing (physiological sinks) are the fractions most susceptible to defoliation-induced stress (source reduction).

Selected Studies Describing the Effects of Annual Weed Competition on Soybean Development

Many reviews have described weeds as undesirable flora or simply, "plants out of place" (e.g., Klingman and Ashton, 1975; Zandstra and Motooka, 1978). Pareja (1976) credits Staniforth (1961) with originating a more useful agronomic definition. He reportedly concluded, "plant species may be considered weeds when their exclusion from the artificially maintained habitat becomes a major problem in crop production." Rapidity of growth, efficiency and timeliness in the utilization of limited environmental resources, and a prolific or troublesome nature are characteristics which often cause man to regard a persistent uncultivated plant an important weed.

Many of the most important weeds in soybeans are species which parallel the crop in phenology of germination, growth, and maturity, or are those species which are extremely persistent. Thus, the most enduring and recurring problems are the summer annuals and creeping perennials. Pedigo et al. (1981) summarized growth characteristics and regions of primary importance of 43 of the most common and troublesome soybean weeds (31 annuals and 12 perennials). Six broad categories of adaptive characteristics were listed by these authors as contributing to the success of these weeds. These key characteristics included (1) prolific seed production, (2) effective propagule dispersal, (3) lengthly viable nature of propagules, (4) differential dormancy, (5) strict germination requirements, and, for some, (6) asexual reproduction.

Extended competition or interference between weeds and soybeans often has a deleterious effect on grain yield. Weeds may restrict yield through a reduction in productive crop plant stands (via death or barrenness). More commonly, however, are losses in the quantity or quality of seed produced by crop plants (especially from those plants in close proximity to the weed). Many studies of interspecific competition imply that the weed in question helped cause the yield-limiting stress by effectively reducing (to suboptimal levels) the amounts of light, moisture, and(or) nutrients available for use by the crop. However, the 'weed effect' reported in the majority of studies has not been partitioned into the component light, moisture, or nutrient fractions because of the unavoidable intrinsic confounding. Thus, only indirect inferences as to the identity of the overriding stress in each situation is usually possible. For these reasons, this review will examine only a few detailed studies of soybean-weed

stress, supplemented occasionally by nonweed studies of physiological stress (e.g., shading in general). Other more general reviews of crop and weed competition which should be consulted include Clements et al. (1929), Donald (1951, 1963), Pimentel (1981), and Trenbath (1976).

Weeds are unique pests in that their continued existence in a production environment is not inexplicably connected to the presence of a specific cultivated crop. Additionally, differential seed dormancy (including enforced, innate, and induced forms) helps maintain potentially damaging populations over extended weed-free intervals. This pernicious trait, in particular, serves to complicate weed management largely by enhancing longevity (Khedir and Roeth, 1981; Lueschen and Anderson, 1980). However, several studies have shown that many species have definite periods during which many of the seeds have a heightened probability of germinating. For instance, velvetleaf (*Abutilon theophrasti* Medic.), giant ragweed (*Ambrosia trifida* L.), common ragweed (*Ambrosia artemisiifolia* L.), and Pennsylvania smartweed (*Polygonum pensylvanicum* L.) showed peak germination in central Illinois from early April through May. Although the latter 3 species did not germinate after June 1, velvetleaf also had minor flushes of germination during late May through June (Stoller and Wax, 1973). Only after the seeds have germinated and vegetative growth is underway do the weeds become susceptible to the most commonly employed weed control practices. Until this time, tillage or other soil disturbances may simply encourage additional seeds to germinate. If the stimulatory tillage corresponds to the planting of the crop, developing weeds may encounter an environment where interspecific competition becomes significant (commonly resulting in various degrees of mutual suppression).

One of the most common of environmental stresses which intensifies the importance of continuing interspecific stress would be inadequate moisture. Plants normally lose water via transpiration through open stomata during the uptake of carbon dioxide for photosynthesis. The degree and importance of the water loss is largely dependent on the combined influence of the atmospheric demand, magnitude of the stomatal openings, and availability of water from the surrounding soil. As leaf water potentials in soybeans fall (indicative of developing moisture stress) several physiological functions may eventually become impaired. Among these impairments would be a reduction in cell expansion and photosynthesis (although the latter is more resistant to moderate water deficits than the former). Depending on stress phenology, a smaller bean number (through fewer nodes formed or increased pod abortion) and(or) lower bean weight may contribute to yield reductions.

It seems reasonable that an effective increase in plant density (such as occurs when weeds are not controlled) may be expected to prolong or increase moisture stress under limited moisture conditions. For instance, to produce 454 g of dry matter, a common cocklebur requires approximately 188 kg of water (Hughes, 1976). Cocklebur populations of 7400 to 16,500 plants/ha are reportedly not uncommon in Mississippi alluvial-floodplain soybean fields (McWhorter and Hartwig, 1972). Because each full-season cocklebur plant may produce 0.15 kg or more of dry matter (Davis et al., 1965), the denser infestations have the potential to deprive soybeans of more than 1 million kg of water per ha (Pedigo et al., 1981). It also seems reasonable that timely irrigations, abundant precipitation, or unnaturally high levels of available soil moisture may lessen the importance of such a weed-induced increase in demand for water.

The deleterious effects of interspecific competition between crop and weeds for moisture seems to be more obvious when a definite sequence of events unfolds. Yield reductions often are most severe when moisture supplies were adequate early in the season (planting to prereproductive stages) followed by severe midsummer deficits (during the reproductive stages; Eaton et al., 1973; Staniforth, 1958). Combined, dense weed and crop stands remove significant amounts of available moisture before moisture-sensitive reproductive development begins. The direct effect of such moisture deficits is further confounded by a slowing in soybean root expansion rates as more photosynthetic energy is partitioned into developing reproductive structures (Scott and Oliver, 1976).

The amount of photosynthetically active radiation available to and utilized by a crop often is limited by effective leaf area index, canopy density, canopy configuration and duration, and the relative interference between crop and weeds (in altering the quality and quantity of incident light). Soybeans will outgrow (vertically) many weedy dicots for the first 15 cm of growth, if establishment occurs under conditions of an equal-start situation (typical of conventionally prepared production environments; Frazee and Stoller, 1974). After this period, weed vertical growth rates often exceed soybean growth rates, eventually reversing the height differential. Pedigo et al. (1981) noted that 29 of the 43 notable soybean weeds frequently exceed the crop in average height, and, thus, have the capability for reducing realized production below potential levels of efficiency. However, side-shading should not be forgotten when light attenuation is considered a limiting factor in dry-matter production. Bush and Staniforth (1962) showed that side-shading (weeds \leq soybeans in height), if prolonged,

also can effectively reduce soybean yield. In many situations, side-shading may be a primary component of weed stress (perhaps when considering many vining weeds, in particular).

Several studies have shown that developing weed canopies may limit the light received by soybeans enough to reduce increases in crop leaf area. Eight weeks of competition with tall morningglory (1 weed/61 cm of row) effectively reduced soybean leaf area index (LAI) values by 31% when crop plants were sampled 8 weeks after emergence (Oliver et al., 1976). Morningglory-stressed soybeans possessed only 58% of the LAI of nonstressed control plants at full-bloom. Increasing full-season morningglory densities to 1 weed/15 cm of row resulted in soybean LAI reductions of 60%. Hagood et al. (1980) reported that soybeans competing with 10 velvetleaf/ m^2 of soil surface displayed an LAI of 3.5 to 3.9 by 11 or 12 weeks after emergence. In contrast, weed-free soybeans possessed an LAI of 6.3 to 6.6 after the same interval had passed.

Weed competition also can limit soybean dry matter production. Hagood et al. (1980) reported leaf, stem, root, and reproductive component reductions when soybeans from weedy (velvetleaf) plots were compared with weed-free soybeans. Higher weed densities resulted in an earlier detection of significant differences and a greater magnitude of difference. Crop leaf-weight seemed the most responsive, followed by stem-weight, and finally, root-weight reductions. Oliver (1979) reported similar results and noted that significant reductions in crop growth rates (g/m^2 soil surface/day) were definable. Staniforth and Weber (1956) noted that the above-ground dry matter production of weed-free soybeans commonly equalled the combined

dry matter production of weeds and soybeans when interspecific competition continued until harvest. In addition to reducing dry weights of the structural components, Wahau and Miller (1978) reported that shading (in general) can reduce total nodule N_2 -fixing capabilities.

Definitive field studies showing that weeds have created severe nutrient deficits, which subsequently altered crop growth, have not been widely published. Analyses of plant nutrient content have shown that wide differences exist between species. For instance, barnyardgrass, common lambsquarters, and pigweeds contain significant concentrations of magnesium, potassium, calcium, and phosphorus (Vengris et al., 1953). Thus, dense populations of these weeds may remove substantial quantities of these elements (but proof that suboptimal levels remained for producing an acceptable crop was not confirmed). It would seem that the long-term application of artificial fertilizers (at least on many well-managed farms) would have decreased the likelihood of severe and direct crop/weed competition solely for nutrients. However, it may be possible that excessive nitrogen fertilization of soybeans may enhance weed competition (relative to situations where no supplemental nitrogen was supplied; Staniforth, 1962). This result might occur because well-nodulated soybeans (as a rule) probably would not respond to the same degree (vegetatively) as the nonnodulated, nitrogen-deficient weeds).

Patterson and Flint (1980) speculated that the competitiveness of a species eventually may become dependent upon the type of photosynthetic pathway (e.g., C_3 - Calvin-Benson pathway or C_4 - dicarboxylic acid pathway). These authors conducted a growth analysis study (component biomass

evaluations through time), in which environmental CO₂ concentrations were increased. Patterson and Flint concluded that C₃ species (e.g., soybeans and velvetleaf) showed a greater response in net assimilation rate (rate of dry matter production per unit leaf area) than C₄ species (corn and itchgrass). Thus, the gradual increase in global atmospheric CO₂ concentrations (caused by the accelerated use of fossil fuels) may eventually alter relative dry weight assimilation rates. If true, current competitive relationships between C₃ and C₄ species may be altered in the future because of heightened environmental demands of C₃ types for light, water, and nutrients.

Selected Studies Describing the Effects of Annual Weed Competition on Soybean Yield

The level of competition or interference provided by a weedy species is largely a function of many interacting components including density, distribution, form, and relative developmental rates (to name only a few of the more important criteria). This review will be most concerned with the effects of density and duration in enhancing interspecific competition between weeds and soybeans.

Dense, uncontrolled weed stands may effectively reduce soybean plant populations by causing early death (an absolute reduction) or enhancing barrenness (a relative reduction in crop stand). Unfortunately, the stand losses often peak after the nearby crop plants have already passed through the developmental stages during which significant degrees of compensation might have been possible. Thus, these reproductively-deficient soybeans have become 'weeds' (in the economic sense) because their contribution

to harvestable yield is either entirely absent or extremely limited. Additionally, these lost soybeans undoubtedly modified the local resource-pool by requisitioning resources which would have otherwise remained available for use by adjacent productive soybean plants. For instance, densities of 100,000 common cocklebur plants/ha reduced soybean stands from 15 to 18 plants/m down to approximately 6 plants/m after ≥ 12 weeks of competition (Barrentine, 1974). Similarly, other studies have reported crop stand reductions when weeds are not adequately controlled (Burnside, 1978). In addition to physiological stand reductions, some studies have reported an increase in the prevalence of early lodging which results in heightened harvest losses.

At least 2 contrasting types of damage/loss thresholds have been developed for improving weed management. The need for corrective action under each concept is based on relative emergence times of crops and weeds and the potential for development of significant competitive stress. These thresholds have been designated the critical duration for weed competition and the critical weed-free requirement (Buchanan, 1977). Admittedly, these critical periods are not foolproof. It is well-known that the time required for significant stress development may vary, depending on the relative weed and crop densities, various environmental conditions, and several other factors potentially influencing competition. However, representative critical periods have been established for many weed and crop combinations (Pimentel, 1981). It should be noted that (for the most part) these thresholds are most applicable to a vigorous, well-managed crop under normal growing conditions. Growers should realize, however, that both the critical duration for weed competition and the

critical weed-free requirements were developed to provide information on physiological yield losses and do not consider the harvest interference aspects of noncompetitive infestations.

The critical duration of competition is defined as the period of time after which a soybean crop can no longer tolerate a continued drain of requisites by weeds which emerged with the crop. Significant losses in grain yield will result if the current weed infestation remains after this period of time. Critical duration of weed competition intervals has been established for at least 13 troublesome soybean weeds (Pedigo et al., 1981). Significant losses were noted in equal-start situations by 4 to 12 weeks after emergence. Seemingly, competitive stresses continuing through the soybean reproductive stages have the greatest potential for inducing yield losses. Many weeds have exceeded the soybean canopy in height by this time. The light-attenuation stress may be further confounded by potential increases in internal crop water deficits, because root development slows once reproductive development begins. As might be expected, early stress reduces bean number (through reductions in nodes and pod numbers), whereas a continuation of stresses may limit final seed size. Crop managers employing this type of threshold should realize that the longer controls are delayed, the lower the chances of obtaining acceptable suppression.

The critical weed-free requirement has been defined as the period of time that weeds must be suppressed (after emergence of the crop) for the crop to have a permanent competitive advantage. Knowledge of this relationship can prevent 'luxurious control expenditures'. Such a relationship essentially separates economic losses from less important and largely

cosmetic infestations. In essence, further competitive losses from newly germinating weeds will be inconsequential. Critical weed-free requirement intervals have been established for several weeds. Pedigo et al. (1981) compiled a listing of many of these studies and should be consulted for species-specific information. In soybeans, preventing weed establishment for 4 to 6 weeks after emergence will usually prevent the development of significant interspecific competition favoring the weed. Essentially, the dense, developing soybean canopy prevents successful establishment and (or) normal development of newly emerging weed seedlings. Crop management activities that help insure the development of a highly competitive crop (e.g., the use of high vigor seed, narrow row arrangements, and timely cultivations or herbicidal treatments) will shorten the interval during which costly artificial controls are required.

Post-emergence weed management is largely concerned with ascertaining the importance of residual weed populations. If previous control efforts (especially preplant-incorporated and preemergence herbicides and (or) early cultivations) were successfully employed, the residual populations may cause interspecific stress of questionable importance. Thus, damage/loss relationships based on experiments which combine various competitive intensities and durations become invaluable in defining the seriousness of the situation. Regression analyses of extensive weed-density (Thurlow and Buchanan, 1972) and (or) weed dry-matter (Staniforth et al., 1965) on grain yield frequently confirm strong inverse relationships. If adequately validated, tables which combine critical duration periods with economic thresholds may prove valuable in predicting potential yield

losses (thereby defining relevance of control alternatives). Barrentine and Oliver (1977) have published such a table for common cocklebur. Yield loss is cross-referenced as a function of cocklebur density and duration in their approach. Before a binding recommendation is accepted, the experimental environmental conditions should be critically compared with conditions prevailing in the management situation. Even if strong similarities are noted, future environmental conditions may invalidate the basis for decision by upsetting the weed-to-crop competitive relationship.

Many of the quantitative data on weed-induced soybean yield losses were recently summarized (Pedigo et al., 1981). This review will be restricted to a few of the studies which have examined soybean yield losses from velvetleaf competition.

Several studies have been concerned with documenting the yield-limiting effects of velvetleaf competition. Pareja (1976) reported that full-season competition by velvetleaf spaced at 360 cm, 270 cm, 180 cm, 90 cm, and 30 cm intervals could cause 2.7, 6.6, 14.5, 18.3, and 44.0% soybean grain yield reductions. Oliver (1979) reported that soybean yield was depressed 13 to 27% by 61 and 30 cm spaced full-season velvetleaf. Staniforth (1965) determined that yields were depressed 31% when 3 velvetleaf/30 cm of row remained for the entire growing season. Hagood et al. (1980) also confirmed that increasing velvetleaf densities would cause greater soybean yield losses. Full-season densities of only 2.5 velvetleaf/m² of soil surface (randomly located weeds) caused significant yield reductions (26%). Eaton et al. (1976) reported that dense stands of velvetleaf (130 to 204 plants/m²) reduced soybean yield an average of 23%. Very

dense stands (such as employed by Eaton et al., 1976) induce yield losses that are not proportional to weed density. Intraspecific competition between neighboring velvetleaf suppressed growth of individual weeds enough to effectively reduce the interspecific stress (when expressed on an individual weed basis). Pods/plant are the yield components most often reported as significantly reduced (Hagood et al., 1980; Eaton et al., 1976). Less loss was observed for equivalent velvetleaf densities if soil moisture was abundant during the reproductive stages. Delaying the planting of soybeans also effectively reduced the competitiveness of velvetleaf (Oliver, 1979). Seemingly, this weed is strongly photo-induced (begins reproductive development) somewhat early in the season, which severely limits continued high rates of late season vegetative development (because of carbohydrate supply reallocations).

If velvetleaf establishment is prevented for approximately 3 weeks after soybean emergence, significant yield reductions are uncommon (Eaton et al., 1976; Hagood et al., 1980). However, Eaton et al. (1976) reported that maximal yield could not be assured if suppression was only maintained for 10 days.

Selected Studies Evaluating Insect and Weed

Interactions on Host Plant Development and Yield

Very little published information is available that defines the deleterious effects of combinations of weed competition and insect defoliation on plant growth and yield. Several studies have reported the effects of vertebrate grazing (cattle) on community composition (e.g., see Johnson, 1956), but no invertebrate grazing information directly concerned with

weed and field crop competitive relationships was located. The paucity of information in this regard is reflected by the complete lack of treatment in a publication entitled "The ecological role of weeds in insect pest management systems. A review illustrated by bean (*Phaseolus vulgaris*) cropping systems" (Altieri et al., 1977). This review covered such topics as (1) effects of weeds on beneficial insects, (2) weeds as physical barriers to insects, (3) weed effects in modifying crop microclimate suitability for insects, and (4) alteration of colonization conditions. Another weed and insect interaction review also recently summarized beneficial aspects of weeds in insect pest management (Zandstra and Motooka, 1978). As noted for the preceding citation, no space was devoted to weed and insect stress combinations.

One grazing study that did involve insects is of particular interest. Bentley and Whittaker (1979) reported on altered competitive relationships between 2 closely-related pasture weeds when 1 was preferentially defoliated by a chrysomelid beetle. The weed which usually became dominant (competitively and numerically) under insect-free conditions often lost its competitive advantage when subjected to heavy defoliation by the beetle. Thus, circumstances do exist in unmanaged environments whereby interspecific competition between plant species can be altered by the effects of insect feeding.

PART I. PRE-HARVEST MORPHOLOGICAL CHARACTERISTICS
OF SOYBEANS STRESSED BY SIMULATED GREEN CLOVERWORM
DEFOLIATION AND VELVETLEAF COMPETITION

ABSTRACT

The separate and combined effects of velvetleaf competition and simulated green cloverworm defoliation on soybean morphological development were evaluated in a 3-year field study. Statistical confirmation of velvetleaf competition stress was limited to soybeans in weed-proximate positions. Pre-harvest, weed-induced reductions in nodes with unrolled and fully-developed leaves (1981 only) and transient effects on leaf area development were determined statistically significant. In comparison, the SGCW defoliation procedure reduced soybean leaf area, height, pre-harvest lodging, and lower-leaf abscission (1 of 2 years). Nodal development lagged slightly in 1980 defoliated plots. No treatment altered soybean stand counts, branching, reproductive phenology, or gravimetric soil moisture determinations significantly. Although limited evidence of apparent weed-altered SGCW effects was noted, actual statistical confirmation of velvetleaf x SGCW treatment interactions was not realized in this study.

INTRODUCTION

Soybeans are subjected to significant biological stresses from a vast diversity of pest types. Pedigo et al. (1981), in reviewing approximately 400 published sources, concluded that the reported soybean pest complex in the United States was composed of at least 39 insects, 43 weeds, 31 infectious diseases, and 17 nematodes of varying economic importance. One important observation noted in this and other recent reviews and policy statements (Allen and Bath, 1980; Barfield and Jones, 1979; Chiarappi et al., 1972; Edens and Koenig, 1980) is that published pest-stress studies have often emphasized discipline-oriented research to the exclusion of interdisciplinary efforts.

Without structured interdisciplinary research involving pest combinations, the implementation of usable and truly integrated pest management (IPM) guidelines may be limited to educated 'guesstimates' at best. If the joint influence of the multiple pests involved is interactive or synergistic, rather than simply additive, then the failure potential of such unsupported recommendations is increased. In addition, the subsequent failure of recommendations made on this basis may result in the added disadvantage of enhancing grower suspicion of IPM recommendations in general, and effectively forestall the adoption of accurate interdisciplinary recommendations.

Another shortcoming noted in many pest-induced crop-stress studies is the limited quantification of plant response to evolving stresses during the growing season. With a few notable exceptions (e.g., Hagood et al., 1980; Oliver, 1979; Oliver et al., 1976), pest treatments traditionally

have been applied to a crop and effects have been assessed only on yield. Yield at harvest maturity, although important from an economic sense, incorporates all anomalies of the season into a few discrete values. Thus, treatments which vary in effect or phenology may have important differences masked at harvest (because of yield component compensation), leading to the erroneous conclusion that crop development was not significantly altered (Evans, 1972). In essence, invaluable managerial information on plant morphological plasticity, compensatory growth (or the lack thereof), and phenological variation in crop susceptibility to stresses is often overlooked when plant sampling is restricted to yield only or a few token growing-season evaluations.

A cooperative study involving entomology and weed science was conducted from 1979 through 1981 near Ames, Iowa, to provide some factual information on the effects of pest combinations on soybeans. Velvetleaf (*Abutilon theophrasti* (Medic.)), a common broadleaved annual weed, and the green cloverworm (GCW, *Plathypena scabra* (F.)), a middle- to late-season insect pest, were chosen as a representative competitor and defoliator of soybeans, respectively. Both pests have widespread distribution (Pedigo et al., 1981), and their joint occurrence in many soybean fields makes a study of these pest combinations especially relevant to crop management.

The current discussion (Part I) is limited largely to a quantitative analysis of soybean pre-harvest morphological development as influenced by varying degrees of velvetleaf competition, simulated green cloverworm (SGCW) defoliation, and combinations of these stresses. The separate and combined effects of these stresses on rate of soybean dry matter accumulation are presented in a companion study (Part II).

METHODS AND MATERIALS

These studies were conducted from 1979 through 1981 near Ames, Iowa. The primary soil type was a Nicollet-Webster complex in 1979 and alachlor was applied preemergence at 2.25 kg/ha to control the grass-weed complex. In 1980 and 1981, the studies were conducted on a Coland clay loam treated with preplant-incorporated alachlor at 2.25 kg/ha. Hand hoeing was employed, as needed, to control undesirable weeds.

A split-plot design with 4 replications was used in each year. Soybeans (*Glycine max* (L.) Merr., variety 'Amsoy 71') were mechanically planted in east-west rows on 16 May 1979, 22 May 1980, and 20 May 1981. The 7 main-plot treatments (1 main plot = 19-m long by 20 - (1979 and 1980) or 25 - (1981) rows wide, with a 76-cm interrow spacing) consisted of a factorial arrangement of 2 velvetleaf densities persisting for 3 competition duration intervals, as well as a weed-free control. Weed densities of 1 and 2 velvetleaf/3.0 m of row (or 4386 and 8772 weeds/ha) were established by manually space-planting weed seed within 16 h of soybean seeding, using a cord template. Weed seeds were placed on the south side and approximately 8 to 10 cm from the crop row to simulate a residual weed population surviving cultivation and possessing high competitive potential. Velvetleaf in adjacent soybean rows were offset to insure uniformity of competition. Crop and weeds emerged simultaneously on 24 May 1979, 30 May 1980, and 23 May 1981. Two days after emergence, soybeans were hand-thinned to 9 plants/30 cm of row to establish uniform populations in all plots. Weeds (2450 to 3000 locations) were thinned to desired densities (one per location) within 2 weeks of velvetleaf emergence. Realistic

duration of competition intervals of 0, 4, 5.5 or 6.5, and 12 to 14 weeks (full-season competition) post-emergence were achieved through no weeds, weed removal with bentazon (1.13 kg/ha), manual removal (roguing), and nonremoval, respectively.

Incremental densities of GCW larvae, feeding on soybeans from small larvae through cohort pupation, were manually simulated in each main plot to create subplot treatments (1 subplot = 3 m long by 3 rows wide; adjacent subplots were separated by 2 weed-free border rows). Throughout the study, the following SGCW-subplot levels were used: 1979 — 0, 15, 30, and 45 SGCW/30 cm of soybean row; 1980 — 0, 18, 36, and 54 SGCW/30 cm of soybean row; and 1981 — 0, 12, 24, 36, and 48 SGCW/30 cm of soybean row. These levels were chosen to represent the full range of reported GCW densities. Although the punch simulation employing cork borers (described below) was restricted because of labor and time constraints to a 3.0-m section of the center subplot row, more than 2.3×10^6 holes (2.85 cm² each) were required to accomplish this study.

Besides sham-defoliating (via a nail-studded flail) and weed-stressing subplot border regions, several other measures were initiated within the punched row solely to maintain the integrity of the primary simulation treatments. *Bacillus thuringiensis* (an entomopathogen) was applied to all plots, as needed, to control natural GCW populations. The normal phenology of outbreak GCW populations in Iowa (Pedigo, 1974) required that the SGCW defoliations be initiated when soybeans were in full bloom (15 July 1979, 14 July 1980, and 13 July 1981). Individual defoliators were assigned different plots each day to minimize systematic errors. Previous

studies (Poston et al., 1976) revealed that simulations which bisected the soybean midrib altered net photosynthesis in a manner not equivalent to natural GCW feeding. A companion study (Hammond and Pedigo, 1981) indicated that the water lost through foliage remaining after actual GCW defoliation was more closely simulated by hole-punching than commonly-employed trifoliolate-excision methods. Natural GCW defoliation is also concentrated in the upper canopy stratum (nodes 6 through 12 at R2 were defoliated in this study) because of larval feeding preferences (Poston and Pedigo, 1976). In addition, intensity of actual GCW defoliation increases in response to larval size and nutritional demands, particularly during the final days of the larval stage. Therefore, a nonmidrib, hole-punching technique was employed to artificially defoliate soybeans at a realistic rate, determined by a temperature-dependent GCW defoliation-developmental model (procedures detailed in Table 1). Defoliation terminated approximately 12 days later when cumulative degree days predicted cohort pupation. Soybeans in insect-free (control) plots also were handled to prevent treatment confounding through undesired thigmomorphogenesis (Jaffe and Biro, 1979), even though Thomas et al. (1978) indicated that this activity may be unnecessary. In 1981, a cone penetrometer (Nelson et al., 1975) was used to determine if soil compaction, as indicated by penetration resistance, was altered by differential defoliator traffic.

Soybean growth and development parameters were determined weekly, beginning approximately 2 weeks (3 weeks in 1979) after soybean emergence. Data on plant height, vegetative and reproductive growth stages (after Fehr and Caviness, 1977), and branches were nondestructively determined

Table 1. Procedures followed to determine daily SGCW defoliation on soybeans (adapted from Hammond and Pedigo, 1982; Hammond et al., 1979a, 1979b)

-
1. Simulated insect defoliation actually begins at 335 GCW degree days (DD), when soybeans reach full bloom (feeding negligible before this time).
 2. Previous day's maximum and minimum temperatures ($^{\circ}\text{F}$) are used to calculate DD_n to be used in the current day's defoliation. Cardinal limits of 85°F and 52°F are observed.

$$\text{DD}_n = ((\max ^{\circ}\text{F} - \min ^{\circ}\text{F}) \times 0.5) - 52 ^{\circ}\text{F}.$$
 3. Daily DD are summed to obtain cumulative DD (CDD) since cohort egg hatch.
 4. Predicted cumulative defoliation per larva (CDL) to date in cm^2 on field-grown soybeans is calculated.

$$\text{CDL}_n = 35.33 - 0.25334(\text{CDD}_n) + 0.00045(\text{CDD}_n)^2.$$
 5. Defoliation predicted for the day per larva (PDL_n) is calculated by subtraction.

$$\text{PDL}_n = \text{CDL}_n - \text{CDL}_{n-1}.$$
 6. Necessary simulated defoliation for the day on a plot (SDP) basis is calculated.

$$\text{SDP}_n = \text{PDL}_n \times \text{larval density simulated per plot}.$$
 7. Punches per plot for the day are determined.

$$\text{Punch number}_n = \text{SDP}_n / (\text{area in cm}^2 / \text{punch}).$$
 Punches are imposed with a cork borer and a rubber stopper or wooden block.
 8. Day $n+1$. Return to Step 2 and repeat Steps 2-3. Defoliation terminates when 630 CDD are realized (simulated cohort pupation).
-

for all (28 in 1979 and 1980, and 35 in 1981) treatment combinations from a minimum of 3 replications. A portable, automatically integrating planimeter (LiCor[®], Model 3000) provided nondestructive estimates of soybean-leaf area for all weed treatments, but its use was restricted to the 0 and 45 SGCW (1979) and 0 and 36 SGCW (1980 and 1981) defoliation combinations (SGCW densities/30 cm of row). Weed-proximate samples were obtained from a randomly selected soybean plant in the 5-plant group located immediately adjacent a velvetleaf after the soybeans possessing the largest and smallest basal stem diameters were deleted from consideration. Weed-distant samples were obtained in a similar manner from the 5-plant group located the maximum in-row distance away from the weed (centered 75 cm away in high weed density plots and 150 cm away in low weed density situations). This selection procedure was employed twice per plot for each weekly sample date, and the duplicate samples were averaged. Plants sampled in control plots were chosen in a similar manner, with one location arbitrarily defined as weed-proximate. These restrictions on randomization served as checks on the validity of weed proximity tests (viz., significant proximity effects in the weed-free control plot indicated that random sampling variation may be responsible for any observed differential weed location effects) and uniformity of SGCW defoliation distribution (viz., a significant SGCW x proximity interaction in soybean leaf area measurements may indicate non-uniformity in artificial defoliation).

Occurrence and magnitude of lower-leaf abscission were monitored in 1980 and 1981. Pre-harvest lodging was evaluated in all plots during weeks 9 and 12 in 1980. Plant stands were determined on 3 dates (thinning at emergence, immediately before SGCW defoliation, and harvest maturity) in

each year. Soil moisture percentages were determined gravimetrically 4 to 6 times each year from plots of contrasting stresses. Weather records were obtained from a nearby N.O.A.A. station.

Standard analyses of variance and orthogonal contrasts were employed to determine the significant velvetleaf density, velvetleaf duration, SGCW and interaction effects of these stresses on soybean morphology and development with respect to distance from weed location. Separation of data sets according to weed proximity was deemed essential before the study began because weeds act as stress-point sources; i.e., soybeans sampled farther from the weed show less evidence of weed competition. In this experiment, analyses treating locations as split-split plots were not adequately discriminating because restrictions on orthogonal contrasts imposed at the main plot level and higher treatment averaging effectively prevented pertinent comparisons (viz., especially when the weed effect was evident only with full-season competition and only in weed-proximate locations), and, thus, valid velvetleaf treatment effects were often masked. Separating the data sets by location had the added advantage of improving the chances of statistically confirming or refuting the existence of velvetleaf x SGCW-treatment interactions (which would probably be most evident in weed-proximate locations if such interactive effects are definable at these treatment levels). Where proximity effects were definable, t-tests were conducted on control and treatment plots to insure that differential location significances were not the result of random sampling variation. Although combining data sets often resulted in the loss of significant weed effects (because of the limited distance influences of competition), SGCW

treatments that were only approaching significance ($0.05 < p < 0.09$) occasionally became significant when such pooled analyses were conducted. All such responses are noted in the text, with type of test documented.

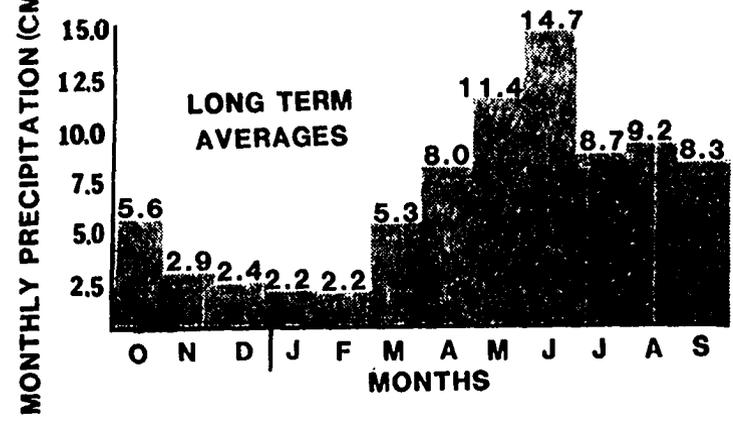
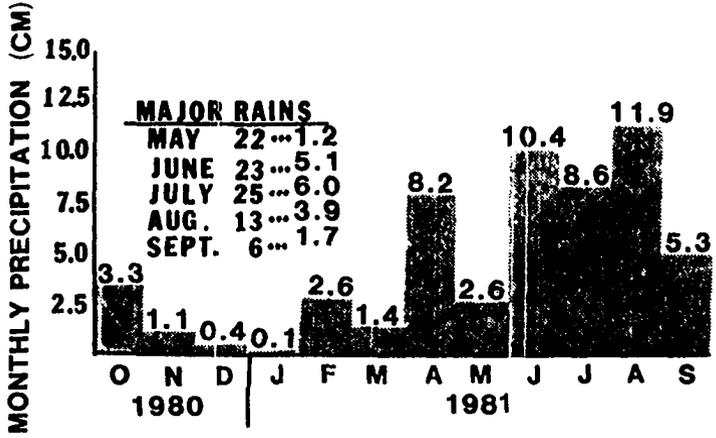
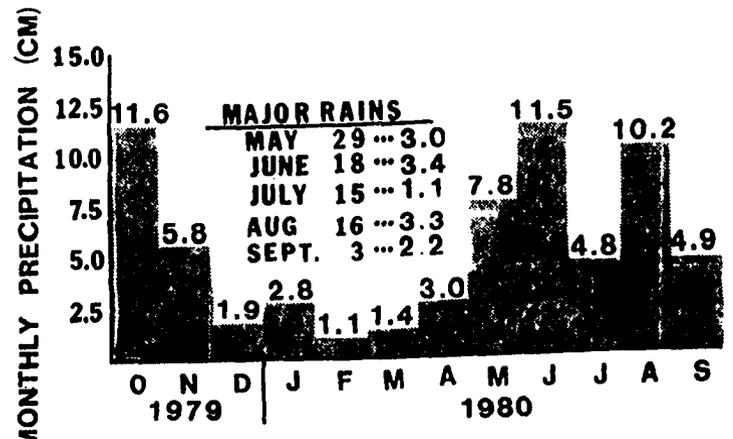
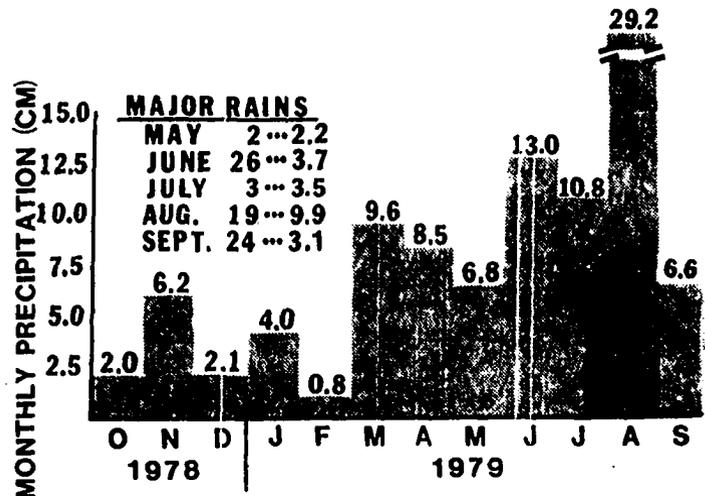
RESULTS AND DISCUSSION

Rainfall data are summarized in Figure 1. The 5-month growing season total (May through September) for 1979, 1980, and 1981, deviated +23.3 cm, -13.1 cm, and -13.5 cm from long-term averages. Precipitation for 1979 was very near normal except for a very wet August. The years 1980 and 1981 were characterized by moderate and severe May through late July precipitation deficits, respectively. In general, soil moisture trends (to 25 cm) declined as the season progressed, with varying degrees of recovery after periods of heavy precipitation. No weed density, weed duration, SGCW defoliation, or treatment interactions caused significant changes in soil moisture reserves.

Penetration resistance measurements obtained in 2.5 cm increments from the soil surface to 15 cm deep at 4 locations per plot increased slightly with depth, as expected, but no significant treatment effects were detected. This result is interpreted to mean that any soil compaction differences that might otherwise have been caused by unequal defoliation traffic were largely eliminated by our program of intentionally treading upon interrow regions of undefoliated treatments.

Values presented in the following graphs are averaged across treatments and locations (for simplicity and clarity), except where specific treatments caused significant changes in growth characteristics. In addition to these graphed treatment effects, which represent consistent patterns of significance, specific treatment differences of a short-term nature are discussed in the text.

Figure 1. Monthly and long-term precipitation falling near the velvetleaf and simulated green cloverworm study sites



Soybean Leaf Area Development and Retention

Soybeans without weed, insect, or combination stresses achieved and maintained maximum leaf-area dimensions from 9 through 11 or 12 weeks after emergence in all 3 years. Similar control plot leaf area indices (LAI) of 5.73 and 5.69 were achieved in 1979 and 1980, respectively. Far below normal precipitation from planting through late July (Week 8) in 1981 limited nontreated soybeans to 82% of comparable 1979 and 1980 leaf areas. In 1979, hail drastically reduced soybean LAI soon after the Week 12 sample was recorded (Figure 2).

Several studies (Geddes et al., 1979; Oliver, 1979; Oliver et al., 1976) have reported soybean leaf area reductions because of broadleaf weed competition, but most have dealt with higher (and perhaps less realistic) full-season weed to crop density ratios. None of the listed studies have reported weed proximity influences of velvetleaf within the soybean row. In this study, soybeans directly shaded by intercropped full-season velvetleaf consistently developed somewhat smaller leaf area in late season when compared to weed-free soybeans (although the differences were rarely statistically significant). Significant weed-induced, soybean-area reductions of brief duration (Weeks 8 and 9 of approximately 22 and 12.8%, respectively) in weed proximate locations of full-season velvetleaf plots were observed in 1979. The same combination of weed stresses caused a similar brief, but significant, reduction (14%) in soybean leaf area during Week 10 in 1980. These isolated and transient weed-treatment significances reflect the limited competitive potential of residual velvetleaf densities on soybean leaf area production. Much higher densities of

Figure 2. The development of soybean leaf area as influenced by simulated green cloverworm defoliation

Figure 2. (continued)

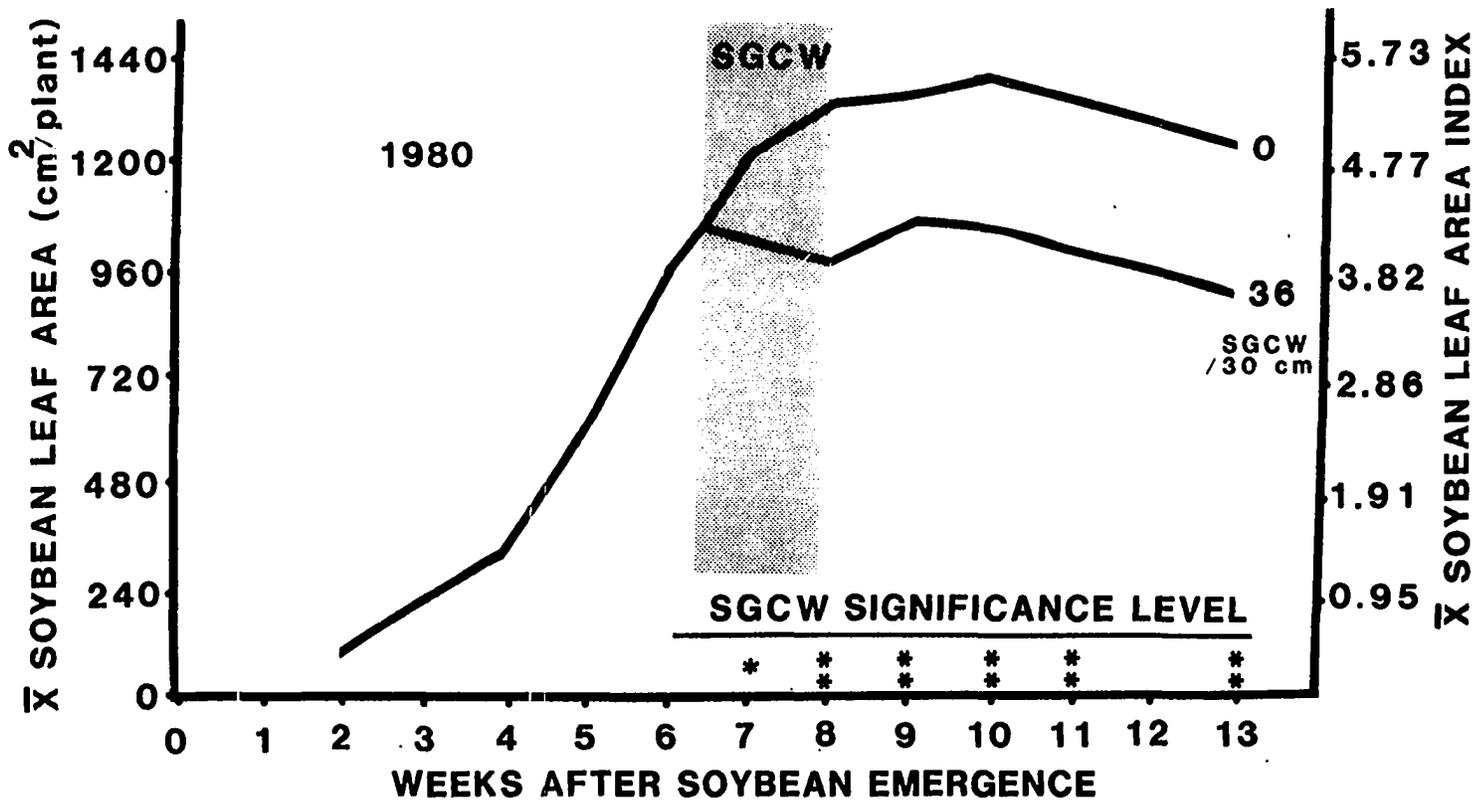
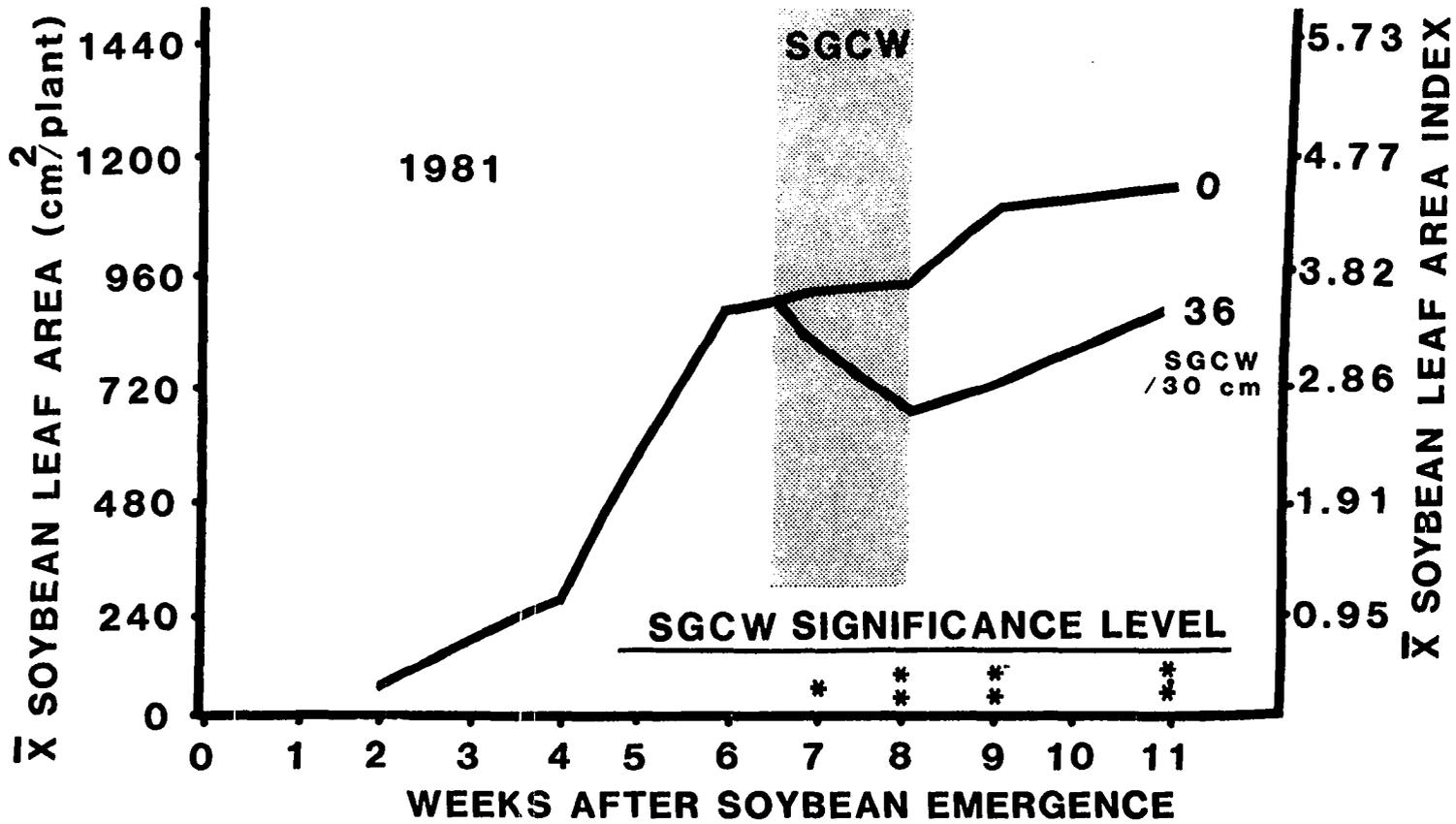


Figure 2. (continued)



velvetleaf (1 weed/30 cm of row) have been shown to reduce soybean LAI up to 23% on a plot basis by 12 weeks after emergence (Oliver, 1979).

In each year, the primary treatment influencing soybean LAI was the direct physical reduction imposed by the insect simulations (Figure 2). No SGCW x weed proximity interactions were significant during Weeks 7 and 8 (Weeks 8 and 9 in 1979), suggesting that defoliators distributed punches uniformly along the plot as instructed. The Week 8 samples (taken 4 to 5 days into the defoliation process) revealed significant differences in soybean leaf area between 0 and 45 SGCW/30 cm of row in 1979 when responses were averaged over all weed treatments. Significant defoliation-induced differences were also noted early in the simulation procedure (Week 7) in 1980 and 1981 between 0 and 36 SGCW/30 cm of row. By this time, from 443 to 480 GCW degree days had accumulated and larvae were predicted to have 68 to 79% of their total defoliation potential remaining. At pupation (630 GCW degree days), the difference in leaf area between the insect-free controls and plots with 36 SGCW/30 cm of soybean row plateaued.

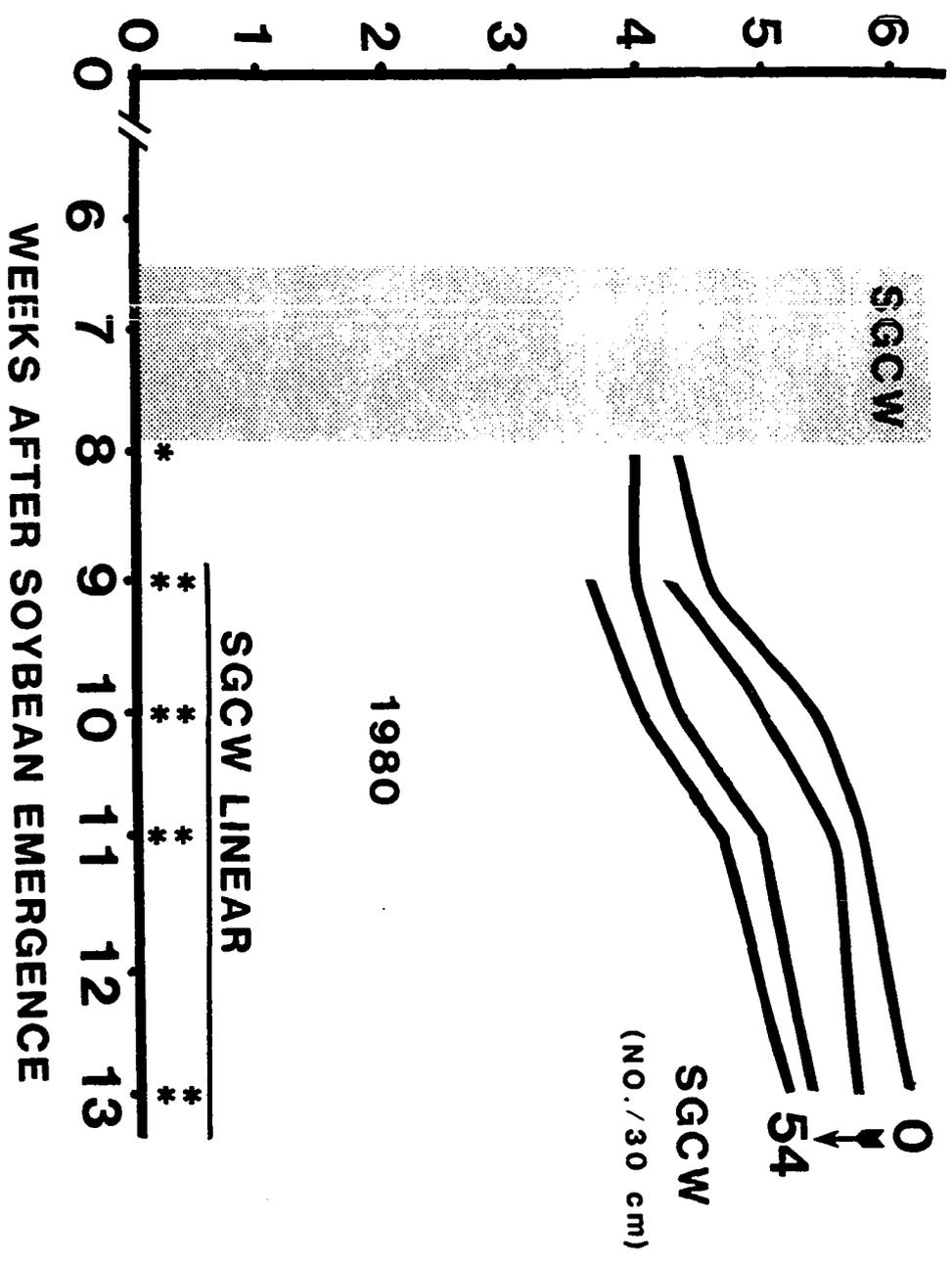
Leaf expansion is commonly cited as one of the first readily observable growth parameters to decline with increasing moisture stress (Boyer, 1970; Mitchell, 1970). The severity of the 1981 moisture shortage is reflected in leaf expansion rates that were drastically curtailed from Weeks 6 through 8 (when compared to other years). Rainfall patterns switched from an extended period of severe deficiency to above normal levels, immediately after the post-pupation measurements were completed. No offsetting compensatory growth in leaf area of defoliated plants was detected on any post-pupation date ($P > 0.05$, all tests). In fact, the only significant difference in rate of leaf area accumulation (post-pupation)

between defoliated and insect-free plots favored the undefoliated control from Week 8 through Week 9 in 1981. Seemingly, in 1981, soybeans stressed jointly by SGCW defoliation and extended periods of low soil moisture responded less rapidly to the return of favorable growth conditions than drought-stressed control plants. No weed x SGCW interactions were determined significant on any sample date.

Plant compensation to defoliation may be expressed through changes in rates of lower leaf senescence, in addition to modified expansion rates. In the absence of defoliation, the lowest leaves become shaded by the developing canopy until photosynthetic photon flux densities at this level become inadequate to support and maintain normal leaf integrity, resulting in leaf senescence (Shibles et al., 1975). However, if supplemental light is provided to these lower leaves, they may again become photosynthetically efficient (Beuerlein and Pendleton, 1971; Johnston et al., 1969). Soybean nodes missing primary trifoliolate leaves were counted weekly (beginning Weeks 8 and 6 in 1980 and 1981, respectively) to determine if increasing numbers of SGCW, feeding on the upper canopy and, thus, presumably increasing light infiltration, would alter the lower-leaf abscission rate. In 1980, a small, but significant, increase in lower-leaf retention (equals reduced abscission) was observed with 36 SGCW/30-cm of row when compared to 0 SGCW/30-cm of row (Figure 3). All 4 SGCW densities were sampled beginning Week 9. On all subsequent dates, a consistent inverse linear relationship was demonstrated between numbers of SGCW and leaf-free soybean nodes. Once linearity was established, no date x SGCW interactions tested were significant (i.e., no change in slope occurred between dates). A strong tendency for similar responses was recorded in

Figure 3. Mean number of nodes/soybean plant missing primary leaves in 1980 under selected levels of simulated green cloverworm defoliation

(SOYBEAN NODES
MISSING PRIMARY TRIFOLIOLATES)
LOWER LEAF ABSCISSION



1981, however, no significant differences were detected. It is hypothesized that the extremely dry conditions of early 1981 contributed to the greater variability in abscission rates observed in that year. Interspecific competition with velvetleaf, either alone or in combination with SGCW defoliation, did not alter the soybean abscission response, in spite of the additional shading provided by the weed. It would be expected that much denser velvetleaf infestations could cause the light attenuation necessary to influence (viz., increase) soybean lower-leaf abscission rates regardless of soybean defoliator density.

Soybean Plant Height

In 1979 and 1980, soybeans grown without velvetleaf, SGCW, or combined stresses achieved maximum heights of approximately 120 cm by 11 or 12 weeks post-emergence. In 1981, moisture stress during vegetative and early reproductive development stunted untreated plants approximately 17 cm when compared to earlier years.

A review of relevant literature sources showed that plants do not necessarily respond to defoliation and weed competition in the same manner. Defoliation has resulted in plant height responses ranging from no change to various degrees of stunting (Fehr et al., 1981; Teigen and Vorst, 1975; Weber, 1955), whereas competition may result in more variable effects on the plant height of the interaction species (Eaton et al., 1973; McWhorter and Hartwig, 1972; Rhodes and Stern, 1978). In the current study, soybeans developed a consistently shorter ground to apex height as SGCW defoliation increased (Figure 4). In contrast to leaf-area differences, these linear reductions in height were not detected until after the

1

Figure 4. The development of soybean height as influenced by simulated green cloverworm defoliation

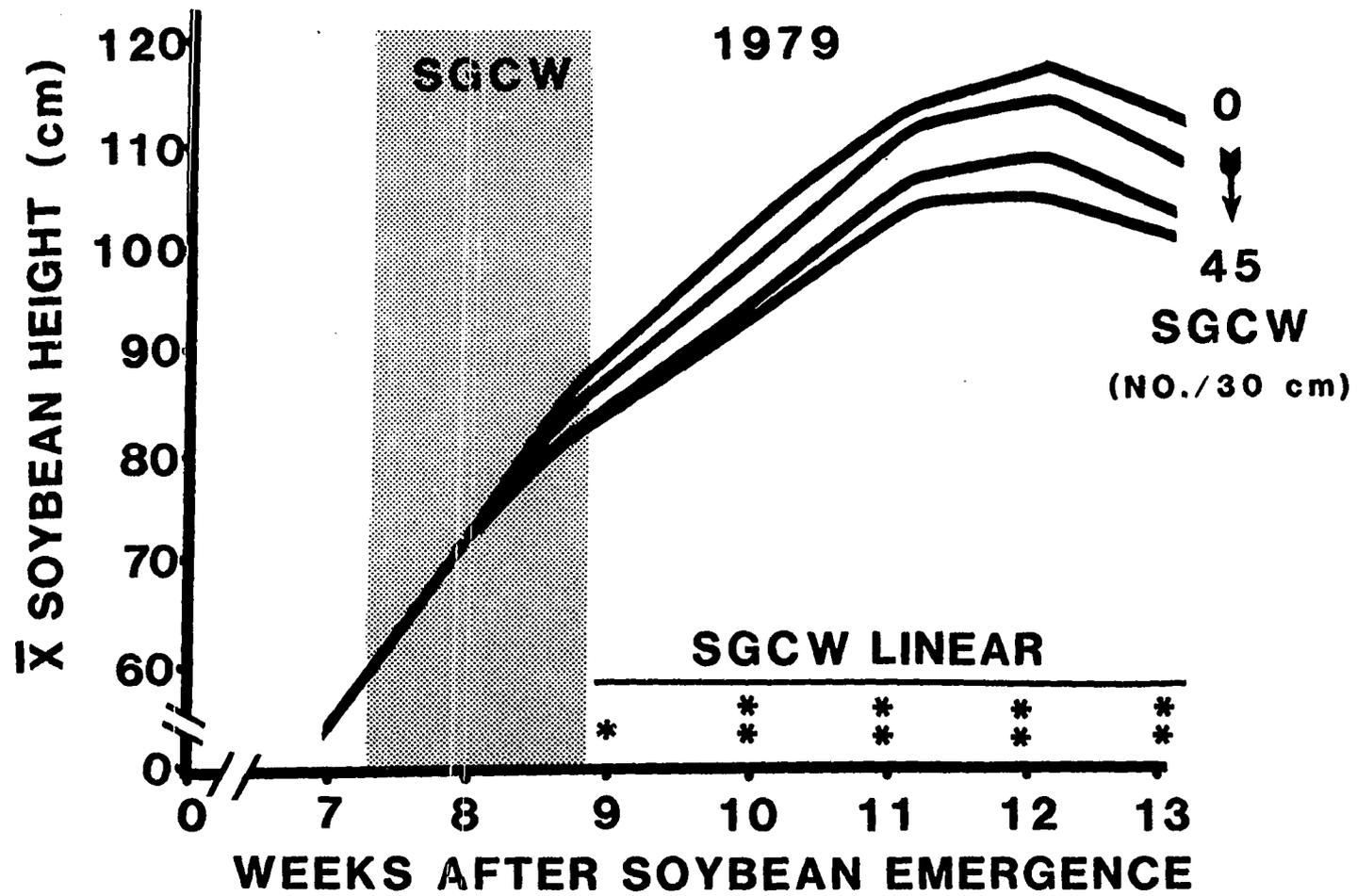


Figure 4. (continued)

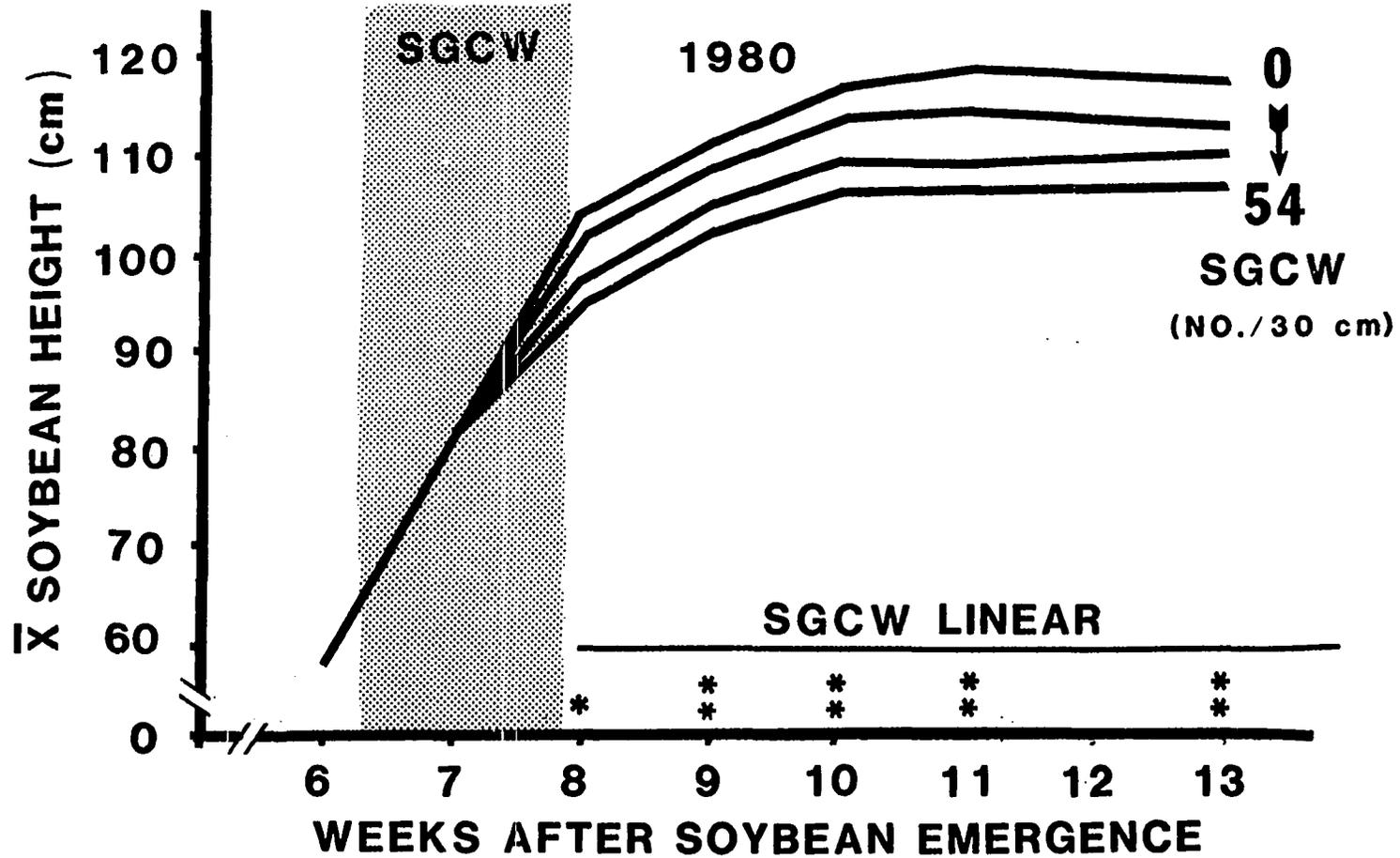
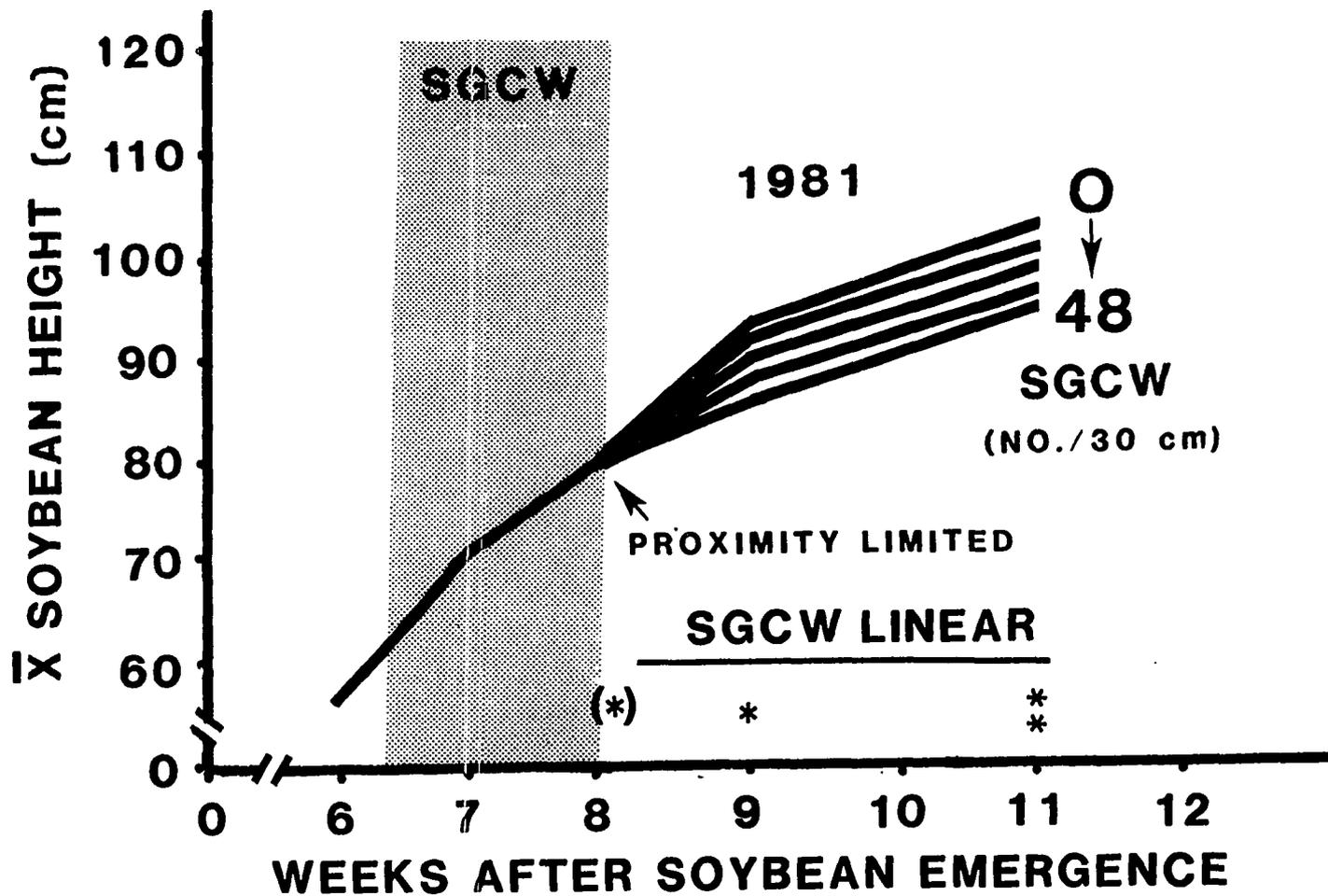


Figure 4. (continued)



defoliation schedule was completed. In 1981, velvetleaf proximity influenced soybean height indirectly by delaying the observable response to insect defoliation in weed-proximate locations. Specifically, soybeans 75 cm from the weeds exhibited significant SGCW-induced stunting by the time punching terminated, as in the previous years. In contrast, the defoliated soybeans immediately adjacent full-season weeds in 1981 did not exhibit the typical stunting until Week 9, even though no differences in leaf area reductions between locations were detectable. Except for this one transient significance, velvetleaf stresses failed to alter soybean plant height. No direct evidence of treatment interactions was detected.

Abundant precipitation, occurring immediately after 1981 simulations were concluded, may have helped offset the effects of defoliation on plant height that year. Nearly equivalent levels of defoliation resulted in 12-cm height reductions in 1979 and 1980, whereas 1981 reductions averaged only about 6 cm. Once maximum differentials in height were established by SGCW defoliation, the differences persisted virtually unaltered throughout the sampling period ($p > 0.05$, all tests). The delayed nature of the height-reduction response probably would preclude its use as a direct indicator for insect management. In the instance of the GCW, a majority of the population would have safely pupated before apparent reductions in plant height triggered the need for an insecticidal treatment. In contrast, the stunting influence of insect defoliation on soybean height could alter the phenology of late season weed management options (Part III).

Soybean Vegetative and Reproductive Development

Soybeans not receiving weed, SGCW, or combination stresses differed somewhat between years in numbers of nodes with unrolled and fully-developed leaves (as defined by Fehr and Caviness, 1977) during the 11 to 13 week sampling season. In 1979, 1980, and 1981, untreated soybeans unrolled approximately 18, 16, and 15 primary leaves during this period, respectively. Treatments did not influence leaf production in 1979 (data not shown), but significant effects were detected in the other 2 years (Figure 5). Although no treatment interactions were significant, the important main effects varied between years. In 1980, slightly fewer nodes with fully-developed leaves were recorded beginning Week 9 from subplots which had received SGCW defoliation. Defoliation beginning in the reproductive stages would be expected to alter the rate of development more than change the total number of primary leaves expanded because 3 or 4 more trifoliolate leaves are present in the terminal bud than unrolled at any given time. Probably this is why the linear response to SGCW defoliation persisted through Week 13 in 1980, but was not verifiable as nodal differences in harvest subsamples (Higgins et al., 1982).

In contrast to the 1979 and 1980 results, soybeans sampled beneath full-season velvetleaf possessed significantly fewer nodes by Week 11 than soybeans with all other treatment combinations. Similar data in 1980 showed a nonsignificant 0.5 node advantage for weed-free plots in the final 2 sampling periods. The significant 1981 node reduction also was substantiated in plants subsampled for a yield component analysis at harvest (Higgins et al., 1982). Other soybean and weed competition studies have also

Figure 5. The development of soybean nodes with fully-developed leaves as influenced by simulated green cloverworm defoliation in 1980 and velvetleaf competition in 1981

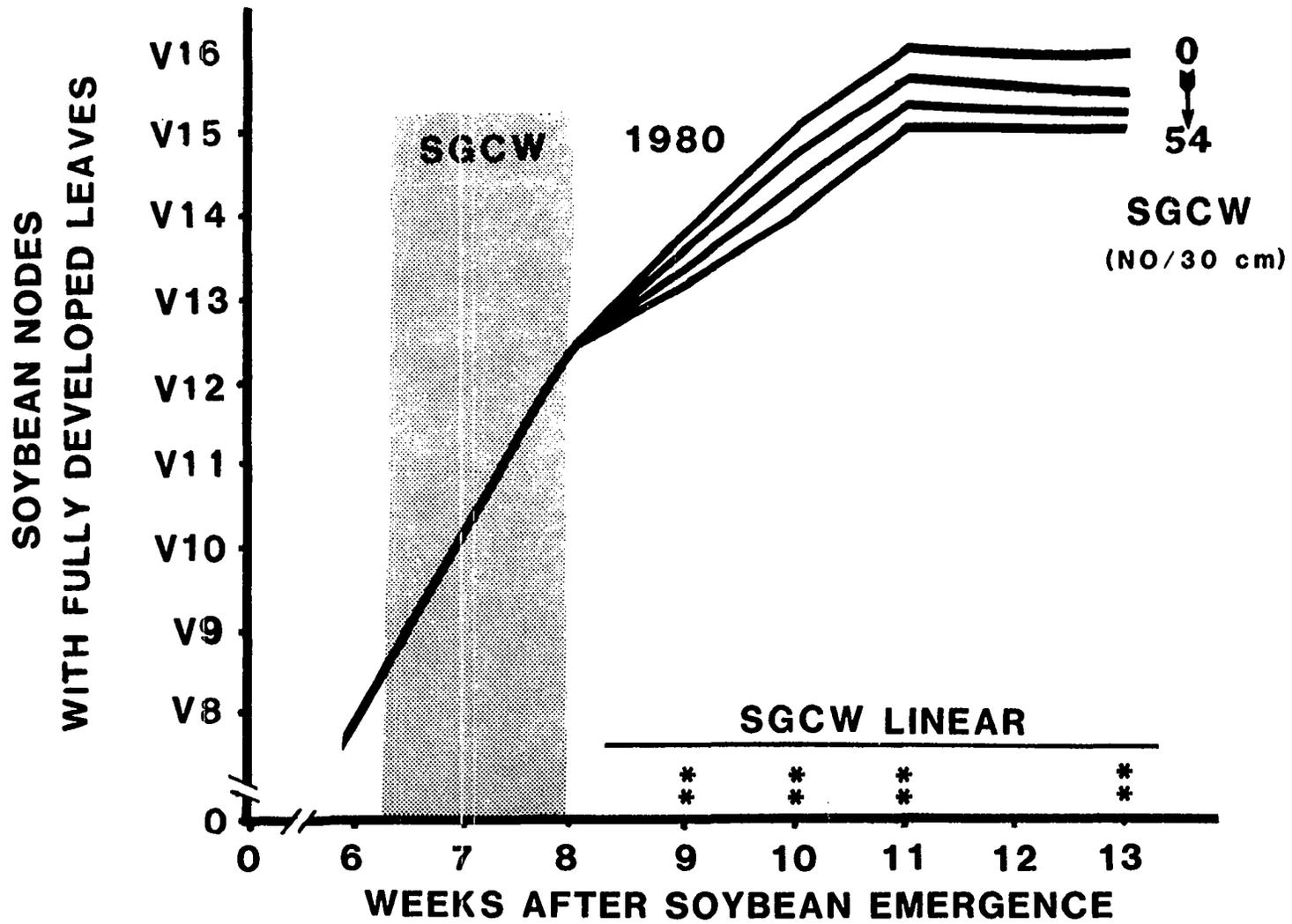
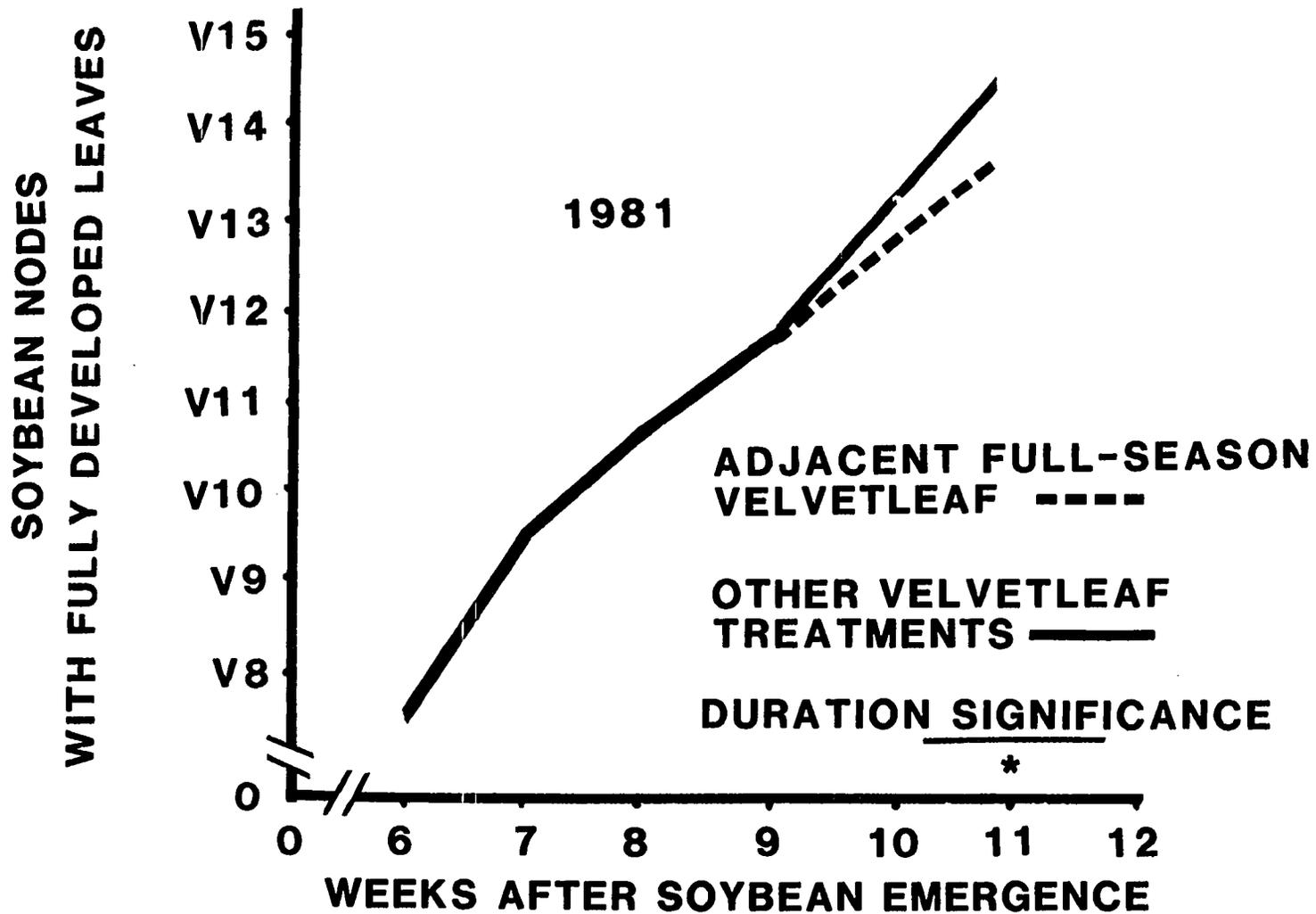


Figure 5. (continued)



reported reduced soybean nodal development with full-season weed competition (Eaton et al., 1976; Orwick and Schreiber, 1979).

Soybeans entered the full-bloom, podding, and bean-fill stages about the same calendar date each year. No significant treatment differences in rate of reproductive development were detected.

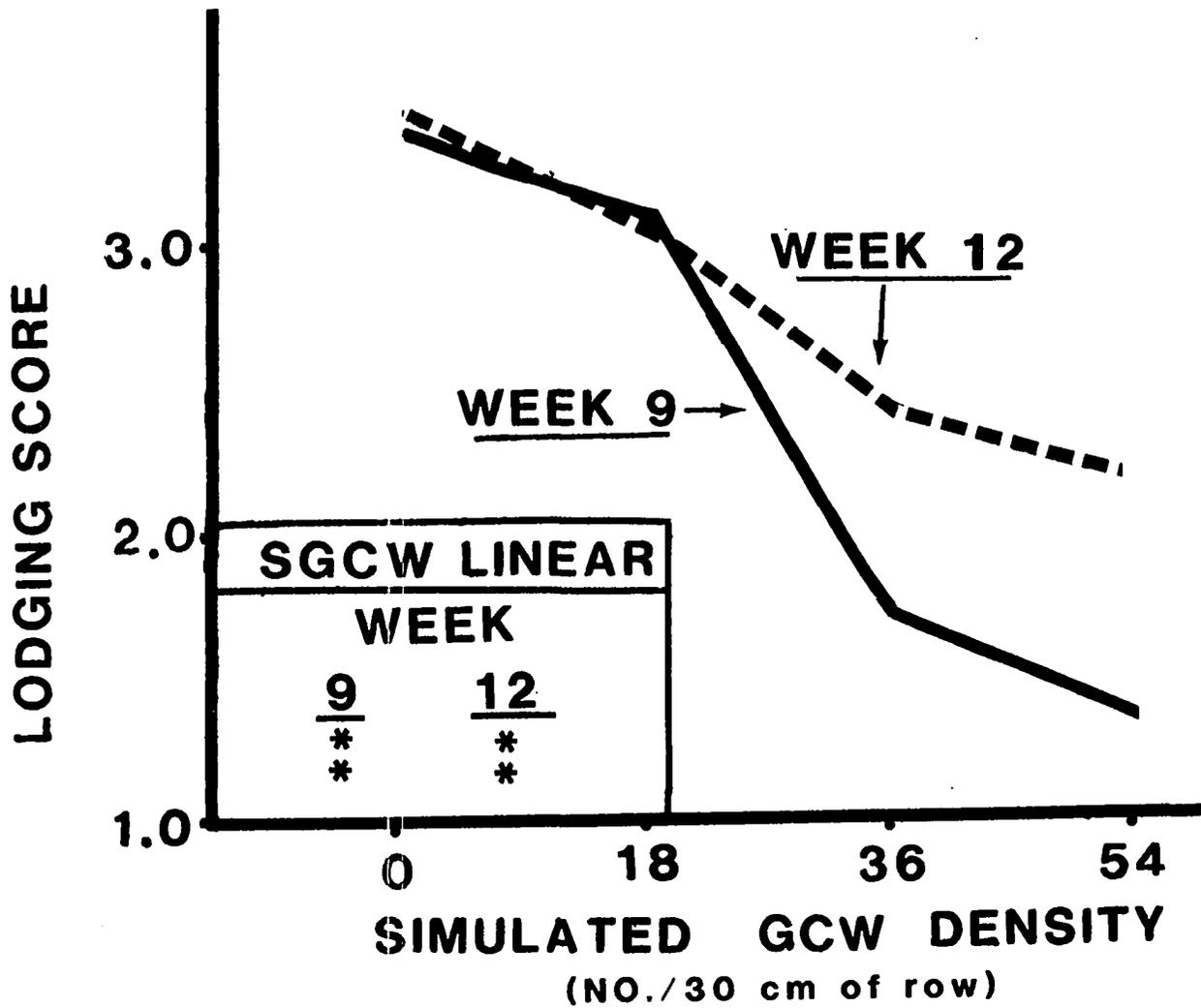
Stand Counts, Branching, and Lodging

No reductions in soybean plant stands or changes in rates of branching could be attributed to any treatment combination. Branches were only evident late in the growing season and even then were virtually nonexistent.

Lodging was quantified in all plots on 2 pre-harvest dates in 1980 when obvious treatment differences were noticed after winds had buffeted the plots (Figure 6). The most striking difference was quantified one week after defoliations were terminated (Week 9). A significant inverse linear relationship between the lodging score and SGCW density was still evident 3 weeks later. The stunted plant height and increased wind infiltration (allowed by leaf tissue removal) probably jointly contributed to decreasing or delaying the lodging susceptibility of defoliated plants. A similar phenomenon was observed in 1981, but, unfortunately, an unusually heavy, driving rainstorm lodged all plants before treatment differences were quantified. No weed density, weed duration, or interactive effects on lodging were significant in 1980.

Studies seeking to compare simple defoliation effects might be adversely affected by wind and rain enhancing differences in canopy architectures. Fortunately, the present study was concerned with understanding

Figure 6. The effects of simulated green cloverworm defoliation on soybean pre-harvest lodging scores (erect = 1, prostrate = 5) in 1980



the effects of insect, or at least insect-like, defoliation on soybeans under field conditions. Specifically, in the instance of insect damage/loss studies, reductions in crop lodging susceptibility may well be a part of the insect/loss syndrome. If so, attempts to artificially prevent such plant responses (e.g., by staking of plants) may make results less applicable for production management. If simple defoliation effects were the only interest, the differences attributed herein to the SGCW densities may well be less than expected in situations where lodging was prevented. In field situations, the SGCW-stressed soybeans exhibited greater persistence of optimal leaf displays through reduced lodging. This response should partially offset the deleterious effects of defoliation by maintaining a more efficient use of incident sunlight.

PART II. PARTIAL GROWTH ANALYSIS OF SOYBEANS
STRESSED BY SIMULATED GREEN CLOVERWORM
DEFOLIATION AND VELVETLEAF COMPETITION

ABSTRACT

Soybean dry weight (DWT) accumulation under selected combinations of velvetleaf competition and simulated green cloverworm (SGCW) defoliation was evaluated with traditional growth analysis techniques in a 2-year field study. Discernible weed-stress effects (detected 42 or more days after emergence) were restricted to soybeans developing in weed-proximate locations (viz., significant velvetleaf effects were not detected 75-cm away from in-row velvetleaf). In general, weed proximate soybeans in full-season velvetleaf plots exhibited smaller component DWTs, mean crop growth rates ($\overline{\text{CGRs}}$), and mean relative growth rates ($\overline{\text{RGRs}}$) than weed-proximate soybeans in plots where velvetleaf competition was terminated within 5.5 weeks of emergence. In contrast to velvetleaf stress, SGCW defoliation (36 SGCW/30 cm of row), did not alter reproductive DWT or growth rates within 75 days of emergence. Competition and defoliation (numerically equivalent in stressor density and duration) significantly altered more soybean DWT characteristics in 1981 than 1980. This differential response is attributed to the more unfavorable soil-moisture conditions prevailing the first 8 weeks of 1981. Statistical confirmation of velvetleaf and SGCW treatment interactions was not realized in this study.

INTRODUCTION

Physical stresses (extremes of drought, temperature, light, etc.) commonly limit field-plant growth rates below genetic potentials. Biological stresses (insects, weeds, plant diseases, and nematodes) can also restrict dry matter accumulation either directly (through consumption or other injury) or indirectly (through interspecific or intraspecific competition). However, unlike physical stresses which often are beyond the control of the grower, the effects of biological stresses often can be partially alleviated through cultural, biological, or chemical control measures. Pest management options and requirements may be clarified if the temporal development of specific effects of physiological stresses on the crop is known.

Numerous studies have employed 'growth analysis' to define physical stress effects on plant development (e.g., Blackman and Wilson, 1951; Evans, 1972; Watson, 1947). Until recently, growth analysis techniques have not been widely exploited to quantify the effects of known levels of specific biological stressors on crop growth. For the above reasons, a 2-year study of the separate and combined effects of insects (using simulated green cloverworm defoliation) and weeds (velvetleaf competition) on dry weight (DWT) accumulation in field soybeans was initiated. The effects of these stresses on specific soybean morphological characteristics over 3 years is reported in a companion study (Part I).

METHODS AND MATERIALS

Experimental conditions, phenological and morphological observations, and manner of establishing treatments are detailed in the companion study (Part I). A split-plot design was used each year. Velvetleaf competition duration formed the main-plot treatments and densities of SGCW defoliation were the subplot treatments. Velvetleaf duration (2 weeds/3.0 m of row, equivalent to 8772 weeds/ha) included 0, 4, 5.5, and 12 to 14 (full season) weeks of competition. These weed treatments were formed by preventing weed establishment, removal of intentionally seeded weeds with bentazon (1.13 kg/ha), manual removal of seeded weeds (roguing), and nonremoval of seeded weeds, respectively. SGCW defoliations (equivalent to 0 and 36 GCW/30 cm of row) were imposed with cork borers. Defoliation realistically increased in intensity as predicted by a temperature-dependent, defoliation-development model (Hammond et al., 1979a, 1979b; Hammond and Pedigo, 1982).

Accumulated dry matter was determined by destructively subsampling soybeans on 5 important dates. The 5 harvests were: Harvest 1, immediately before bentazon treatment; Harvest 2, immediately before manual weed removal by roguing; Harvest 3, immediately before or very early in the SGCW defoliation procedure; Harvest 4, immediately after SGCW defoliation terminated at pupation (approximately 8 weeks after emergence); and Harvest 5, approximately 2.5 weeks after defoliations were terminated. Six soybeans per plot (3 each from weed-proximate and weed-distant locations or former weed locations) were removed from each of 8 plots in 3 (1980) and 4 (1981) replications at each harvest. No attempt was made to recover

material excised naturally during development or removed through defoliation. Sampled plants were divided into leaf, supporting, and nonflower reproductive components and oven-dried to a constant weight. Component and total dry matter, mean crop growth rates,¹ $\overline{\text{CGR}}$ s, and mean relative growth rates,² $\overline{\text{RGR}}$ s, were statistically analyzed for treatment effects. Traditional growth analysis formulae, as presented by Radford (1967), were used to calculate growth rates on a plot-by-plot basis to facilitate the statistical analyses. Net assimilation rates were not calculated because dry matter and leaf area estimates were obtained from separate plants.

Analysis of variance was computed on each soybean growth parameter for each evaluation date and for the intervals separating adjacent harvests. Significant differences were determined by using orthogonal treatment comparisons.

$${}^1\overline{\text{CGR}} = (\text{DWT}_{n+1} - \text{DWT}_n) / (t_2 - t_1) \text{ in g/m}^2 \text{ soil surface/day.}$$

$${}^2\overline{\text{RGR}} = (\log_e(\text{DWT}_{n+1}) - \log_e(\text{DWT}_n)) / (t_2 - t_1) \text{ or 'interest rates'.$$

RESULTS AND DISCUSSION

Results are summarized in Tables 2 through 5. Caution should be employed in interpreting the abnormally low DWT values reported for Harvest 3 (1980 only). Processing errors and not treatment effects or environmental vagaries are suspected as causing aberrant values at this harvest. Errors associated with a single DWT measurement may alter contiguous growth rate determinations drastically (in opposite directions). Therefore, Tables 4 ($\overline{\text{CGR}}$) and 5 ($\overline{\text{RGR}}$) have been modified by adding a 37- to 56-day calculation (Interval 5) to eliminate the confounding effects of 1980 Harvest 3 data. Similar composite statistics are presented, for comparative purposes, in 1981.

Dry Weights of Soybean Components

Dry weight increased throughout the growing season in support (stem and petiole, SDWT) and total above-ground (TDWT) fractions of control plants (Table 2). Leaf DWT (LDWT) seemed more responsive to dry conditions and even decreased slightly during 1 droughty mid-season interval in 1981. Seemingly, significant lower-leaf abscission and very limited production of new growth served to restrict canopy development through late July in 1981 (Harvest 4) after which time precipitation was again satisfactory. Competition for photosynthate from the developing reproductive fraction may have prevented a detectable increase in LDWT between Harvests 4 and 5 in both years. Pod DWT (PDWT) was not registered until the final harvest dates.

Table 2. Mean above-ground DWT partitioned into support (SDWT), leaf (LDWT), pod (PDWT) and total (TDWT) fractions of the untreated soybean control and a summary of significant velvetleaf, SGCW, and combination treatments^a in 1980 and 1981

Harvest	Elapsed time from emergence		SDWT		LDWT		PDWT		TDWT	
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
	days		g/3 plants							
1	28	27	2.02 NS	2.25 NS	4.68 NS	4.19 NS	0	0	6.70 NS	6.44 NS
2	35	37	4.83 NS	10.05 NS	7.87 NS	11.03 NS	0	0	12.70 NS	21.08 NS
3	42 ^b	46	8.88 NS	13.13 NS	6.83 NS	10.48 NS	0	0	15.72 NS	23.60 NS
4	56	58	22.95 WP	18.26 ID	14.25 WP,(I)	12.69 IP,ID	0	1.43 WP	37.20 WP	32.38 WP,IP,ID
5	75	76	26.02 IP	26.01 WP,IP,ID	14.78 IP	11.48 WP,IP	11.97 NS	11.25 WP	52.77 IP	48.74 WP,IP,ID

^aWP = weed effect proximate to velvetleaf significant; WD = weed effect distant from velvetleaf significant; IP = SGCW effect proximate to velvetleaf significant; ID = SGCW effect distant from velvetleaf significant; () = Only when data were pooled across weed locations was the effect significant; WP X IP, WD X ID, and W X I designate significant treatment interactions; NS = no significant treatment effects.

^bValues reported for the 42-day sample (1980 only) believed artificially low because of processing errors.

Velvetleaf treatments caused no significant effects through the third harvest. After Harvest 3, deleterious effects of velvetleaf competition occasionally were detected in soybeans underlying the intermittent weed canopy (weed-proximate positions or WP). However, significant weed effects were never evident in soybeans located 75 cm away from the velvetleaf (weed-distant locations or WD). By Harvest 4 in 1980, soybeans, weed-free from emergence, had 22.4, 20.7, and 21.4% higher LDWTs, SDWTs, and TDWTs than weed-proximate soybeans in plots having any history of weed presence ($p < 0.05$, all tests). Furthermore, there was a trend for soybeans below full-season velvetleaf to have even lower component DWTs than where weeds were removed, but significant differences between plants in plots with these competition duration intervals were not shown. Significant weed-stress responses were not determined for the final 1980 soybean harvest. Velvetleaf canopies had declined (Part III) by this time (as the weeds matured), thus lessening the level of interspecific stress considerably.

Weed-induced reductions in soybean PDWT (25.5%, $p < 0.05$), SDWT (16.3%, $p > 0.05$) and LDWT (17.6%, $p > 0.05$) contributed to an overall reduction in TDWT (17.3%, $p < 0.05$) in 1981 Harvest 4 samples. By Harvest 5 in 1981, each soybean component showed significant weed stress through lower DWTs. Although significant weed effects in reducing SDWT were resolved, differences could not be found between velvetleaf durations. In other words, the average SDWT of soybeans in plots once possessing velvetleaf was significantly smaller (14.8%) than SDWT in the control plots. However, plots with full-season velvetleaf competition did not have an

average soybean SDWT that was significantly below SDWT in plots where velvetleaf competition developed and then was terminated artificially (by roguing at 5.5 weeks or bentazon at 4 weeks after emergence). The orthogonal comparisons provided more resolution in the origin of the specific weed duration treatments reducing LDWT (11.1%), PDWT (16.6%), and TDWT (14.4%). In 1981, the weed effect on these components of Harvest 5 soybeans was significantly more pronounced (17 to 20%) in full-season velvetleaf locations than in weed-proximate locations where the weed had been removed at 4 or 5.5 weeks after emergence. The differences in intensity and duration of the weed competitive effect on component soybean DWT between years are largely attributed to the striking differences in weed leaf-area development and maturity. Unlike 1980 weeds, leaf area in 1981 velvetleaf plants was still increasing when the final sample was removed (Part III).

Although mean LDWT values were 10.7% smaller in defoliated than in control plots in 1980 (Harvest 4), this difference was not statistically significant when locations were analyzed separately ($p = 0.09$). However, significant SGCW reductions in LDWT were detectable ($p < 0.03$) when the larger data set (formed by combining locations) was analyzed for significant defoliation effects (after proximity effects were shown not significant). The relatively small effect of defoliation on LDWT in 1980 probably reflects initially greater soybean LAI, defoliation-reduced lower-leaf abscission (Part I), and less precision (because 1980 DWT information was limited to 3 replications, whereas all 4 replications were sampled in 1981). In contrast to 1980, highly significant reductions in Harvest 4

LDWT (24%, regardless of weed location) were evident immediately after defoliations were terminated in 1981. Significant SGCW-induced reductions in SDWT were detectable in weed-distant locations (13.0%, $p = 0.03$) and were approaching significance in weed-proximate locations (12.2%, $p = 0.06$). Together, these SGCW-altered components caused lower TDWT (17%) regardless of velvetleaf treatment or sample location.

Simulated GCW defoliation reduced all nonreproductive DWT fractions by Harvest 5. Each weed-proximate insect effect (designated IP in Table 2) indicates that the defoliation effect was only statistically significant near the weeds, although reductions usually were noted in weed-distant locations. For example, in Harvest 5 of 1980, SGCW defoliation (weed-proximate, IP) reduced LDWT, SDWT, and TDWT an average of 19.6, 17.5, and 18.7% below undefoliated control levels. In contrast, the weed-distant defoliation induced reductions (ID) were a nonsignificant 3.0, 4.3, and 5.9%, respectively. In 1981, the LDWT reduction (caused by defoliation) was slightly greater near the weed (15.8%, $p = 0.02$) than away from the weed (10.8%, $p > 0.05$), agreeing with 1980 LDWT results. In comparison, the susceptibility of SDWT (15.4% reduction) and TDWT (13.0% reduction) to defoliation was not influenced by weed proximity.

The majority of TDWT was accounted for by LDWT early in the growing season (Table 3, LPCT). The support components, collectively responsible in maintaining adequate leaf distribution for optimal light interception, gradually developed to become the dominant DWT fraction during the sampling period. Mean SDWT exceeded LDWT by the third harvest (42 to 46 days after emergence).

Table 3. Mean percentage of TDWT contributed by support (SPCT), leaf (LPCT) and pod (PPCT) fractions in the untreated soybean control and a summary of significant velvetleaf, SGCW, and combination treatments^a in 1980 and 1981

Harvest	Elapsed time from emergence		SPCT		LPCT		PPCT	
	1980	1981	1980	1981	1980	1981	1980	1981
	days		%					
1	28	27	29.9 NS	35.1 NS	70.1 NS	64.9 NS	0	0
2	35	37	38.1 NS	47.7 NS	61.9 NS	52.3 NS	0	0
3	42 ^b	46	56.6 NS	55.6 NS	43.4 NS	44.4 NS	0	0
4	56	58	61.7 IP, ID	56.5 IP, ID	38.3 IP, ID	39.2 IP, ID	0	4.3 NS
5	75	76	49.2 NS	53.6 NS	28.1 NS	23.5 NS	22.8 NS	22.9 NS

^aWP = weed effect proximate to velvetleaf significant; WD = weed effect distant from velvetleaf significant; IP = SGCW effect proximate to velvetleaf significant; ID = SGCW effect distant from velvetleaf significant; () = only when data were pooled across weed locations was the effect significant; WP X IP, WD X ID, and W X I designate significant treatment interactions, NS = no significant treatment effects. Untransformed means are presented in Table 3. An arcsine transformation was applied before the data were analyzed.

^bValues reported for the 42-day sample (1980 only) believed artificially low because of processing errors.

Treatments did not alter the proportion of TDWT partitioned into leaf or support components until the fourth harvest. Defoliation (36 SGCW/30 cm of row), caused the percentage of TDWT contributed by LDWT to decline and, thus, resulted in an apparent increase in SDWT percentage. These differences in component percentages of TDWT from the undefoliated control plants averaged 1.8% in 1980 and 3.1% in 1981 regardless of weed competition duration or location. The more severe change observed in 1981 (with equivalent tissue area removed) resulted from the smaller leaf area produced and maintained when soil moisture was limiting (conditions especially prevalent before late July in 1981). Additional variability may have been created by the large physiological changes that accompany rapid pod development, thereby masking any treatment effects persisting in the Harvest 5 percentage-of-TDWT data. No velvetleaf duration X SGCW defoliation effects were significant.

Crop Growth Rates of Soybean Components

Note that in comparing Table 2 (DWTs) with Tables 4 (\overline{CGRs}) and 5 (\overline{RGRs}) fewer significant treatment differences are detected in the latter. This finding was not especially surprising because treatments which cause a small change in growth rates often produce significantly different amounts of endproduct if the interval between samples is relatively large. It should be noted also that classical equations of growth analysis (*sensu* Watson, 1952) are known to produce more variable growth rates than recently advocated regression techniques (Buttery, 1969; Radford, 1967). However, regression growth analyses have the unfortunate disadvantage of often masking the influence of important short-term environmental stresses

(Buttery, 1969). Because the intensity of weed competition often varies as a result of specific environmental conditions, traditional growth analysis techniques were considered more appropriate than regression forms for this study.

Total above-ground crop growth rates (TCGRs) in unstressed soybeans generally increase until middle seed development stages (Buttery, 1969; Koller et al., 1970). Leaf (LCGR), support (SCGR), and pod (PCGR) fractions usually peak and decline sequentially. Widely differing results between years in mean component CGRs ($\overline{\text{TCGR}}$, $\overline{\text{SCGR}}$, $\overline{\text{LCGR}}$, and $\overline{\text{PCGR}}$; bar designates traditional formulae, see Radford, 1967) were determined in this study (Table 4).

A normal progression of control component $\overline{\text{CGR}}$ values was observed in 1980 if Intervals 3 and 4 are replaced, as suggested, with the composite Interval 5. Significant $\overline{\text{CGR}}$ responses to velvetleaf competition were only detected in soybeans immediately below the weed canopy, which is consistent with other significant velvetleaf-altered growth parameters. Interval 5 was characterized by a significantly lower $\overline{\text{SCGR}}$ (25.4%) and $\overline{\text{TCGR}}$ (28%) in 1980 weed-treated plots than in plots weed-free from emergence. Although the expected significant difference in $\overline{\text{LCGR}}$, caused by SGCW defoliation, was not detected in 1980 (even when locations were pooled), the $\overline{\text{LCGR}}$ of defoliated plots was only 66% of undefoliated control plants' rates. This surprising lack of significance probably resulted from the inclusion of an extended undefoliated period in the interval, differences in lower-leaf retention, low precision, or a combination of factors.

Table 4. Mean crop growth rates ($\overline{\text{CGR}}$ s) of control soybeans including support ($\overline{\text{SCGR}}$), leaf ($\overline{\text{LCGR}}$), pod ($\overline{\text{PCGR}}$), and total above-ground ($\overline{\text{TCGR}}$) fractions and a summary of significant velvetleaf SGCW, and combination treatments^a in 1980 and 1981

Interval	Time period encompassed		$\overline{\text{SCGR}}$		$\overline{\text{LCGR}}$		$\overline{\text{PCGR}}$		$\overline{\text{TCGR}}$	
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
	— days —		g DWT/m ² soil/day							
1	1 → 28	1 → 27	0.85 NS	1.00 NS	2.01 NS	1.84 NS	0	0	2.86 NS	2.84 NS
2	28 → 35	27 → 37	5.28 NS	10.24 NS	5.97 NS	8.97 NS	0	0	11.24 NS	19.20 NS
3	35 → 42 ^b	37 → 46	7.59 NS	4.48 NS	-1.94 NS	-0.80 NS	0	0	5.65 NS	3.68 NS
4	42 → 56 ^b	46 → 58	13.18 WP	5.62 NS	6.95 WP	2.42 ID	0	0.10 WP	20.13 WP	9.59 ID
5	35 → 56	37 → 58	11.32 WP	5.13 NS	3.99 NS	1.04 ID	NA	NA	15.31 WP	7.06 ID
6	56 → 75	58 → 76	2.18 NS	5.65 (I)	0.37 NS	-0.88 WP, ID	8.26 NS	7.05 WP	10.75 NS	11.93 WP

^aWP = weed effect proximate to velvetleaf significant; WD = weed effect distant from velvetleaf significant; IP = SGCW effect proximate to velvetleaf significant; ID = SGCW effect distant from velvetleaf significant; () = only when data were pooled across weed locations was the effect significant; WP X IP, WD X ID, and W X I designate significant treatment interactions; NS = no significant treatment effects; NA = not applicable.

^bValues calculated for 35-to-42 days and 42-to-56 days (1980 only) should probably be replaced with the composite 35-to-56 day calculation because of processing errors at 42 days.

In 1981, growth rates of control plants showed drastic deviations from normality because of the severe precipitation deficits predominating a major part of the season (Interval 2 through Interval 4). During Interval 3, $\overline{\text{LCGR}}$ was slightly negative in all plots, reflecting the net decline in LDWT over the period. As noted in the DWT discussion, this near-zero change in $\overline{\text{LCGR}}$ corresponds to a temporary plateauing of leaf-area development that year, before maximum areas actually were achieved (see Part I). Although $\overline{\text{SCGR}}$ was still increasing during Interval 3, the mean daily gain in DWT was less than one-half of the preceding period. The small 1981 increase in control $\overline{\text{LCGR}}$ during Interval 4 contrasts sharply with the negative $\overline{\text{LCGR}}$ ($-1.12 \text{ g/m}^2/\text{day}$) of plots defoliated by 36 SGCW/30 cm of row that year. These significant reductions in $\overline{\text{LCGR}}$ also caused comparable declines in $\overline{\text{TCGR}}$. Significant declines in $\overline{\text{LCGR}}$ occurred only in weed-distant locations, although nonsignificant reductions were recorded in weed-proximate locations. Similar responses were observed in Interval 5, but differences were smaller because an extended undefoliated interval also was included.

In 1981, the $\overline{\text{SCGR}}$ was significantly reduced (20.8%) during Interval 6 by SGCW defoliation when data sets were pooled across locations. Of particular interest, however, were the trends in $\overline{\text{LCGR}}$ (Interval 6). These trends were reversed (both locations) so the defoliated plants were undergoing apparent increases ($+\overline{\text{LCGR}}$) and the undefoliated plots had begun to decline slightly ($-\overline{\text{LCGR}}$). Significant differences between defoliated plots and undefoliated plots were limited to weed-distant soybeans, and the advantage (in absolute value) of defoliated-plant $\overline{\text{LCGR}}$ was small ($0.50 \text{ g/m}^2/\text{day}$). However, the opposing trends in control and defoliated $\overline{\text{LCGR}}$ s

were capable of statistically masking differences in weed-distant LDWT (ID) on the fifth harvest in 1981 (Table 2).

Relative Growth Rates of Soybean Components

Soybean development in unstressed plants is normally accompanied by a regular decline in \overline{RGR} (Buttery, 1969). With minor fluctuations, the pertinent control data (Table 5, excluding Intervals 3 and 4, 1980 only) follow this expected progression in 1980, but much less consistency was observed in 1981. Thus, the 'rate of interest' (\overline{RGR}) in component DWT fractions also reflected the environmental stresses of a temporarily limited soil moisture environment.

No treatment-induced differences in soybean components RGRs were detected in 1980. In contrast, Interval 4 and the broader Interval 5 of 1981 demonstrated SGCW-induced reductions in leaf \overline{RGR} (\overline{LRGR}) and total above-ground \overline{RGR} (\overline{TRGR}) that were more readily detectable in weed-distant than weed-proximate locations (although RGRs at both locations tended to be reduced below control plant levels). As with \overline{LCGR} in 1981, the \overline{LRGR} calculation exhibited slightly more positive values in weed-distant defoliated plants during Interval 6 than with weed-proximate defoliated soybeans. Perhaps more importantly, plants in both defoliation locations (IP and ID) exhibited declining (in comparison with earlier intervals), but positive, \overline{LRGR} values, whereas plants in both control locations exhibited declining and negative \overline{LRGR} values. Thus, some measure of compensatory growth or a delay in maturity seemingly was evident in defoliated plots. Significant differences between control and defoliated \overline{LRGR} s were limited to the weed-distant soybeans. This differential response may be

Table 5. Mean relative growth rates (\overline{RGRs}) of control soybeans including support (\overline{SRGR}), leaf (\overline{LRGR}), pod (\overline{PRGR}) and total above-ground (\overline{TRGR}) fractions and a summary of significant velvetleaf, SGCW, and combination treatments^a in 1980 and 1981

Interval	Time period encompassed		\overline{SGCR}		\overline{LRGR}		\overline{PRGR}		\overline{TRGR}	
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
	— days —		Component $\overline{RGRs} \times 100$							
1	1 → 28	1 → 27	8.15 NS	8.92 NS	8.73 NS	8.64 NS	--	--	8.56 NS	8.74 NS
2	28 → 35	27 → 37	12.83 NS	14.95 NS	7.54 NS	9.69 NS	--	--	9.29 NS	11.87 NS
3	35 → 42 ^b	37 → 46	8.70 NS	3.00 NS	-2.05 NS	-0.50 NS	--	--	3.03 NS	1.30 NS
4	42 → 56 ^b	46 → 58	6.77 NS	2.70 NS	5.26 NS	1.50 ID	--	21.48 WP	6.15 NS	2.56 ID
5	35 → 56	37 → 58	7.41 NS	2.83 NS	2.82 NS	0.64 ID	NA	NA	5.11 NS	2.02 ID
6	56 → 75	58 → 76	6.37 NS	2.04 NS	1.88 NS	0.50 WP, ID	24.76 (I)	11.78 WP	1.83 NS	2.35 WP

^aWP = weed effect proximate to velvetleaf significant; WD = weed effect distant from velvetleaf significant; IP = SGCW effect proximate to velvetleaf significant; ID = SGCW effect distant from velvetleaf significant; () = only when data were pooled across weed locations was the effect significant; WP x IP, WD x ID, and W x I designate significant treatment interactions; NS = no significant treatment effects; NA = not applicable.

^bValues calculated for 35-to-42 days and 42-to-56 days (1980 only) should probably be replaced with the composite 35-to-56 day calculation because of processing errors at 42 days.

attributable to continued velvetleaf competitive pressure in weed-proximate positions which might be depressing the magnitude of the recovery-from-defoliation response. As with all other parameters, however, direct statistical evidence of velvetleaf x SGCW treatment interactions was not confirmed in these samples (collected before soybean harvest maturity).

Pod \overline{RGR} (\overline{PRGR}) in 1980 showed no weed-treatment effects. In contrast, \overline{PRGR} in 1981 was significantly reduced by velvetleaf competition during contiguous Intervals 4 and 6 (an initial PDWT of 0.1 g was assumed to facilitate the testing of treatment effects). As with all other growth characteristics, the weed effect was only evident in weed-proximate positions. During Interval 4, the 11% reduction in \overline{PRGR} from the weed-free control was statistically detectable when all weed treatments were averaged. In Interval 6, however, the full-season weed-proximate locations had a 21.5%, lower \overline{PRGR} ($p < 0.01$) than all other velvetleaf treatment combinations. In 1980, Interval 6 exhibited a 4% reduction in \overline{PRGR} of defoliated plants that was significant when locations were pooled ($p = 0.045$), but not when locations were analyzed separately ($p = 0.07$, each position).

PART III. VELVETLEAF MORPHOLOGICAL CHARACTERISTICS
AND YIELD COMPONENTS UNDER INTRASPECIFIC
AND INTERSPECIFIC COMPETITION WITH
DEFOLIATED AND UNDEFOLIATED SOYBEANS

ABSTRACT

Velvetleaf morphological characteristics under selected combinations of intraspecific competition with defoliated and undefoliated soybeans were evaluated in a 3-year field study. A standardized velvetleaf vegetative and reproductive developmental system was proposed. Doubling the density of monocropped velvetleaf (from 1 to 2 weeds/3.0 m of row) did not appreciably alter the morphological development of the weeds. Monocropped velvetleaf consistently exceeded intercropped velvetleaf in leaf area, canopy width, nodes with fully-developed leaves, branches, and number of capsules as early as 3, 4, 3, 5, and 8 weeks after emergence, respectively. Intercropped velvetleaf were initially shorter than the soybean canopy (through 4 weeks), became equivalent to the crop in height (during Week 5 and(or) 6), and finally, exceeded the crop in canopy height. Simulated green cloverworm defoliation of adjacent soybeans did not alter weed heights significantly, but did affect the development of weed-soybean canopy height differentials (by stunting the crop). Furthermore, an analysis of weed-soybean canopy-height differentials indicated that the temporal feasibility of certain late-season weed control devices (rope-wick applicators and recirculating sprayers) may vary, depending on the level of insect defoliation previously tolerated. Defoliation of soybeans (up to 40%) at the full-bloom stage did not consistently alter most velvetleaf characteristics. Seemingly, the lack of a significant response in velvetleaf morphological development resulted because the weeds had already become photo-induced (began reproductive development) about the same time that soybean

defoliation began. Adults of an undescribed beetle of the family Bruchidae emerged from velvetleaf seed collected from plants in the study plots.

INTRODUCTION

Crop and weed competition create varying degrees of stress for each involved species, depending on intrinsic (e.g., morphological and physiological) and extrinsic (e.g., moisture) factors. Weeds survive intense competition (of intraspecific or interspecific origin) by exhibiting considerable latitude in morphological plasticity (Harper and Gajic, 1961). The ability to compete effectively for requisites (especially light) varies directly with structure and size of specific morphological components. Therefore, studies seeking to understand the basis for competition in a specific situation should quantify weed and crop development throughout the season. Such a dual quantification of development is particularly important if the weed management techniques under consideration require specific minimal morphological differentials between crop and weed. For example, recirculating sprayers and rope wick applicators rely on differences in weed and crop height to prevent nonselective herbicides from causing unacceptable levels of crop damage.

For these reasons, a quantitative analysis of velvetleaf morphological development and dry weight accumulation was undertaken each year from 1979 through 1981 to complement the soybean studies reported in Parts I and II. Part III is a summary of morphological characteristics of velvetleaf (including yield components) developing under various intraspecific and interspecific environments. The effects of these stresses in altering velvetleaf dry matter accumulation and allocation are reported in Part IV. Direct comparisons between velvetleaf development in intraspecific and interspecific environments were used to establish the onset of significant

interspecific stress between velvetleaf and soybeans (viz., velvetleaf served as the stress indicator species).

METHODS AND MATERIALS

Eight additional full-season velvetleaf plots were randomized at the main-plot level within the split-plot design (presented in Part I) during planting. These 8 plots either had soybeans removed at emergence (1979 and 1980) or never planted (1981) so that each density of velvetleaf established therein (1 and 2 weeds/3.0 m of row) developed under intraspecific competition only.

Beginning 2 or more weeks after soybean emergence, nondestructive estimates of velvetleaf leaf area, lower-leaf abscission, canopy width, height, vegetative and reproductive growth stages, and branches were gathered weekly. To sample these characteristics, 2 weeds from each intraspecific (velvetleaf only) and interspecific (velvetleaf and soybean) plot were measured from at least 3 replications. Xerographic leaf images of known areas in graded increments were used to estimate areas of velvetleaf leaves which exceeded the scanning-head width of the electronic planimeter. Reproductive effort was assessed by determining capsules/plant, carpels/capsule, and seeds/carpel. These data then were used to generate estimates of total seed production through Week 13 on a plot-by-plot basis to facilitate statistical analysis of numbers/plant and numbers/m² of soil surface.

Standard analyses of variance and orthogonal contrasts were used to separate treatment means on a week-by-week basis. Main-plot analyses were conducted by only considering data from weeds in plots not receiving weed-control treatments to date. Appropriate adjustments in orthogonal contrasts were observed, where necessary, to accommodate the weed-removal

treatments. Data from the intraspecific plots were deleted before analysis of SGCW defoliation effects so that only the relevant variability from the interspecific competition treatments was included. Where appropriate, the orthogonal contrasts included velvetleaf density, velvetleaf duration, SGCW defoliation level, and all interactions. Summary figures are used to present significant treatment effects of a consistent pattern for clarity and simplicity. All significant treatment effects and the statistical sources thereof are discussed in the text.

RESULTS AND DISCUSSION

Velvetleaf Leaf Area Development, Leaf Retention,
and Canopy Widths

Leaf area of velvetleaf growing under intraspecific competition only (Figure 7, solid lines) increased through Week 10 in 1979, Week 11 in 1980, and at least Week 11 in 1981. The largest intraspecific velvetleaf sampled in this study had developed over 60,600 cm² of leaf surface by Week 11 in 1981. No leaf-area differences were detected between 1 and 2 velvetleaf/3.0 m of row (thus, only one solid line in each year is shown), suggesting intraspecific competition between in-row or across-row locations was not severe. By Week 13, leaf area had declined 76% in 1979 and 92% in 1980 from maximum intraspecific levels. Rates of natural canopy decay were confounded 12 weeks after emergence in 1979 by a brief, but intense, hail-storm.

Each year, the monocropped velvetleaf developed substantially more leaf area than velvetleaf intercropped with soybeans (dashed lines). Significant interspecific stress between crop and weeds was determined by quantifying differential velvetleaf development between intraspecific (INTRA) and interspecific (INTER) environments (significance is denoted by the separation of solid and dashed lines in the accompanying figures). If velvetleaf leaf-area differences are used as stress indicators, interspecific competition was first detected 7 weeks after emergence in 1979 (a normal rainfall year), 3 weeks after emergence in 1980, and 4 weeks after emergence in 1981 (the latter 2 years had sub-optimal early-season precipitation). Leaf area differences, once established, increased until maturity

Figure 7. Velvetleaf leaf area development under intraspecific competition only (INTRA or solid lines) and velvetleaf leaf area development under interspecific competition with defoliated and undefoliated soybeans (INTER or broken lines)

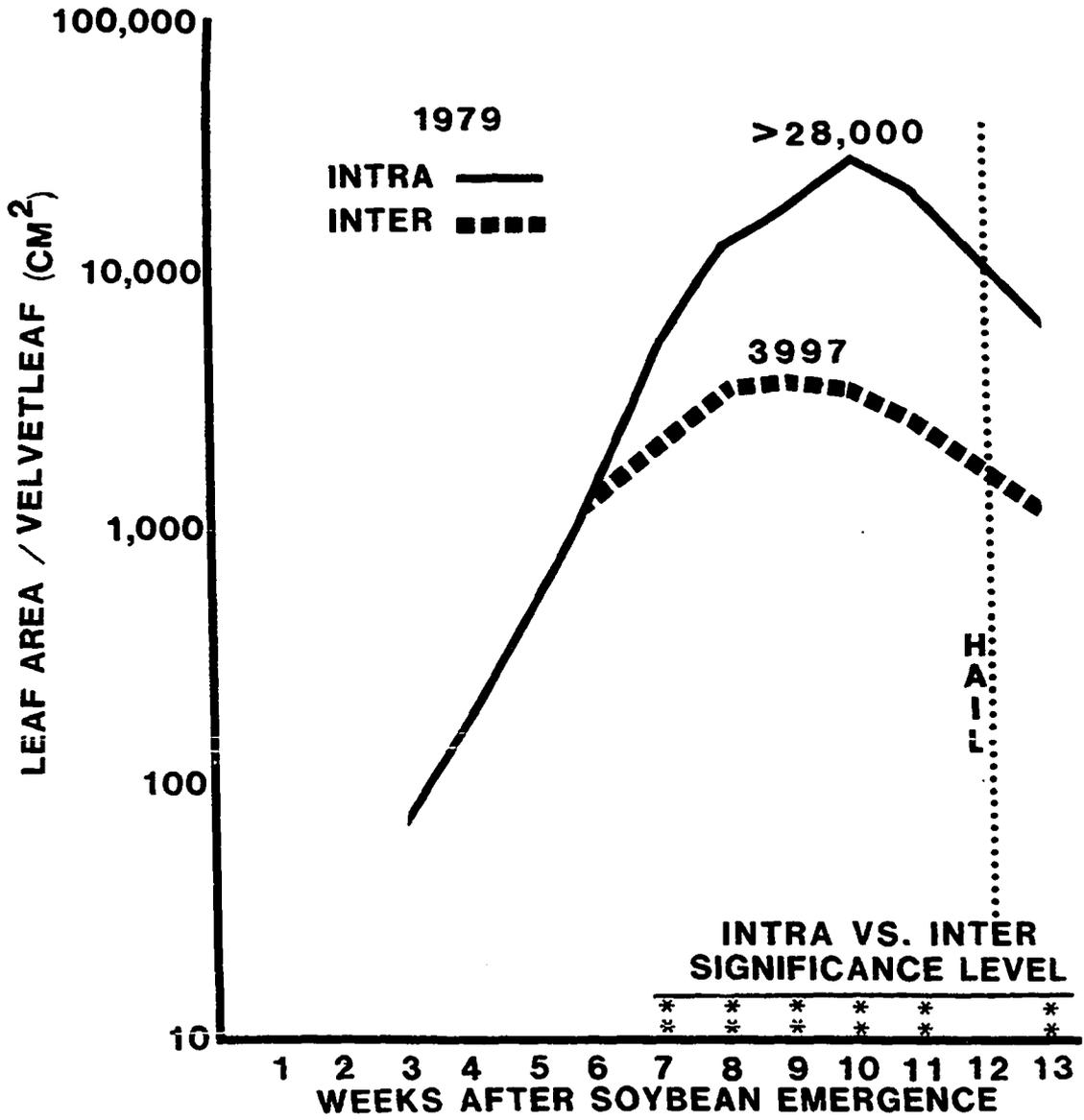


Figure 7. (continued)

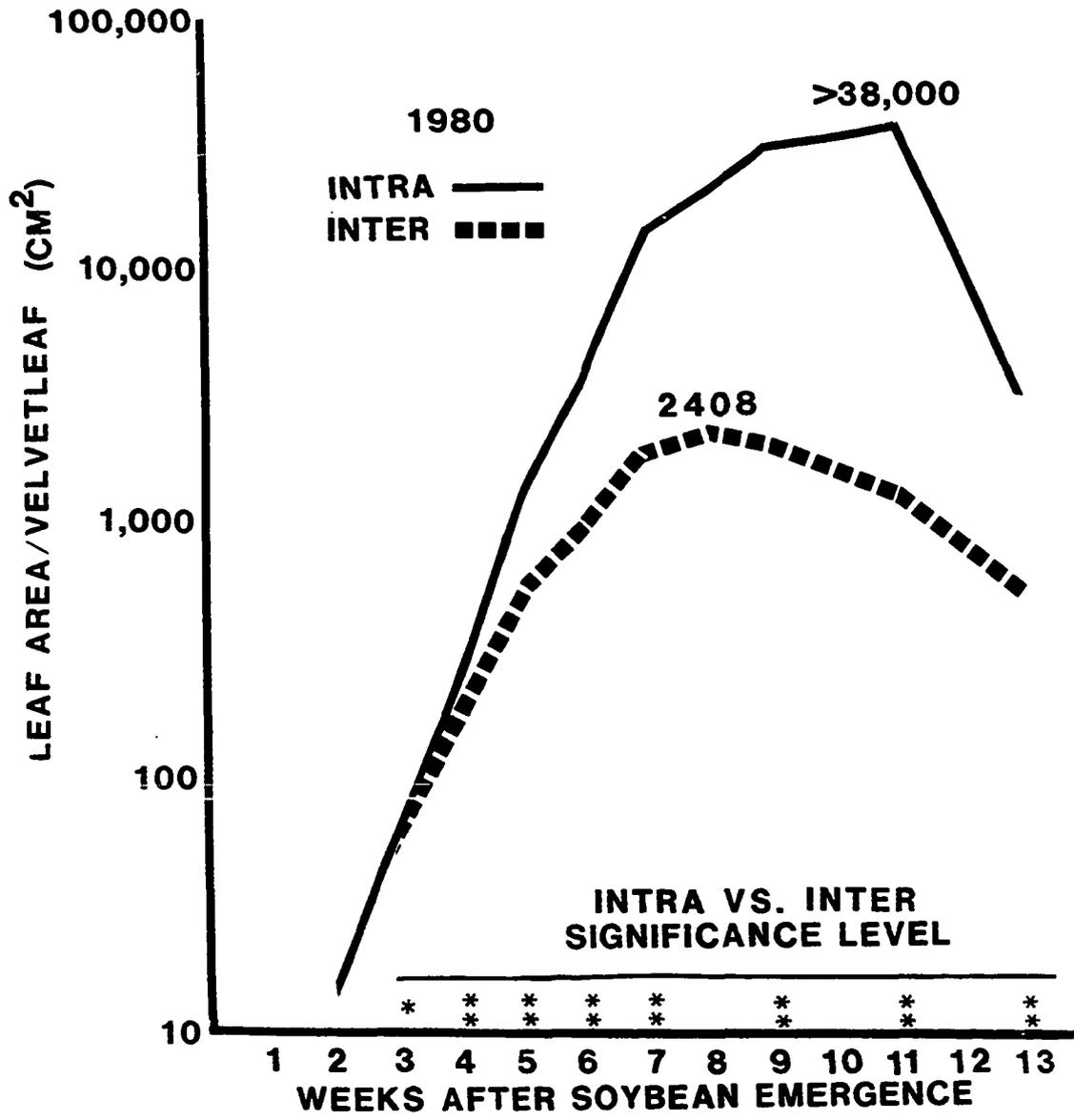
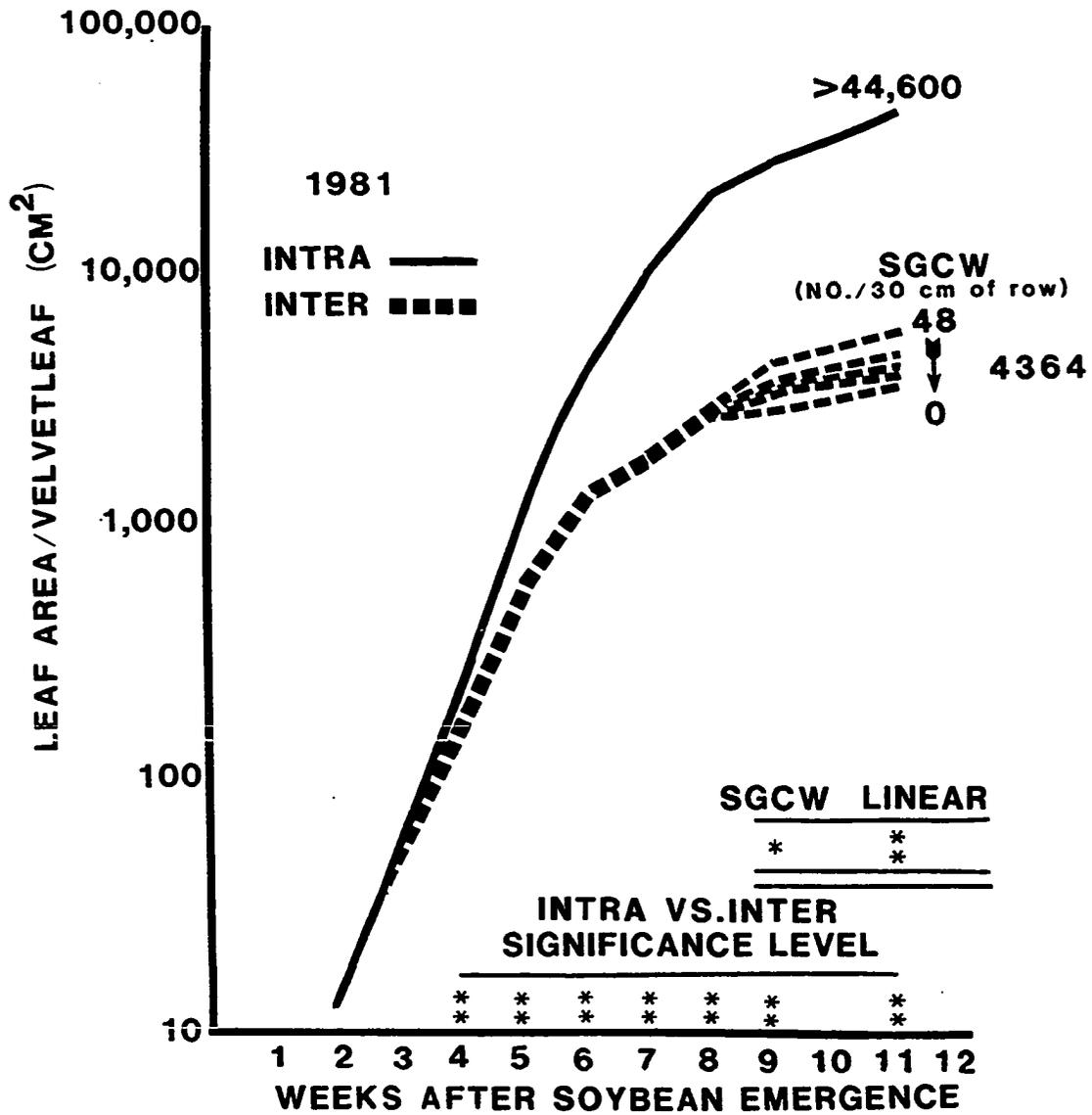


Figure 7. (continued)



caused weed canopies in each environment to rapidly decline. Representative interspecific velvetleaf (same densities as intraspecific weeds) achieved leaf areas which averaged only 14% of 1979, 6.3% of 1980, and 9.8% of 1981 monocropped velvetleaf, respectively. In 1979 and 1980, interspecific velvetleaf had achieved maximum leaf area values and were declining before monocropped velvetleaf leaf areas peaked.

SGCW defoliation of full-bloom soybeans in 1979 ($\leq 32\%$) or 1980 ($\leq 40\%$) did not significantly alter subsequent leaf-area development of intercropped velvetleaf. In 1981, velvetleaf-leaf area (post-defoliation) was directly related to the density of GCW larvae simulated and, therefore, directly related to level of defoliation applied to the adjacent soybeans (1 and 3 weeks after defoliations were terminated). On Week 11 (3 weeks after simulated pupation), plots with soybeans defoliated by 0, 12, 24, 36, and 48 SGCW/30 cm of soybean row (up to 40% defoliation) had interspecific velvetleaf averaging 3552 cm², 3803 cm², 4190 cm², 4633 cm², and 5646 cm², in canopy leaf area, respectively. Velvetleaf-leaf number also indicated that interspecific weed growth had increased in response to SGCW defoliation of soybeans by 9 weeks after emergence in 1981. Densities of 0, 12, 24, 36, and 48 SGCW/30 cm of soybean row resulted in 25.9, 29.5, 32.8, 35.9, and 45.6 leaves/velvetleaf on the Week 11 sample date. Thus, insect defoliation of crops seemingly can shift the competitive balance between crop and weeds in favor of the weeds in certain situations. A strong trend towards parallel increases in component and total velvetleaf dry weight components with soybean defoliations was also noted (Part IV).

A commonly observed result of shading is for the stressed plants to exhibit above-normal rates of lower-leaf abscission. Doubling the density

of intraspecific velvetleaf (from 1 to 2 weeds/3.0 m of row) did not affect the rate of abscission. However, from 1 to 4 more lower leaves were abscised by interspecific velvetleaf than intraspecific velvetleaf, regardless of density, at 8 (1981), 9 (1981), and 11 (1980) weeks after emergence ($p < 0.05$, all tests). The additional light attenuation caused by the adjacent soybean canopy probably caused the interspecific weeds to experience increased leaf loss. In contrast, by Week 11 in 1981, an average of 2 fewer nodes were missing leaves on interspecific than intraspecific weeds. A similar, but not statistically significant reversal also was observed on Week 13 in 1980. The late-season reversals probably occurred largely because intraspecific velvetleaf had developed significantly more nodes from which leaves could potentially be lost than interspecific plants. Level of SGCW defoliation of adjacent soybeans did not affect the number of velvetleaf nodes retaining leaves during either year of this study.

It seems reasonable that weed canopy widths could be a useful growth parameter to monitor, especially when dealing with a relatively sparse weed population that provided only intermittent shading to the crop canopy. Because the weed densities employed did not produce such a continuous weed canopy, canopy widths of velvetleaf developing under the various competition environments also were quantified. Data were collected weekly on maximum weed canopy widths (paralleling the soybean row) beginning 4 weeks after emergence in 1980 and 2 weeks after emergence in 1981 (Figure 8). In intraspecific environments, average maximum canopy widths of 145 cm (1980) and 168 cm (1981) were achieved 11 weeks after emergence, regardless of velvetleaf density. In contrast, velvetleaf intercropped with soybeans achieved average maximums of 65 cm (1980) and 72 cm (1981). Intraspecific

Figure 8. Development of velvetleaf canopy widths under intraspecific competition only (INTRA or solid lines) and development of velvetleaf canopy widths under interspecific competition with defoliated and undefoliated soybeans (INTER or broken lines)

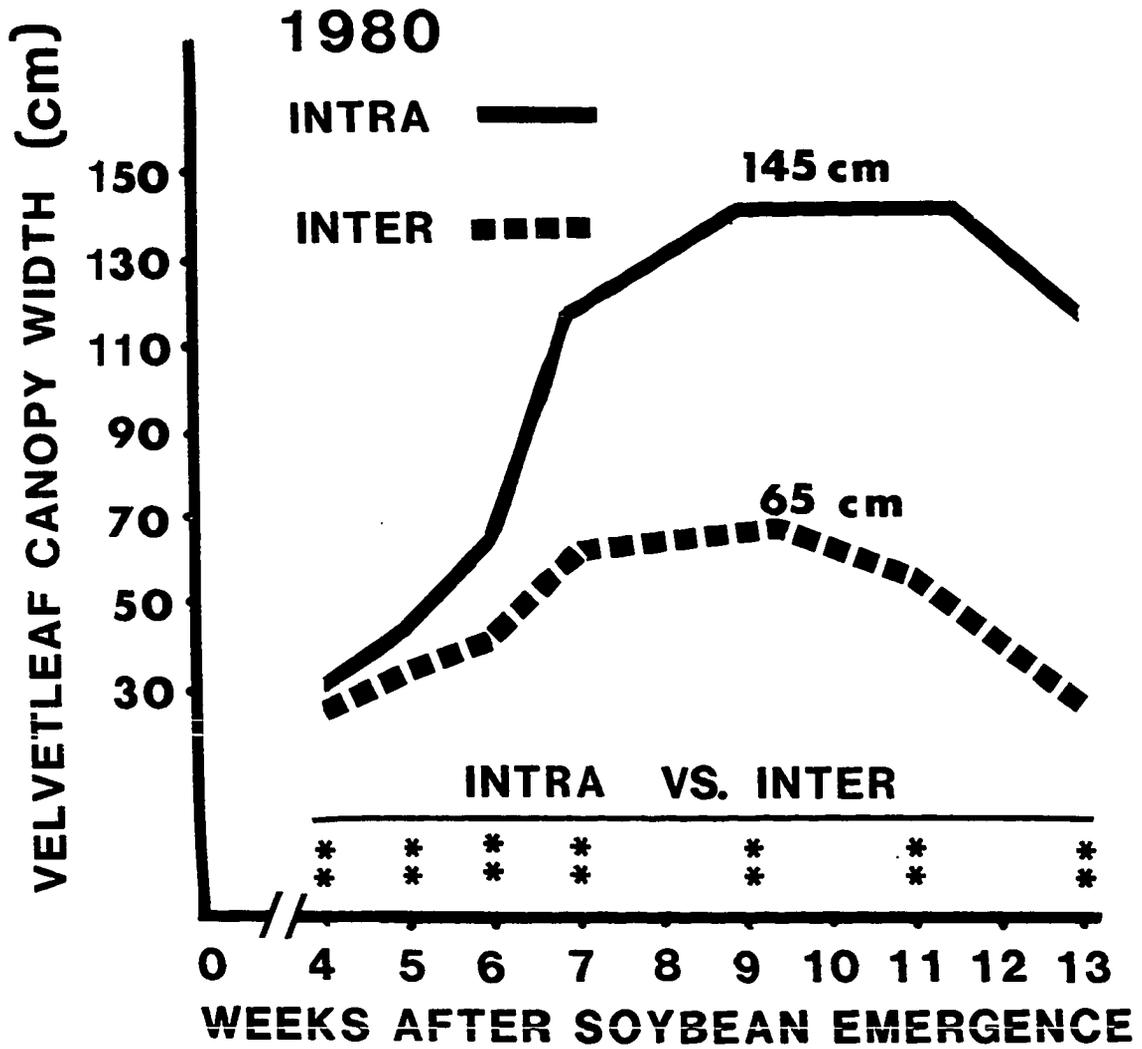
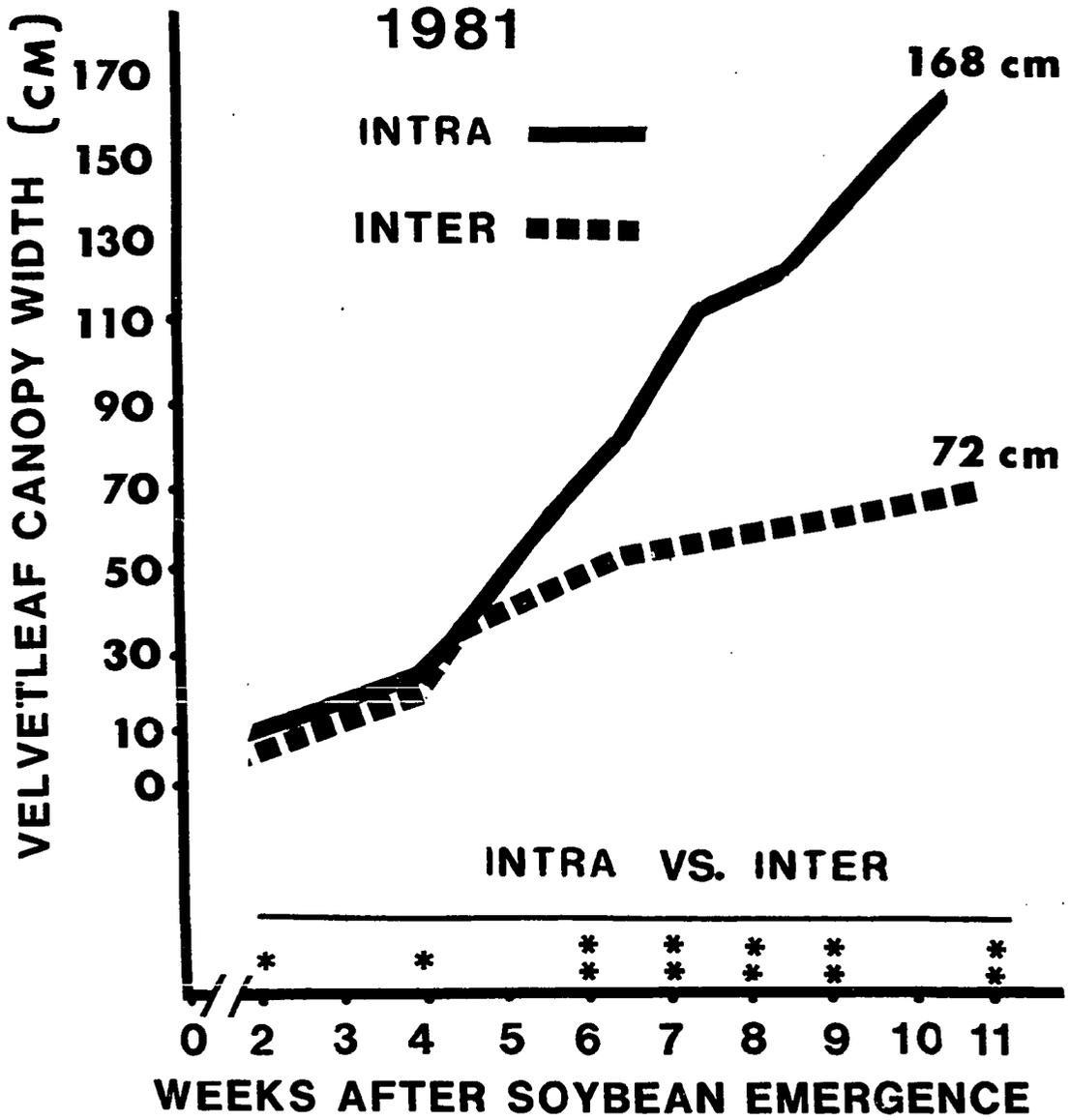


Figure 8. (continued)



velvetleaf canopies were consistently wider than interspecific velvetleaf canopies beginning 4 (1980) and 6 (1981) weeks after emergence. Although intraspecific canopy widths seemed wider than those of interspecific weeds at 2 and 4 weeks after emergence in 1981, differences were not detected 5 weeks after emergence. Canopy widths of interspecific velvetleaf declined after the Week 9 samples were recorded in 1980. Perhaps because of the abundant precipitation beginning during Week 8, canopy widths in 1981 did not begin to decline through at least Week 11. Defoliation of the soybeans in interspecific plots did not cause the intercropped velvetleaf to respond by producing significant wider canopies during the 1980 and 1981 sampling seasons.

Velvetleaf Height and Relationship to Height of Competing Soybeans

Velvetleaf monocropped at densities of 1 and 2 weeds/3.0 m of row (4386 and 8772 weeds/ha, respectively) did not differ significantly in height during the 3-year study (Figure 9). The rapid increase in height, occurring from Week 7 through Week 9 in 1979, may be characteristic of velvetleaf vertical growth under conditions of adequate soil moisture. In contrast, more gradual mid-season increases in height were observed during the much drier years of 1980 and 1981. Significant amounts of precipitation (beginning during Week 8) maintained or slightly increased late-season vertical growth rates in 1981. By Week 11, intraspecific velvetleaf were 10 to 15 cm taller than the maximum seasonal weed heights recorded in the 2 preceding years.

Figure 9. Development of velvetleaf canopy height under intraspecific competition only (INTRA or solid lines) and development of velvetleaf canopy height under interspecific competition with defoliated and undefoliated soybeans (INTER or broken lines)

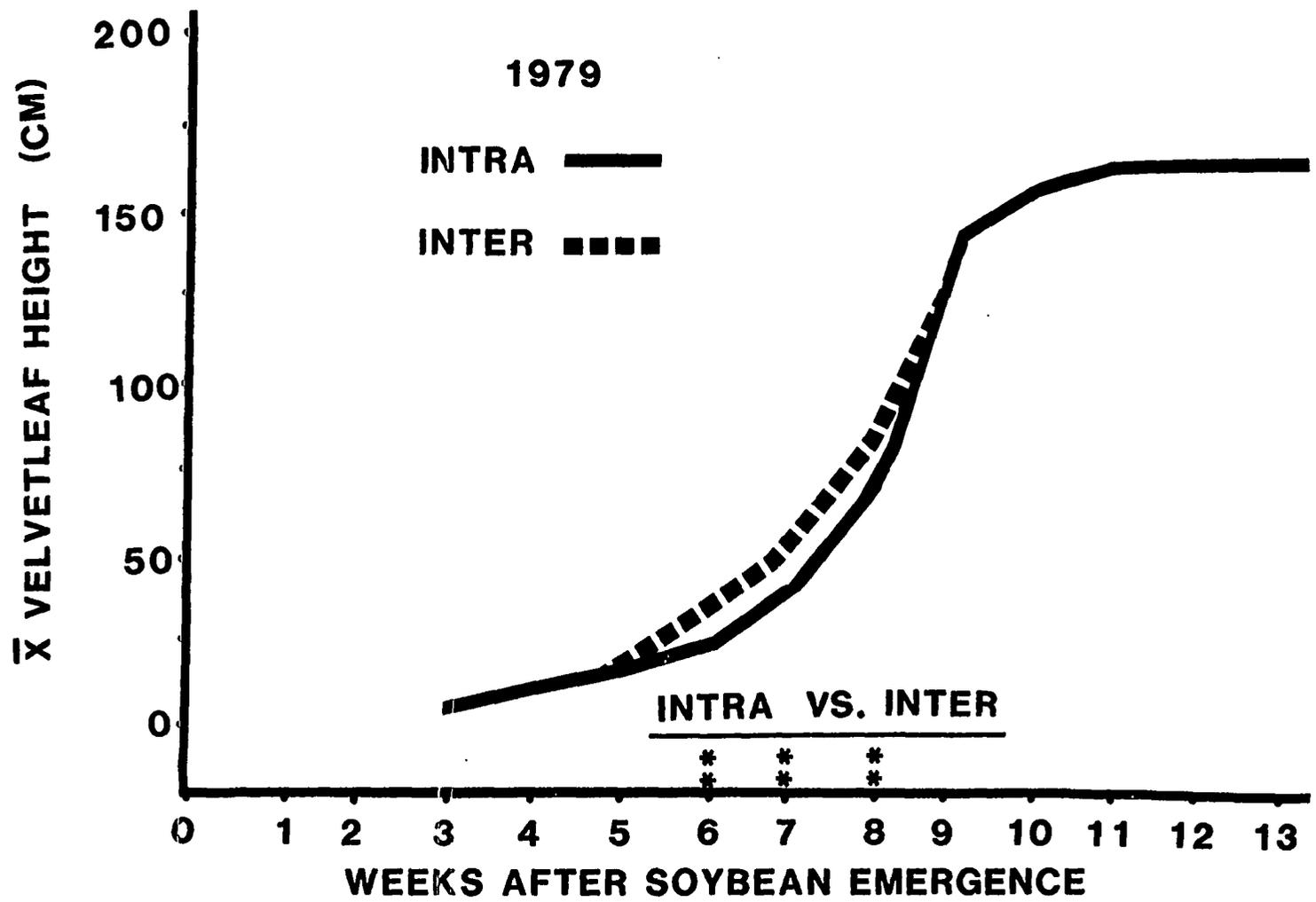


Figure 9. (continued)

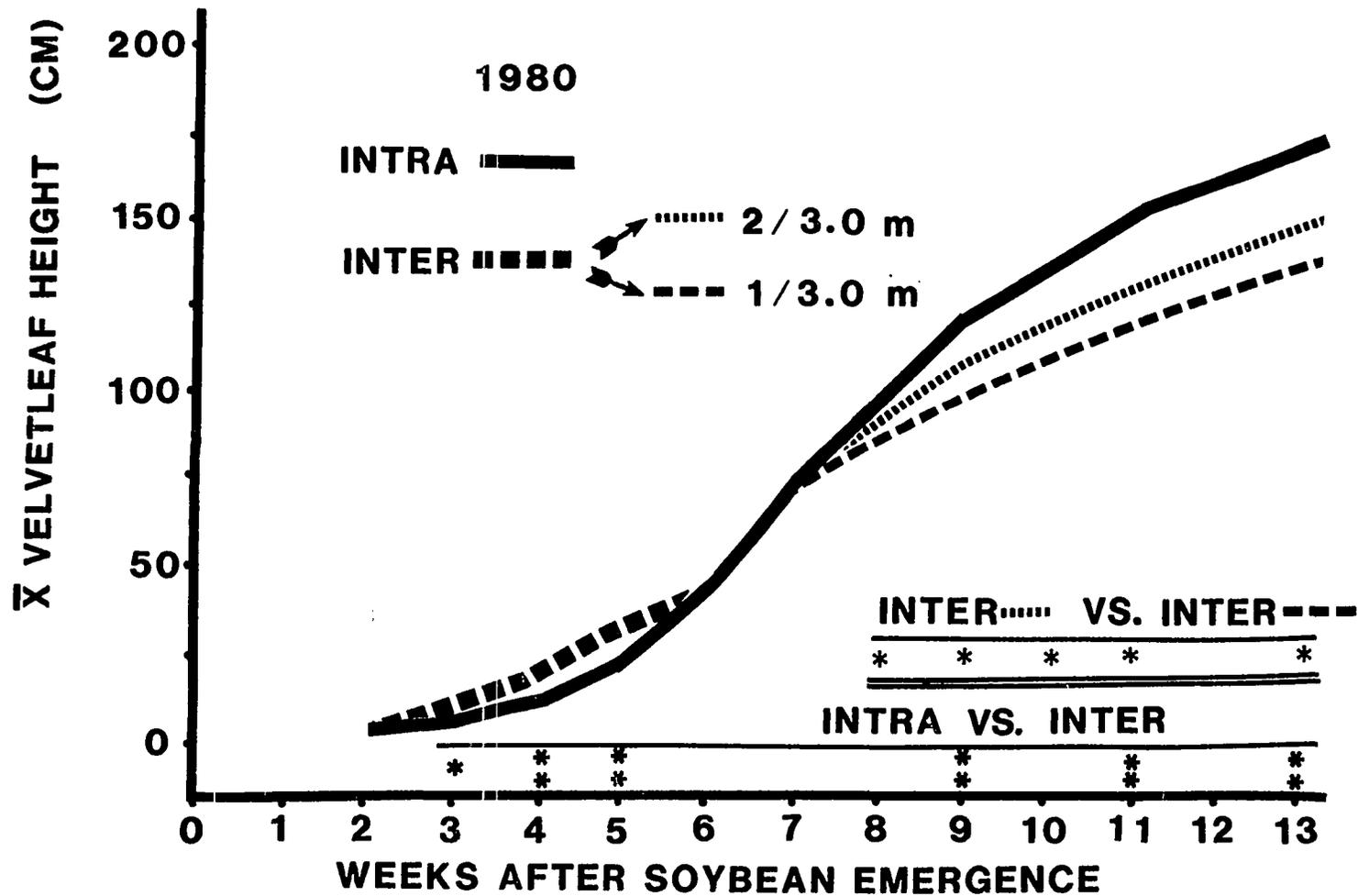
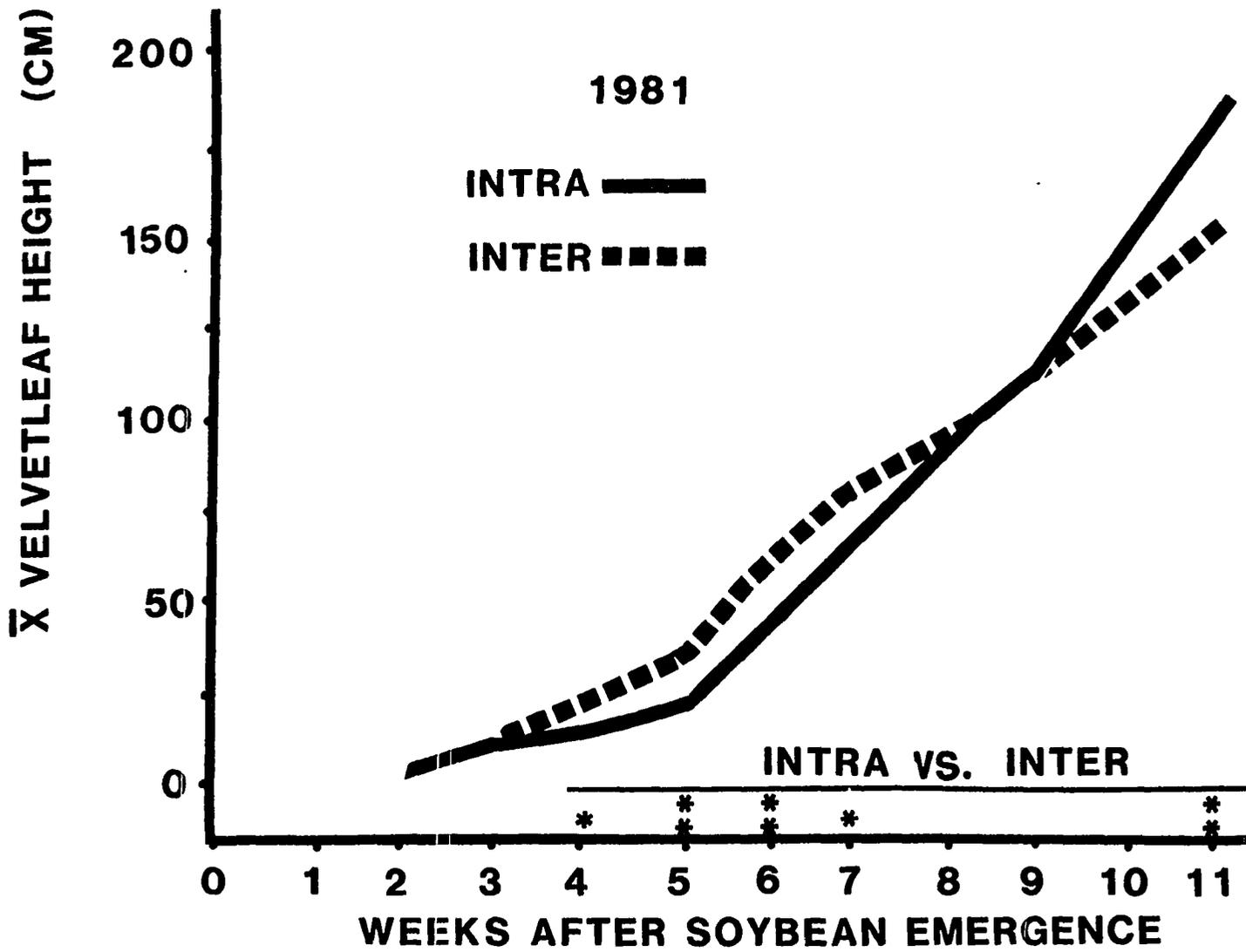


Figure 9. (continued)



Seemingly, only in 1980 was velvetleaf density important in determining the height of weeds intercropped with soybeans. For an unknown reason, doubling the velvetleaf density produced 14-cm taller weeds beginning approximately 8 weeks after emergence that year. An examination of velvetleaf canopy widths (Figure 8) indicates that even with high density velvetleaf plantings (weeds every 150 cm), the in-row gap between the extended leaves of adjacent interspecific weeds averaged 85 cm at the peak of the 1980 weed canopy development. Therefore, there is little evidence to support the notion that the weed height differences noted in 1980 interspecific environments resulted from interaction between adjacent weeds.

A consistent pattern emerged when interspecific velvetleaf heights were compared weekly, throughout the season, with heights of monocropped velvetleaf. Initially, the weed and weed-plus-soybean environments did not produce velvetleaf which differed significantly in height. However, by 6 weeks (1979), 3 weeks (1980), and 4 weeks (1981) after emergence, the velvetleaf intercropped with soybeans developed significantly greater heights than did monocropped weeds. The greater elongation response in the interspecific weeds probably resulted from a buildup of auxins in these soybean-shaded velvetleaf. Similar levels of auxins would not have been expected in the monocropped weeds at this time because these hormones are believed to be rapidly degraded by sunlight (which in this instance is not limited by a nearby soybean canopy). Eventually, however, the dense, compact canopy developed by monocropped velvetleaf provided enough self-shading that a similar rapid internodal elongation occurred in these monocropped weeds also. Thus, the height differences were effectively equalized and no longer detectable by 9 weeks, 6 weeks, and 8 weeks after emergence

in 1979, 1980, and 1981, respectively. Finally, the relatively-unstressed monocropped weeds surpassed their soybean-stressed counterparts in height. In 1979, sample variance was great enough to prevent the 11.5-cm advantage of intraspecific weeds from being significantly different from the inter-cropped values.

Glyphosate is a popular post-emergence herbicide often used late in the growing season for removing tall weeds from soybeans. This herbicide is not physiologically selective. Instead, selectivity is achieved through specially designed applicators (primarily rope wick applicators and recirculating sprayers), which make use of a distinct weed-to-soybean height differential. Consequently, the herbicide is only applied to, and only controls, weeds protruding above the soybean canopy. Thus, the magnitude of the weed-to-soybean height deviation is important in determining when a given applicator may be useable.

To reduce the potential for crop damage, the glyphosate label¹ requires that each of these devices be operated to apply the herbicide at least 5 cm above the crop canopy (Level 1). The glyphosate label also recommends that for optimal efficacy the targeted weeds should exceed the crop canopy by at least 15 cm in height (Level 2). A more conservative crop safety and control efficacy recommendation was recently proposed specifically for recirculating sprayers. After testing a recirculating sprayer under various weed-to-soybean height differences, Carlson and Burnside (1981) concluded that weeds should extend a minimum of 45 cm above the crop level (Level 3). Regardless of the recommendation preferred, published

¹Glyphosate (Roundup®) Label. 1981. Monsanto.

data are inadequate on the development of velvetleaf-to-soybean height differentials. Additionally, no data are available which quantify the effects of crop defoliation by insects on the development of these height differences. It seems possible that such confounding stresses, by altering relative vertical growth rates, may enhance or restrict the potential weed-management alternatives.

In this study, various intensities of SGCW defoliation of full-bloom soybeans did not affect the height achieved by intercropped velvetleaf ($p > 0.05$, all tests). In contrast, the soybean height data (reported in Part I) revealed a consistent linear increase in severity of stunting as defoliation level increased. Therefore, it seemed reasonable that the velvetleaf-to-soybean height deviation probably showed a similar linear response. Thus, the period of time required before a given level (safety or legal) is reached may vary, depending upon the insect defoliation history of the crop. This hypothesis was tested by calculating weed-to-soybean height differentials weekly on a plot by plot basis and analyzing each week for significant SGCW-linear effects. The results are summarized in Figure 10.

The canopies of interspecific velvetleaf remained significantly shorter than the intercropped soybean canopies for the first 5 weeks after emergence in each year. A brief period (1 to 2 weeks) of no significant height differences then occurred shortly after velvetleaf vertical growth rates began rapidly increasing. The intercropped velvetleaf exceeded soybeans significantly in height by 7 weeks after emergence in 1981 and 8 weeks after emergence in 1979. Greater variability in weed heights and more substantial early-season soybean height advantages delayed the development of

Figure 10. Mean velvetleaf and soybean canopy height differentials (interspecific competition) throughout the growing season as influenced by level of simulated green cloverworm defoliation of soybeans. Three height differentials relevant to late-season weed management also are shown

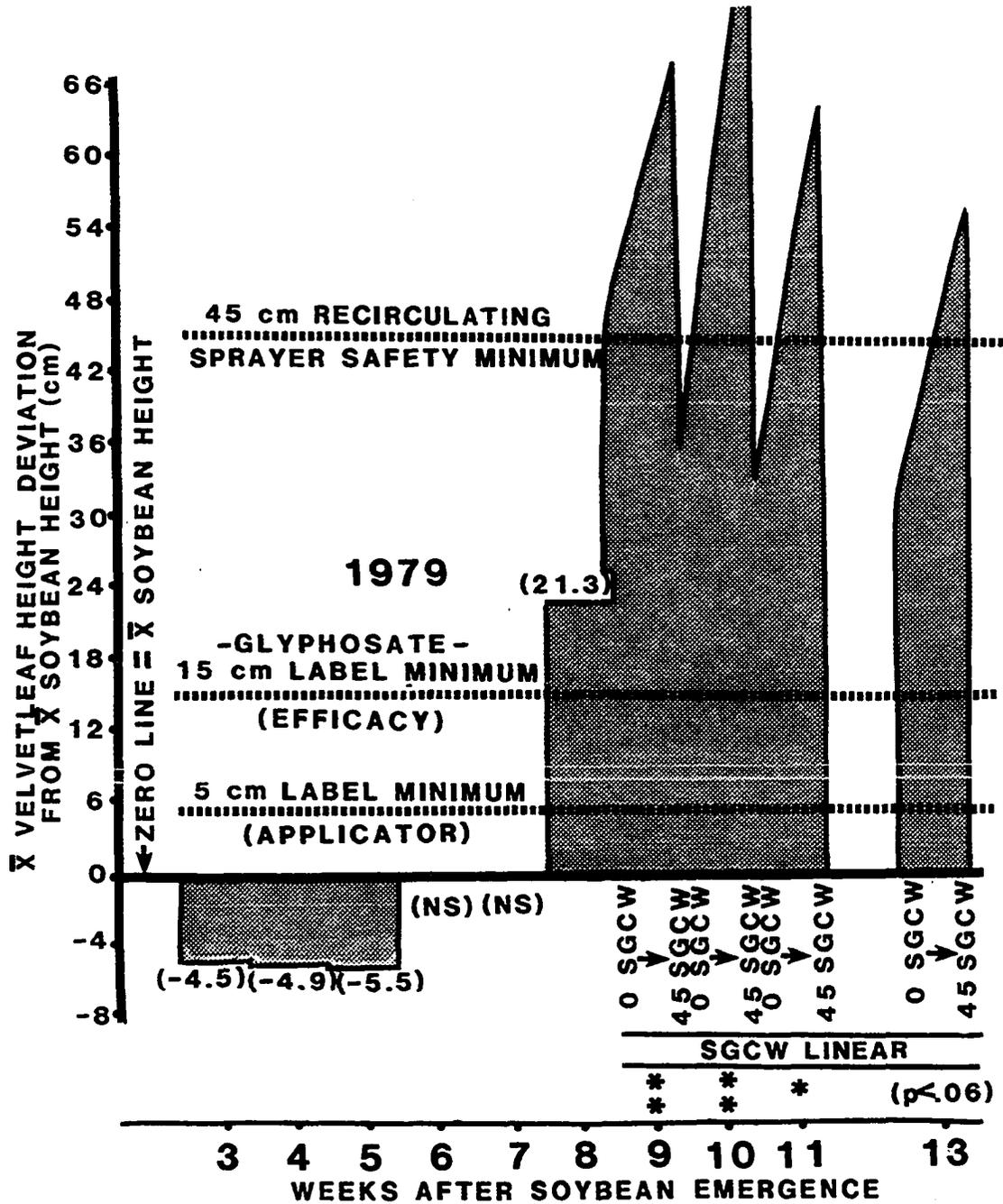


Figure 10. (continued)

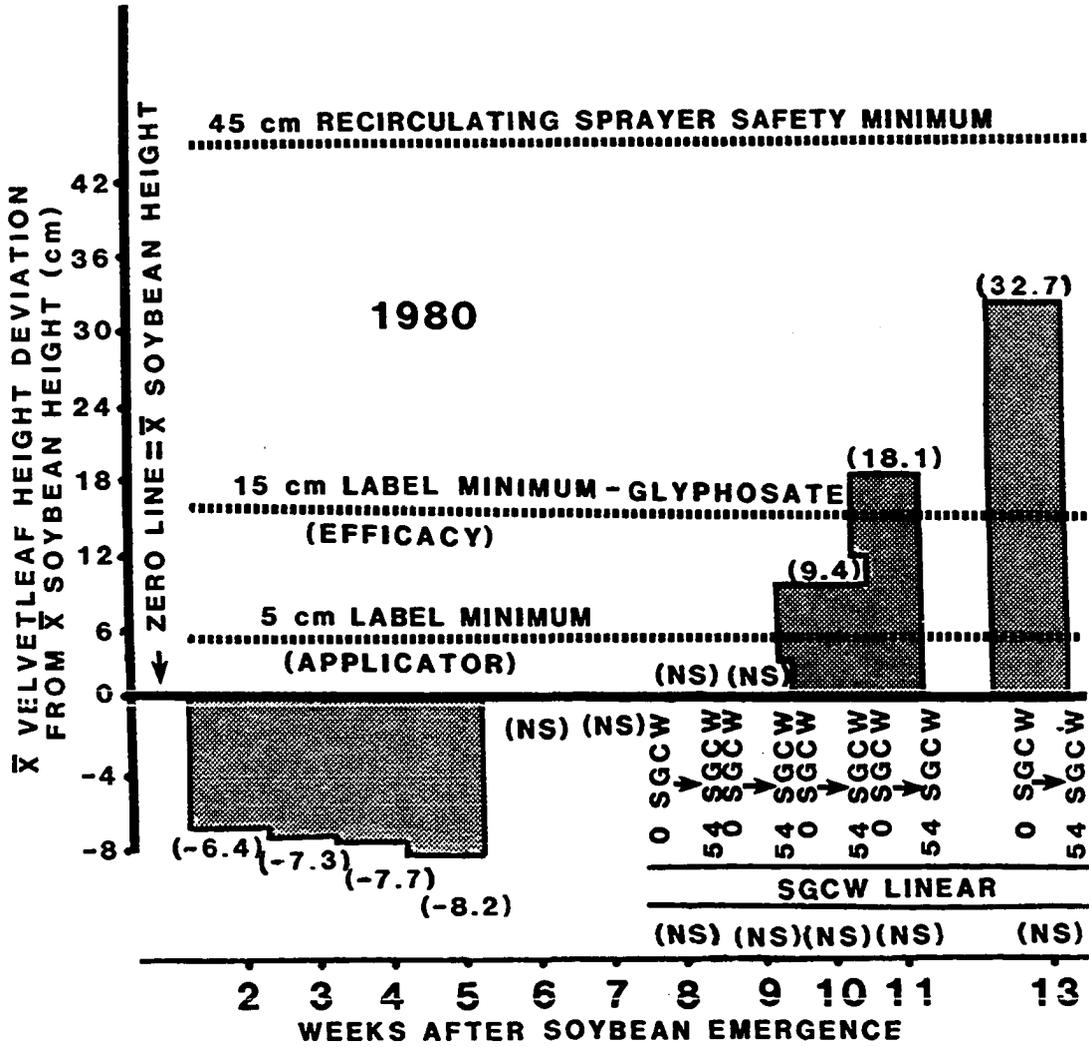
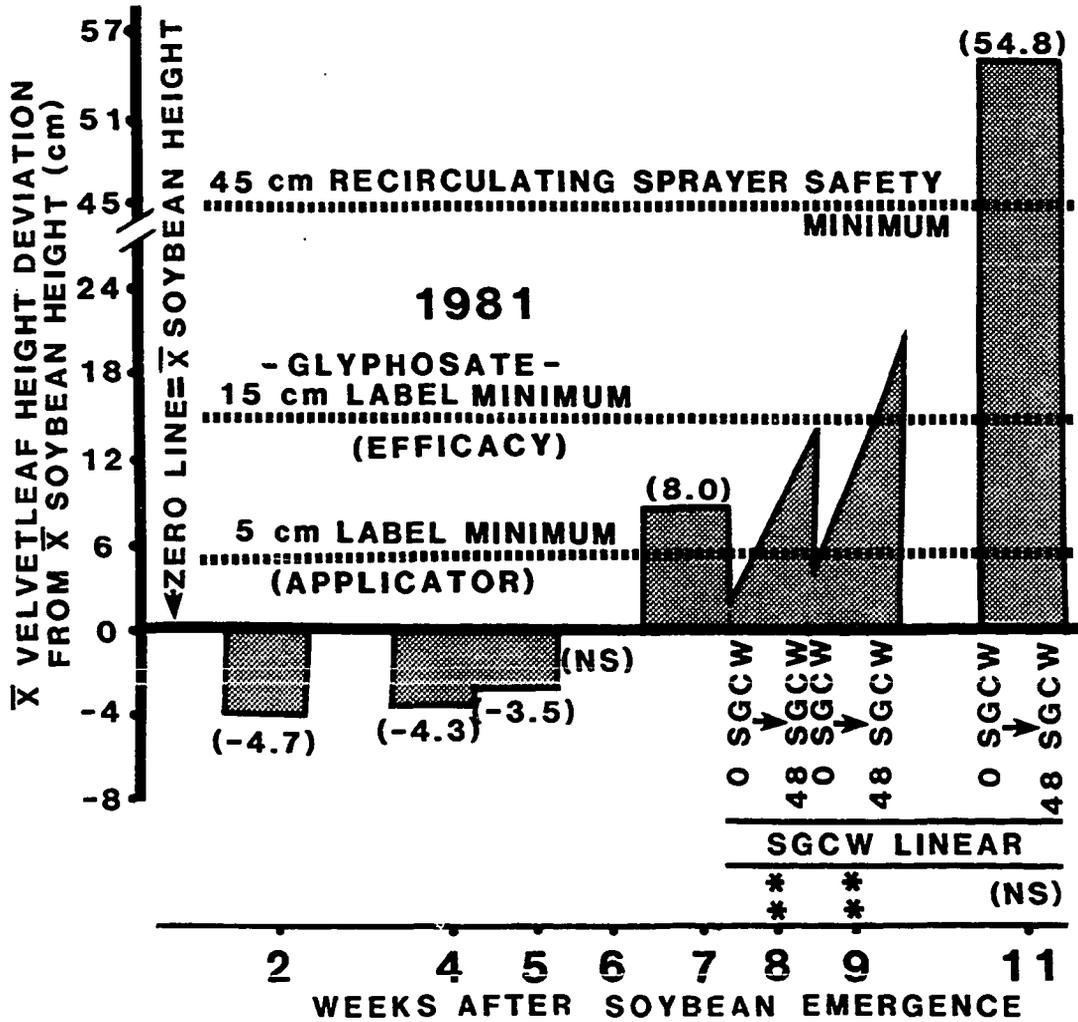


Figure 10. (continued)



this difference during 1980. These factors combined to prevent the average velvetleaf canopy height from significantly surpassing the soybean canopy until 10 weeks after emergence that year. In 1980, the intercropped weeds also failed to achieve the 45-cm differential suggested for recirculating sprayers. Thus, velvetleaf may not be equally predisposed to control by these specialized sprayers every year.

Weed-height variability was great enough in 1980 so that no significant SGCW-induced trends in soybean-to-weed height differentials were detected. Unlike 1980, the time required before the critical height differentials (Levels 1, 2, and 3) were attained often varied, depending on the density of GCW larvae simulated (which is directly related to the level of defoliation applied to the full-bloom soybeans). In each instance that defoliation intensity was important, a linear increase in SGCW density caused correspondingly greater differences in average canopy heights. Thus, toleration of greater levels of insect defoliation (and the resulting soybean stunting) would have permitted earlier use of rope wick applicators and recirculating sprayers.

For instance, in 1981, Level 1 (the closest to the crop that glyphosate can be safely applied) was exceeded at 8 weeks after emergence only if GCW populations ≥ 13.6 larvae/30 cm of soybean row had been tolerated (soybean defoliation occurred during the full-bloom stage, terminating approximately 8 weeks after emergence). In contrast, by waiting until Week 9, only an estimated 1.9 GCW larvae/30 cm of row would have had to be tolerated during the soybean full-bloom stage. In comparison, weeds would have exceeded soybeans by the label recommended 15 cm (Level 2) approximately 9

weeks after emergence in 1981 only if an estimated 31.4 GCW larvae/30 cm of row were tolerated during the earlier full-bloom stages. However, because GCW densities exceeding 15 larvae/30 cm of row are considered economically deleterious (DeWitt et al., 1978), insecticides probably would have been applied. This action, if undertaken, would have effectively lowered the potential level of insect defoliation, and, as a consequence, smaller height differentials would be realized. In contrast, if no GCW larvae had been tolerated, the weed-height advantage predicted for Week 9 would only have averaged 4.3 cm during Week 9. It should be obvious that this limited difference in height does not exceed any of the glyphosate thresholds. Therefore, all of the listed control recommendations would suggest delaying herbicidal treatment (assuming velvetleaf was the primary weed targeted for control).

Note that, by Week 11 in 1981, GCW larval density (at soybean full-bloom) was not important in determining whether velvetleaf and soybeans were separated in height by more than 45 cm. Therefore, the crop probably would experience only a minimal amount of herbicide injury from a properly adjusted recirculating sprayer. In 1979, the earlier and more rapid velvetleaf vertical growth rates (perhaps associated with the very favorable soil moisture supplies) allowed all weed and soybean height differentials to exceed each decision level by Week 9, regardless of the density of GCW larvae simulated. Later in the 1979 season, the magnitude of the weed-to-soybean height difference declined somewhat. This reduction in canopy-height differentials resulted from a termination of velvetleaf vertical growth compounded with continuation of soybean vertical growth (Amsoy 71

is an indeterminate variety). Thus, for velvetleaf to achieve the necessary 45-cm height advantage at 10, 11, or 13 weeks after emergence in 1979, the adjacent soybeans would have to have been defoliated at the full bloom stage by a GCW population of at least 15.4, 22.1, or 27.7 larvae/30 cm of soybean row, respectively.

The preceding discussion seemingly indicates that insecticidal sprays, applied in a timely manner to prevent foliage loss, also can effectively forestall late-season weed-control efforts by preventing or delaying the development of adequate weed-to-soybean height differentials. In this instance, the pest management specialist may need to consider the consequences of several actions (or the lack thereof). These consequences include: (1) the anticipated significance of various degrees of insect defoliation on yield, (2) the significance of continued weed competition on yield, (3) the significance of increased interference caused by larger weeds on harvest losses, (4) the importance of increased weed-seed production, (5) stress interactions, and (6) costs and efficacy of each control measure employed. Obviously, if pest management decisions are to be truly integrated in a comprehensive manner, the consequences of a single management action on a significant portion of the pest community should probably be understood. However, from a practical standpoint, only a few of the most relevant factors can probably be considered in a given situation.

Velvetleaf Vegetative and Reproductive Development

Standardized terminology defining plant development has been published for several field crops (e.g., Fehr and Caviness, 1977; Hanway, 1966; Kalu and Fick, 1981). Without such standardized terminology, researchers cannot be sure that similar experiments separated by time and space are directly comparable. Table 6 summarizes a developmental staging system proposed for velvetleaf based on the progression of readily observable morphological characteristics. The forerunner of the current system initially was developed in 1978 using greenhouse plants. Various improvements were incorporated (in the reproductive stages only) after field testing was completed in 1979. The vegetative stages (viz., V(n)) proposed by Fehr and Caviness (1977) to describe soybean growth were largely adequate to describe velvetleaf leaf initiation and nodal development. Note that, in both systems, fully-expanded and fully-developed are not equivalent terms. A leaf is considered fully-developed for node-counting purposes when the edges of the leaves arising from the node above are no longer touching, whereas a leaf is fully-expanded when it has achieved maximum leaf area. The systems also differ in that velvetleaf unfolds its leaf edges, whereas soybeans unroll their new leaves. The V-count continues to increase as long as leaf-bearing nodes are added. After the opposite cotyledons and opposite unifoliolate leaves are initiated, velvetleaf develops a single unifoliolate leaf/node approximately over 125° to 140° around the main stem. This upward, spiral-like production of new leaves creates an environment where intraplant competition for light is effectively reduced. The first 6 reproductive stages (R1 through R6) are based on the development of flowers and capsules arising from main-stem leaf-axils. Total

Table 6. A velvetleaf vegetative and reproductive development system based on readily identified morphological changes

Stage number	Stage name	Description
VE	Emergence	Cotyledons above the soil surface
VC	Cotyledon	Edges of opposite unifoliolate leaves unfolded so they are no longer touching one another
V1	First-node	Fully-developed unifoliolate leaves ^a
V2	Second-node	Fully-developed primary leaf at the node above the node possessing the opposite unifoliolate leaves
.	.	.
.	.	.
.	.	.
V(n)	nth-node	n Main stem nodes with fully-developed leaves
R1	Beginning bloom	One open flower on the main stem in the axil of a primary leaf
R2	Full bloom	At least 1 open flower on 1 of the top 4 nodes with fully-developed leaves
R3	Capsule 1	At least 1 capsule ^b on the main stem in the axil of a primary leaf
R4	Capsule 2	At least 2 green capsules on the top 4 main-stem nodes
R5	Capsule 3	At least 1 mature capsule with exposed seeds on the top 4 main-stem nodes
R6	Capsule 4	Three of 4 capsules on the top 4 main stem nodes are mature with exposed seeds
R7	Late maturity	Only capsules are present (no flowers) on the weed; leaf drop progressing rapidly
R8	Full maturity	Ninety-five percent of the capsules on the entire weed have reached their mature pod color

^aLeaves are considered fully-developed for node counting purposes when the node above has a leaf with leaf edges not touching one another (unfolding).

^bCapsules are not counted until they attain at least 2-cm in diameter (dime-sized).

plant development, encompassing branches as well as main-stem reproductive parts, is used in defining R7 and R8.

Doubling the density of monocropped velvetleaf (from 1 to 2/3.0 m of row) did not significantly alter the rate of vegetative development (Figure 11). As expected, similar increases in interspecific weed densities also failed to change rates of leaf initiation. Monocropped weeds significantly exceeded their soybean-intercropped counterparts in number of fully-developed leaves from 3 to 6 weeks after emergence. Eleven to 13 weeks after emergence, monocropped velvetleaf had produced an average of 6 to 11 more nodes than velvetleaf stressed by soybeans. In addition to fewer nodes, greater internodal lengths were characteristic of velvetleaf developing in mixed plantings. Seemingly, node production rates of velvetleaf intercropped with soybeans increased after the adjacent soybeans were defoliated by SGCW larvae. However, only during Weeks 10 and 11 of 1979 were the defoliation-induced increases statistically confirmed. The subsequent loss of significance by Week 13 probably resulted from variations in maturity.

Velvetleaf reproductive development during 1980 and 1981 is summarized in Table 7 and Figure 12. Flowers were not detected until Week 6 in 1980 and Week 7 in 1981 (Table 7). Capsules (at least 2 cm in diameter) were detected on a few weeds during Week 7 each year. The presence or absence of soybeans did not significantly alter the time of floral initiation or capsule development. However, soybeans did stress weeds enough to curtail the number of flowers and pods produced (relative to weeds in soybean-free environments). Fewer flowers were developed by soybean-stressed weeds than monocropped weeds beginning 7 weeks after emergence in 1981. Fewer capsules also were evident 1 week later that year. Although 1980 data are not

Figure 11. Velvetleaf nodes with fully-developed leaves under conditions of intraspecific competition only (INTRA or solid lines) and velvetleaf nodes with fully-developed leaves under conditions of interspecific competition with defoliated and undefoliated soybeans (INTER or broken lines)

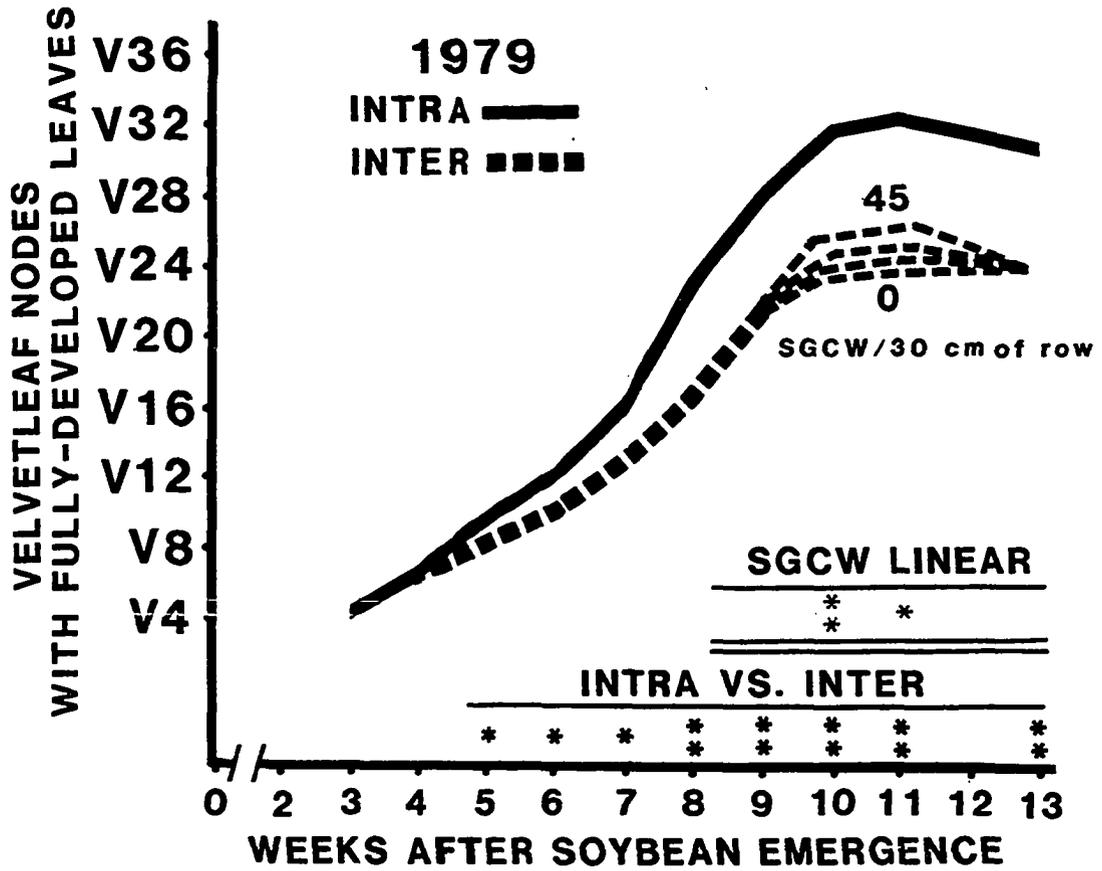


Figure 11. (continued)

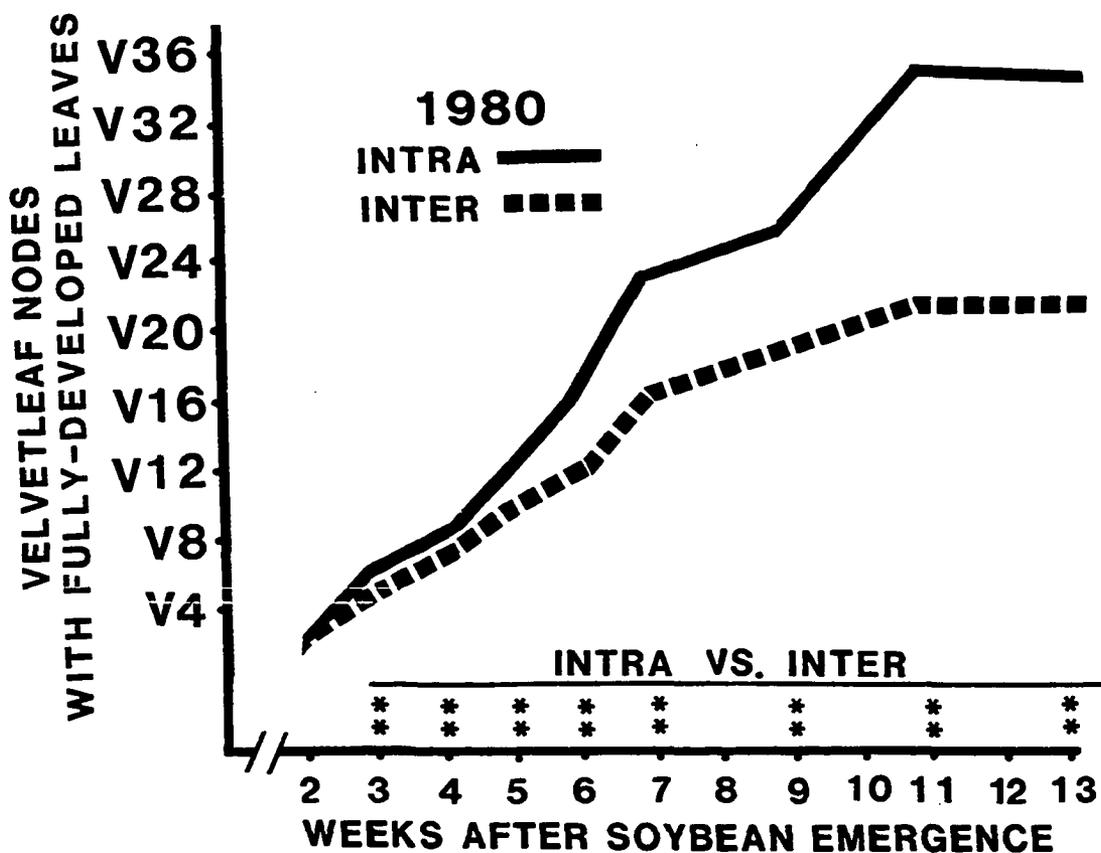


Figure 11. (continued)

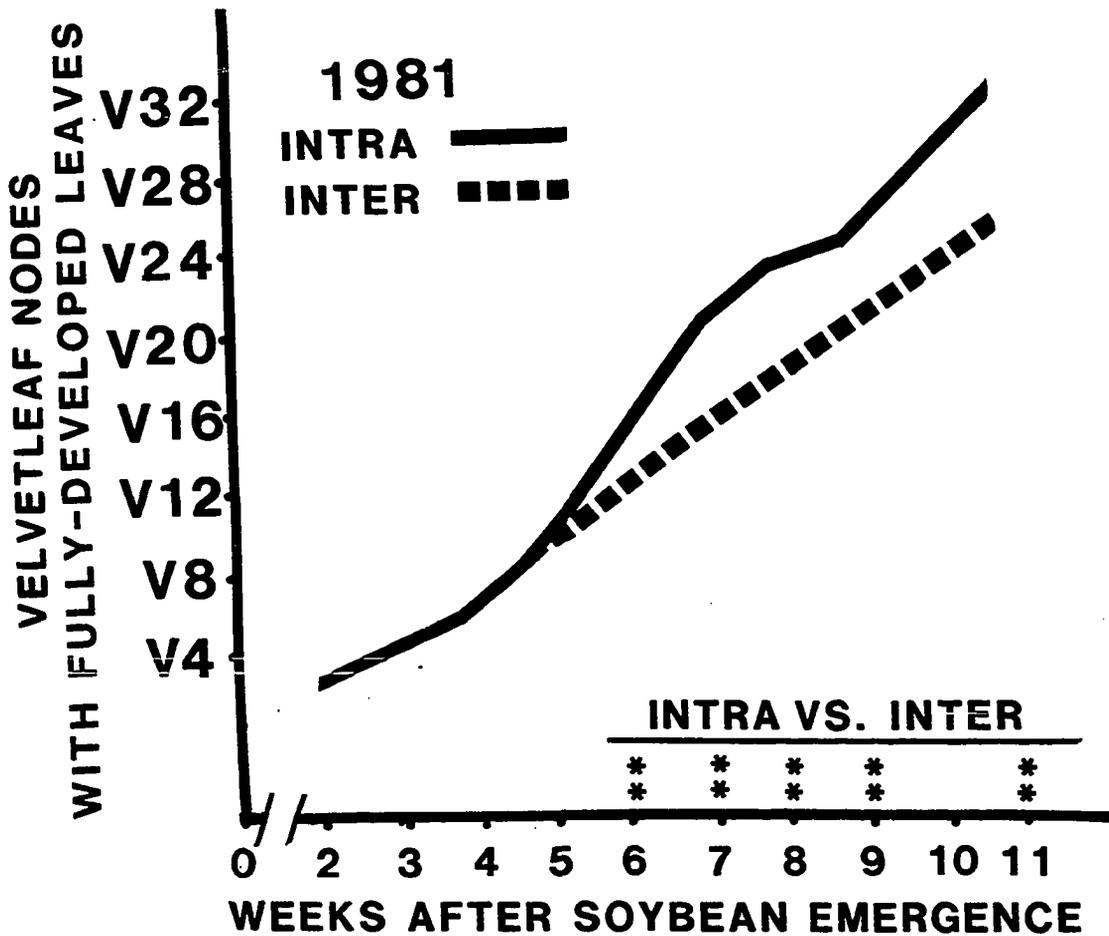


Table 7. Mean values and relevant summary statistics^a for velvetleaf flowers and capsules under intraspecific (INTRA) and interspecific (INTER) competition in 1980 and 1981

Weeks after emergence	Type of competition ^b	— Flowers —		— Capsules —	
		1980	1981	1980	1981
6	INTRA	0.1	0	0	0
	INTER	0.3	0	0	0
	C1:	NS	--	--	--
	C2:	NS	--	--	--
7	INTRA	4.3	1.0	10.3	1.3
	INTER	1.6	2.2	4.3	0.9
	C1:	NS	NS	NS	NS
	C2:	NS	* ^c	NS	NS
	C3:	NS	NS	NS	NS
8	INTRA	--	8.3	--	17.5
	INTER	1.8	2.1	7.6	5.3
	C1:	--	NS	--	NS ^d
	C2:	--	*	--	** ^d
	C3:	NS	NS	NS	NS
9	INTRA	33.8	14.6	40.5	26.6
	INTER	1.6	3.7	7.2	6.8
	C1:	NS	NS	NS	NS
	C2:	**	*	**	**
	C3:	NS	NS	NS	NS
11	INTRA	67.2	92.2	269.9	130.9
	INTER	8.3	16.5	33.0	28.2
	C1:	NS	NS	NS	NS
	C2:	**	**	**	**
	C3:	NS	NS	NS	NS
13	INTRA	35.7	--	380.0	307.4
	INTER	15.4	--	41.4	36.1
	C1:	NS	--	NS	NS
	C2:	NS	--	**	**
	C3:	NS	--	NS	NS

^aAnalysis of variance and orthogonal treatment comparisons were employed to separate treatment means. The relevant comparisons listed include: C1, 1 velvetleaf (INTRA)/3.0 m of row vs. 2 velvetleaf (INTRA)/3.0 m of row; C2, INTRA velvetleaf vs. INTER velvetleaf; C3, SGCW linear in interspecific plots.

^bINTRA = intraspecific competition or velvetleaf monocropped. INTER = interspecific competition or velvetleaf intercropped with soybeans.

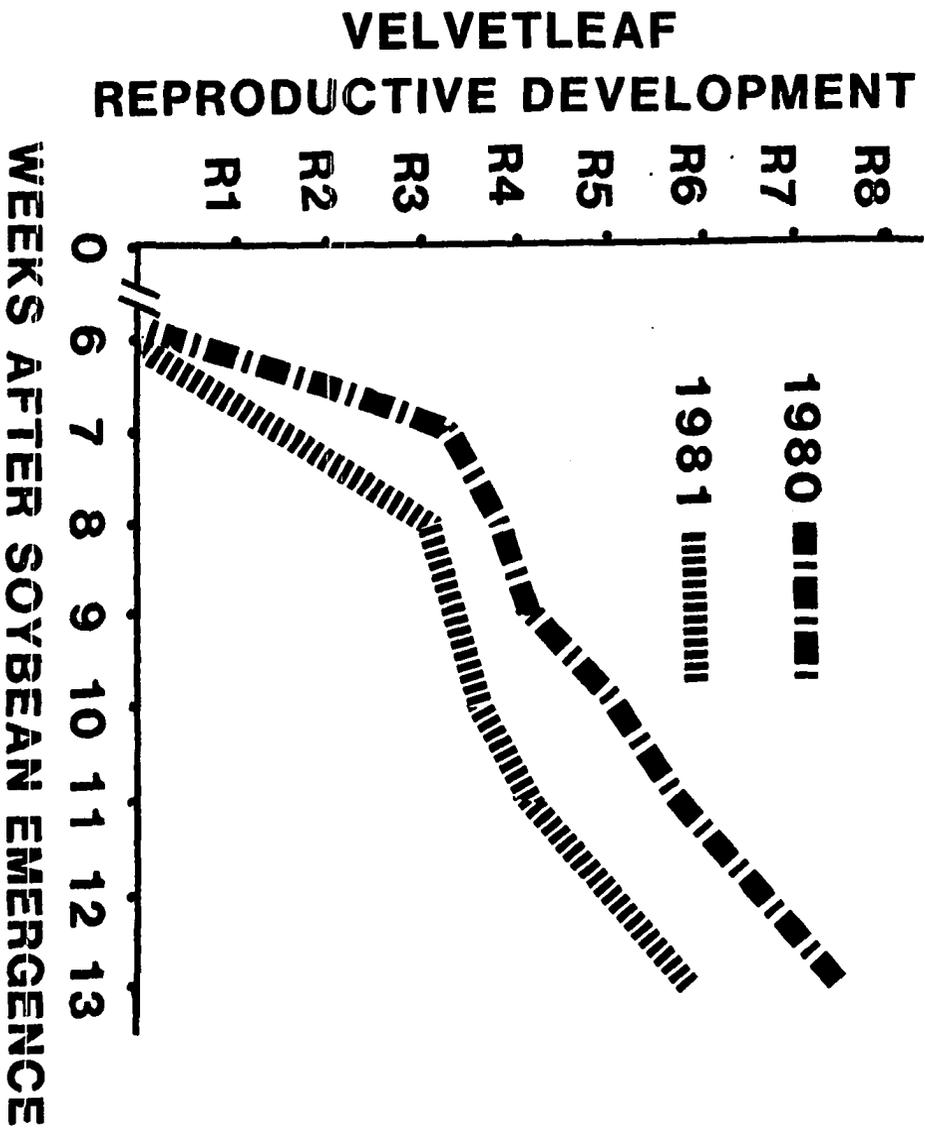
^c* = Significant at the 0.05 level.

^d** = Significant at the 0.01 level.

as complete, similar differences had been established in both components by at least 9 weeks after emergence. The average number of capsules present on soybean-stressed weeds by Week 13 was only 10.9% (1980) to 11.7% (1981) of numbers present on monocropped weeds. SGCW defoliation (equivalent to 48 (1981) or 54 (1980) GCW larvae/30 cm of soybean row) did not alter the number of reproductive structures successfully developed on weeds intercropped with soybeans.

Characteristically, crop plants in a given field are very similar genetically and pass through their various developmental stages as a unit, with little plant-to-plant variation. In contrast, a field infestation of velvetleaf develops from many parental lines. For this reason, greater variation between individuals should be anticipated even when weeds emerge nearly simultaneously (as in this study, or where a final pre-plant tillage operation results in a flush of newly germinating weeds). Therefore, the greater variability in R-stage observed for velvetleaf than soybeans on any sampling date seems to be a logical outcome of greater genetic diversity. The occasional apparent lack of agreement (described below) between Table 7 and Figure 12 was actually caused by variation in weed reproductive development. For instance, the average velvetleaf R-stage on Week 7 in 1981 was R1.6 (Figure 12) and not R3 (even though Table 7 shows an average of 1 capsule/weed). This apparent discrepancy arises because a few weeds have several capsules, whereas the majority lacked any capsules on this date. A similar explanation applies to the velvetleaf reproductive development presented for Week 13 in 1980. The average velvetleaf R-stage on this date was R7.2 (Figure 12, indicating that most weeds presented only capsules and no flowers). The presence of flowers

Figure 12. Mean velvetleaf reproductive development across all treatment combinations in 1980 and 1981



in Table 6 on the same sample date means that a few weeds continued to retain a large number of flowers.

The vast majority of velvetleaf capsules (hence seeds) are formed on branches and not in the axils of the primary leaves (unlike soybeans). Normally, only 1 capsule to a primary leaf axil was present, although in a very small number of weeds a few nodes would have 2 capsules at 1 or more leaf axils. Because of their important role in contributing to seed production and canopy leaf distribution, velvetleaf branches were counted weekly in all plots. To be counted as a branch, the edges of 2 leaves/axillary shoot must have been unfolded enough so the edges were no longer touching one another (i.e., at least 1 fully-developed leaf/branch was present). Branches were not detected until velvetleaf developed 9 to 10 nodes. Significantly more branches were present on intraspecific weeds than interspecific weeds 5 to 6 weeks after emergence (Figure 13). Twenty to 24 nodes developed branches by 11 weeks after emergence on weeds in intraspecific environments. However, less than one-half this number of branches were present on soybean-stressed weeds. No branching differences between weed densities were significant in either environment. Shading caused by the adjacent soybean canopy effectively prevented the development of basal branches on the interspecific weeds. Thus, rapid branch development was delayed for these weeds until 8 or more weeks after emergence (when velvetleaf exceeded soybeans in height). However, increasing the level of SGCW defoliation of soybeans did not cause a concomitant increase in intercropped velvetleaf branch number.

Figure 13. Development of velvetleaf branches under conditions of intraspecific competition only (INTRA or solid lines) and development of velvetleaf branches under conditions of interspecific competition with defoliated and undefoliated soybeans (INTER or broken lines)

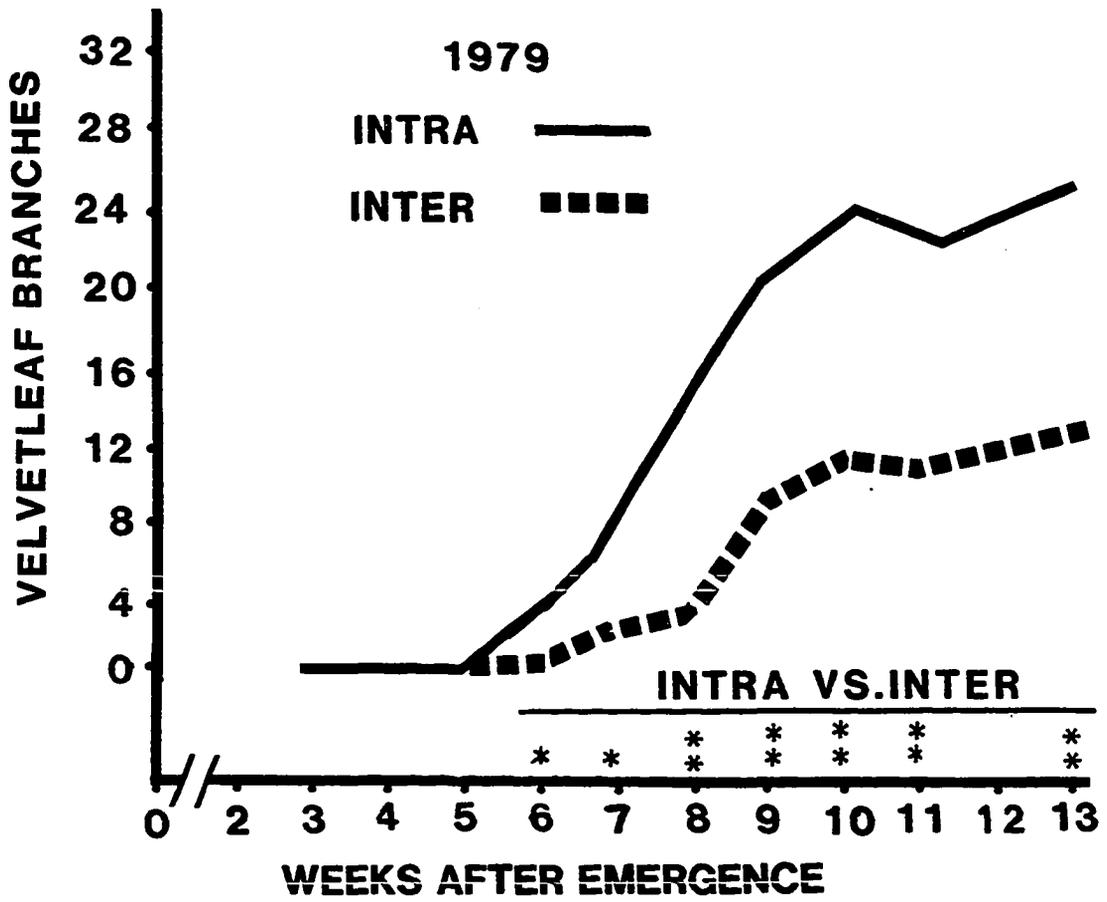


Figure 13. (continued)

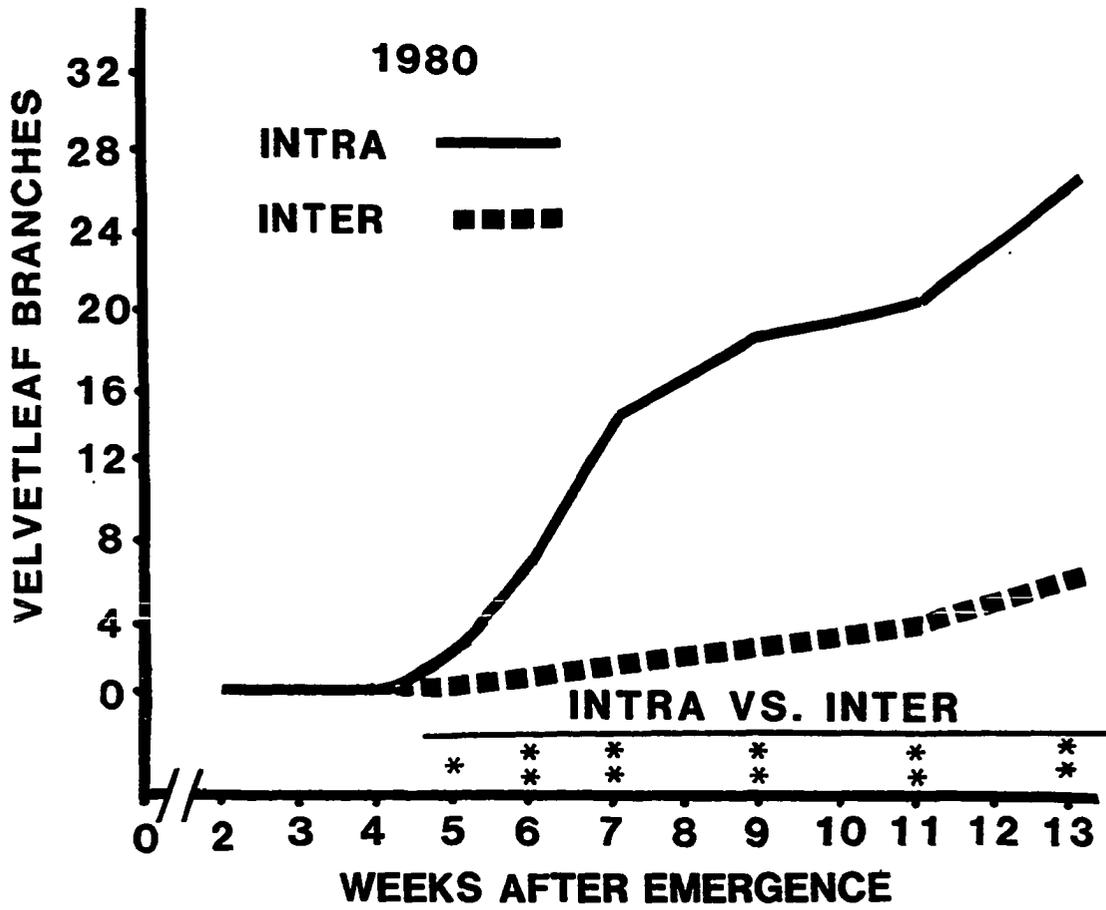
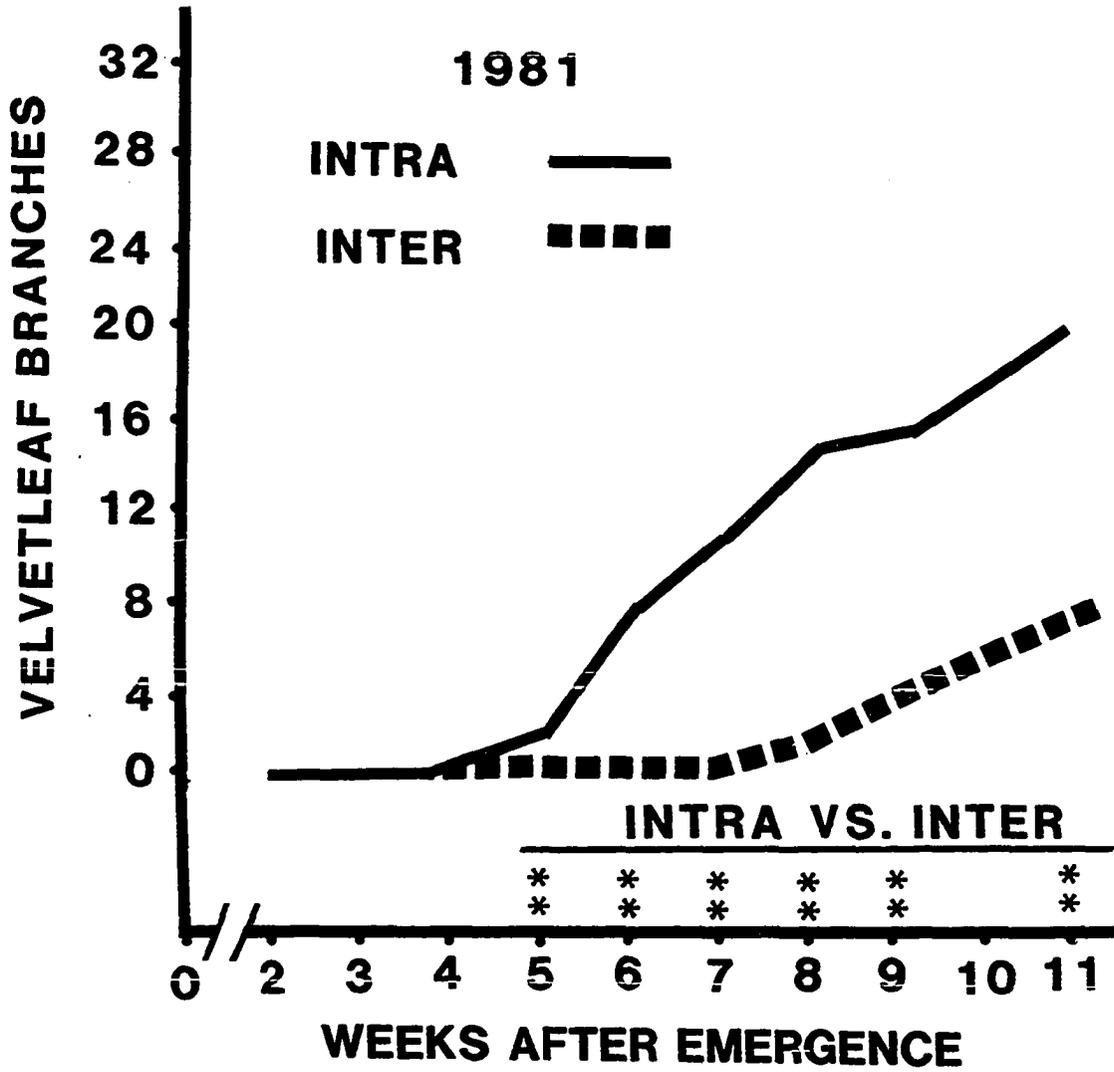


Figure 13. (continued)



Velvetleaf Yield Component Analysis

An important objective of annual-weed management is to limit the quantity of viable weed seeds returned to the soil. However, plants stressed by biological or physical factors often have their reproductive capabilities already substantially restricted. Therefore, weed-seed production should be quantified on weeds developing under representative stress environments, if the data are to be applicable to specific situations. Additionally, some components of seed yield may respond to specific stresses by decreasing or increasing quantity or size, whereas others may not be capable of any variation. To better understand the resilience of velvetleaf-seed yield under a variety of intraspecific and interspecific stresses, each important yield component was evaluated. Treatment effects on capsules/plant, carpels/capsule, and seeds/carpel were quantified. Seed weight, unlike the components affecting seed number, was not thought important enough to necessarily warrant investigation (in contrast to crop-yield situations where seed weight can be very important from a monetary standpoint). The results of the yield-component analyses and estimates of weed-seed yield derived therefrom (on a plant and m^2 of soil surface basis) are presented in Table 8.

Treatments removing weeds by 5.5 weeks after emergence (bentazon or roguing) prevented any seed production. In fact, other data on capsule development (Table 7) indicate that capsules were not developed until sometime between 6 and 7 weeks after emergence. Although the 2-cm size may or may not correspond to the formation of viable seeds within the capsule, 6

Table 8. Seed yield component analysis of velvetleaf under intraspecific competition and interspecific competition with undefoliated and defoliated (36 SGCW/30 cm of soybean row) soybeans

Velvetleaf density	Treatment combination			Capsules/plant	
	Velvetleaf duration	Type of competition	SGCW density	1980	1981
All	5.5 weeks	All	--	0	0
1/3.0 m	Full-season	Inter	0	42.5	28.3
2/3.0 m	Full-season	Inter	0	40.8	34.8
1/3.0 m	Full-season	Inter	36	37.8	42.8
2/3.0 m	Full-season	Inter	36	44.3	38.3
1/3.0 m	Full-season	Intra	--	334.3	311.3
2/3.0 m	Full-season	Intra	--	425.8	303.5

Results of relevant orthogonal treatment comparisons applied to velvetleaf yield component data

C4: (1/3.0-m Inter vs. 2/3.0-m Inter)	NS ^a	NS
C5: (0 SGCW/30 cm of row vs. 36 SGCW/30 cm or row)	NS	NS
C6: (C4 x C5)	NS	NS
C7: (1/3.0-m Intra vs. 2/3.0-m Intra)	NS	NS
C8: (Intra vs. Inter)	** ^b	** ^b

^aNS = Not significant.

^b** = Significant at the .01 level.

^c* = Significant at the .05 level.

<u>Carpels/capsule</u>		<u>Seeds/carpel</u>		— Estimated seed production —			
1980	1981	1980	1981	Velvetleaf basis		m ² soil-surface- area basis	
				1980	1981	1980	1981
--	--	--	--	0	0	0	0
14.4	14.6	2.95	2.94	1826	1204	801	528
14.3	14.0	2.95	2.92	1718	1432	1507	1256
14.7	14.3	2.93	2.92	1614	1787	643	784
14.5	13.9	2.94	2.94	1877	1556	1647	1365
14.5	14.9	2.94	2.92	14149	13557	6206	5955
14.4	14.8	2.94	2.93	18024	13161	15811	11545

NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	**	**
NS	* ^C	NS	NS	**	**	**	**

weeks is a seemingly valid (conservative) velvetleaf weed-seed free interval (in both intraspecific and interspecific environments, assuming a late May emergence).

Each velvetleaf growing in any full-season plot eventually produced capsules containing fully-formed seeds. However, certain treatments differed in numbers of capsules produced on each plant. In both 1980 and 1981, substantially more capsules were produced on intraspecific velvetleaf than interspecific (soybean-stressed) velvetleaf. Interspecific velvetleaf produced an average of 36.1 (1981) to 41.4 (1980) capsules regardless of weed density or soybean defoliation level. In contrast, monocropped weeds yielded 307.4 (1981) to 380.5 (1980) capsules/plant, with no significant differences caused by doubling the weed density. The greatest capsule production, on a plant basis, in intraspecific and interspecific environments was 711 and 83, respectively.

Capsules possessed from 11 to 16 carpels each, with approximately 14.5 carpels/capsule being the average. Only in 1981 were treatment differences noted. Monocropped weeds seemed to average slightly more carpels/capsule than weeds intercropped with soybeans that year. Each carpel contained between 2 and 3 seeds, but averaged a remarkably consistent 2.94 seeds/carpel. The various competitive environments tested did not alter the number of seeds/carpel significantly. Seeds/capsule (the product of carpels/capsule and seeds/carpel) varied from 33 to 47. An overall average of 42.8 seeds/capsule was recorded. However, even the minimum number noted in this study substantially exceeded the average number/capsule reported in a regional research report (5 to 15 seeds/capsule) as typical for the species (Illinois Agricultural Experiment Station, 1974). Chandler and Dale (1974) also

recently reported an average capsule production of approximately 42 seeds. None of the tested SGCW defoliation and weed density levels altered carpels/capsule, seeds/carpel, or the composite seeds/capsule component significantly.

Seed production estimates were initially calculated within each replication (on a plant and m^2 -of-soil-surface basis) to facilitate statistical analyses of treatment effects. Monocropped velvetleaf produced approximately 9 times the seed (on a plant basis) as the average soybean-stressed velvetleaf. The maximum seed yield recorded for a single velvetleaf in this study was estimated at 29,760 seeds when weeds were monocropped. Intercropping velvetleaf with soybeans reduced the maximum single plant production to about 3,620 seeds. Defoliating the adjacent soybeans by the equivalent of 36 GCW larvae/30 cm of soybean row (20 to 26% at the full-bloom stage) did not significantly increase velvetleaf seed production. However, the importance of weed density became more evident when seed production was expressed in more practical terms (number/ m^2 of soil surface). Doubling the density of maturing weeds effectively doubled the seed production/ m^2 of soil surface because weed-to-weed interference was not great enough to substantially reduce seed production at the tested levels. Thus, it was not surprising that significant differences were detected between monocropped velvetleaf planted at 1 and 2 velvetleaf/3.0 m of row. Substantial variability in seed production of soybean-stressed weeds prevented the tendencies for greater weed-seed yield/ m^2 in high-density interspecific environments from being significant.

Discovery of an Unknown Velvetleaf Seed Predator

Velvetleaf seed from intraspecific and interspecific competition plots (30 August 1981 only) were sequestered in insect-tight plastic cases in lots of 15 capsules each for later use in a proposed germination study. Approximately 2 months later (25 October) several small, gray, ovoid beetles were found clinging to the vertical walls of the container. Closer examination revealed an equivalent number of variously hollowed seed coats with hinged flaps (operculum) cut through the testa. Many other seeds were distinctly translucent and each of these had a single hemispherical operculum well-defined to facilitate emergence of the adult beetle. Dr. J. M. Kingsolver of the USDA Insect Identification and Beneficial Insect Introduction Institute in Beltsville, Maryland, identified this seed predator as an undescribed species of the insect family Bruchidae (*Abutiloneus* new species). Other species in this family frequently destroy large numbers of seeds, but their most common hosts occur in the Leguminosae. Depending on the economic value of the host, the seed destruction may be considered beneficial or deleterious. The potential of this species for biological control of velvetleaf has not yet been explored. An examination of the numerous seeds in each zipper case revealed a broad range in the number of seeds damaged or destroyed. From 1 to 22% of the seeds had been destroyed (overall average of 4.5%). No differences in bruchid attack rates between intraspecific and interspecific seed lots were detected.

PART IV.

PARTIAL GROWTH ANALYSIS OF VELVETLEAF STRESSED BY
INTRASPECIFIC COMPETITION AND INTERSPECIFIC COMPETITION
WITH UNDEFOLIATED AND DEFOLIATED SOYBEANS

ABSTRACT

Velvetleaf dry weight (VDWT) accumulation under selected combinations of intraspecific (velvetleaf only) and interspecific (velvetleaf and defoliated or undefoliated soybeans) competition were evaluated in a 2-year field study. Dry weights of monocropped velvetleaf planted at 2 weeds/3.0 m of row (76-cm centers) showed limited evidence of interference between adjacent plants by 42 days after emergence. Intraspecific weeds exceeded interspecific weeds in leaf VDWT (VLDWT), support VDWT (VSDWT), and reproductive VDWT (VCDWT) within 27, 37, and 56 days of emergence, respectively. By 76 days after emergence, intraspecific velvetleaf possessed over 9 times the dry matter of interspecific velvetleaf. Defoliating soybeans (20 to 26% LAI reduction) resulted in little evidence of significantly increased VDWT production. However, 76 days after emergence (18 or 19 days after defoliation was terminated) strong trends for increased component VDWTs were evident. In general, treatments had a more adverse effect on VDWTs than weed growth rates.

INTRODUCTION

Agronomic 'growth analysis' is finding increasing usage in studies of field crop development. Recently, weed scientists have begun using this technique to better understand the nature of varying degrees of biological stress resulting from interplant interference. Information on velvetleaf dry-weight (VDWT) accumulation has been published in at least 4 studies, 3 of which have dealt with velvetleaf in soybeans (Eaton et al., 1976; Chandler, 1976; Hagood et al., 1980; Oliver, 1979). However, only Oliver (1979) formally presented weed (= crop) growth rates. None of the listed studies partitioned total above-ground dry weight of velvetleaf into leaf, support, and reproductive components.

To date, all published studies quantifying the mutual suppression of weeds and row crops have been limited to situations where the crop was intentionally protected from additional stress caused by other biological organisms. However, it seems feasible that certain defoliating insects (in consuming the foliage of a weed-stressed crop) may shift the interspecific competitive advantage more in favor of the weed. Such a shift may result in substantially increased weed growth which, potentially, aggravates the level of competitive interference through intensified moisture demands, shading, and nutrient removal. Although the adverse ramifications to growers and pest management specialists of such a scenario should be self-evident, no published information on potential interactions between these 2 pest types is available.

For these reasons, the dry weight development of velvetleaf under various levels of intraspecific and interspecific stress was examined. Data were collected on a component basis for a more flexible and descriptive interpretation of treatment effects.

METHODS AND MATERIALS

Velvetleaf were destructively subsampled on 5 dates in 1980 and 1981 from the established competition and defoliation stress-interaction experiment described in the preceding sections. Plots selected for the weed-growth analysis included: 1 and 2 velvetleaf/3.0 m of row developing under intraspecific competition, and all interspecific competition plots with densities of 2 weeds/3.0 m of soybean row and 0 or 36 SGCW/30 cm of soybean row. A minimum of 2 weeds/treatment were removed from each replication, divided into leaf, support (stem and petiole), and nonflower reproductive (capsule) fractions and oven-dried to a constant moisture content before weighing. Component and total mean velvetleaf weed growth rates (\overline{WGRs} , g/m² soil/day) and mean relative growth rates (\overline{RGRs} , 'interest rates') were calculated (on a plot basis), according to formulae presented by Radford (1967), before analyses of treatment differences were conducted. Analyses of variance and relevant orthogonal contrasts were employed for separation of means.

RESULTS AND DISCUSSION

Results are summarized in Tables 9 through 12. To prevent unnecessary repetition, the results of each relevant statistical test are summarized in a column below the listed treatment means. The orthogonal comparison 'C1' summarizes significant differences in dry weight (DWT) characteristics between 1 and 2 velvetleaf/3.0 m of row (intraspecific competition, soybeans removed at emergence). A significant C1 test indicates probable interference between adjacent velvetleaf (originating either from in-row or across-row locations). Differences between velvetleaf growing alone (intraspecific competition or intraspecific weeds) and velvetleaf growing alongside a soybean row (interspecific competition or interspecific weeds) are noted in 'C2'. Therefore, significant C2 tests reflect the development of interspecific stress between adjacent soybeans and velvetleaf. Any abnormal increase in interspecific weed DWT, resulting from SGCW-defoliation of the adjacent full-bloom soybeans, is described by significance of 'C3'. Only the appropriate data sets were included in each analysis.

Velvetleaf Dry Weight Accumulation and Allocation Under
Conditions of Intraspecific Competition Only

Comparison C1 showed only a temporary difference in the leaf DWT (VLDWT) on monocropped velvetleaf in 1980 (Table 9). Low-density (1 weed/3.0 m of row) and high-density (2 weeds/3.0 m of row) intraspecific velvetleaf had 14.8% more or less VLDWT, respectively, than the overall 242.7 g average. However, no differences were evident in the subsequent sample. In 1981, more consistent evidence of interference was noted. That year,

^aRelevant orthogonal treatment comparisons.

C1: 1 weed/3.0 m (INTRA) vs. 2 weeds/3.0 m of row (INTRA).

C2: INTRA vs. INTER.

C3: 0 SGCW/30 cm of row (INTER) vs. 36 SGCW/30 cm of row (INTER).

^bNS = not significant.

^c** = Significant at the 1% level.

^d* = Significant at the 5% level.

the Harvest 4 advantage of low-density weeds was 17.8% for support DWT (VSDWT) and 31.9% for total above-ground DWT (VTDWT), above the overall intraspecific averages. Although not significant, relative increases in VLDWT (12%) and capsule DWT or VCDWT (22%) of low-density intraspecific weeds also contributed to the large, but temporary, significant differences in Harvest 4 VTDWT. Harvest 5 in 1981 showed additional evidence of interference between individual weeds at the high monocrop density. Low-density weeds had VLDWTs, VSDWTs, and VCDWTs that differed +23.5, +15.9, and -34.3% from the listed intraspecific average, whereas the trends in high-density weeds were reversed by an equivalent amount. Together, these differences resulted in only a 10% change in VTDWT ($p = 0.08$), favoring the low-density weeds.

The above data indicate that changes in one component were not automatically accompanied by equivalent responses in other components on the same plant. The substantial differences reported between intraspecific VCDWTs in 1981 (Harvest 5, samples collected nearly 11 weeks after emergence) was not corroborated late in Week 13, however. No differences were recorded in capsule number or estimated velvetleaf seed production between intraspecific densities at that time (Part III), indicating that VCDWTs probably were not very different either. Also noted in Part III, however, was that, by Week 11 (1981), velvetleaf were not yet declining in leaf area. These weeds also were not as advanced reproductively as in the preceding year. Additionally, the only significant difference in component percentages of intraspecific TDWTs favored the population-stressed (high-density) weeds (Table 10). Specifically, 24.5% of high-density VTDWT was

Table 10. Mean percentage of VTDWT contributed by leaf (VLPCT), support (VSPCT), and capsule (VCPCT) components under conditions of intraspecific (INTRA) and interspecific (INTER) competition and a summary of significant orthogonal treatment comparisons^a in 1980 and 1981

Harvest	Elapsed time from emergence			VLPCT		VSPCT		VCPCT	
	1980	1981		1980	1981	1980	1981	1980	1981
	days			%					
1	28	27	INTRA:	--	78	--	22	--	0
			INTER:	72	74	28	26	0	0
			C1:		NS ^b		NS		
			C2:		NS		NS		
2	35	37	INTRA:	--	62	--	38	--	0
			INTER:	63	55	37	45	0	0
			C1:		NS		NS		
			C2:		NS		NS		
3	42	46	INTRA:	--	60	--	40	--	0
			INTER:	44	46	56	54	0	0
			C1:		NS		NS		
			C2:		** ^c		**		
4	56	58	INTRA:	44	44	50	50	6	6
			INTER:	30	35	64	60	6	5
			C1:	NS	NS	NS	NS	NS	NS
			C2:	**	**	**	**	NS	NS
			C3:	NS	NS	NS	NS	NS	NS
5	75	76	INTRA:	23	26	58	57	19	17
			INTER:	20	29	56	60	23	11
			C1:	NS	NS	NS	NS	NS	** ^d
			C2:	NS	NS	NS	NS	NS	* ^d
			C3:	*	NS	NS	NS	NS	NS

^aRelevant orthogonal treatment comparisons.

C1: 1 weed/3.0 m (INTRA) vs. 2 weeds/3.0 m of row (INTRA),

C2: INTRA vs. INTER,

C3: 0 SGCW/30 cm of row (INTER) vs. 36 SGCW/30 cm of row (INTER).

^bNS = Not significant.

^c** = Significant at the 1% level.

^d* = Significant at the 5% level.

already allocated to capsules in Harvest 5 samples, whereas only 9.6% of the low-density weed DWT was in capsules. For the above reasons, it is quite possible that differences in VCDWT evident in Week 11 (Harvest 5) in 1981 were real, but may have diminished before the weeds actually matured.

Velvetleaf Dry Weight Accumulation and Allocation when Comparing
Weeds from Intraspecific and Interspecific
Competition Environments

Highly significant differences in VDWT accumulation between intraspecific and interspecific environments were evident early in development (Table 9). Values of VLDWT and VTDWT were significantly smaller (59.2 and 57.1%, respectively) in soybean-stressed plots at the first harvest in 1981. Although the average VSDWT of interspecific weeds was only 50% of monocropped velvetleaf at Harvest 1, statistically significant differences were not detected until Harvest 2 in 1981. The first time capsules were detected, large differences in VCDWT were present in the samples. All components were significantly smaller in interspecific than intraspecific environments by Harvest 4 in both years. At Harvest 5, interspecific plots possessed only 6.4 to 11.3% of the VLDWT, 7.7 to 10.5% of the VSDWT, 7.2 to 11.2% of the VCDWT, and 8.0 to 10.2% of the VTDWT, determined in plots where velvetleaf was monocropped. The higher values characteristic of VLDWT, VSDWT, and VTDWT in 1981 versus 1980 closely paralleled similar late season differences in velvetleaf leaf area, canopy width, and weed-to-soybean height differentials between years (Part III).

A significantly higher proportion of VTDWT was maintained longer as VLDWT in monocropped velvetleaf than where weeds were intercropped with

soybeans (viz VLPCT in Table 10). The apparent increase in the proportion of intraspecific VSDWT (denoted VSPCT) probably resulted from the higher levels of lower-leaf abscission (Part III) and concomitant overall younger average leaf age. Plants growing under partially-shaded or light stressed environments (herein caused by the close proximity of the soybean canopy) characteristically develop this type of DWT distribution. Monocropped weeds (Harvest 5), on the average, had allocated a greater proportion of the VTDWT to VCDWT (denoted VCPCT) in 1981 than intercropped weeds. However, no difference in VCPCT was noted in 1980.

Velvetleaf Dry Weight Accumulation and Allocation when Comparing
Interspecific Competition with Defoliated and
Undeveloped Soybeans

The SGCW-defoliation procedure, initiated and completed between Harvests 3 and 4, had reduced soybean LAI by 20 to 26% and soybean LDWT by 10.7 to 24.0% in 1980 and 1981, respectively (Parts I and II). No significant changes in component VDWT were detected subsequent to the completion of the defoliation schedule (C3 in Table 9). An examination of SGCW treatment means showed no consistent pattern on Harvest 4, with only very small differences present (limited to 5% of the overall mean). By Harvest 5, however, every characteristic of VDWT was substantially heavier in the plots where the defoliation (equivalent to 36 SGCW/30 cm of soybean row) was imposed. A ranking of components from the most responsive through the least responsive (strictly on a percentage basis) would show: VCDWT (+55%), VLDWT (+25.8%), VTDWT (+24.5%), and VSDWT (+13.7%). Seemingly, the intrinsic variability of velvetleaf nearing maturity and stressed throughout the

season by soybean competition was great enough to overrule this consistent trend. Probably an earlier defoliation treatment or more replications would reveal that soybeans defoliated by insects lose some of their ability to suppress weed development. Unfortunately, additional velvetleaf plants could not be spared in this study for a more thorough destructive analysis of weed DWT resilience.

Without exception, velvetleaf in SGCW-defoliated soybean plots had, by Harvest 5, a larger percentage of VTDWT composed of VLDWT (4 to 8% more) and VCDWT (4 to 7% more) than weeds competing with undefoliated soybeans. Conversely, these same defoliated-plot velvetleaf had a lower proportion of VTDWT partitioned into VSDWT (11 to 12% less). However, only in 1 instance was the difference significant (Table 10). These trends are probably largely explainable in terms of increased availability of light, directly resulting from the SGCW defoliation of adjacent soybeans. Thus, although it seems possible for defoliation to alter the weed to crop competitive status, firm evidence to support this hypothesis (statistically) was not realized. It may be that soybean defoliation occurring earlier in the season than the full-bloom phenology (characteristic of the green cloverworm) used in this study would have a more substantial weed-releasing effect.

Weed Growth Rates and Relative Growth Rates of Velvetleaf

Under Conditions of Intraspecific Competition Only

Intraspecific velvetleaf leaf \overline{WGR} (\overline{VLWGR}) and support \overline{WGR} (\overline{VSWGR}) showed the largest period increases during Intervals 4 and 5 (Table 11; these intervals correspond to Interval 4 and 6, respectively, in the

soybean DWT section, Part II). As expected, this period of rapid DWT growth also closely paralleled the rapid increase in leaf area and height of these weeds (Part III). Greater component \overline{WGR} s of low-density intraspecific weeds, relative to high-density weeds (indicating weed-to-weed interference), also were restricted to these last 2 sampling intervals. These differences between intraspecific \overline{WGR} s were detectable in 1981 but not in 1980. The larger volume occupied by 1981 velvetleaf (leaf area/plant of 44,600 cm² and canopy widths of 168 cm) than 1980 velvetleaf (leaf area/plant of 38,000 cm² and canopy widths of 145 cm) may have contributed to this differential response (Part III). In 1981, the population-stressed weeds had 15.8 (Interval 5) to 22 (Interval 4) percent smaller \overline{VSWGR} s, a 33.5% smaller \overline{VLWGR} (Interval 5), and a 20.9% smaller total above-ground \overline{WGR} (\overline{VTWGR} , Interval 4) than the overall intraspecific means (Table 11). Consequently, their low-density counterparts had correspondingly higher values in these component growth rates. Surprisingly, no differences between densities in \overline{VTWGR} s were detected during Interval 5. This lack of significance in \overline{VTWGR} was caused by an offsetting, greater capsule \overline{WGR} (\overline{VCWGR}) (43.7%) in high-density weed plots. If these 1981 differences are accurate, they indicate that velvetleaf may respond to competition developing late in the season by increasing reproductive growth relative to vegetative growth.

The pattern of velvetleaf \overline{RGR} of plants under intraspecific competition varied somewhat in 1981, but, in general, component and total \overline{RGR} declined as the season progressed (Table 12). Only in 1 instance did density significantly influence the 'rate of interest' or \overline{RGR} . As with \overline{VCWGR} ,

^aRelevant orthogonal treatment comparisons.

C1: 1 weed/3.0 m (INTRA) vs. 2 weeds/3.0 m of row (INTRA).

C2: INTRA vs. INTER.

C3: 0 SGCW/30 cm of row (INTER) vs. 36 SGCW/30 cm or row (INTER).

^bNS = Not significant.

^{c**} = Significant at the 1% level.

^{d*} = Significant at the 5% level.

^aRelevant orthogonal treatment comparisons -

C1: 1 weed/3.0 m (INTRA) vs. 2 weeds/3.0 m of row (INTRA).

C2: INTRA vs. INTER.

C3: 0 SGCW/30 cm of row (INTER) vs. 36 SGCW/30 cm of row (INTER).

^bNS = not significant.

^{c**} = Significant at the 1% level.

^{d*} = Significant at the 5% level.

Interval 5 capsule \overline{RGR} (\overline{VCRGR}) was greater in the population-stressed monocrop planting. Plots with 2 velvetleaf/3.0 m of row had a $\overline{VCRGR} \times 100$ value of 16.0, whereas values in plots with only 1 velvetleaf/3.0 m of row were approximately one-half this magnitude.

Weed Growth Rates and Relative Growth Rates of Velvetleaf
Under Conditions of Intraspecific
and Interspecific Competition

Soybean competition reduced growth rates of intercropped velvetleaf substantially below weed growth levels in soybean-free environments. Values of \overline{WGR} calculated for leaf, support, capsule, and total above-ground fractions were consistently smaller in soybean-stressed plots beginning sometime during Intervals 1, 2, 4, and 2, respectively (Table 11). During the final interval sampled, weeds intercropped with soybeans were only adding 8.5 to 10.8% of the VLDWT, 6.3 to 8.1% of the VSDWT, 6.6 to 11.5% of the VCDWT and 7.9 to 8.3% of the VTDWT of monocropped weeds on a daily basis.

Component \overline{RGR} s of weeds competing with soybeans had mean values less than the soybean-free weeds during each sampling interval. However, significant differences were not consistently obtained (Table 12). Smaller leaf \overline{RGR} s (\overline{VLRGR} s) reduced total above-ground \overline{RGR} s (\overline{VTRGR} s) of interspecific velvetleaf through Interval 2 in 1981. A significantly reduced \overline{VTRGR} again was realized during the final sample interval. In this instance a smaller support \overline{RGR} (\overline{VSRGR}) was the component causing the reduction. Interval 4 in 1981 was characterized by a smaller \overline{VCRGR} in interspecific environments.

Weed Growth Rates and Relative Growth Rates of Velvetleaf
Competing with Defoliated and Undefoliated Soybeans

No significant differences in component \overline{WGRs} and \overline{VRGRs} were determined either year in response to defoliation of adjacent soybeans at the full-bloom stage (Tables 11 and 12). However, a consistent trend of reduced \overline{WGRs} was noted in the final interval, indicating that substantial responses were occurring in many plants. During this interval, the \overline{VLWGR} , \overline{VSWGR} , \overline{VCWGR} , and \overline{VTWGR} of interspecific velvetleaf in 1980 defoliated plots averaged 0.24, 1.05, 0.97, and 2.27 g/m² soil/day. Velvetleaf adjacent undefoliated soybeans were adding an average of 0.13, 0.46, 0.25, and 0.84 g/m² soil/day, respectively, during the same interval in 1980. Similarly, the defoliated plot weeds in 1981 also seemed to have some components growing faster during Interval 5. Average daily increases of 0.82 g/m² in \overline{VLWGR} , 1.39 g/m² in \overline{VSWGR} , 0.16 g/m² in \overline{VCWGR} , and 2.69 g/m² in \overline{VTWGR} were recorded for the weeds adjacent defoliated soybeans. In comparison, the weeds in undefoliated plots were limited to a mean daily gain of 0.39 g/m², 1.38 g/m², 0.09 g/m², and 2.06 g/m² for each component, respectively. The nonsignificant differences in \overline{VRGR} caused by defoliation ranged from a high of 56% in \overline{VLRGR} (1981) to no detectable difference in \overline{VSRGR} the same year. Once again, the highest values were associated with weeds growing in the defoliated plots.

GENERAL SUMMARY AND CONCLUSIONS

Soybean and velvetleaf pre-harvest growth and development were evaluated in a 3-year field experiment using selected combinations of annual weed competition and(or) simulated insect defoliation. The experiment consisted of 2 velvetleaf densities, 3 velvetleaf durations (plus a weed-free control), and 3 or 4 simulated green cloverworm densities (plus an insect-free control). Bentazon and roguing were used to terminate weed competition about 4 and 5.5 (6.5 in 1979) weeks after emergence, respectively. Full-season competition was terminated by natural weed senescence 12 to 14 weeks after emergence. A temperature-dependent hole-punching procedure was employed to insure the proper temporal intensity of the defoliation treatments (simulating equally-spaced densities of green cloverworm larvae). A split-plot design was used such that a factorial arrangement of weed density and duration formed the main-plot treatments, and density of simulated green cloverworm larvae formed the subplot treatments. Selected vegetative and reproductive morphological characteristics of both soybeans and velvetleaf were determined weekly. Component (leaf, support, and reproductive) dry matter accumulations of the crop and weeds also were evaluated on 5 significant dates. Sampling and statistical analyses were conducted by considering developmental information obtained from selected weed-proximate or weed-distant soybeans separately (to enhance the chances of detecting stress interaction).

The primary conclusions ascertained from this study can be summarized as follows:

- 1) Statistical confirmation of velvetleaf competition stress was limited to soybeans in weed-proximate positions (viz., significant velvetleaf treatment effects were not evident on soybeans located ≥ 75 cm from the nearest in-row weed).
- 2) Weed-proximate soybeans responded to full-season velvetleaf competition by occasionally producing fewer nodes. Transient effects on soybean leaf area also were noted.
- 3) Weed-proximate soybeans in full-season velvetleaf plots did not exhibit significant reductions in component dry weights (DWTs), mean crop growth rates ($\overline{\text{CGRs}}$), and mean relative growth rates ($\overline{\text{RGRs}}$) until at least 42 days after emergence.
- 4) Simulated green cloverworm (SGCW) defoliation reduced soybean leaf area, height, pre-harvest lodging, and lower-leaf abscission (1 of 2 years). Nodal development lagged slightly in the defoliated plots during one year.
- 5) Although SGCW defoliation (36 SGCW/30 cm of row) reduced leaf DWTs (usually significantly), reproductive DWTs and growth rates were not retarded 18 or 19 days after defoliation had been terminated (75 or 76 days after emergence).
- 6) Tested levels of velvetleaf competition and simulated green cloverworm defoliation did not alter soybean stand counts, branching, or reproductive phenology.
- 7) Gravimetric soil moisture determinations did not differ significantly between any of the sampled stress-treated soybean plots on any date tested.

- 8) Statistical confirmation of velvetleaf and simulated green cloverworm treatment interactions was not realized through the analysis of soybean growth and development.
- 9) A proposed velvetleaf vegetative and reproductive staging system showed promise for standardizing reports of velvetleaf development.
- 10) The morphological development of velvetleaf was not appreciably altered when monocropped weed densities were doubled (from 1 to 2 weeds/3.0 m of row). In comparison, DWT data indicated that at least a limited amount of interference existed between adjacent plants of the upper density (when monocropped) beginning 42 or more days after emergence
- 11) Monocropped velvetleaf consistently exceeded intercropped velvetleaf in leaf area, nodes with fully-developed leaves, canopy widths, branches, and number of capsules as early as 3, 3, 4, 5, and 8 weeks after emergence, respectively.
- 12) Intraspecific velvetleaf exceeded interspecific velvetleaf in leaf, support, and reproductive DWT within 27, 37, and 56 days of emergence, respectively. By 76 days after emergence, intraspecific velvetleaf possessed over 9 times the dry matter of interspecific velvetleaf.
- 13) Intercropped velvetleaf were initially shorter than the soybean canopy (through 4 weeks), became equivalent to the crop in height (during Week 6 and(or) Week 7), and finally, exceeded the crop in canopy height.
- 14) Simulated green cloverworm defoliation of adjacent soybeans did not

alter weed heights significantly, but did affect the development of weed/soybean canopy heights differentials (by stunting the crop). Furthermore, an analysis of weed/soybean canopy height differentials indicated that the temporal feasibility of certain late-season weed control devices (rope-wick applicators and recirculating sprayers) may vary, depending on the level of insect defoliation previously tolerated.

- 15) Few velvetleaf morphological characteristics exhibited substantial increases in developmental rate after intercropped soybeans were defoliated. However, substantial nonsignificant increases in the DWTs of certain velvetleaf components were evident 18 or 19 days after defoliations were terminated. Velvetleaf reproductive development had commenced about the time that defoliation of soybeans began. Thus, from a physiological standpoint, the weeds may not have been able to use the additional resources (e.g., sunlight) toward enhancing the development of structural features (thereby further limiting the opportunity for interaction between competition and defoliation).
- 16) Six weeks is a seemingly valid (conservative) velvetleaf weed-seed free production interval (in both intraspecific and interspecific environments, assuming a late May emergence).
- 17) An examination of selected velvetleaf seed yield components (capsules/plant, carpels/capsule, and seeds/carpel) revealed that the tested levels of stressors restricted the number of capsules/plant (largely through a reduction in branch number) more than the other measured yield parameters.

- 18) Interspecific competition (full-season) with soybeans reduced the seed-production capabilities of velvetleaf approximately 9-fold. Defoliation of full-bloom soybeans (20 to 26%) did not significantly increase the seed production of nearby velvetleaf.
- 19) Adults of an undescribed beetle of the family Bruchidae (*Abutiloneus* new species) emerged from velvetleaf seed collected from plants in the 1981 study plots.

Special attention should be given to the fact that significant treatment interactions between annual-weed competition and simulated-insect defoliation (at the tested treatment levels) were not observed in this study. One possible interpretation is that weeds and insects are largely acting independently in their physiological effect on the crop and that losses may be additive rather than interactive or synergistic. An in-depth analysis of soybean yield and yield components (Higgins et al., 1982) supports the contention that little detectable interaction existed in this study. Higgins et al. (1982) reported that consistency in statistically determined interaction between selected combinations of competition and defoliation was restricted to weed-proximate soybeans, seemingly at the sub-plant level. However, it should be noted that a lack of substantial interaction between stressors in altering development and yield does not mean that management should be restricted strictly within disciplines (e.g., note Item 14 in the above discussion).

LITERATURE CITED

- Allen, G. E. and J. E. Bath. 1980. The conceptual and institutional aspects of integrated pest management. *Bioscience* 30:658-664.
- Altieri, M. A., A. van Schoonhoven and J. Doll. 1977. The ecological role of weeds in insect pest management systems: A review illustrated by bean (*Phaseolus vulgaris*) cropping systems. *PANS* 23:195-205.
- Barfield, C. S. and J. W. Jones. 1979. Research needs for modeling pest management systems involving defoliators in agronomic crop systems. *Florida Entomol.* 62:98-114.
- Barrentine, W. L. 1974. Common cocklebur competition in soybeans. *Weed Sci.* 20:600-603.
- Barrentine, W. L. and L. R. Oliver. 1977. Competition, threshold levels, and control of cocklebur in soybeans. *Mississippi Agric. For. Exp. Stn. Tech. Bull.* 83. 27 pp.
- Begum, A. and W. G. Eden. 1965. Influence of defoliation on yield and quality of soybeans. *J. Econ. Entomol.* 58:591-592.
- Bentley, S. and J. B. Whittaker. 1979. Effects of grazing by a chrysomelid beetle, *Gastrophysa viridula*, on competition between *Rumex obtusifolius* and *Rumex crispus*. *J. Ecol.* 67:79-90.
- Beuerlein, J. E. and J. W. Pendleton. 1971. Photosynthetic rates and light saturation curves of individual soybean leaves under field conditions. *Crop Sci.* 11:217-219.
- Blackman, G. E. and G. L. Wilson. 1951. Physiological and ecological studies in the analysis of plant environment. 7. An analysis of the differential effects of light intensity on the net assimilation rate, leaf-area ratio, and relative growth rate of different species. *Ann. Bot.* 15:373-408.
- Blomquist, R. V. and C. A. Kust. 1971. Translocation pattern of soybeans as affected by growth substances and maturity. *Crop Sci.* 11:390-393.
- Boote, K. J., J. W. Jones, G. H. Smerage, C. S. Barfield and R. D. Berger. 1980. Photosynthesis of peanut canopies as affected by leafspot and artificial defoliation. *Agron. J.* 72:247-252.
- Boyer, J. S. 1970. Leaf enlargement and metabolic rates of corn, soybean, and sunflower at various leaf water potentials. *Plant Physiol.* 46:233-235.

- Buchanan, G. A. 1977. Weed biology and competition. Pages 25-41 in B. Trueblood, ed. Research methods in weed science. S. Weed Sci. Soc. Auburn Printing, Inc., Auburn, Alabama.
- Burnside, O. C. 1978. Mechanical, cultural, and chemical control of weeds in a sorghum-soybean rotation. *Weed Sci.* 26:362-369.
- Bush, L. P. and D. W. Staniforth. 1962. Shading effects of annual weeds in soybeans. *N. Centr. Weed Contr. Conf.* 15:46-47.
- Buttery, B. R. 1969. Analysis of the growth of soybeans as affected by plant population and fertilizer. *Can. J. Plant Sci.* 49:675-684.
- Capinera, J. L. and W. J. Roltsch. 1980. Response of wheat seedlings to actual and simulated migratory grasshopper defoliation. *J. Econ. Entomol.* 73:258-261.
- Carlson, D. R. and O. C. Burnside. 1981. Use of the recirculating sprayer to control tall weed escapes in crops. *Weed Sci.* 29:174-179.
- Carner, G. R., M. S. Shepard and S. G. Turnipseed. 1974. Seasonal abundance of insect pests of soybeans. *J. Econ. Entomol.* 67:487-493.
- Caviness, C. E. and J. D. Thomas. 1980. Yield reduction from defoliation of irrigated and non-irrigated soybeans. *Agron. J.* 72:977-980.
- Chandler, J. M. 1976. Competition of spurred anoda, velvetleaf, prickly sida, and Venice mallow in cotton. *Weed Sci.* 25:151-158.
- Chandler, J. M. and J. E. Dale. 1974. Comparative growth of four Malvaceous species. *Proc. South. Weed Sci. Soc.* 27:116-117.
- Chiarappi, L., H. C. Chiang and R. F. Smith. 1972. Plant pests and diseases: Assessment of crop losses. *Science* 176:769-773.
- Clements, F. E., J. E. Weaver and H. Hanson. 1929. Plant competition. Carnegie Institute of Washington Publ. No. 398.
- Coggin, D. L. and G. P. Dively. 1980. Effects of depodding and defoliation on the yield and quality of lima beans. *J. Econ. Entomol.* 73:609-614.
- Davidson, A. 1973. Computerized plant growth analysis of the interactions of arthropod pests and other factors with the cotton plant. Ph.D. thesis. Univ. of California, Berkeley. 192 pp.

- Davis, R. G., A. F. Wiese and J. L. Pafford. 1965. Root moisture extraction profiles of various weeds. *Weeds* 13:98-100.
- DeWitt, J. R., H. J. Stockdale and R. B. Hammond. 1978. Green cloverworm control on soybeans. Ia. Coop. Ext. Serv. IC-436.
- Donald, C. M. 1951. Competition among pasture plants. I. Interspecific competition among annual pasture plants. *Aust. J. of Agr. Res.* 2:355-376.
- Donald, C. M. 1963. Competition among crop and pasture plants. *Adv. in Agron.* 15:1-118.
- Dornhoff, G. M. and R. M. Shibles. 1970. Varietal differences in net photosynthesis of soybean leaves. *Crop Sci.* 10:42-45.
- Eaton, B. J., K. C. Feltner and O. G. Russ. 1973. Venice mallow competition in soybeans. *Weed Sci.* 21:89-94.
- Eaton, B. J., O. G. Russ and K. C. Feltner. 1976. Competition of velvet-leaf, prickly sida, and Venice mallow in soybeans. *Weed Sci.* 24:224-228.
- Edens, T. C. and H. E. Koenig. 1980. Agroecosystem management in a resource-limited world. *Bioscience* 30:697-701.
- Egli, D. B. and J. E. Leggett. 1976. Rate of dry matter accumulation in soybean seeds with varying source-sink ratios. *Agron. J.* 68:371-374.
- Egli, D. B., D. R. Gossett and J. E. Leggett. 1976. Effect of leaf and pod removal on the distribution of ^{14}C labeled assimilate in soybeans. *Crop Sci.* 16:791-794.
- Enyi, B. A. C. 1975. Effects of defoliation on growth and yield in groundnut (*Arachis hypogea*), cowpeas (*Vigna unguiculata*), soybean (*Glycine max*), and green gram (*Vigna aurens*). *Ann. Appl. Biol.* 79:55-66.
- Evans, G. E. 1972. The quantitative analysis of plant growth. University of California Press, Berkeley, Calif. 734 pp.
- Fehr, W. R. and C. E. Caviness. 1977. Stages of soybean development. Iowa State Univ. Coop. Ext. Serv. Spec. Rep. 80.
- Fehr, W. R., C. E. Caviness and J. J. Vorst. 1977. Response of indeterminate and determinate soybean cultivars to defoliation and half-plant cut-off. *Crop Sci.* 17:913-917.
- Fehr, W. R., B. K. Lawrence and T. A. Thompson. 1981. Critical stages of development for defoliation of soybean. *Crop Sci.* 21:259-262.

- Frazee, R. W. and E. W. Stoller. 1974. Differential growth of corn, soybean, and seven dicotyledonous weed seedlings. *Weed Sci.* 22:336-339.
- Geddes, R. D., H. D. Scott and L. R. Oliver. 1979. Growth and water use by common cocklebur (*Xanthium pensylvanicum*) and soybeans (*Glycine max*) under field conditions. *Weed Sci.* 27:206-212.
- Gould, G. E. 1963. Japanese beetle damage to soybeans and corn. *J. Econ. Entomol.* 56:776-781.
- Hagood, E. S., T. T. Bauman, J. L. Williams and M. M. Schreiber. 1980. Growth analysis of soybeans (*Glycine max*) in competition with velvetleaf (*Abutilon theophrasti*). *Weed Sci.* 28:729-734.
- Hammerton, J. L. 1972. Effects of weed competition, defoliation, and time of harvest on soybeans. *Exp. Agric.* 8:333-338.
- Hammond, R. B. 1979. Green cloverworm phytophagy and simulation of insect defoliation on soybeans. Ph.D. thesis. Iowa State University Library, Ames, Iowa. 91 pp.
- Hammond, R. B. and L. P. Pedigo. 1981. Effects of artificial and insect defoliation on water loss from excised soybean leaves. *J. Kans. Entomol. Soc.* 54:331-336.
- Hammond, R. B. and L. P. Pedigo. 1982. Determination of yield-loss relationships for two soybean defoliators by using simulated insect-defoliation techniques. *J. Econ. Entomol.* 75:102-107.
- Hammond, R. B., L. P. Pedigo and F. L. Poston. 1979a. Green cloverworm leaf consumption on greenhouse and field soybean leaves and development of a leaf-consumption model. *J. Econ. Entomol.* 72:714-717.
- Hammond, R. B., F. L. Poston and L. P. Pedigo. 1979b. Growth of the green cloverworm and a thermal-unit system for development. *Environ. Entomol.* 8:639-642.
- Hanway, J. J. 1966. How a corn plant develops. Iowa State Univ. Coop. Ext. Serv. Special Rep. No. 43.
- Harper, J. L. and D. Gajic. 1961. Experimental studies on the mortality and plasticity of a weed. *Weed Res.* 1:91-104.
- Higgins, R. A., L. P. Pedigo and D. W. Staniforth. 1982. Yield and yield components of soybeans stressed by simulated insect defoliation and annual weed competition. Submitted to *J. Econ. Entomol.*
- Hinson, K., R. H. Nino and K. J. Boote. 1978. Characteristics of removed leaflets and yield response of artificially defoliated soybeans. *Soil and Crop Soc. of Florida* 37:104-109.

- Hughes, H. A. 1976. Crop chemicals - Fundamentals of machine operation. John Deere Service, Moline, Ill. 195 pp.
- Illinois Agricultural Experiment Station. 1974. Weeds of the North Central States. North Central Regional Publication. No. 36. Illinois Agric. Exp. Stn. Circular 718. 262 pp.
- Ingram, K. T., D. C. Herzog, K. J. Boote, J. W. Jones and C. S. Barfield. 1981. Effects of defoliating pests on soybean canopy CO₂ exchange and reproductive growth. *Crop Sci.* 21:961-968.
- Jaffe, M. J. and R. Biro. 1979. Thigmomorphogenesis: The effect of mechanical perturbation on the growth of plants, with special reference to anatomical changes, the role of ethylene, and interaction with other environmental stresses. Pages 25-51 in H. Mussell and R. C. Staples, eds. *Stress physiology in crop plants*. John Wiley and Sons, New York.
- Johnson, W. M. 1956. The effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges in central Colorado. *Ecology* 37:790-798.
- Johnston, T. J. and J. W. Pendleton. 1968. Contribution of leaves at different canopy levels to seed production of upright and lodged soybeans (*Glycine max* (L.) Merrill). *Crop Sci.* 8:291-292.
- Johnston, T. J., J. W. Pendleton, D. B. Peters and D. R. Hicks. 1969. Influence of supplemental light on apparent photosynthesis, yield, and yield components of soybeans (*Glycine max* L.) *Crop Sci.* 9:577-581.
- Kalton, R. R., C. R. Weber and J. E. Eldredge. 1949. The effect of injury simulating hail damage to soybeans. *Iowa Agr. and Home Econ. Exp. Stn. Res. Bull.* 359:736-796.
- Kalu, B. A. and G. W. Fick. 1981. Quantifying morphological development of alfalfa for studies of herbage quality. *Crop Sci.* 21:267-271.
- Khedir, K. D. and F. W. Roeth. 1981. Velvetleaf (*Abutilon theophrasti*) seed populations in six continuous-corn (*Zea mays*) fields. *Weed Sci.* 29:485-490.
- Kincade, R. E., M. L. Laster and E. E. Hartwig. 1971. Simulated pod injury to soybeans. *J. Econ. Entomol.* 64:984-985.
- Klingman, G. C. and F. M. Ashton. 1975. *Weed science: Principles and practices*. J. Wiley and Sons, New York. 431 pp.
- Kogan, M. 1976. Evaluation of economic injury levels for soybean insect pests. Pages 515-533 in L. D. Hill, ed. *World soybean research. Proc. World Soybean Res. Conf.* Interstate Printers and Publ., Danville, Ill.

- Koller, H. R., W. E. Nyquist and I. S. Chorush. 1970. Growth analysis of the soybean community. *Crop Sci.* 10:407-412.
- Lawn, R. J. and W. A. Brun. 1974. Symbiotic nitrogen fixation in soybeans. I. Effects of photosynthetic source-sink manipulations. *Crop Sci.* 14:11-16.
- Lockwood, J. L., J. A. Perich and J. N. Maduwesi. 1977. Effect of leaf removal simulating pathogen-induced defoliation on soybean yields. *Plant Dis. Repr.* 61:458-462.
- Lueschen, W. E. and R. N. Anderson. 1980. Longevity of velvetleaf (*Abutilon theophrasti*) seeds in soil under agricultural practices. *Weed Sci.* 28:341-346.
- McAlister, D. F. and O. A. Krober. 1958. Response of soybeans to leaf and pod removal. *Agron. J.* 50:674-677.
- McWhorter, C. G. and E. E. Hartwig. 1972. Competition of johnsongrass and cocklebur with six soybean varieties. *Weed Sci.* 20:56-59.
- Mitchell, R. L. 1970. *Crop growth and culture.* Iowa State University Press, Ames, Iowa. 349 pp.
- Mueller, A. J. and B. W. Engroff. 1980. Effects of infestation levels of *Heliothis zea* on soybean. *J. Econ. Entomol.* 73:271-275.
- Nelson, W. E., G. S. Rahi and L. Z. Reeves. 1975. Yield potential of soybean as related to soil compaction induced by farm traffic. *Agron. J.* 67:769-772.
- Oliver, L. R. 1979. Influence of soybean (*Glycine max*) planting date on velvetleaf (*Abutilon theophrasti*) competition. *Weed Sci.* 27:183-188.
- Oliver, L. R., R. E. Frans and R. E. Talbert. 1976. Field competition between tall morningglory and soybean. I. Growth analysis. *Weed Sci.* 24:482-488.
- Orwick, P. L. and M. M. Schreiber. 1979. Interference of redroot pigweed (*Amaranthus retroflexus*) and robust foxtail (*Setaria viridis*) var. *robusta-alba* or var. *robusta-purpurea* in soybeans (*Glycine max*). *Weed Sci.* 27:665-674.
- Pareja, M. R. 1976. Soybean yield losses from varying levels of weed infestation. M.S. thesis. Iowa State University Library, Ames, Iowa. 76 pp.

- Patterson, D. T. and E. P. Flint. 1980. Potential effects of global atmospheric CO₂ enrichment on the growth and competitiveness of C₃ and C₄ weed and crop plants. *Weed Sci.* 28:71-75.
- Pedigo. 1974. Bioeconomics of Iowa soybean insects. *Proc. N. Cent. Branch Entomol. Soc. Am.* 29:56-61.
- Pedigo, L. P., R. B. Hammond and F. L. Poston. 1977. Effects of green cloverworm larval intensity on consumption of soybean leaf tissue. *J. Econ. Entomol.* 70:159-162.
- Pedigo, L. P., J. D. Stone and G. L. Lentz. 1973. Biological synopsis of the green cloverworm in central Iowa. *J. Econ. Entomol.* 66:665-673.
- Pedigo, L. P., R. A. Higgins, R. B. Hammond and E. J. Bechinski. 1981. Soybean pest management. Pages 417-537 *in* D. Pimentel, ed. *Handbook of pest management in agriculture*, Vol. 3. C.R.C. Press, Boca Raton, Fla.
- Pimentel, D. 1981. *Handbook of pest management in agriculture*, Vol. 3. C.R.C. Press. Boca Raton, Fla. 656 pp.
- Poston, F. L. and L. P. Pedigo. 1976. Simulation of painted lady and green cloverworm damage to soybeans. *J. Econ. Entomol.* 69:423-426.
- Poston, F. L., L. P. Pedigo, R. B. Pearce and R. B. Hammond. 1976. Effects of artificial and insect defoliation on soybean net photosynthesis. *J. Econ. Entomol.* 69:109-112.
- Puckridge, D. W. 1969. Photosynthesis of wheat under field conditions. 2. Effect of defoliation on carbon dioxide uptake of the community. *Aust. J. Agr. Res.* 20:623-627.
- Radford, P. J. 1967. Growth analysis formulae - Their use and abuse. *Crop Sci.* 7:171-175.
- Rhodes, I. and W. R. Stern. 1978. Competition for light. Pages 175-189 *in* J. R. Wilson, ed. *Plant relations in pastures*. CSIRO, East Melbourne, Australia.
- Scott, H. D. and L. R. Oliver. 1976. Field competition between tall morningglory and soybean. II. Development and distribution of root systems. *Weed Sci.* 24:454-460.
- Shibles, R. M., I. C. Anderson and A. H. Gibson. 1975. Soybean. Pages 151-190 *in* L. T. Evans, ed. *Crop physiology*. Cambridge University Press, Cambridge.

- Staniforth, D. W. 1958. Soybean-foxtail competition under varying soil moisture conditions. *Agron. J.* 50:13-15.
- Staniforth, D. W. 1961. Crop-weed ecology in relation to weed control research. Paper presented at the 14th Southern Weed Conference. Dept. of Botany and Plant Pathology, Iowa State University, Ames, Iowa.
- Staniforth, D. W. 1962. Responses of soybean varieties to weed competition. *Agron. J.* 54:11-13.
- Staniforth, D. W. 1965. Competitive effects of three foxtail species on soybeans. *Weeds* 13:191-193.
- Staniforth, D. W. and W. G. Lovely. 1974. Postemergence application of bentazon for velvetleaf control in soybeans. *Res. Rep. 31st Ann. North Cent. Weed Control Conf.*
- Staniforth, D. W. and C. R. Weber. 1956. Effects of annual weeds on the growth and yield of soybeans. *Agron. J.* 48:467-471.
- Staniforth, D. W., W. G. Lovely and F. B. Cady. 1965. Sampling procedures for estimates of weed yields in corn plots. *Weeds* 13:357-360.
- Stickler, F. C. and A. W. Pauli. 1961. Leaf removal in grain sorghum. I. Effects of certain defoliation treatments on yield and components of yield. *Agron. J.* 53:99-102.
- Stoller, E. W. and L. M. Wax. 1973. Periodicity of germination and emergence of some annual weeds. *Weed Sci.* 21:574-580.
- Stone, J. D. and L. P. Pedigo. 1972. Development and economic-injury level of the green cloverworm on soybean in Iowa. *J. Econ. Entomol.* 65:197-201.
- Teigen, J. B. and J. J. Vorst. 1975. Soybean response to stand reduction and defoliation. *Agron. J.* 67:813-816.
- Thaine, R., S. L. Ovenden and J. S. Turner. 1959. Translocation of labelled assimilates in the soybean. *Aust. J. Biol. Sci.* 12:349-369.
- Thomas, G. D., C. M. Ignoffo, K. D. Biever and D. B. Smith. 1974. Influence of defoliation and depodding on yield of soybeans. *J. Econ. Entomol.* 67:683-685.
- Thomas, G. D., C. M. Ignoffo, D. B. Smith and C. E. Morgan. 1978. Effects of single and sequential defoliations on yield and quality of soybeans. *J. Econ. Entomol.* 71:871-874.

- Thrower, S. L. 1962. Translocation of labelled assimilates in the soybean. II. The pattern of translocation in intact and defoliated plants. *Aust. J. Biol. Sci.* 15:629-649.
- Thurlow, D. L. and G. A. Buchanan. 1972. Competition of sicklepod with soybeans. *Weed Sci.* 20:379-384.
- Todd, J. W. and L. W. Morgan. 1972. Effects of hand defoliation on yield and seed weight of soybeans. *J. Econ. Entomol.* 65:567-570.
- Trang, K. M. and J. Giddens. 1980. Shading and temperature as environmental factors affecting growth, nodulation and symbiotic N₂ fixation by soybeans. *Agron. J.* 72:305-308.
- Trenbath, B. R. 1976. Plant interactions in mixed communities. Pages 129-170 *in* Multiple cropping. ASA Special Publication No. 27. ASA-CSSA-SSSA, Madison, Wisconsin.
- Turnipseed, S. G. 1972. Response of soybeans to foliage losses in South Carolina. *J. Econ. Entomol.* 65:224-229.
- Vengris, J., M. Drake, W. G. Colby and J. Bart. 1953. Chemical composition of weeds and accompanying crop plants. *Agron. J.* 45:213-216.
- Wahau, T. A. and D. A. Miller. 1978. Effects of shading on the N₂-fixation, yield and plant composition of field-grown soybeans. *Agron. J.* 70:387-392.
- Watson, D. J. 1947. Comparative physiological studies on the growth of field crops. *Ann. Bot.* 11:41-76.
- Watson, D. J. 1952. The physiological basis for variation in yield. *Adv. in Agron.* 14:101-145.
- Weber, C. R. 1955. Effects of defoliation and topping simulating hail injury to soybeans. *Agron. J.* 47:262-266.
- Weber, C. R. and B. E. Caldwell. 1966. Effects of defoliation and stem bruising on soybeans. *Crop Sci.* 6:25-27.
- Whittaker, J. B. 1979. Invertebrate grazing, competition, and plant dynamics. Pages 207-239 *in* R. M. Anderson, B. D. Turner and L. R. Taylor, eds. Population dynamics. Symposium of the British Ecological Society, No. 20. Blackwell Scientific Publications, Oxford.
- Zandstra, B. H. and P. S. Motooka. 1978. Beneficial effects of weeds in pest management - A review. *PANS* 24:333-338.

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