Arthropod injury and plant gas exchange : Current understandings and approaches for synthesis

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ABSTRACT

Despite the importance of arthropod injury on plant growth and yield, the mechanisms by which plants respond to these stressors are poorly understood. We present here current understandings of the impact of arthropod herbivores on plant gas exchange processes and suggest approaches for synthesis in this area. We believe several issues must be addressed before meaningful synthesis can occur. More specifically, we identify and discuss four key areas: the level of plant organization, the role of extrinsic factors, experimental limitations, and research objectives.

INTRODUCTION

The impact of insect-induced injury on plants bears directly on questions concerning the role of herbivory on plant population dynamics, plant evolution, plant-insect coevolution, life history strategies, community structure, successional processes, and ecosystem nutrient cycling. In agricultural systems, insect injury may reduce crop yields, resulting in increased inputs into the agroecosystem, usually in the form of insecticide applications.

There is extensive evidence that insect herbivores affect plant growth and yield in both agricultural and natural systems (Bardner and Fletcher 1974; Harper 1977; Crawley 1989). However, the mechanisms by which plants respond to these biotic stresses are poorly understood (Higley et al. 1993). Research on biotic stress traditionally has focused on the biological agents producing the injury, rather than on the physiological responses of plants to the injury (Higley et al. 1993). The paucity of research on physiological responses to biotic stress is especially apparent in the area of arthropod-induced plant stress, even though insect and mite injury represents one of the most important and apparent types of biotic stress.

In this paper, we examine current understandings of the impact of insect herbivores on plant gas exchange processes. It is not our intention to review the studies con-

ducted to date; Welter (1989) provides a thorough literature review of the effect of arthropods on plant gas exchange. Rather, we will demonstrate the need for integration in this area and suggest approaches for synthesis.

Synthesis is critical because we must move beyond merely surveying the responses of each plant species to each insect species. Welter (1989) recognized this, stating, "...if researchers are not going to be fettered forever to repeating experiments for each plant-arthropod combination, then a more general understanding of plant responses is required." We believe sufficient research has been conducted to begin developing general understandings in this area of investigation. The lack of synthesis in this area is not unique; indeed, most topics in plant-insect interactions have yet to be integrated (e.g., the role of herbivory in plant allelochemical production, plant genetics, and community structure and the role of plants on herbivore feeding specialization and speciation). Although the influence of arthropod herbivores on plant gas exchange may seem of limited importance to population and community level processes, the characterization of physiological responses of plants to these stresses, and the variation within and among species, may help refine research questions and methodologies at these higher levels of biological organization.

STRESSORS, STRESS, AND PHYSIOLOGICAL RESPONSE

Arthropod feeding can directly or indirectly influence several plant gas exchange processes, including photosynthesis, water-vapor transfer, and respiration. These processes are crucial determinants of plant growth, development, and fitness; consequently, impacts of herbivory on these processes may have repercussions throughout subsequent growth. Also, gas exchange processes, such as photosynthesis, rapidly respond to external factors, so measuring how insect injury alters gas exchange provides an immediate indication of plant stress. Characterizing

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these physiological responses can provide a common basis for understanding how plants respond to insect-induced stress (Welter 1989; Higley et al. 1993).

Insects injure plants in a variety of ways. Although injury from injecting toxins and vectoring pathogens is important, the most common and significant injuries are caused by arthropods consuming host tissues or fluids (Pedigo et al. 1986). Insects traditionally have been placed in feeding guilds according to their taxonomic status. However, more recently researchers recognized that injury mechanisms are not unique for each insect species. Therefore, arthropods that feed on plant tissues and fluids can be grouped into injury guilds based on the general physical appearance of the injury (Metcalf et al. 1962; Bardner and Fletcher 1974). Examples include leaf mining, leaf skeletonizing, stem boring, fruit scarring, and seed feeding. Boote (1981) refined the classification of injury guilds by placing emphasis on the physiological responses of plants to different injury types. He categorized insects as belonging to five injury types: stand reducers, leaf-mass consumers, assimilate sappers, turgor reducers, and fruit feeders. An additional injury type, architectural modifier, has been proposed by Pedigo et al. (1986). Higley et al. (1993) incorporate the six injury types and several others into categories of physiological impact. With this scheme, insects can be grouped into categories that better describe their differential impact on host physiology.

Welter's (1989) review considered current understandings by placing arthropods in injury guilds and evaluated the responses of plants to these guilds. The feeding guilds, based on Root's (1973) classification, included defoliators, mesophyll feeders, gall formers, epidermal feeders, phloem feeders, stem borers, and root feeders.

Phloem Feeding

The effects of phloem feeding on plant gas exchange parameters primarily have been characterized for aphids. Photosynthetic responses to aphid injury have been highly variable, from increases, to no changes, to decreases in rates per unit area (Welter 1989). The mechanisms to explain the responses with no changes or increases in photosynthetic rates have not been elucidated. The mechanism underlying reductions in rates has been determined for only a few phloem feeders: *Schizaphis graminum* on sorghum, *Melanocallis caryaefoliae* on pecan, and *Macrosiphum euphorbiae* on potato (Gibson et al. 1976; Veen 1985; Wood et al. 1985; Ryan et al. 1987). Aphid feeding has been shown to inhibit normal phloem transport, which then interrupts the delivery of nitrogen to cells and disrupts the flow of photosynthates from leaves to stems, reproductive structures, and roots. Lack of nitrogen and suspected alterations of source-sink feedback signals lead to reduced ribulose bisphosphate regeneration.

Another mechanism for photosynthesis reduction in aphids occurs when honeydew physically blocks stomatal openings. This type of blockage prevented CO_2 uptake in wheat, which lowered photosynthetic rates (Rabbinge et al. 1981). However, honeydew effects on gas exchange were not observed in sorghum (Ryan et al. 1987).

Gall Forming, Epidermal Feeding, Root Feeding, and Stem Boring

Gas exchange responses to gall formation, epidermal feeding, root feeding, and stem boring have not been studied sufficiently to generalize about mechanistic responses. Galled areas might exhibit lower photosynthetic rates because of decreases in chlorophyll and increases in non-photosynthesizing tissue (Veen 1985). Epidermal feeding by mites and thrips generally causes a decrease in photosynthesis and stomatal conductance (Castro et al. 1972). However, it is not known whether uninjured tissue is affected or why photosynthetic rates are reduced. The effects of root feeding on gas exchange parameters have only been characterized in one study. Detling et al. (1980) observed reductions in net photosynthesis after simulated insect injury on *Bouteloua gracilis*. The reductions occurred most likely because of an inhibition of water transport. Similarly, stem boring injury produced reductions in photosynthetic rates most likely because of vascular tissue impairment (Heichel and Turner 1973; Madden 1977). Welter (1989) cautions that many of these studies were unmanipulated and contained only one replication, so the information presented is only of limited interpretive value.

Mesophyll Feeding and Leaf Mining

Most mite-induced injury can be classified as mesophyll feeding. Mesophyll tissue, such as chloroplasts, is selectively consumed. Nearly all of the studies characterizing gas exchange responses to mite injury indicate that photosynthesis is reduced because of decreases in leaf chlorophyll content (Welter 1989). Similar responses and mechanisms have been observed for scale, leafhopper, and whitefly feeding (Welter 1989; Buntin et al. 1993).

Of the relatively few studies on mining injury, most have been conducted with dipteran species in the family Agromyzidae (Fujiie 1982; Proctor et al. 1982; Johnson et al. 1983; Parella et al. 1985; Trumble et al. 1985; Daley and McNeill 1987; Martens and Trumble 1987). Agromyzid larvae produce "serpentine" mines, with feeding concentrated in mesophyll tissue. On tomato, Johnson et al. (1983) observed negative linear correlations between photosynthetic rates and stomatal conductances of unmined areas and the percentage of mined tissue produced by *Liriomyza sativae*. However, mechanisms for these reductions have not been identified. Similar results were observed on celery injured by *L. trifolii* (Trumble et al. 1985) and on chrysanthemum injured by *L. trifolii* and *L. huidobrensis* (Parrella et al. 1985). Daley and McNeill (1987) observed no impact from *Agromyza frontella* on the total canopy photosynthesis of alfalfa. However, mined areas were not quantified, so results are only of limited interpretive value. Two studies

have been conducted on lepidopteran leaf miners. Proctor et al. (1982) observed reduced net photosynthetic rates on apple after mining injury by the spotted tentiform leafminer, *Phyllonorycter blancardella*, which produces "blotch" mines (Hill 1987). Photosynthetic rates for pear leaves injured by the pear leaf miner, *Bucculatrix pyrivorella*, were negatively correlated with larval densities per leaf (Fujiie 1982). Most of the results from studies on leaf mining injury and gas exchange responses are difficult to interpret because of a lack of quantification of injury and because of incomplete descriptions of photosynthesis measurement protocols.

Leaf-Mass Consumption

Most studies on plant gas exchange and arthropod-induced injury have focused on leaf-mass consumers (defoliators). In previous studies, insect defoliation produced a continuum of responses, from decreases to increases in photosynthetic rates of remaining leaf tissue (Welter 1989). These responses have been observed for individual leaves, individual plants, and plant canopies.

Most studies indicate that removal of either partial or entire leaves by insects results in an increase in photosynthetic rates of remaining leaf tissue. Mechanisms for these increases have not been characterized in any detail, although several extrinsic (environmental) and intrinsic (physiological) causal factors have been proposed (Welter 1989). Intrinsic factors may include increased assimilate demand after defoliation (Neales and Incoll 1968), reduced competition between leaves for mineral nutrients necessary for cytokinin production (Wareing et al. 1968), and delayed leaf senescence (Gifford and Marshall 1973; Caldwell et al. 1981; Nowak and Caldwell 1984). It should be noted that some researchers who observed rejuvenated photosynthetic rates in remaining leaves removed whole shoots or branches, so the defoliation techniques may not have fidelity to actual insect injury (Hodgkinson 1974; Satoh et al. 1977).

Several studies have observed no changes in photosynthetic rates per unit area of remaining leaves in response to defoliation injury (Davidson and Milthorpe 1966; Hall and Ferree 1976; Poston et al. 1976; Syvertsen and McCoy 1985; Welter 1991; Higley 1992; Peterson et al. 1992). Decreases in photosynthetic rates per unit area also have been observed, but the reductions were temporary (Alderfer and Eagles 1976; Hall and Ferree 1976; Li and Proctor 1984). Reductions in CO_2 exchange generally have been demonstrated at the canopy level (Detling et al. 1979; Boote et al. 1980; Ingram et al. 1981). These reductions were caused by decreased leaf area indices, smaller leaf size, and decreased light interception.

The most thoroughly studied level of response has been the individual leaf. However, mechanisms responsible for changes in photosynthesis have not been characterized. For example, on apple, Hall and Ferree (1976) observed reductions in photosynthetic rates of remaining tissue after greater than 10% simulated insect defoliation. Insect defoliation was simulated using different circumference-sized cork borer punches. Differences in rates were observed one day after treatments were imposed. Moreover, differences continued to be expressed 14 days after injury was imposed. Increased circumference of the leaf area caused greater photosynthetic reductions. Also, injury to major lateral leaf veins caused greater photosynthetic reductions when compared to leaves with only interveinal injury. This result implies that interruption of water transport to leaves may play a significant role in reducing rates. However, the authors did not determine transpiration rates or stomatal conductances, so it is impossible to determine the reason for the reductions in photosynthetic rates that they observed.

Li and Proctor (1984) cut across midrib veins and main lateral veins on apple leaves with a scalpel and observed reductions in photosynthetic rates both two and ten days after treatments were imposed. However, transpiration rates were not affected. The authors did not characterize stomatal conductances, so the results are difficult to interpret. More intensive research is needed to determine if gas exchange rate reductions occur in apple. Moreover, research needs to be directed toward characterizing the mechanisms which cause perturbation of rates.

Much research already has been conducted characterizing the gas exchange responses of soybean to leaf-mass consumption injury (e.g., Poston et al. 1976; Hammond and Pedigo 1981; Ingram et al. 1981; Ostlie and Pedigo 1984; Higley 1992). Indeed, the most comprehensive work to date has been on soybean. Previous studies have demonstrated that both simulated and actual insect defoliation does not perturb photosynthetic rates of remaining tissue. Water loss from the cut edges of injured leaves was significant and was correlated with the perimeter length of cut tissue. However, it was also transient, and did not seem to affect photosynthesis (Ostlie and Pedigo 1984).

APPROACHES FOR SYNTHESIS

There currently is much confusion in the literature concerning the physiological responses of plants to insect injury. This is especially true for responses to defoliation injury. Interpretations have varied with the diverse methodologies used, the ability to quantify injury accurately, and the central focus of the study (i.e., individual leaf versus plant canopy). It is unclear whether responses are inherently variable among species and insect stressors or whether external factors are affecting observed responses.

Characterizing how plants respond to stresses from different injury guilds represents an important step toward developing more complete understandings of how insect injury affects plant gas exchange processes. Recent work suggests that there may be similarities in plant physiolog-

ical responses associated with each insect injury guild (Welter 1989; Welter 1991; Higley 1992; Peterson et al. 1992; Higley et al. 1993). Welter and Steggall (1993) have demonstrated that the response of wild and domesticated tomato to defoliation is similar; differences were observed, but they were quantitative, not qualitative. Research by L. G. Higley and colleagues (unpubl. data) indicates that leaf-mass consumption by green cloverworm, soybean looper, grasshopper species, bean leaf beetle, and velvetbean caterpillar produce photosynthetic responses of soybean that are not statistically different from each other or from undefoliated controls. Unfortunately, there have not been enough experiments to determine if there are homogeneities of response with other injury types.

A more complete picture of gas exchange responses has begun to emerge in recent years. Instrumentation for reliable gas exchange determinations in field environments has only been available for the past 10 years. New instrumentation and plant gas exchange methodologies have helped stimulate research efforts in this area. Also, research has only recently been directed specifically toward characterizing gas exchange processes. In many previous studies, the focus was not limited to photosynthetic parameters; often, growth, developmental, yield, and fitness responses were also determined. Consequently, gas exchange responses were reported, but not thoroughly interpreted.

The brief review presented above highlights four issues that we believe must be addressed before meaningful synthesis of the effects of arthropod injury on plant gas exchange can occur. These areas include: the level of plant organization, the role of extrinsic factors, experimental limitations, and research objectives.

Plant Organization

Characterizing the mechanisms by which insects affect different plant organizational levels is critical to understanding how plants respond to herbivore stress. Insect injury may stress plants at several levels of biological organization, from organelles to populations (Peterson et al. 1992) (Fig. 1). Moreover, responses may be different at different organizational levels. For example, in alfalfa and soybean, defoliation does not alter photosynthetic rates of remaining tissue of individual leaflets (plant organs) (Poston et al. 1976; Higley 1992; Peterson et al. 1992). However, defoliation *does* alter the normal leaf senescence pattern of plants (organisms) (Higley 1992; Peterson et al. 1992). Similarly, Detling et al. (1979) observed an increase in photosynthetic rates of remaining *Bouteloua gracilis* leaves, but canopy carbon assimilation decreased.

Because there are differences in response among organization levels, it is critical that researchers identify their research questions carefully and interpret their results accurately. Welter (1989) stated, "...if the question is to examine the effects of herbivory on the productivity or 'fitness' of a plant, then total canopy measurements would provide a better indicator. If the authors are interested in specific plant buffering mechanisms, then use of individual leaves should provide a more detailed understanding."

Ultimately, we are interested in understanding responses at all levels of plant organization. Evolutionary, ecological, and agricultural understandings of the impact of herbivory depend upon characterizing how plant populations and communities are affected by insect injury. Describing mechanisms of plant response to different types of injury and identifying injury guilds require a focus on physiological, cellular, and molecular processes (Higley et al. 1993). However, most research has focused on responses between these extremes. Describing how individual leaves respond to injury is appropriate given that these are the organs most immediately affected by herbivory. But responses of individual leaves have not been related to responses at higher levels of organization. For example, in the literature on plant gas exchange and herbivory, there are scores of papers on individual leaf response to herbivory (Welter 1989), but we are aware of only three studies directly examining canopy responses to herbivory (Boote et al. 1980, Ingram et al. 1981, Daley and McNeill 1987). Similarly, documenting changes in leaf gas exchange associated with injury does not provide information on how such changes occur. Work on leaf responses is needed to guide research on mechanisms of response, but describing those mechanisms requires work at lower levels of organization. Consequently, developing a more encompassing understanding of herbivory requires that greater attention be given to responses at organizational levels above and below that of individual leaves.

Intrinsic and Extrinsic Factors

As discussed previously, the literature reveals that insect defoliation produces a continuum of responses, from decreases to increases in photosynthetic rates of remaining leaf tissue (Welter 1989). However, changes in photosynthetic rates may occur not because defoliation is perturbing the remaining photosynthetic apparatus, but rather because numerous extrinsic factors interact with the gas exchange responses to injury (Welter 1989).

Insect-induced Plant Stress
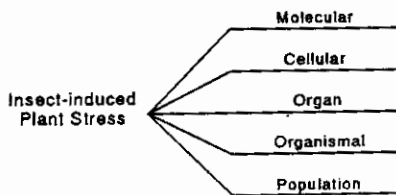Molecular
Cellular
Organ
Organismal
Population

Figure 1. Arthropod-induced stress may impact plants at several levels of organization. Gas exchange responses to stressors can differ among different levels.

By determining the direct responses of insect injury on plant physiology, interactive effects can be assessed more accurately (Fig. 2). This is especially pertinent in natural systems because extrinsic factors constraining optimal plant growth, both temporally and spatially, are common. Numerous extrinsic factors can interact with the direct effects of injury. Extrinsic factors may include light penetration, water availability, and nutrient availability (Welter 1989; Peterson et al. 1992). The variable responses reported in the literature may be attributable to the interaction of these extrinsic factors with insect injury. Clearly, the sensitivity of gas exchange processes to confounding factors needs to be determined.

If physiological responses to injury among plant species are similar, then general models can be constructed and indirect factors that influence plant response can be evaluated more effectively (Higley et al. 1993). For example, in an optimal growing environment defoliation injury to a leaf may not alter its photosynthetic rate per unit area of remaining tissue. If water and nitrogen are limiting, defoliation injury may result in increases in photosynthetic rates of remaining leaves because the remaining leaves would no longer be water and nitrogen stressed. This mechanism may have occurred in reported results from grassland system studies by McNaughton (1983) and Detling et al. (1979). Increases in gas exchange rates of individual leaves, then, would not be because of intrinsic factors, but rather because of the interaction of extrinsic factors.

Experimental Limitations

Recognizing how injury affects different levels of plant organization and distinguishing between intrinsic and extrinsic factors both relate to the experimental question of how we characterize plant responses to injury. To an extent, we believe our progress in understanding herbivory and plant responses has been constrained by experimental
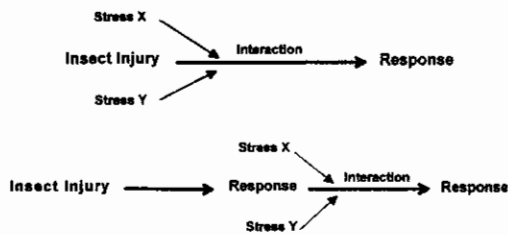

Figure 2. Insect injury interacts with other biotic and abiotic stresses to produce plant responses that may be attributable solely to the insect stressor (top). Substantial progress will be made by first characterizing the direct responses of plants to insect injury, and then characterizing how extrinsic factors interact with insect stress (bottom).

limitations. Broadly, these limitations involve experimental objectives and experimental procedures.

Experimental objectives focus research onto specific questions; are we asking questions about herbivory and plant response that lead to broad understandings or are we posing narrow questions that preclude such understandings? Much research on herbivory and plant gas exchange has been observational, in the sense that we observe plant responses to different types of insect injury. This work is important in establishing the general nature of plant response to herbivory, but of itself it does not provide explanations for the observed effects. Elsewhere (Higley et al. 1993) we have argued for an emphasis on mechanisms of stress, specifically physiological responses to injury, as a basis for broader understandings of plant stress. We will return to experimental objectives in the next section, but the key point to be made is that if we are to develop broad understandings of how insects affect plants, then our experimental objectives must focus on mechanisms and not just observations of responses.

The second experimental issue is that of experimental procedures. We believe problems in conducting experiments on plant responses to herbivory have constrained, and continue to constrain, our understanding of herbivory. Procedural issues can be separated into questions of quantification (or measurement) and of control (maintaining treatment integrity).

For work on plant gas exchange, the ability to measure gas exchange easily and accurately had been an important obstacle, but the development of portable infrared gas analyzers for measuring carbon exchange rates solved this problem, at least for single leaf measurements. Measurements of canopy gas exchange parameters are not as straightforward, and although canopy measurement systems can be constructed (Garcia et al. 1990), their complexity and experimental challenges in their use (such as establishing plots or maintaining a uniform light environment across treatments) have limited their use in studies on herbivory.

Another measurement issue involves quantifying injury. It is well established that responses to herbivory are a function of the amount of injury (Tammes 1962, Bardner and Fletcher 1974, Pedigo et al. 1986, Higley et al. 1993), but many studies on herbivory and plant response do not provide adequate assessments of injury. This problem is particularly relevant for some types of insect injury, such as leaf mining or those producing chlorosis, which are very difficult to quantify. However, recent advances in digital imaging provide a means for discriminating between even subtle differences between most injured and uninjured tissues.

A final quantification question relates to biochemical measurements. For example, assessing differences in ribulose bisphosphate carboxylase/oxygenase (rubisco) levels

between injured and uninjured plants can be important in determining direct effects of injury on the photosynthetic apparatus. However, rubisco assays are expensive, time consuming, and cannot be conducted for all plant species. Similar arguments apply to other molecules of interest in stress response. These limitations tend to restrict our work to plant species whose biochemistry and physiology is relatively well known. As an experimental approach, it may be necessary to develop detailed understandings of physiological response in only a few model systems rather than across many plant species, because the physiological and biochemical background needed for such work is unavailable in most species.

Many problems associated with quantification have been eliminated or lessened through the development of new instrumentation or procedures, and we anticipate this trend will continue. In total, these limitations are by no means barriers to work on plant stress and herbivory, but they are constraints.

Experimental limitations associated with control involve the recognition that characterizing plant gas exchange responses to insect injury requires controlling the array of other factors that may influence and confound gas exchange responses to injury. Plant gas exchange processes, such as photosynthesis, vary across individual plants, plant ages, and plant tissues, and are highly sensitive to many factors including light, temperature, relative humidity, and plant water status. Ideally, all of these factors should be uniform across treatments. At a minimum, a failure to control for factors such as light or leaf age will contribute to increased variation in measurements. More importantly, lack of control can lead to systematic errors. We are troubled that much of the literature on plant gas exchange and herbivory does not include explicit discussion of potential confounding or of experimental procedures used to maintain treatment uniformity. In the absence of such discussion, we cannot help but wonder how much of the variability in reported gas exchange responses may be attributable to confounding from external factors rather than intrinsic differences in plant response to herbivory.

Another potential control problem arises through how herbivory treatments are imposed. Techniques such as caging or insecticides used to manipulate insect numbers (and thereby injury) have the potential to interact with injury. For example, cages reduce the light environment of the plant, and insecticides can alter plant physiology. These concerns do not invalidate the techniques, but they do indicate the need for special attention in experimental design. For instance, caged and uncaged controls can be used to help identify potential cage effects.

Maintaining uniform treatment conditions is not the only way to address control problems. Measurements by treatment of potential confounding factors, such as light intensity, can be used to remove the effect of the factor in

analyses of the influence of herbivory (such as by analysis of covariance). One caution in using this approach is that it assumes there is no interaction between responses to the factor in question (e.g., light) and responses to insect injury, which may not be true. Nevertheless, measuring potential confounding factors to account for their influence may be the only method available for many studies. This is particularly true for work in natural systems, where positive controls may be impractical or impossible.

Indeed, it is the problem of control that makes work in most natural systems so difficult. The recent finding that natural and cultivated species did not have qualitative differences in response to insect injury (Welter and Steggall 1993), suggests it may be possible to develop models of plant response in cultivated species (where external factors are more easily controlled). These models can then be used as a basis for characterizing plant responses in more variable systems.

Identifying and addressing potential sources of confounding is a key issue in plant gas exchange experiments. In our opinion, failing to distinguish between intrinsic and extrinsic factors influencing responses to herbivory has been responsible for much of the experimental difficulties we see in the literature. Fundamentally, the issue is not one of having every experiment control all factors; different objectives call for different experimental procedures. However, discussions of experimental procedures should be explicit in the precise rationale behind a given approach and should recognize potential confounding factors and distinguish the type of response (intrinsic, extrinsic, or both) being evaluated.

Research Objectives

We have argued that a focus on plant physiology provides a common language for characterizing plant stress and is essential for integrating understanding of stress (Higley et al. 1993). Physiology may include measurements from plant populations, plants, and plant parts, as well as biochemical and molecular measurements more typically associated with the notion of plant physiology. Consequently, most of the literature on plant gas exchange and herbivory already addresses questions of physiological response. Therefore, the key issue, in our view, is not so much changing the nature of our experiments as it is changing their direction.

As we have argued in the preceding section, most of our research to date describes responses rather than mechanisms. This is appropriate given our current understandings, and considerable descriptive work remains. However, sufficient descriptive work is available to allow for a transition to explanatory research. We mean by this, studies that focus on the underlying mechanisms associated with observed plant responses. Why, for example, do photosynthetic rate reductions occur in response to injury? Does injury alter mesophyll or stomatal limits to photosyn-

thesis? We have data in some systems on these questions, but we do not have general models or hypotheses that might direct research.

We believe the construction of models and hypotheses regarding plant responses to herbivory is a crucial activity for advancing our understanding. At this point, it matters less that a given model or hypothesis is correct than that such models and hypotheses lead to research providing broader insights into plant stress. Obviously, many problems exist in striving for broad interpretations. Many different types of insect injury occur, plant responses may differ between C_3 and C_4 species or between annuals and perennials, and responses may vary under different environmental regimes. However, these potential differences provide a starting place for identifying commonalities. For example, we might ask how gas exchange responses to all types of insect injury compare within a single plant system. Do different plant species demonstrate the same type of response to a given injury? How does water stress influence responses to injury? Examining such questions can provide a foundation for more comprehensive interpretations.

CONCLUSIONS

Determining the conditions under which gas exchange rates increase, decrease, or do not change after insect-induced injury will add to our knowledge of how plants respond to these stressors. But learning how and why changes in gas exchange rates occur will do more to advance our understanding of plant stress from herbivory. With such a focus, we believe herbivore stress and other factors, such as plant competitive interactions, diseases, and mineral stress, can be integrated into a more encompassing view of plant stress at the individual plant and plant population levels (Louda et al. 1990; Tilman 1990; Louda and Collinge 1992; Higley et al. 1993). Just as Chapin (1991) has suggested a conceptual integration for abiotic stress, we believe research can lead to a conceptual integration of biotic stress. Hopefully, these integrated views of abiotic and biotic stress will themselves lead to a synthesis in understanding all types of plant stress.

ACKNOWLEDGEMENTS

REFERENCES CITED

Alderfer, R. G. & Eagles, C. F. 1976. *Bot. Gaz.,* *137*:351-355.

Bardner, R. & Fletcher, K. E. 1974. *Bull. Entomol. Res.,* *64*:141-160.

Boote, K. J. 1981. ASAE Pap. 81-4007, American Society of Agricultural Engineers. St. Joseph, MI.

Boote, K. J., Jones, J. W., Smerage, G. H., Barfield, C. S., &

Berger, R. D. 1980. *Agron. J.,* *72*:247-252.

Buntin, G. D., Gilbertz, D. A. & Oetting, R. D. 1993. *J. Econ. Entomol., 86*:517-522.

Caldwell, M. M., Richards, J. H., Johnson, D. A., & Dzurec, R. S. 1981. *Oecologia 50*:14-21.

Castro, P. R. C., Pitelli, R. A., & Passilongo, R. L. 1972. *Ann. Entomol. Soc. Braz., 1*:5-10.

Chapin, F. S. III. 1991. *Bioscience 41*:29-36.

Crawley, M. J. 1989. *Annu. Rev. Entomol., 34*:531-564.

Daley, P. F. & McNeill, J. N. 1987. *Can. J. Plant Sci., 67*:433-443.

Davidson, J. L. & Milthorpe, F.L. 1966. *Ann. Bot., 30*:185-198.

Detling, J. K., Dyer, M. I., & Winn, D. T. 1979. *J. Econ. Entomol. 72*:403-406.

Detling, J. K., Winn, D. T., Procter-Gregg, C., & Painter, E. L. 1980. *J. Appl. Ecol.17*:771-778.

Fujiie, A. 1982. *Appl. Entomol. and Zool., 17*:188-193.

Garcia, R. L., Norman, J. M., & McDermitt, D. K. 1990. *Remote Sensing Rev., 5*: 141-162.

Gibson, R. M., Whitehead, D., Austin, D. J., & Simkins, J. 1976. *Ann. Appl. Biol. , 82*:151-153.

Gifford, R. M. & Marshall, C. 1973. *Austral. J. Biol. Sci., 26*:517-526.

Hall, F. R. & Ferree, D. C. 1976. *J. Econ. Entomol., 69*:245-248.

Hammond, R. B. & Pedigo, L. P. 1981. *J. Kan. Entomol. Soc., 54*:331-336.

Harper, J. L. 1977. Population biology of plants, Academic Press, London.

Heichel, G. H. & Turner, N. C. 1973. *Ann. Appl. Biol., 75*:401-408.

Higley, L. G. 1992. In: Copping, L. G., Green, M. G. & Rees, R. T. (Eds.) Pest management in soybean. Elsevier Science Publishers, London.

Higley, L. G., Browde, J. A., & Higley, P. M. 1993. In: Buxton, D. R. (Ed.). International Crop Science I. Crop Science Society of America, Madison, WI. *in press.*

Hill, D. S. 1987. Agricultural insect pests of temperate regions and their control. Cambridge University Press, Cambridge.

Hodgkinson, K. C. 1974. *Austral. J. Plant Physiol., 1*:561-568.

Ingram, K. T., Herzog, D. C., Boote, K. J., Jones, J. W. & Barfield, C. S. 1981. *Crop Sci., 21*:961-968.

Johnson, M. W., Welter, S. C., Toscano, N. C., Ting, I.P., & Trumble, J. T. 1983. *J. Econ. Entomol., 76*:1061-1063.

Li, J. & Proctor, J. T. A. 1984. *HortScience 19*:815-817.

Louda, S. M., Keeler, K. H., & Holt, R. D. 1990. In: Grace, J. B. & Tilman, D. (Eds.). Perspectives in plant competition. Academic Press, New York, N. Y.

Louda, S. M. & Collinge, S. K. 1992. *Ecol., 73*:153-169.

Madden, J. L. 1977. *Bull. Entomol. Res., 67*:405-426.

Martens, B. & Trumble, J. T. 1987. *Environ. Entomol.,* *16*:374-378.

McNaughton, S. J. 1983. Encyclopedia of Plant Physiology, 12C.

Metcalf, C. L., Flint, W. P., & Metcalf, R. L. 1962. Destructive and useful insects. McGraw-Hill, 4th ed. New York, N. Y.

Neales, T. F. & Incoll, L. D. 1968. *Bot. Rev., 34*:107-125.

Nowak, R. S. & Caldwell, M. M. 1984. *Oecologia* *61*:311-318.

Ostlie, K. R. & Pedigo, L. P. 1985. *Environ. Entomol., 13*:1675-1680.

Parrella, M. P., Jones, V. P., Youngman, R. R., & Lebeck, L. M. 1985. *Ann. Entomol. Soc. Am., 78*:90-93.

Pedigo, L. P., Hutchins, S. H., & Higley, L. G. 1986. *Annu. Rev. Entomol., 31*:341-368.

Peterson, R. K. D., Danielson, S. D., & Higley, L. G. 1992. *Environ. Entomol., 21*:501-507.

Poston, F. L., Pedigo, L. P., Pearce, R. B., & Hammond, R. B. 1976. *J. Econ. Entomol., 69*:109-112.

Proctor, J. T. A., Bodnar, J. M., Blackburn, W. J., & Watson, R. L. 1982. *Can. J. Bot., 60*:2734-2740.

Rabbinge, R., Dress, E. M., Van der Graff, M., Verberne, F. C. M., & Wesselo, A. 1981. *Nether. J. Plant Pathol.,* *87*:217-232.

Root, R. B. 1973. *Ecol. Monogr., 43*:95-124.

Ryan, J. D., Johnson, R. C., Eikenbary, R. D., & Dorschner, K. W. 1987. *Crop Sci., 27*:283-288.

Satoh, M., Kreidmann, P. E., & Loveys, B. R. 1977. *Physiologia Plantarum 41*:203-210.

Syversten, J. P., & McCoy, C. W. 1985. *Fla. Entomologist 68*:386-393.

Tammes, P. M. L. 1961. *Tijdschr. Plantenziekten 67*:257-263.

Tilman, D. 1990. *Oikos 58*:3-15.

Trumble, J. T., Ting, I. P., & Bates, L. 1985. *Entomol. Exp. Appl., 38*:15-21.

Veen, B. W. 1985. *Ann. Appl. Biol., 107*:319-323.

Wareing, P. F., Khalifa, M. M., & Treharne, K. J. 1968. *Nature 220*:453-457.

Welter, S. C. 1989. In: Bernays, E. A. (Ed.). Insect-plant interactions.Vol. 1. CRC Press, Boca Raton, FL.

Welter, S. C. 1991. *Environ. Entomol., 20*:1537-1541.

Welter, S. C. & Steggall, J. W. 1993. *Ecol. Applic., 3*:271-278.

Wood, B. W., Tedders, W. L., & Thompson, J. M. 1985. *J. Am. Soc. Hort. Sci., 110*:393-397.