22 November 1985, Volume 230, Number 4728 SCIENCE

Resource Availability and Plant Antiherbivore Defense

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Summary. The degree of herbivory and the effectiveness of defenses varies widely among plant species. Resource availability in the environment is proposed as the major determinant of both the amount and type of plant defense. When resources are limited, plants with inherently slow growth are favored over those with fast growth rates; slow rates in turn favor large investments in antiherbivore defenses. Leaf lifetime, also determined by resource availability, affects the relative advantages of defenses with different turnover rates. Relative limitation of different resources also constrains the types of defenses. The proposals are compared with other theories on the evolution of plant defenses.

Herbivores exert a major impact on plants, both in ecological and evolutionary time scales. Insects have caused greater economic loss to American agriculture than the combined effects of damage from drought and freezing and have caused greater tree mortality than does logging. On average, more than 10 percent of the plant production in natural communities is consumed annually by herbivores (*1*). This loss to herbivory is greater than the average allocation to plant reproduction (*2*), the investment that most directly determines plant fitness. Thus herbivores exert a strong selective influence on plants by increasing plant mortality and by removing biomass that might be allocated to growth or reproduction.

Herbivory, however, is not equally distributed among all plant species. In a tropical rainforest, insects remove from 0.0003 to 0.8 percent of the leaf area per day, depending on the tree species (*3*). In arctic shrub tundra and boreal forests the frequency of both insect and vertebrate herbivory on different species can range from 0 to 100 percent during herbivore population outbreaks (*4*). This orders-of-magnitude range in herbivore damage among species within a single community is primarily a reflection of palatability differences among species. Although the nutritional quality of leaves and twigs can influence herbivore food choice (*5*), chemical and structural defenses are generally the major determinants of leaf and twig palatability (*6, 7*). Plants have evolved an extraordinary array of secondary metabolites which act as antiherbivore defenses and which appear not to be waste products nor to serve any other known function in the plant (*8*). Clearly, the production of defenses is only favored by natural selection when the cost of production is less than the benefit of enhanced protection from herbivores.

A major goal in the study of plant-herbivore interactions is to understand why plant species differ in their commitment to defenses and hence in their susceptibility to herbivores. If plants have the potential to defend themselves effectively against herbivores, why do many species suffer high levels of herbivory? We present evidence that both the nature and quantity of plant defenses are determined by the resources available in the local habitat. We suggest that natural selection favors plants with slow growth rates and high levels of defense in environments with low resource availability and that plants with faster growth rates and lower defense levels are favored under conditions of high resource availability. We will first outline the proposal and present the evidence from natural systems and then discuss how these ideas compare with current theories on plant apparency and the evolution of plant defenses.

Resource Limitation and Plant Growth Characteristics

All plants are dependent on the availability of light, water, and nutrients as essential resources for growth. In nature there is a continuum of habitat types, from resource-poor habitats that support little or no plant growth, to resource-rich habitats that can potentially support rapid plant growth. This variation in habitat quality can occur over long distances, as in the change from nutrient-poor white sands forests in the northern Amazon basin to the nutrient-rich forests covering southwestern Amazonia. Habitat quality can also vary substantially over only a few meters, as, for example, when one moves from a shady forest understory, where plants are light-limited, to a sunny light gap created by a fallen tree.

The evolutionary response of plants to resource limitation has been a suite of interdependent characteristics associated with an inherently slow growth rate (Table 1) (*9, 10*). There are many examples of inherently slow growth rates in species from infertile sites (*11*), in species from shaded habitats (*3, 12*), and in species and even populations growing in arid areas (*13*). Such plants grow slowly even in the most favorable environments and have low capacities to photosynthesize and absorb nutrients (*9, 10, 14*). The low respiratory and photosynthetic rates in these inherently slow-growing species are associated with low levels of leaf protein (*15*). Slow growth resulting from a low metabolic demand may confer a greater ability to withstand chronically

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stressful environments and therefore to outcompete more rapidly growing species adapted to resource-rich environments (*9, 10*).

Because inherently slow-growing plants occur in environments where resources are not readily replaced, they tend to have long-lived leaves and twigs. Slow turnover of plant parts is advantageous in a low-nutrient environment because each time a plant part is shed, it carries with it approximately half of its maximum nitrogen and phosphorus pool (*10*). Similarly, in shady and perhaps in cold or dry environments, where the potential for energy (carbon) acquisition is low, carbon loss can be minimized by having a slow leaf turnover rate.

In contrast, resource-rich environments such as agroecosystems, old-field habitats, and many tropical regions have favored plant species that have the potential for rapid growth (*9, 10*). These species exhibit a characteristic set of traits (Table 1) that include a high capacity to absorb nutrients and high respiratory and light-saturated photosynthetic rates. Such species generally show a biochemical and morphological plasticity that allows them to take advantage of pulses in resource availability (*9, 10, 16*). Since photosynthetic rates decline with age, and older leaves are often shaded by younger ones, energy acquisition in high-resource sites is maximized by a rapid turnover of leaves (*10, 14, 17, 18*). The inevitable nutrient and carbon loss associated with rapid turnover of plant parts is not a strong selective influence on plants in a high-resource environment because nutrients and light are more readily available.

Growth Rates, Herbivory, and Antiherbivore Defenses

In addition to differing in general plant and leaf characteristics, inherently fast- and slow-growing plants also have consistent differences in their antiherbivore characteristics (Table 1). Fast-growers adapted to resource-rich habitats suffer higher rates of damage from herbivores and have both lower amounts and different types of defensive chemicals than slow-growing species. Observations in a variety of communities have revealed that vertebrate and invertebrate herbivores prefer feeding on fast-growing plant species of resource-rich environments (Table 2). For example, in boreal systems, herbivory by vertebrates and insects is greatest on rapidly growing trees that colonize recently disturbed areas along rivers rather than on slowly growing species characteristic of the adjacent resource-limited sites (*7, 19, 20*). In a neotropical rainforest, fast-growing tree species are eaten 6 times as rapidly by insects as inherently slow-growing species in the same microhabitat (*3*). Leaf-eating *Colobus* monkeys from nutrient-poor forests in Africa avoid the leaves of most tree species and rely more heavily on seeds than do their congeners from forests on richer soils (*21*). Leaves that are eaten by *Colobus* come disproportionately from deciduous tree species as compared to evergreens (*22*). In feeding preference tests, fast-growing temperate plants from fertile soils were preferred by snails (*23*), and early successional species were preferred by slugs (*24*), caterpillars (*25*), and several species of sap- and leaf-feeders (*26*).

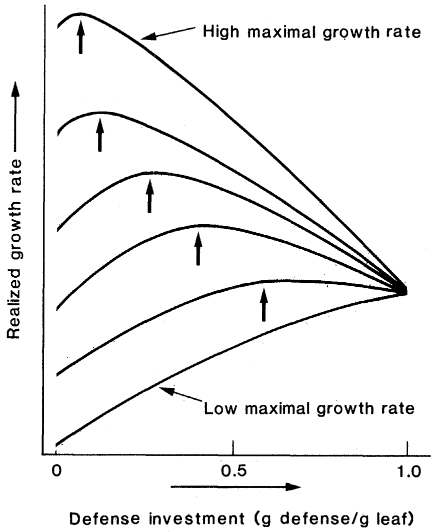

Fig. 1. Effect of defense investment on realized growth. Each curve represents a plant species with a different maximum inherent growth rate. Levels of defense that maximize realized growth are indicated by an arrow. Realized growth (dC/dt) is calculated as $dC/dt = G^*C^*(1 - kD^{\alpha}) - (H - mD^{\beta})$ where G (g g^{-1} d^{-1}) is the maximum inherent growth rate permitted by the environment (without herbivores), C (g) is the plant biomass at time zero, D (g g^{-1}) is the defense investment, k (g d^{-1}) and α are constants that relate an investment in defense to a reduction in growth. The entire term $(1 - kD^{\alpha})$ is the percentage of reduction in growth due to investment in defenses. The term H (g d^{-1}) is the potential herbivore pressure in the habitat (assuming no defense). Potential herbivory is reduced by a function of defense investment, (mD^{β}), where m (g d^{-1}) and β are constants that determine the shape of the defense effectiveness curve. The entire negative term $(H - mD^{\beta})$ is the reduction in realized growth (g d^{-1}) due to herbivory. Since it is subtracted from growth, this assumes herbivores consume fixed amounts of leaf tissue and not fixed percentages of plant productivity. The model's results depend on the extent to which this assumption is true. To further conform to biological reality, the herbivory term $(H - mD^{\beta})$ cannot be less than zero, regardless of the value of D.

The observations that inherently slow-growing plants are less preferred by herbivores are consistent with both the amount and type of defenses (Table 1). The absolute concentrations of defenses in leaves of slow-growers from resource-limited sites tend to be at least twice as high as those in leaves of fast-growers from resource-rich sites (*3, 21, 27–29*). The defenses of slow-growers are primarily chemicals such as lignins or polyphenolic compounds that may have dosage-dependent effects on herbivores (*28–31*). In addition, lignin, or fiber content serves as structural support in the leaf (*32*). These types of metabolites are most often present in large concentrations (*28–30*) and exhibit low rates of turnover during the life of the leaf (*33–34*). In contrast, the chemical defenses of fast-growing species include a myriad of diverse chemicals that are present and effective in lower concentrations (*28, 29, 35*). These types of metabolites exhibit high turnover rates (*36, 37*) and thus represent a reversible commitment to defense.

Predictions for Amount of Defense

Our resource availability hypothesis suggests that the observed associations of inherent growth rates and antiherbivore defenses of plants (Table 1) is one of causality (*38*). We suggest that the optimal level of defense investment increases as the potential growth rate of the plant decreases (holding herbivore pressure constant) for several reasons. First, as potential growth rates become more limited by resource availability, replacement of resources lost to herbivores becomes more costly. Since this increases the relative value of limiting resources, one would expect to see higher levels of defense in resource-limited environments (*39*). Second, a given rate of herbivory (grams of leaf removed per day) represents a larger fraction of the net production of a slow-grower than that of a fast-grower. Therefore, because the relative impact of herbivory increases as inherent growth rate declines, we would again expect higher defenses in slower growers. And third, a percentage reduction in growth rate due to the cost of producing defenses represents a greater absolute growth reduction for fast-growing species than for slow-growing ones (*40*). In other words, because the relative cost of defense increases as growth rates increase, we would expect lower levels of defense in resource-rich environments.

Our hypothesis that the level of defense investment increases as the plant's potential growth rate decreases can be formalized mathematically (Fig. 1). We assume that in a world without herbivores, the maximum potential growth rates would be determined by the resource availability in the environment (modified slightly by allocation patterns of individual species). As noted above, evidence suggests that over evolutionary time plants have adjusted their inherent growth rates to match the degree of resource limitation in their preferred habitats. Let us now add herbivores to the model. We assume that they remove a biomass of plant material that is a function of the herbivore biomass and therefore a fixed amount, rather than a fixed percentage of the plant's productivity. Any plant that invests in defenses will reduce its losses to herbivores. The resultant plant growth rate is the balance between a growth reduction due to defense costs and a growth increase due to better protection from herbivores. The shape of this relationship between defense investment and actual growth rate is a curve with intermediate levels of defense causing maximum growth rates (Fig. 1). Below this optimal defense level (indicated by arrows), growth is reduced because of high losses to herbivores and above it, because of an excessively high cost of defense. Figure 1 shows a family of curves where only the maximum potential growth rate permitted by the environment varies. The sharp peak in the curves for fast-growing species (upper curves) suggests that deviations from the optimal defense levels have a larger negative impact on realized growth than they would for slow-growing species (lower curves). As the inherent growth rate decreases (from upper to lower curves), the optimal level of defense increases, and the level of actual herbivory decreases. These two predictions, increased defense and decreased herbivore damage in slow-growing species, have not been explained by previous models and are the major patterns observed in nature.

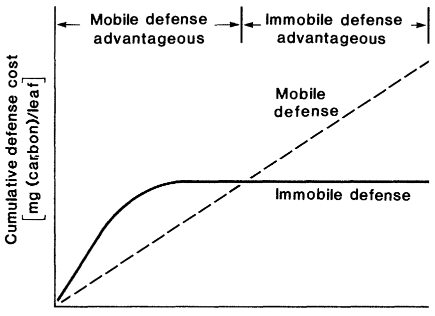

Fig. 2. The cumulative cost of defending a leaf with a large amount of an immobile defense that has negligible turnover compared to a small amount of a mobile defense that continues to turnover throughout the life of the leaf.

Predictions for Type of Defense

Inherent growth rates of plants may influence the type of defense as well as the amount. Because of the increased conservation of resources, slow-growing plants of resource-limited environments have longer-lived leaves than fast-growing species (Table 1) (*18*). We suggest that there should be a relation between the length of leaf lifetime and types of defense. Defense compounds, such as polyphenols and fiber [quantitative defenses as defined by Feeny (*28*)], are present in high concentrations and thus represent a high initial construction cost. They are fairly inactive metabolically, so that continued maintenance costs are small. However, because of this metabolic inactivity, these compounds are immobile, being retained in senescent leaves and lost to the plant upon leaf death (*34*). These types of defense, which we shall refer to as immobile defenses, would therefore be advantageous in long-lived leaves which have more time over which to spread these fixed costs (Fig. 2). Data from 41 tree species in a neotropical forest support this, showing a significant increase in polyphenol and fiber content as leaf lifetime increases (*3*, *41*).

The other end of the defense spectrum is represented by mobile defenses such as alkaloids, phenolic glycosides, and cyanogenic glycosides [qualitative defenses as defined by Feeny (*28*)], which are present in low concentrations and therefore initially represent a low total construction cost. Although the concentration of these compounds in a leaf may remain constant and small, the pool is continually turning over. For example, in several species of mint, the biological half-lives of mono- and diterpene defenses are 10 to 24 hours (*42*), and in several unrelated agricultural species, half-lives of various alkaloids range from 7.5 hours to 6 days (*37*). This high metabolic activity allows compounds to be recovered from a leaf during senescence, but also means that there is a continued metabolic cost associated with turnover. Mobile defenses are therefore not expected to be common in long-lived leaves, because the continued metabolic costs summed over leaf lifetime would likely be larger than a fixed investment in immobile defenses (Fig. 2) (*43*). These same arguments predict that mobile defenses would be favored in short-lived leaves. Furthermore, the metabolic turnover of mobile defenses may allow a greater plasticity in the expression of defense, as has been noted for some species (*44*, *45*).

The types of resources available in the environment will also place constraints on the types of defenses that will be favored through evolutionary time. Clearly, in extremely nutrient-limited environments, nitrogen-based defenses would have high relative costs compared to carbon-based defenses, and should be rare (*20*, *46*). Nitrogen-containing alkaloids are unusually common in legumes with nitrogen-fixing symbionts. Desert shrubs growing under conditions of unlimited light frequently produce such

Table 1. Characteristics of inherently fast-growing and slow-growing plant species.

Variable	Fast-growing species	Slow-growing species
Growth characteristics		
Resource availability in preferred habitat	High	Low
Maximum plant growth rates	High	Low
Maximum photosynthetic rates	High	Low
Dark respiration rates	High	Low
Leaf protein content	High	Low
Responses to pulses in resources	Flexible	Inflexible
Leaf lifetimes	Short	Long
Successional status	Often early	Often late
Antiherbivore characteristics		
Rates of herbivory	High	Low
Amount of defense metabolites	Low	High
Type of defense (sensu Feeny)	Qualitative (alkaloids)	Quantitative (tannins)
Turnover rate of defense	High	Low
Flexibility of defense expression	More flexible	Less flexible

large quantities of carbon-based terpenes that they perfume the air. Although species that grow in the forest understory, a low-carbon environment, also often have carbon-based defenses, this may reflect a compromise with other nutrient limitations and the leaf lifetime considerations discussed above. Presumably because phosphorus is limiting in almost all environments, there are no naturally occurring phosphorous-based defenses. The effectiveness of organophosphate pesticides probably arises from their novelty to herbivores.

Evolution of Plant Defenses

Another model for the evolution of plant defenses was presented by Feeny (*28*) and Rhoades and Cates (*29*). They were the first to point out many of the patterns of defense investment outlined in Table 1 and suggested that it was a plant's apparency that influenced the type of defense. They defined apparent plants as being distributed predictably in time and space, giving late successional species as an example. Because of their predictability, it was hypothesized that apparent plants were easily discovered by herbivores and should therefore show a large investment in broadly effective defenses (quantitative defenses). Unapparent plants were defined as having ephemeral or unpredictable distributions as, for example, those in early successional sites. Unapparent species were expected to rely on escaping discovery by specialist herbivores and therefore needed only to invest in less costly chemical defenses (qualitative defenses) effective against nonadapted generalist herbivores. The defense differences between apparent and unapparent plants were suggested to reflect differential effectiveness of qualitative and quantitative defenses against specialist and generalist herbivores and differential selection pressure by generalists and specialists due to plant apparency.

Because the extremes of resource availability are often associated with habitat disturbance and successional stages, considerations of resource availability or plant apparency often lead to the same predictions. Both theories suggest that successional status should be correlated with defense investment; Feeny (*28*) and Rhoades and Cates (*29*) attribute this pattern to an increase in apparency through time, whereas we suggest that it is because of a decrease in resource availability and, hence, inherent growth rates. There are, however, several studies of defense patterns of plants that separate the effects of apparency from resource availability. In the following examples, differences in defenses (Table 1) are observed between plant species that have similar apparency in time and space but occur along a resource gradient. Grime (*9*) was one of the first to identify this relation, noting an increase in defenses in many British plants associated with an increase in environmental stress. In Cameroon, tree species growing in nutrient-poor soils contain twice the concentration of phenolic compounds as species in similar rainforest vegetation but growing in richer soils (*21*), a pattern which is probably repeated in many nutrient-poor areas (*39, 47*). In a neotropical forest, the mature canopy is composed of fast-growing shade-intolerant trees as well as slow-growing shade-tolerant species (*48*). Although both groups of species have similar apparency, the fast-growing species are eaten more by herbivores and show lower concentrations of immobile defenses than do the slow-growing species (*3*). In boreal communities, where species diversity is low and early successional riparian habitats are widespread and predictable, it is difficult to see that certain tree species would be more apparent than others. However, a gradient in resource availability and plant growth rate is well correlated with palatability to vertebrate herbivores (*7, 19, 20*).

Table 2. Field studies of herbivore preferences for fast- or slow-growing plant species in natural communities. Herbivory is expressed as the relative consumption of fast-growers over slow-growers, considering only mature plants.

Herbivore	Herbivory	Reference
Tropical forest		
Insect	6	(*3*)
Black *Colobus* monkey	20	(*22*)
Boreal forest		
Moose (winter)		
Alaska	*	(*53*)
Newfoundland	3	(*54*)
Finland	3	(*55*)
Moose (summer)		
Alaska	*	(*56*)
Snowshoe hare (winter)		
Alaska	4	(*20, 57*)
Michigan	10	(*58*)
Newfoundland	3	(*54*)
Snowshoe hare (summer)		
Alaska	*	(*56*)
Mountain hare (winter)	8	(*59*)
Mountain hare (summer)	28	(*59*)
Caribou	57	(*60*)
Beaver	*	(*61*)
Arctic tundra		
Insect	8	(*19*)
Microtus	*	(*62*)
Dicrostonyx	*	(*62*)
Lemmus	*	(*62*)
Spermophilus	4	(*63*)
Arctic hare	6	(*64*)
Musk-oxen	*	(*65*)
Caribou	*	(*66*)
Reindeer	*	(*67*)

*Little or no recorded use of slow-growing evergreen species.

We suggest that resource availability better explains the observed patterns of plant defense (Table 1) than apparency in several ways. Apparency theory argues that apparent and unapparent plants have evolved different types of defenses as a result of differential pressure from specialist and generalist herbivores. However, this is not generally supported by empirical evidence on the relative effectiveness of defense types against specialists or generalists (*26, 31, 49*), nor is it supported by the relative abundance of herbivore types on apparent and unapparent plants (*50*). Furthermore, apparency theory implies that all species should suffer similar rates of damage, with some species avoiding damage by escape and others by chemical defenses. Although the mechanisms of apparency theory do not seem appropriate to explain the observed patterns of herbivory and plant defense (*3, 51*), the predictability of a plant in time and space may influence the degree of herbivore pressure, particularly in comparisons of species having different leaf lifetimes. In this sense, it should be included as a complementary factor when considering plant-herbivore interactions. The resource availability hypothesis, however, provides a more general and comprehensive explanation of the differences between species in herbivory and defense.

Conclusions

Other investigators have recognized the importance of resource availability in directing the evolution of a variety of plant characteristics (*10, 52*), and Grime (*9*) has made specific reference to an increase in plant defenses with an increase in habitat stress. We extend this idea and propose that resource availability in the environment is the major factor influencing the evolution of both the amount and type of plant defense. Resource limitation selects for inherently slow growth rates, which in turn favor large investments in defense. Leaf lifetime, also determined by resource availability, affects whether mobile or immobile defenses will be more advantageous. Further constraints on the types of defenses are imposed by the relative limitation of different resources.

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45. We prefer the terms mobile and immobile defenses as opposed to qualitative and quantitative because the latter imply two distinct modes of action against herbivores, and these have not been well supported. The terms mobile and immobile defenses refer to physiological properties of the defenses in the plant and encompass a continuum of metabolic activity and mobility. We also think that they more accurately describe the defense characteristics of major importance to the plant.
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68. We thank M. Aide, D. Davidson, M. Geber, T. Kursar, and B. Stubblefield for discussions. Supported by NSF grant DEB-820 7170 (to F.S.C.) and by funds from the University of Utah (to P.D.C.).