PLANT COMPENSATION FOR ARTHROPOD HERBIVORY

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INTRODUCTION

Plant compensation for arthropod damage is a general occurrence of considerable importance in both natural and agricultural systems. In natural systems, plant species that can tolerate or compensate (e.g. recover equivalent yield or fitness) for herbivore feeding have obvious selective advantages that lead to genotype maintenance. Scientists publishing in this area often cite an optimal strategy for enhancing fitness (90, 108). In agricultural crops, reports of plant compensation mostly are concerned with yields rather than fitness (164). However, variation in compensatory response also affects sampling strategies and economic threshold levels [sensu Stern (166)] and provides a viable tactic for breeding insect resistance to key arthropod pests into plants. Not surprisingly, the relative importance of the various forms of compensation in agricultural and natural systems is still relatively unknown. Therefore, a primary purpose for this review is to integrate the forms of compensation reported in the literature in the context of natural and agricultural habitats.

Several previous reviews and articles have had a significant impact on the development of an understanding of plant compensatory responses. Some provide extensive lists of examples of plant compensation and the pest-yield relationship (4, 164), while others stress the complexity and interrelatedness

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of the physiological processes affected by arthropod feeding (15, 68, 102, 135). The hypothesis that herbivory benefits plants by causing an overcompensation response has produced several excellent articles, which furnish evidence for potential mechanisms of plant compensation to herbivore damage (9, 26, 122, 137, 139). More recently, information on some local environmental factors influencing the potential degree of plant compensation has been reported (113). In addition, a comprehensive review of the effects of arthropods on photosynthetic activity and related processes in plants has been published (193). With few exceptions, the authors of these articles tend to support either the view that herbivory is detrimental to plants or that herbivory results in an overcompensation response that benefits the plants. Like Maschinski & Whitam (113) and Doak (40), we feel that the answer is not a biological absolute that favors only one of these contradictory hypotheses. Rather, we believe that the compensatory responses vary, and the impact of that response on fitness or yield is determined by a variety of habitat-, plant-, and damage-specific components.

This review does not address all aspects of several important topics. Specifically, the contentious hypothesis that herbivore damage benefits plants is not discussed. Likewise, even though resource allocation within plants is central to the understanding of compensation responses, this paper is not designed to review the vast literature on resource allocation. Finally, the reader is referred to Metcalf et al (125) for examples of the types of plant damage that arthropods can cause. This review does discuss specific examples of the impacts of some feeding strategies, selected types of physical damage resulting in pruning or weakening, and key mediating influences. However, inclusion of all possible arthropod effects on plants is not possible.

KEY PROBLEMS IN EVALUATING PLANT COMPENSATION

Historically, one of the most significant problems delaying an understanding of plant compensatory responses has been the erroneous assumption of linearity between plant growth (usually assumed to be equal to yield) and leaf area based simply on the presumption that carbohydrate production increases with leaf area (65). During the 1960s and 1970s, this generally accepted presumption greatly inhibited the understanding of compensatory responses. Because differences in growth versus yield can be dramatic, with arthropod damage to foliage greatly stimulating one at the expense of the other, conclusions were often apparently contradictory. In addition, the relative importance of growth versus yield is substantial when comparing evolutionary or ecological fitness with agricultural suitability, but these concepts were often considered equivalent. Fortunately, the pursuit of this hypothesized linear

relationship between leaf area and yield led to a body of knowledge that allowed researchers to recognize the limitations of this assumption and stimulated investigation into a variety of important mechanisms affecting plant compensation.

Probably the foremost reason for the lack of a consistent linear relationship between carbohydrate production and growth or yield is the complexity and variability of the plant resource-allocation infrastructure (108). The exact mechanisms associated with the partitioning and allocation of photoassimilates in plants are poorly understood at best (110). Clearly, such allocation of carbon at the cellular level is not just a consequence of concentration gradients between sources and sinks as implied in the mass-flow hypothesis. Partitioning of carbon between chloroplasts (or plastids in general) and the cytosol (cytoplasm) is highly regulated by exogenous factors such as light and temperature and by endogenous factors including the rates of CO_2 assimilation and the concentration of substrates, products, and effector molecules. Starch, the primary storage carbon compound of plants, is synthesized in plastids, of which the chloroplast is the most thoroughly studied. Sucrose, the primary carbon compound translocated in most plants, is synthesized in the cytosol prior to allocation by translocation to various sinks. Transport of carbon between chloroplasts and cytosol is largely mediated by a phosphate translocator involving a stoichiometric one-to-one reciprocal transfer of triosephosphates out of and orthophosphate into the plastid.

The translocation of sucrose from source to sink depends upon many factors including the concentrations in source and sink and the rates of synthesis at the source and use at the sink. In many sinks that have a storage function, the process of sucrose to starch synthesis is reversed between cytosol and the starch storing plastids of the sink. Carbohydrate metabolism and ultimate allocation is regulated by the effector metabolite fructose 2,6-bisphosphate, which is in itself regulated by environmental factors, e.g. light (82). Thus, a variety of environmental components including arthropod feeding would be expected to alter the carbon partitioning and allocation within the plant. Even though an exact mechanism cannot be proposed, an understanding of the regulation of the allocation processes gives useful insight into the compensatory responses of plants to perturbations from arthropods.

Watson & Casper (188) and Watson (187) pointed out that resource allocation between sources and sinks is quite variable in that sinks may be positionally related to sources. Restricted allocation may be caused by morphology, anatomy, and physiology, among other factors, and limited to internodal regions, adjacent leaves, individual fruits, inflorescences, or branches. Plants such as monocots with a limited number of sinks and extensive vascular systems may not show such restricted allocation (188). Importantly, the extent of allocation to any one sink may change with age

and/or reproductive status, and can be readily manipulated experimentally. Certainly, environmental perturbations such as herbivory influence allocation. Thus, knowing the endogenous limitations to resource allocation within a plant system and having knowledge of their change in response to perturbations is critical to understanding resource allocation and reallocation during herbivory (70). Not surprisingly, in such a complex and interrelated regulation system where changes in yield or growth result from interacting metabolic and physiological activities rather than just simple alterations in carbohydrate supply, elucidation of mechanisms of compensation can be complicated. Alteration of one process can impact another dramatically; the literature abounds with examples of changes in hormone titer affecting nitrogen utilization, fruit set, or the onset of senescence (78).

Additionally, other factors can impact the complexity of plant responses. Variability in environments (27, 80) creates a mosaic of possible outcomes from arthropod herbivory, which is further complicated by changes in plant physiology and concomitant compensatory events that vary with vegetative or reproductive stages (40, 204). Annual or perennial habits, and reproductive differences, create further diversity in plant responses. The differences in photosynthesis, carbohydrate economy, and nitrate and sulfate metabolism between plants with C_3 and C_4 photosynthesis should greatly impact both plant responses and insect feeding behavior (13, 14). These differences are not only of basic metabolism, but also of anatomical compartmentation of photosynthetically related events by many C_4 species (42). Thus, one might expect that compensatory responses would differ between C_3 and C_4 species.

An additional confounding factor is that insects actually may be rather distant from the physiological event leading to yield change. For example, insects may inject toxins that affect production of hormones impacting translocation of assimilates (23, 78), thereby increasing sink stimulation of metabolic centers and enhancing photosynthetic activity. Arthropod feeding also may be temporally distant from resulting yield affects; several studies have demonstrated that insect damage may affect storage for next season's growth, thus causing a delayed stunting in some perennials (6, 70, 102).

Measurement of plant compensation is not always a simple process. No single perfect factor or process has been reported for predicting yield or growth, but photosynthetic activity has been successfully correlated with yield in some cases (91, 178). This measure is not always consistent because all leaves do not have the same productivity. One approach to reduce variability has been to evaluate all leaves rather than just a representative sample (28). However, carbohydrate production is not always the key process responsible for yield or fitness. For example, flower production in water hyacinth was shown to be inversely correlated with clonal growth, suggesting that meristem production may be more important for plant fitness than gross carbohydrate production (188).

One of the most pervasive and significant problems in evaluating plant compensation to arthropod damage is the presence of an abundance of literature that has been largely segregated by topic within discipline-specific journals. The entomological and ecological literature contain many examples of plant compensatory responses to arthropod damage. Particularly important are cause-and-effect studies that place data for agricultural-crop yield or fitness in an ecological context. The more recent ecological literature has many reports describing tests of hypotheses proposed to explain plant compensation for herbivory. The botanical, horticultural, and ecological literature, and to a lesser extent the forestry literature, contain reports of potential physiological mechanisms resulting in compensation. This literature is particularly rich in resource-allocation information. The agronomy literature provides examples of physical mechanisms (e.g. canopy architecture) of compensatory responses. Journals in all of the above disciplines contain studies evaluating photosynthetic responses to various forms of stress.

In the most recent literature (past five years) on plant-insect interactions and plant-stress chemistry, reports cross the established boundaries of many fields. While this is desirable, most studies still do not consider the wealth of information available on compensatory responses in the available literature. Unfortunately, many current researchers are apparently unaware of much of the previous work, and an exceptional amount of effort is being spent on duplicative research. Thus, this chapter also provides researchers with a broad overview of the information available on plant compensatory responses, and draws lines of relationship that should be considered when designing further studies or conceptualizing new hypotheses.

ENDOGENOUS FACTORS AFFECTING PLANT COMPENSATION

Endogenous factors affecting plant compensation are defined as those mechanisms that are primarily influenced by allocation or reallocation of resources within the plant. These include regrowth patterns, photosynthetic activity, senescence, leaf morphology, and canopy architecture. Variable distribution of resources can result in major changes in the form of plant compensatory responses and is strongly influenced by source-sink relationships. For example, sink-limited plants are characterized by lack of yield reduction following leaf loss (48, 78, 187). In such plants, carbohydrates may be stored in structures other than leaves; up to 40% of the stem weight of corn may be sucrose. Major reductions in leaf area do not affect yield of tomatoes because of overproduction of photosynthates (140, 169). Thus, even though leafmining by *Liriomyza sativae* can reduce apparent photosynthesis by 60% in affected leaves (91), relationships between leafmining and reduced tomato yield have been difficult to document (200). Judging the degree of sink limitation is often

difficult because of variable importance of other compensatory factors, including hormonal balance effects on translocation (79) or assimilate release by senescing tissues (179).

In contrast, source-limited plants usually suffer marked yield (or growth) reductions following a decrease in leaf area [but see Aggarwal et al (2) for an exception]. For example, even moderate levels of mining of celery leaves by *Liriomyza trifolii* results in stunting (178). This damage extends the growth period up to seven weeks, with attendant losses in economic value because of additional fertilizer, water, labor, and pesticide inputs. Many common crop plants are source-limited, and the literature provides numerous examples of yield loss due to arthropod removal of leaf area (164). The relative effects of sink or source limitation on yield of agricultural crops are likely to vary with cultivar, growing conditions, and stress. This variability represents a major challenge for plant breeders attempting to utilize plant compensation for arthropod resistance.

Photosynthetic Enhancement

Herbivory can influence photosynthesis and respiration through a variety of effects ranging from physical to biochemical on the plant. Net photosynthesis (P) is defined as the difference between total gross photosynthesis (P_g) and respiration (R) including photorespiration (172): $P = P_g - R$. Thus, injury by herbivory may decrease P by directly affecting P_g at any level and/or by stimulating an increase in R. Measurements of photosynthesis, for example, by gas-exchange techniques, do directly give information about net photosynthesis (P) but do not as such give insight into the mechanisms involved.

Net photosynthesis (P) also can be readily described using a gas exchange equation of the following form: $P = D/R_s + R_m$, where D is the difference between external and internal CO_2, R_s is the resistance to CO_2 uptake due to stomata, and R_m is the intracellular resistance to CO_2 uptake and includes a diffusional and transport component as well as components for the biochemical and photochemical events of photosynthesis (172). The latter components include chlorophyll and the photochemistry of photosynthesis, carboxylases, sources and sinks, and all internal aspects that may affect CO_2 assimilation.

Most measurements of net photosynthesis are conducted on single leaves and the problems of scaling to canopies, agricultural populations, or natural stands are complex (133). Thus, one must use caution when interpreting net photosynthetic measurements in terms of whole-plant photosynthesis.

An increase in net photosynthetic activity may occur following arthropod damage because leaves often function below maximum capacity (108, 114, 185). Two general mechanisms have been proposed that would allow for such an increase. First, limitations of the assimilate transport system and/or utilization rate inhibit gross CO_2 fixation, presumably because of an accumu-

lation of photosynthetic products in the leaf, i.e. starch, which inhibit photosynthesis perhaps by an effect on intracellular CO_2 transport (i.e. R_m) (130, 131, 171). Second, although partial defoliation reportedly has variable effects on net photosynthesis (193), it has been shown to increase assimilate demand by previously existing or new sinks (e.g. replacement tissue) thereby increasing photosynthetic activity of remaining leaves (28, 69, 185). In the case of *L. trifolii* mining on lima beans, the increase in sink demand related to restitutive tissue allowed an overcompensation response resulting in a net increase in apparent photosynthetic activity in damaged plants (117).

A variety of physiological responses potentially responsible for changes in photosynthetic activity following defoliation have been demonstrated. Partial defoliation may result in an increased supply of leaf cytokinins (124) or root-derived cytokinins (185) due to less competition within the plant for the hormone. Increased levels of cytokinins have been shown to increase net CO_2 fixation as a result of enhanced assimilate transport and nutrient uptake (153), to delay senescence (134, 172), and to decrease intracellular resistance to CO_2 transport, i.e. R_m (79, 153, 185). Additionally, less leaf area may improve water availability for the remaining leaves, thereby improving water status resulting in stomata remaining open longer in dry periods (46, 162). Similarly, an increased availability of nitrogen due to either reduced leaf area or a feeding-induced (premature) senescence could enhance protein synthesis (29). An increase in production of the carboxylating enzyme ribulose bisphosphate carboxylase could be expected to increase photosynthetic activity (79, 171). Finally, compensatory responses resulting in either an increased chlorophyll content in the remaining leaf tissue (153) or restitutive cell growth with new chloroplasts (117) would also increase photosynthetic capacity. Defoliation, however, during the critical stage of fruit set frequently results in reduced yields (86).

One can conclude from the above-cited studies that most herbivory-related compensatory responses are the result of a decrease in R_m (79, 153, 185) and not a decrease in R_s. However, debudding of *Xanthium* sp. resulted in an increased net photosynthetic rate because of a decrease in R_s (185). Variable or changing responses over time tend to complicate evaluation of potential compensation responses. Several reports note that net photosynthetic activity following arthropod damage may remain the same initially (36, 62, 63, 92, 94), and then increase following leaf-area recovery to levels above the undamaged control plants (36, 54, 124). Such variability ·in response is not unexpected given the range of plant species characteristics involved (grasses vs broadleaf plants, perennials vs annuals) and the expectation that the type of arthropod feeding associated with various guilds (193) could directly influence photosynthetic tissues, assimilate transport, or sink strength. In addition, the age class of the leaves at the time of defoliation could affect

potential compensation (116). As early as 1974, researchers had demonstrated that increased cell division could occur in response to arthropod damage but that the potential was related to leaf age; growth from meristematic tissue ceased when immature tissues reached 25–75% of mature size (4, 183). Thus, the ages of the plants examined for compensation responses undoubtedly contribute to the observed variability in the literature.

Finally, as described in detail by Welter (193), an important caveat applies to reports documenting increases in photosynthetic activity following defoliation. Many of the published experiments have been interpreted too broadly. Although tissues remaining after partial defoliation may increase in photosynthetic activity, the increase may not be adequate to replace the productivity of the leaf area lost.

Reallocation of Available Assimilates

According to Gifford & Evans (57), a typical or characteristic pattern of assimilate distribution occurs within plants. Under normal growth conditions, assimilates produced within leaves are partitioned between (a) leaf growth [structural and metabolic processes, often related to meristematic tissue, see Turgeon (179) and references therein], (b) storage in numerous cellular sinks, or (c) export to other foliage, stems, roots, or fruit. In sink-regulated systems, assimilate apportionment is related to the relative strength of each sink, which varies with the stage of development of the plant (141). However, resource allocation after partial defoliation can be dramatically altered in several ways.

A commonly tested hypothesis is that reallocation to new, restitutive, or replacement tissues occurs at the expense of other growth and metabolic centers. Considerable direct evidence of such reallocation is available from ^{14}C tracer experiments with grasses (152), field crops (171), and conifers (46, 47). Smith et al (161) provided additional evidence by showing that amino acid concentrations in extra-floral nectaries increased following simulated herbivory on *Impatiens sultani* (Balsaminaceae). They speculated that this reallocation was adaptive against herbivores, as omnivorous ants foraging on plants with extra floral nectaries are known to prefer nectars with high levels of amino acids (105, 161).

A substantial body of circumstantial evidence also exists for resource reallocation following herbivory, much of which has been developed in agricultural systems. For example, early season feeding on cucumbers by spider mites produced plants that out-yielded controls (84); tiller production was stimulated in some range grasses following feeding by grasshoppers (35, 41); yields were enhanced or unaffected by partial defoliation of cotton or tobacco (real or simulated) by the tobacco budworm (71, 100, 101); and feeding by a lepidopterous pest caused multiple stalks in some thistles, leading to a three-fold increase in seed production (87). More recently, Karban &

Courtney (94) demonstrated that even high levels of pierid damage did not affect seed set in a crucifer. In a similar study, low levels of simulated defoliation by a lepidopteran at the preheading or heading stage in cabbage improved yields over undamaged plants (158). In addition, in spite of some vascular-system damage, apparent net photosynthesis increased in corn with low population levels of the European corn borer, *Ostrinia nubilalis* (59). In the nonagricultural plant *Rubus chaemaemorus* (Rosaceae), removal of up to 50% of the female ramets that had initiated fruit had no effect on fruit or seed set or total seed mass per fruit (3).

Reallocation of resources also may occur following release from apical dominance. Dominant apical meristems are often the target of arthropods as the new-growth tissue tends to be more succulent than older, lignified foliage (148). In addition, the new growth, as a site of protein synthesis and use, may be more attractive because of higher nitrogen content (97, 119). When dominant meristems are removed, an increase in meristematic activity at nonapical locations can lead to increased branching (68). This has been demonstrated for mammals grazing on *Ipomopsis arizonica* (Polemoniaceae) (113) as well as for a variety of arthropod herbivores (11, 40). Such branching can compensate for both foliage and seed predation if damage occurs in an early stage of plant development and if resources are adequate (11, 170, 189). Increased branching probably has the greatest potential impact for those plants that flower at the branch terminals (11). However, benefits may accrue primarily for plants grown singly and not in competition (1). Regardless, such branching will not always be compensatory. In agricultural systems, increased branching may result in unacceptable size or timing of yield. In natural systems, reduced plant height affecting seed dispersal or predation may not balance benefits.

Horticulturalists have known of stress-induced reallocation of assimilates to fruiting structures for many years, but relatively few studies have examined the role of arthropod stress. Recently, Reichman & Smith (150) found that early removal of one or more flowers of *Tragopodon dubius* (Asteraceae) stimulated more production of flowers and biomass than that in undamaged plants. Root feeding by the scarabaeid *Phyllopertha horticola* caused reallocation of resources to reproductive growth in an annual herb, *Capsella bursa-pastoris* (Brassiceae), which subsequently increased levels of soluble nitrogen and stimulated aphid population development (55). Some plants may respond to herbivory by the production of parthenocarpic (seedless) fruit; in wild parsnip, such fruit is highly attractive and apparently diverts feeding of a lepidopterous herbivore from the fruit with seeds (202). Hendrix & Trap (73) found that even after extensive floral herbivory, numbers of seed produced by the desert/rangeland plant *Pastinaca sativae* (Apiaceae) were not different from undamaged plants, but the size of the seeds from partially

defoliated plants was smaller. In general this would be considered a fitness-reducing effect as smaller seeds have less available nutrients at germination. However, the smaller seeds of this species allocate more biomass to root production, and produce seedlings with better survivorship during periods of drought (50). Thus, the advantage of a seed population producing drought-resistant seedlings may, over evolutionary time, increase fitness in *P. sativae*. Similarly, although fewer seeds of the rangeland plant *Gutierrezia sarothrae* (Asteraceae) are produced on branches with leaves tied together by insect herbivores, seeds developing from tied branches germinate faster and at a higher percentage than seeds from untied controls (198). These two systems demonstrate a concern recently voiced by Prins & Nell (146) that studies based on performance of individual plants may be insufficient for predicting fitness at the population level.

Even for a single plant, prediction of reallocation effects can be difficult. Kirkwood (98) suggested that a "suicidal" reallocation of resources from repair to reproduction following herbivory may increase fitness in plants with annual or determinant growth patterns. In plants with indeterminate growth, a balance will be struck between somatic longevity and reproductive output. Optimal allocation for repair or reproduction then would occur at the level that most closely approximates indefinite survival.

Factors affecting assimilate reallocation are complex and poorly understood. It is generally accepted that the strength of sink demand controls resource distribution in source-limited plants (179, 185). As noted previously, fruiting structures often become the strongest sinks following partial defoliation (93). However, in the absence of reproductive sinks, new tissues are generally stronger sinks for carbon resources than roots (152, 182, 194) [but see Detling et al (37) for effects of root feeding]. This concept provides some of the rationale for the horticultural practice of stimulating fruit development and maturation through water deprivation (6). The defoliation-induced shifts in assimilate allocation last only until the new growth can provide for its internal carbon needs (152). Thus, reallocation is a temporary process if the plant can replace lost tissue. Nonetheless, even if reallocation is temporary, negative fitness or yield effects may result if the plant loses synchrony with others of the same species (89, 144).

Utilization of storage reserves, which can be used to buffer the effects of arthropod damage, will also affect resource allocation following defoliation. The key storage sites vary with plant age and stage, but are typically found within leaves, along the route of translocation, or in specialized storage structures such as roots, tubers, and rhizomes (47, 128, 179). The availability of storage will relate to the the sink strength of the storage sites prior to arthropod damage. The most readily available reserves for reallocation are nonstructural carbohydrates such as sucrose, fructose, starch or nonstarch

polysaccharides, oligosaccharides, alditols, and cyclitols (96). Imported sucrose is used preferentially for the synthesis of structural carbohydrates in immature leaves in several species (38, 179).

Gifford & Evans (57) list several additional factors that affect assimilate distribution. Hormones impact sink strength through effects on many physiological processes, including translocation and gas exchange (23, 78, 193, 195). In addition, light and energy availability affect the productivity of sources, thereby determining if a source will meet its own carbon requirements or provide an excess. These factors are discussed in more detail in the following section.

Changes in Canopy Architecture

The most common measure of canopy architecture is the leaf-area index (LAI), which is the total cumulative leaf area (one surface) per total ground area covered (199). LAI has important implications for plant compensation to herbivory in that it relates to the interception of photosynthetically active radiation (PAR). Lower LAI values indicate fewer layers of foliage. A related concept is the light-extinction coefficient (LEC), which relates to the PAR absorption properties of the canopy and depends in part on the composition and quantity of photosynthetic pigments and leaf orientation (48). The absorption of PAR (A) by the canopy is described by the formula: $A = (LEC) \times (LAI)$.

Most early studies investigating the interactions of LAI with respiration and photosynthesis assumed that respiration was linearly related to LAI (as accumulated dry weight), while photosynthesis increased asymptotically (67, 112). They therefore concluded that there must be an optimum LAI for plant growth. Such optimum LAIs have been reported for several crops (31, 67). Beyond the point of optimum LAI, net photosynthesis of the canopy would be reduced (48, 112). Some evidence indicates that feeding on shaded foliage may not be as detrimental to beech trees as is feeding on sunlit leaves (132). Gold & Caldwell (60) demonstrated that simulated herbivory removing the lower, more horizontal leaf blades of tussock grass reduced the LEC at midday, and photosynthetic activity was maximized. Further, Osborne (135) suggested that defoliating insects may act as biological pruners, removing superfluous leaf area with an excess respiratory load, decreasing mutual shading, and thus improving yields. However, a key assumption, made by proponents of an optimum LAI in the 1960s and early 1970s, is that all the leaves on a plant have essentially equivalent photosynthetic activity. This assumption is, of course, not correct (66). Other studies demonstrated that plant respiration is negatively curvilinear with LAI, resulting in a broad range or plateau of optimum LAI (48, 120; see Figure 1 in 196).

The implication of a broad range of optimum LAI is that canopy architecture

may buffer the effects of arthropod foliar damage. If leaves in the canopy are removed, photosynthetic activity in the remaining leaves will increase, while the LEC will be reduced. Clearly, plants with a broad optimum LAI would have an ecological advantage in being able to sustain some defoliation without loss in assimilate production while not incurring significant additional metabolic costs.

Changes in canopy architecture within a plant species resulting from partial defoliation can profoundly affect both fitness and yield. For example, competitive interactions between plants may be affected; artificial defoliation of white clover in a mixed sward of white clover and ryegrass resulted in white clover–density increases and ryegrass-density decreases (32). Increases in stem length in the white clover, which allowed partial shading of the ryegrass, permitted the white clover to maintain this competitive advantage for several years without additional defoliations. Arthropod damage also increases variation within plant canopies (56, 154). In many cases this variability may lead to reduced fitness and lower survival (56), but such variation can enhance fitness. Variable canopy architecture can reduce survival of defoliators through alterations in host-finding behavior (34), changes in temperature that affect disease susceptibility (72), deleterious exposure of herbivores to UV radiation (177), reduced nutritional status of the foliage (151), or sunlight-enhanced improvements in the success of parasitoids (180).

The location of the damaged plant within a multispecies canopy can affect the compensation response. After attack by scale insects, trees grown in full sun are significantly smaller than those grown in shaded areas even after the heights were adjusted by growth patterns of undamaged control trees (182). Similar results have been reported for artificial defoliation experiments with red oak seedlings (121). In contrast, grasses grown in shade did not recover as rapidly as when grown in full sun, allocated a smaller proportion of available assimilate to roots, and suffered greater mortality from repeated defoliation (143). In addition, because plant compensatory responses can change with leaf age (116), modifications in the population age structure of leaves on plants due to shading (8) should impact plant compensatory responses.

Changes in Leaf Morphology

Changes in leaf morphology following arthropod damage have been reported since the 1800s (74). New leaves may become larger due to increase in cell size via mesophyll elongation (100, 153) or increased cell division (129). Cell expansion may be influenced by chloroplast enlargement due to starch accumulation or via increased turgor pressure (128). Turgor pressure provides the force for cell expansion, which declines if the leaf water content falls below 90%, and ceases entirely below 70%. Thus, partial defoliation during

periods of water stress may improve the water potential of remaining foliage and result in cell expansion.

Subsequent to partial defoliation, the remaining leaves may increase in specific leaf weight (SLW, g/cm^2) (86). SLW increase probably occurs in response to increased light penetration (decreased LEC), which stimulates chloroplast production and carboxylase activity. However, there may be a physiological tradeoff in that an increase in SLW can affect CO_2 diffusion (128). A greater PAR absorption is associated with enhanced thickness, cell-surface area–to–leaf area ratio, and specific leaf weight (111, 142).

An increase in SLW may give the plant additional fitness-enhancing attributes. Some seaweeds show an increase in tensile strength following herbivory (109). Such increases in leaf toughness can have a reciprocal effect on insects. Raupp (147) demonstrated that the mandibles of a leaf beetle wear faster on the tough older leaves of willow, reducing food intake and, eventually, fecundity. Also, any increases in leaf content with nonnutritive fibrous materials may increase density and result in dilution of nutrient-rich tissues with indigestible bulk, leading to reductions in herbivore population growth potentials (20, 149).

Delay in Senescence Following Defoliation

Following partial defoliation, a delay in the onset of senescence may occur (9, 58). Total leaf-area reduction may reduce competition between roots and leaves for root-derived cytokinins, which inhibit mRNA, suppress protein and enzyme degradation, increase stomatal opening, and maintain cell-membrane integrity (17, 62, 185). Other studies have demonstrated a reduction in intracellular resistance to CO_2, a reduction in starch accumulation, increased protein synthesis, and a retention of photosynthetic activity related to the increased sink demand discussed previously (29, 79).

Some insects (typically sucking insects) inject host metabolism–modifying chemicals including phenolics, plant hormones, enzymes, and toxins (68). The many examples of negative effects include stunting and gall formations (23, 43), but the evidence for a compensatory response is less compelling. Regions surrounding the mines of some species of leafminers may remain green and high in protein, and apparently continue to photosynthesize, despite the loss in activity of other regions on the leaf (45, 135). In fact, these regions may remain active even after the leaf abscises. Cytokinin levels in the affected regions are 20-fold higher than in the remaining tissues, suggesting that the insects could sequester or produce cytokinins (44, 45). In addition, saliva deposited by grasshoppers stimulated more rapid plant regrowth as compared to plants artificially defoliated a similar amount (16, 41). The regrowth appeared to be related to increased root respiration and tiller production. However, a subsequent study has suggested that the primary mechanism for

regrowth is a temporarily altered carbohydrate allocation pattern, rather than a stimulatory substance in grasshopper saliva (184). Similarly, a delay in senescence in sycamore leaves fed upon by aphids has been reported (39), but this delay could have resulted from the increased availability of foliar nitrogen deposited as excreta by the aphids because a higher level of nitrogen was found in the affected foliage.

EXOGENOUS FACTORS AFFECTING PLANT COMPENSATION

A variety of exogenous factors that impact plant compensatory responses are not directly under the physiological control of the plant. These include such environmental factors as nutrient availability, intensity and timing of defoliation, herbivore distribution, etc. These are discussed in detail in the following pages.

Nutrient Availability

Predicting plant compensation responses for arthropod damage is complicated by variability in nutrient availability, which can affect not only growth but also the allocation of resources within the plant (197). According to Wilson (197), many plants tend to respond to poor soil nutrition with an increased allocation of resources to root growth (but see 121 and references therein). Nutrient pulses, which occur in both natural and agricultural systems, variably affect leaf and root relative growth rates and allocation to reproductive structures (126, 127, 165). Timing of such nutrient pulses in relation to plant phenology is critical, as late season pulses may selectively be transported to reproductive structures, while earlier pulses reduce the relative growth rate of the roots as compared to leaves (126). The relative level of optimal versus substandard nutrient availability, as well as accessibility of growth related nutrients (e.g. nitrogen, phosphorus, and sulfur) versus other nutrients (potassium, etc), will influence biomass allocation (85, 126). The role of substandard nutrition may be more important in natural systems as opposed to agricultural ecosystems, as most agricultural crops are routinely provided with supplemental nutrition. Thus, because nutrient availability to the roots changes relative sink strengths, and sink strength relates directly to compensation through resource allocation, the nutritional status of the root medium plays a significant role in compensatory responses.

One area of plant nutritional ecology that is commonly overlooked in both natural and agricultural ecosystems is the impact of arthropods. Schowalter et al (156) cite a series of studies documenting rapid nutrient recycling in forest ecosystems following defoliation episodes by arthropods. Even nominal levels of herbivory were shown to induce premature litterfall [with up to 10

times higher levels of nitrogen (99)] and to increase the rate of leaching from damaged foliage. Although the quantity of biomass returned as arthropod feces or tissues is less than from normal litterfall, the arthropod products are more readily processed by soil microorganisms, leading to enhanced biotic activity (greater densities of bacterial decomposers) that improves biotic reduction of leaf litter. Owen & Wiegert (138) suggested that the large quantities of water released by some cercopid species could increase the nutrient uptake by surface roots in otherwise dry conditions. Unfortunately, little information of this nature is available for nonforest vegetation [but see McNaughton (123) for mammalian nutrient cycling]. Lightfoot & Whitford (107) determined that nitrogen excreted by arthropods accounted for nearly 20% of the canopy-to-soil nitrogen flux in a creosotebush community. Hopefully, forthcoming research will address this topic; systems poor in nitrogen would be excellent candidates for further investigation.

Intensity and Timing of Defoliation

Intensity of defoliation includes both degree of leaf loss and number of successive episodes of defoliation. Although plants generally compensate less for multiple defoliations due to chronic herbivory than for episodes of single defoliation (18, 25), some plants can effectively compensate for more than one partial defoliation. For example, even weekly defoliations of 29% of the foliage throughout the growing season did not reduce yield in potatoes (192). Stewart et al (167) reported that cauliflower could tolerate multiple defoliations of up to 36% of the leaf area without significant reductions in head weight or maturation rate. Similarly, three defoliations of 50% of the leaf area are required before flowering or fruit set decreases in a woodland orchid, *Tipularia discolor* (Orchidaceae) (194). For *T. discolor,* resources stored in older corms apparently were mobilized to prevent significant losses in leaf biomass after the first two defoliations.

The relationship between timing of arthropod damage and plant phenological stage is critical to understanding compensation responses. Bardner & Fletcher (4), in an extensive review of the literature up to 1974, reported that the relationship between injury and yield varies with growth stage at the time of injury in the following generalized pattern for annual plants:

1. Plants are intolerant of damage and compensate little immediately following germination.
2. As vegetative growth proceeds, plants become increasingly tolerant.
3. At the onset of flower production, plants become less able to compensate (specifically those species with a short flowering period).
4. As reproductive structures mature (ripen), plants again become tolerant to arthropod defoliation.

Although many exceptions exist [e.g. Sharrow (157) documented late-season defoliation–enhanced yield losses in wheat], this generalized pattern for annual plants is broadly supported by the more recent literature. An illustration is provided by one of the most intensively studied plant-insect systems, potatoes attacked by the Colorado potato beetle, *Leptinotarsa decemlineata*. Wellick et al (192) reported that yield losses were significant when potatoes were defoliated 3–5 weeks after germination. The next critical period when defoliation did not result in compensation was during flowering (24, 65, 155). However, the potential time period available for regrowth is important, as later-maturing potato varieties showed improved yield recovery (24). Within a few weeks of harvest, as tubers fill, even 100% defoliation has no significant impact on yields (52, 65, 203). The data base on defoliation patterns and compensatory responses in potatoes is such that computer models are being used to predict yield losses from field estimates of defoliation during various stages of plant growth (49, 75).

Predicting the compensatory responses of perennial plants is complicated by a host of factors including the wide variety of storage systems that tend to buffer the effects of defoliation. However, a few generalizations are possible. For example, little compensation occurs if flowers are lost by deciduous trees, as can be seen following flower abscission in many fruit trees resulting from late-season frosts. In addition, the effects of the defoliation may not be evident until one or more years after the incident (6, 70, 103). Also, late-season feeding can be extremely detrimental to grasses, as they may not recover reproductive potential (77).

Distribution of Arthropods

The distribution of insects within a field can affect plant compensation for damage. In agricultural systems, plant spacing is such that small losses to the canopy can be readily filled, but if larger areas are damaged, adjacent plants cannot easily compensate (5, 157, 201). Arthropods that feed in an aggregated or clumped dispersion pattern are likely to cause such damage at lower population levels than those with random or systematic dispersion (159). Bardner & Fletcher (4) discuss several mechanisms responsible for aggregated dispersions, including edge effects, obstruction effects, plant density, and plant heterogeneity. Other potential mechanisms include protection or self defense, mating behaviors, feeding strategies, pesticide application, and oviposition patterns (145, 163, 174).

The feeding-site preference of arthropods can impact the compensatory responses of plants. For example, root feeding can increase water stress (55), resulting in a variety of physiological effects (see below). The effects of selective removal of apical dominance, shade vs sun leaves, and old versus new foliage are discussed above in this review. However, feeding-induced

changes in plant-canopy morphology and plant physiology have reciprocal effects on the arthropod populations that may alter feeding-site preference, population growth, and the extent of plant damage. For example, crowding may produce smaller individuals (61) and force feeding on plant parts that are less nutritious and contribute less to yield; thus a nonlinear relationship can develop between arthropod numbers and plant yield or fitness. This is a poorly understood process for most plant species, and the reader is referred to Karban's & Myers' (95) review on induced plant responses to herbivory for additional information.

Other Environmental Stresses

Water and temperature stress can significantly impact plant compensatory capacity, mostly through alteration of allocation and reallocation of resources and stomatal closure effects on gas exchange and photosynthetic capacity (10, 21, 22, 80 and references therein, 118, 121). Most of the physiological changes due to water and temperature stress that influence plant compensation are similar to those already addressed in this review, and are not repeated in detail. The effects of water deprivation, which vary with plant growth stage, are often profound; significant alterations in protein and carbohydrate metabolism, leaf temperature, defensive chemistry, and phytohormone systems have been reported. Considerable information is available on this topic, and Hsiao (81) provides a detailed review of the effects of water stress on plant physiology. Benedict & Hatfield (10) and Holtzer (80) have contributed excellent reviews of the influence of temperature and water stress–induced changes in plant metabolism on arthropod population growth and development, respectively.

Environmental perturbations resulting in water stress and osmotic changes frequently cause a reduction in growth beyond the effects on CO_2 assimilation by photosynthesis (115). And although net photosynthesis may increase or decrease (193), the ratio of growth to CO_2 assimilation may increase. The stress is ordinarily accompanied by hormonal changes such as the production of cytokinins, abscisic acid, and ethylene (33). The excess photosynthate may result in the biosynthesis of a variety of secondary products including both protein and nonprotein amino acids, phenolic compounds, terpenoids, alkaloids, glucosinolates, and cyanogenic glucosides (186).

The effects on compensation for herbivory of intra- and interspecies competition among plants for limited resources vary. Even in the absence of herbivory, resource allocation is commonly altered. Chandrasena & Peiris (19) found that an eightfold increase in density of *Panicum repens* (Gramineae) resulted in less tiller production but not the expected shift to increased rhizome biomass. In contrast, Lieffers & Titus (106) determined that root/shoot ratios increased for pines (*Pinus contorta*) in higher density plantings. Central to

this variability is the resource for which the plants compete. Researchers have suggested that the interplant competition for light is asymmetric; larger individuals have a greater impact on smaller plants (190, 191). In contrast, competition for nutrients may cause a relative growth suppression that is similar for both individuals (190, 191). Not surprisingly, if defoliation of a plant increases photosynthetic activity in another competing plant, thereby allowing more rapid growth, or if nutrients are not distributed equally (possibly because of arthropod tissue/frass deposition or improved nutrient flux beneath damaged plants), variable regrowth potential will result.

Competition effects on regrowth depend on the plant-herbivore system studied. Swank & Oechel (168), examining interactions among arthropod herbivory, resource limitation, and competition between chaparral shrubs and herbs, found strong interactions between all main factors. Fowler & Rauscher (53) observed just the opposite: competition and herbivory effects were additive and independent in a system utilizing a perennial herb [*Aristolochia teticulata* (Aristoloiaceae)], a grass [*Schizachyrium scoparium* (Gramineae)] and another common herb [*Rubus trivialis* (Rosaceae)]. Similarly, little interaction was observed between weed competition and simulated arthropod feeding in soybeans (76). A recent study on mammalian herbivory by Machinski & Whitham (113) provides an intermediate response; association with either grasses or pines tended to reduce fruit set in the herb, *Ipomopsis arizonica* (Polemoniaceae), but only competition with grasses significantly interfered with compensation for foliar damage.

Air pollution, like water stress, can alter plant compensation for arthropod damage. Although most air pollutant episodes are deleterious to plants through lesion development, membrane destruction, or premature senescence (83, 173, 176), wet deposition of pollutants (acidic rain, acidic fog) on foliar surfaces can act as foliar fertilizers (160, 175) that may result in increased photosynthetic activity (51, 88) and thus more rapid recovery from arthropod damage (see previous section on nutrient availability). Following plant exposure to moderate levels of ozone and other pollutants, substantial modifications in the form and content of plant nitrogen (176) and sugars (83) have been reported. These effects include an increase in free amino acids, soluble proteins, free sugars, and reducing sugars, which presumably could provide a readily available pool of assimilates for regrowth. However, because pollutants (*a*) generally decrease photosynthetic activity and increase crop losses (64), (*b*) often maximize the attractiveness and nutritional suitability of affected plants to the benefit of arthropod herbivores (83), and (*c*) can interfere with root function (30), the potential effects of pollution events are likely to negatively impact compensatory responses.

Increasing levels of atmospheric CO_2 alter a variety of plant physiological systems likely to substantially impact plant compensatory responses. In a

detailed review of the possible consequences of increasing global CO_2 levels, Bazzaz (7) lists references that document reduced water requirements, improved biomass accumulation, initial improvements in photosynthesis, specific leaf-area decreases, and increased branching. All of these mechanisms can increase compensatory responses of plants to herbivory. Plants grown in elevated CO_2 atmospheres generally have greater LAI values (104, 181), and therefore may be more tolerant of arthropod defoliation. This tolerance may occur in spite of a tendency by arthropods to consume more leaf area on the relatively nitrogen-poor foliage produced in high CO_2 environments (136). Interestingly, C_3-photosynthetic plants tend to respond more positively to increased atmospheric levels of CO_2 than do C_4-photosynthetic plants because the carboxylation system of C_4 plants is nearly CO_2 saturated at present ambient levels (12). To our knowledge, however, no reports have been published that were designed specifically to test pollutant effects on plant compensatory responses to herbivores.

CONCLUDING REMARKS

Most plants compensate for herbivory to some extent. Depending on the endogenous and exogenous factors discussed in this article, some plants may only partially compensate for arthropod damage while others may even overcompensate and increase yields or fitness. The evolutionary advantages accruing to plants with compensatory abilities are not in question. Whether these capabilities have evolved in response to arthropods and other herbivores, or to evolutionary pressures resulting from plant competition, remains in doubt (1). Nonetheless, although our knowledge of mechanisms resulting in tolerance or compensation is increasing rapidly, our ability to predict the levels of compensation that will occur in any given system is still relatively poor, in part because of a lack of information regarding interactions between ecosystem components. In most systems, interactions between available nutrients, timing and intensity of defoliation, water stress, plant competition, etc are highly significant (168); in other systems, such interactions appear minimal (53). Thus, until a much more substantial data base is developed, few generalizations regarding the ecological or agricultural importance of compensatory responses will be forthcoming. Indeed, development of general theories on plant compensation will rely on the recognition that a broad range of responses are probable in different ecosystems. A thorough knowledge of plant compensation for herbivory would be an asset to sound integrated pest management programs inasmuch as an initial apparent injury may elicit an unwarranted and unnecessary pesticide treatment regime.

Finally, a review of the available literature suggests the need for more closely controlled experimental designs. With few exceptions, mostly from

the contemporary literature, studies have not reported most or even many of the potential exogenous factors affecting plant compensatory responses. Although not all such factors (nutrients, light, water stress, etc) need be varied within a study, they must be controlled, or at least documented, to allow comparison with future research results. Without documentation of these variables, studies can only provide circumstantial evidence for compensatory mechanisms.

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