Overcompensation of plants in response to herbivory and the by-product benefits of mutualism

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Plants that overcompensate for herbivory are relatively healthier when damaged. In this mutualistic association, the herbivore benefits from the plant, and the plant benefits from the herbivore's actions. As long as the benefit to the plant outweighs the costs imposed by browsing herbivores, this interaction should remain stable. Many apparently parasitic associations can be mutually beneficial under some environmental conditions.

Most plants are subject to multiple attackers and employ strategies to defend against or to escape herbivory. Plant defense against herbivory can be loosely categorized into mechanisms that provide resistance against herbivores, tolerance to herbivory or phenological escape from herbivory (Box 1). Resistance traits are those that reduce the preference and/or performance of herbivores. Constitutive and environmentally induced variation in plant resistance to herbivores has been extensively studied in a cost–benefit framework[1–3]. Tolerance traits reduce the negative effects of herbivory on plant fitness after herbivory has occurred[4]. Variation between plants in their tolerance has also recently been examined in the cost–benefit framework, although evidence supporting the cost–benefit model is thus far minimal[4]. An additional defense strategy is phenological escape of plants from herbivores[5]. The examination of plant defense (resistance, tolerance and escape) assumes an antagonistic interaction between plants and herbivores in ecological and evolutionary time. An alternative view is that there are circumstances in which herbivores not only benefit from consuming plants, but that plants also benefit from being consumed by herbivores.

Overcompensation is defined as plants that have higher fitness when they are damaged compared with related plants that are undamaged[6] (Fig. 1). Overcompensation goes beyond our concepts of resistance and tolerance because there is a mutually beneficial relationship between plants and their herbivores. Herbivores benefit by consuming plants, and plants benefit from being eaten. The benefits to the plant might be through induced phenological escape, the release of apical dominance and even growth promoters in herbivore regurgitants[7]. The now classical example of overcompensation in plants is that of scarlet *Gilia* (*Ipomopsis aggregata*),

which is often browsed by ungulates. In some populations of scarlet *Gilia*, browsed or manually clipped plants have higher relative female and male fitness than undamaged plants[8–10].

The concept of overcompensation has met considerable scrutiny, and heated debates have ensued over the existence of the phenomenon[11–14]. However, several field and greenhouse studies have documented overcompensation of plants to herbivory using convincing experimental designs and realistic measures of plant fitness[3,4,8,15–17]. Why is overcompensation hard to believe? Several arguments and questions have to be considered and addressed:

- Must herbivores reduce plant fitness?
- If plants can overcompensate, why do not all plants reproduce maximally?
- What insight comes from considering plant–herbivore interactions in a framework of mutualism?

Must herbivores reduce plant fitness?

Sufficient data now exist showing that tolerance to herbivory is a common phenomenon; that is, plant tissues removed by herbivores might not reduce plant fitness when compared with undamaged plants. For example, wild radish plants (*Raphanus raphanistrum*) with up to 25% of their leaves chewed off by caterpillars have equal growth and reproduction in several male and female fitness characteristics as do undamaged plants[18]. Thus, we can no longer cling to the idea that herbivores must be parasites that reduce plant fitness continually. Overcompensation goes beyond tolerance in that herbivory results in higher plant fitness compared with plants that are not damaged. Tolerance to herbivory (and overcompensation) might be genotypically based and/or environmentally dependent (reviewed in Ref. 4). For example, plants might overcompensate only when there is high light and water levels and low levels of competition, and when the herbivory is early in the season. Where overcompensation is environmentally

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Box 1. Plant responses to herbivory

Defense
Any trait that increases plant fitness by reducing herbivory or its effects compared with plants lacking that trait. Plant defenses typically take the form of resistance, tolerance or phenological escape.

Mutualism
An interaction between species in which individuals of both species benefit from the association compared with individuals not engaged in the association. Benefits should be measured in terms of fitness consequences for each partner in ecological time. The evolutionary history of the interaction is not relevant to this definition.

Overcompensation
Plants have higher fitness when they are damaged by herbivores compared with related plants that are undamaged. This interaction suggests a mutualism between plants and herbivores because both parties benefit.

Phenological escape
Defense of plants is successful when plants are not available when herbivores are most active. For example, it is widely believed that natural selection has favored early growth and reproduction in some plants (e.g. winter annuals), such that plants phenologically escape herbivores that do not emerge until later in the season. Although the idea of phenological escape has long been in the literature, it has not been thoroughly integrated into current cost–benefit models of plant–herbivore interactions[33].

Semelparous
In obligately semelparous organisms (species that reproduce only once during their lifetime), the quantification of fitness components (e.g. seed production) is simplified because multiple measures of reproduction are not required. In species that reproduce repeatedly during their lifetime (i.e. iteroparous), allocation shifts during one or more growing seasons might falsely indicate overcompensation.

Tolerance
The degree to which plant fitness is reduced by herbivore damage relative to the fitness of a related undamaged plant. Plant genotype, environmental conditions and their interaction affect the ability of plants to tolerate herbivory[4].
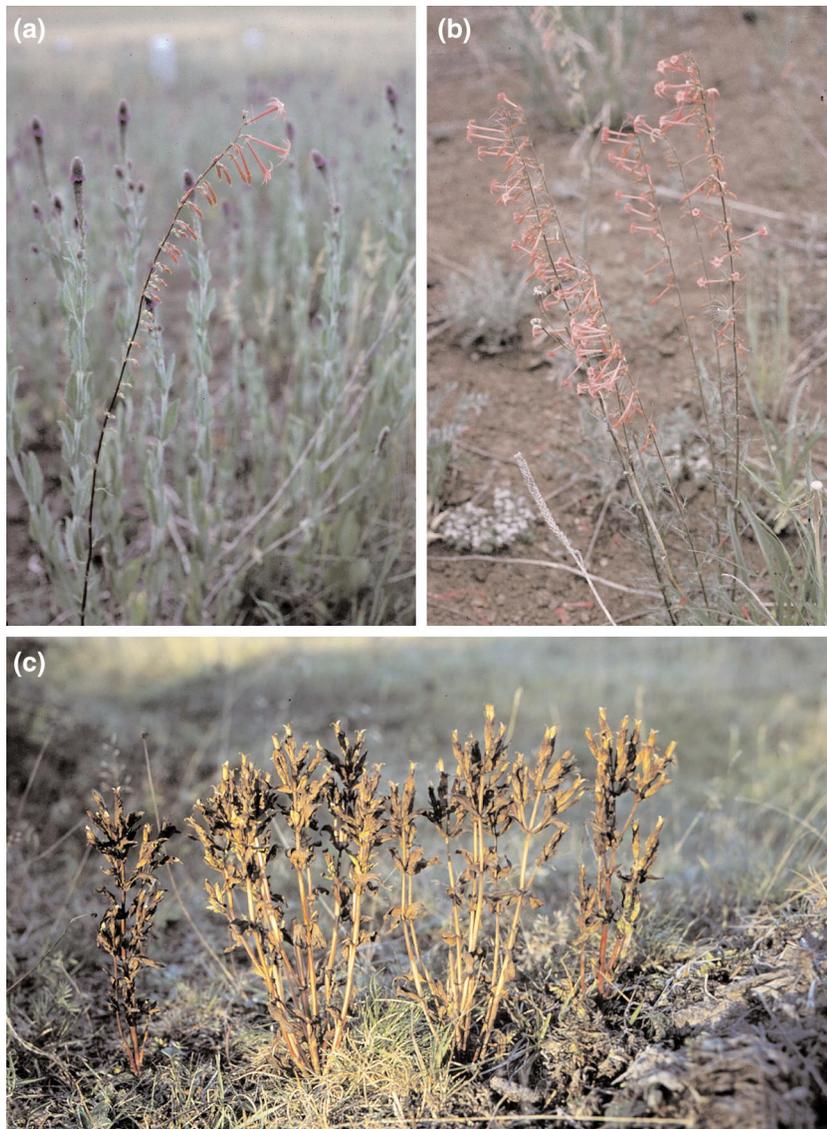

Fig. 1. The benefits of herbivory. (a) Naturally not grazed and (b) grazed individuals of scarlet *Gilia* (*Ipomopsis aggregata*) from a population in Arizona (USA)[8–10]. Natural grazing or artificial clipping of plants causes increased female (seed production) and male (seed siring) fitness compared with undamaged plants in some populations. (c) Field gentians, (*Gentianella campestris*) from populations that have a history of being exposed to grazers, have higher relative fitness when clipped (inner plants) compared with when they are not clipped (outer plants)[16,17]. These plants are from a natural population in Sweden. Plants were matched for having an equal initial size; note that overcompensating clipped (inner) plants have many more meristems than unclipped plants. In such populations, herbivory has apparently increased the overall fitness of plants[4,28]. *(a) and (b) courtesy of Ken Paige, and (c) courtesy of Tommy Lennartsson.*

evolution of overcompensation. In other words, tolerance can make the cost of herbivory small. Thus, a small benefit of herbivory (e.g. in terms of release from apical dominance and/or phenological escape; Fig. 1) for a plant that is mostly tolerant, might make the evolution of overcompensation possible.

The mechanisms of tolerance and overcompensation can be different, although they are certainly not mutually exclusive. Tolerance is more often associated with fast growth and high photosynthetic capacity, whereas overcompensation is more often associated with bud or meristem dormancy[4]. Increased photosynthetic rate and increased water and nutrient uptake have been associated with both tolerance and overcompensation. Tolerance might be favored when resistance is not possible (i.e. for specialized herbivores that are not affected by typical plant defenses) or when resistance is relatively more costly. Overcompensation should be favored when the risk of predictable herbivory is high and the cost of herbivory is low[21].

If plants can overcompensate, why do not all plants reproduce maximally?

Why plants sometimes appear to have lower fitness than is possible is the second puzzle to be addressed. Verbal arguments and mathematical theory have addressed this issue adequately[21–27]. The majority of these models are concerned with the release of apical dominance as the mechanism of overcompensation, and assume:

- A single bout of herbivory (but see Ref. 26).
- The risk of herbivory occurs before flowering.
- Most of the resource acquisition occurs before reproduction and before herbivory[21].

The term 'overcompensation' conjures images of plants that actually benefit from being eaten. Although release of apical dominance might lead to an actual benefit accrued by the plant (more stems, more flowers and more seeds), such release might also be associated with induced phenological escape of the plant. Assume a semelparous plant has the maximum or 'ideal' potential to produce 1000 seeds (Fig. 2). In the models discussed above, such an 'ideal' genotype has no bud (or apical meristem) dormancy, and is not subject to any herbivory. Such a plant might lose 95% of its fitness potential to herbivores that consume the reproductive structures (Fig. 2). Second, consider a genotype that is damaged by predictably migratory herbivores, and that the plant phenologically splits its available reproductive resources, 20% pre-herbivory and 80% post-herbivory, using the herbivory as a cue for low risk to future herbivory; this plant produces 800 seeds (Fig. 2). In this case, the herbivore reduces seed production by 20% compared with the maximally reproducing plant. Now consider a plant identical to the second genotype, except that it is not damaged by the predictably migratory herbivores (Fig. 2). This
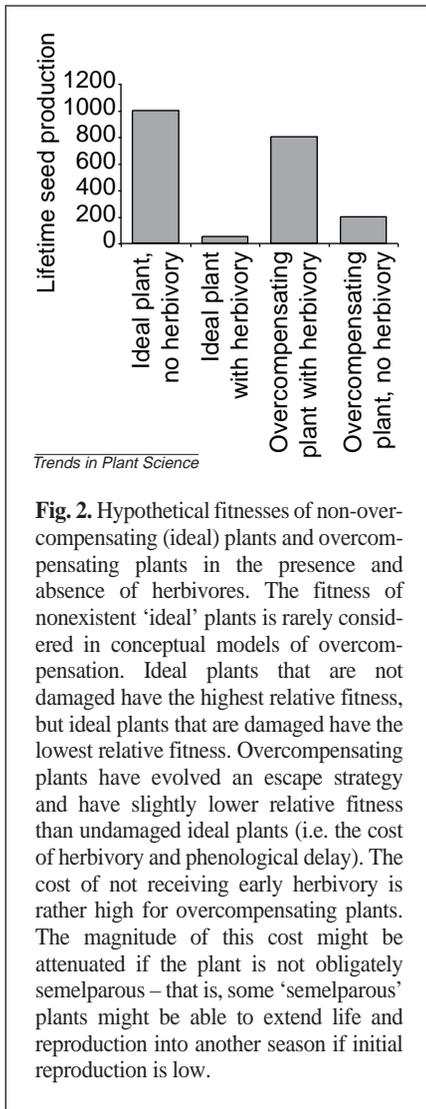
dependent, it can be viewed as a conditional mutualism[19], that is, only mutually beneficial under a subset of favorable conditions.

The field of plant–herbivore interactions is not alone in the realization that parasites do not always reduce host fitness. Tolerance to parasites in many host–parasite systems is now being documented (reviewed in Ref. 20). Evidence for high levels of tolerance to herbivory should not be mistaken as evidence against herbivores having a selective impact on plants. On the contrary, genetic variation in tolerance (a trait that affects fitness) suggests that it is subject to natural selection. In itself, this genetic variation might be circumstantial evidence that herbivory reduced plant fitness in the past and that tolerance strategies were favored by natural selection. The main point is that, for many reasons, herbivores do not always have negative impacts on plant fitness. That herbivory might not reduce plant fitness is relevant to overcompensation, because the benefits of herbivory need not be large. High levels of tolerance lower the cost–benefit threshold for the

Fig. 2. Hypothetical fitnesses of non-over-compensating (ideal) plants and overcompensating plants in the presence and absence of herbivores. The fitness of nonexistent 'ideal' plants is rarely considered in conceptual models of overcompensation. Ideal plants that are not damaged have the highest relative fitness, but ideal plants that are damaged have the lowest relative fitness. Overcompensating plants have evolved an escape strategy and have slightly lower relative fitness than undamaged ideal plants (i.e. the cost of herbivory and phenological delay). The cost of not receiving early herbivory is rather high for overcompensating plants. The magnitude of this cost might be attenuated if the plant is not obligately semelparous – that is, some 'semelparous' plants might be able to extend life and reproduction into another season if initial reproduction is low.

Box 2. Different ways of viewing mutualism

Current theory does not satisfactorily explain the prevalence and apparent stability of mutualisms in nature. Mathematical models incorporating iterated interactions between partners and partner choice, and resource specialization and trade have had some explanatory power in the paradox of mutualisms. In addition, a recent verbal model conceptualizing the benefits of mutualisms has also provided a significant advance[29]. Benefits to one partner in a mutualism can come from:

- By-products of the other partner's activities.
- Investments of costly resources or services made by the other partner.
- Purloining or stealing of resources or other general benefits from the other partner.

A mutualism can occur between two species, irrespective of the source or mechanism of the benefits.

By-product–by-product mutualisms
Should be stable because there are only benefits and no costs.

By-product–investment mutualisms
Should be stable as long as the benefits of the investment are greater than the costs. The benefit-to-cost ratio is crucial, but the ratio is only really important from the perspective of the organism investing.

By-product–purloined mutualisms
Should be stable as long as the by-product benefit is greater than the cost imposed by the purloining. The benefit-to-cost ratio is crucial, but. the ratio is only important from the perspective of the organism being purloined

Investment–investment and investment–purloined mutualisms
Require anti-cheating mechanisms for stability.

Purloined–purloined mutualisms
These are not likely because the benefits to each partner (from purloining) must be greater than the cost imposed by the other partner[29] (Table 1).

plant puts out only its original 20% of resources, does not receive the 'herbivory cue,' and thus produces only 200 seeds: the plant pays a large penalty when not under attack by herbivores. If herbivores consume the 20%, the plant puts out the rest; if herbivores do not consume the plant, only 20% of the maximum is achieved. Thus, overcompensation is functionally demonstrated as a comparison of a plant consumed early in the season with a plant that is not consumed, with no reference to the 'ideal' plant.

Why do plants not pool all of their reproductive effort into one bout? The simple explanation is that fully exposed plants might lose 100% of their production if it is available to herbivores. In other words, if the plant exposes only 20% of its resources to herbivores, it has only 20% to lose. The main assumption here is that initial herbivory events provide reliable information about the low risk of future herbivory (i.e. migratory herbivores)[28]. It makes sense to 'hold back' full reproduction until the plant has received information that the threat has passed. Theory predicts that if the probability of being eaten is greater than 50%, then restrained bud

dormancy will be favored, regardless of the amount of resources taken by the herbivore[22,26]. Overcompensation might really refer to the plant's ability to hold back reproductive resources. The two best examples of repeatable overcompensation in the field, scarlet *Gilia* (*Ipomopsis aggregata*) and field gentians (*Gentianella campestris*; Fig. 1), are both plant–herbivore systems where the probability of initial attack is high and probability of secondary attack is rather low. This explanation of overcompensation is similar to the description of antagonistic co-evolution (i.e. plant response to a fitness-reducing herbivore) that can lead to a mutualism in present ecological time[28].

Plant–herbivore interactions in a framework of mutualism

Mutualistic species interactions are those in which individuals of both species accrue fitness benefits from the association compared with individuals not engaged in the association (Box 2). This functional definition is based in ecological time, with the current net fitness consequence defining the interaction. A presumed evolutionary history of the interaction should not be confused with the ecological definition of mutualism. Overcompensation of plants in response to herbivory is, thus, a mutualism whereby herbivores benefit from eating plants and plants benefit from being eaten. Placing overcompensation in the framework of mutualisms should help us to understand why such

interactions exist, and why they persist. Such apparently parasitic interactions that are, in fact, mutually beneficial appear to be fairly common in plant–animal interactions (Table 1).

Consider a mutualism where an individual from one species benefits by taking resources from individuals of a second species, and individuals of the second species benefit as a simple by-product of the activities of the first (Box 2, Table 1). These mutualisms are special because superficially they appear to be parasitic relationships: herbivores and pathogens eating seeds, roots, leaves, pollen and flowers. However, because there are by-product benefits associated with the purloining 'parasitism', these interactions are, for all purposes, mutually beneficial. The by-product benefits might be the result of direct effects (e.g. deposition of nutrients, protection from other parasites and enhancement of primary functions such as seed germination) or indirect effects (e.g. providing information about future attack; Table 1). By-product benefits might involve the simple release from some constraint (e.g. physiological release from apical dominance) or an evolved response to the partner (e.g. delaying phenology until it is safe), or both. By-product benefits are by-products because there is no investment of resources by the partner or purloining of resources from the partner. The apparently parasitized individuals might be making the best of an apparently negative situation (i.e. the costs of being parasitized are smaller than the

Table 1. Examples of mutualisms where one party purloins benefits from a second, and the second benefits as a by-product of the first's activities[a]

Purloined benefit	By-product benefit	Ref.
Herbivory	Enhanced plant fitness (overcompensation)	3,4,8–10, 16,17
Root herbivory	Mangrove trees less susceptible to falling over during storms	34
Foliar herbivory	Induced defense to temporally or spatially separated herbivores, within and across plant generations	2,35,36
Grazing algae	Increased growth of coral host	37
Aphid herbivory	Plants benefit from ants that remove more damaging herbivores	38,39
Pathogen attack	Induced defense to temporally or spatially separated pathogens	36,40
Seed predation	Other seed predators cannot build up	41
Seed predation	Pollination of plants	42
Seed predation or caching	Forgotten buried seeds are protected from other seed predators and germinate	43
Seed predation	Some seeds are scarified and have enhanced germination	44,45
Epiphylls cover leaves	Leaves protected from herbivory	46
Pollen consumption	Pollination of plants	29

[a]Each of these interactions appears to be conditional[19], in that both parties only benefit under some environmental conditions

by-product benefits). In this case, the costs could take many forms, including the actual cost of being parasitized (i.e. leaf tissue removal) and opportunity costs in the form of resources allocated to traits that enable compensation. Overcompensation of plants in response to herbivory takes this form of mutualism.

Ungulates purloin benefits from plants and apparently do not invest in benefits for the plant. However, the initial herbivory on the plant provides a by-product benefit that could be as simple as the release from apical dominance (i.e. herbivory allows the plant to have multiple flowering stalks), to more complex scenarios regarding the information provided about future attack and increased growth activity in the plant. Mutualism between herbivores and plants should be stable as long as the by-product benefit to the plant outweighs the cost of the ungulates eating their benefits. Those plants that have historically been in an environment with migratory ungulate herbivores hold back their reproduction until the herd has passed. In the absence of the herbivores, these plants would continue to hold back reproduction, and would have lower fitness than in the presence of herbivores. Whether one believes this is truly a mutualism (because plant reproduction in the presence of herbivores might still be lower than it could be if there were never herbivores) is irrelevant, because functionally the relationship is positive for both partners in ecological time. Under present conditions, there are benefits to both partners, and removal of either partner should come at a cost to the other.

Overcompensation considered and beyond

Plants can tolerate herbivory, and present-day herbivores do not always reduce plant fitness. Overcompensation goes beyond tolerance because damaged plants have higher fitness than undamaged plants. Although apparently a paradox, when we consider the potential by-product benefits of herbivory and overcompensation as a strategy of withholding reproduction until the threat of herbivory has passed, overcompensation simply becomes a striking descriptor for a functional process. The conceptual advance in considering the various benefits of mutualisms, and including mutualisms where one party benefits by purloining and the other benefits as a by-product, sheds light on the overcompensation interaction. This interaction should remain stable when the by-product benefits of being eaten are greater than the cost of the purloined benefits to herbivores (i.e. herbivory). This is likely to be the case where herbivores provide a reliable cue that the risk of herbivory in the future will be low.

Some cases of overcompensation and plant–herbivore mutualism might be more palatable if considered as an induced phenological escape of plants. A key component in the success of early reproducing winter annual plants is that these plants phenologically escape herbivory. Plants that delay reproduction until they receive a reliable cue indicating low risk of future attack are likely to receive benefits of a 'phenological escape' defense. This delay in

reproduction, or other mechanisms that allow for the overcompensation, might come at a cost. Alternatively, some cases of overcompensation might involve simple by-product benefits such as release of apical dominance. A distinction between mutualistic versus antagonistic co-evolution helps to clarify the issue of overcompensation as a plant–herbivore mutualism[28]. Because it is assumed that natural selection will always act to increase individual relative fitness, an interaction that is ecologically a mutualism might have arisen as the best solution to an antagonistic situation (i.e. induced phenological escape). A true mutualism, resulting from mutualistic co-evolution, requires absolute fitness (across environments) to be higher in genotypes engaging in the mutualism compared with genotypes not engaging in the mutualism[28]. In some plants, such as the field gentians, herbivory has apparently increased overall plant fitness (regardless of environment) over evolutionary time[4,28].

In conclusion, the exciting contribution that discussion of overcompensation makes to evolutionary ecology is providing an example of mutualisms that might occur between organisms that seemingly have an antagonistic relationship. Such interactions might be common in nature (Table 1), and probably gave rise to many plant–pollinator mutualisms, for example, where bees take pollen from plants and plants were pollinated as a by-product[29]. The challenge now is not only to document intraspecific variation in overcompensation, but to demonstrate experimentally in which environments it is favored. The examination of overcompensation as a phenomenon is contributing to a synthesis of the ecology and evolution of species interactions. Future work should address the following areas:

- Are by-product–purloined mutualisms pervasive in plant–animal interactions? How often are the by-product benefits evolved responses to the purloining (e.g. phenological escape), rather than absolute by-products of the interaction (e.g. nutrient deposition)?
- How common is overcompensation? Although circumstantial evidence for overcompensation abounds, the hard evidence is limited to a few systems. Additional rigorous experimental and descriptive work on which plants overcompensate and under what environmental circumstances is needed.
- How does overcompensation evolve? Is it derived from plants that already have a high level of tolerance? A comparative phylogenetic approach would be useful in this area[30].
- Is there additive genetic variation for overcompensation in response to herbivory (within and between populations)? Circumstantial evidence is strong, but definitive work is lacking.
- What is the role of salivary constituents of herbivores in overcompensation[7]? Herbivore

saliva is of extreme importance in other plant responses to herbivory[31], yet its role in over-compensation has been contentious.
- The best studies of overcompensation involve ungulate herbivores. Do plants tolerate and overcompensate for damage inflicted by other organisms, such as pathogens[32] and insects[3]? Few studies have examined this possibility.
- Is overcompensation associated with induced plant defenses that deter future attack? Alternatively, what fraction of the benefits of induced defenses[2] are due to mechanisms of overcompensation? Because herbivory might be a cue for both induced defenses and overcompensation, there is the potential for interaction and synergism between these responses.

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