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Should plants in resource-poor environments invest more in antiherbivore defence?

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The 'resource availability hypothesis' proposes that low resource availability favours plants with inherently slow growth rates, which in turn favours large investments in antiherbivore defence. Here we present a simple model of evolution of plant defence allocation in a system incorporating plant-resource dynamics, and show that taking into account the feedback of plants on the amount of a limiting resource leads to very different predictions than those from the classical resource availability hypothesis. The latter is based on the assumption that fitness is determined by the potential growth rate, hence, implicitly, on the assumption of unlimited growth in a transient environment where plants do not deplete soil resources. In an environment where plants have accumulated enough biomass to control resource concentration, fitness is determined by the ability to deplete limiting resources if the environment is homogeneous or by other traits correlated with biomass or productivity if the environment is spatially structured. In this case, resource supply and maximum growth rate may either increase, decrease, or in most cases not affect at all, optimal defence investment. Much more detailed data about what determines fitness in 'climax' environments would be necessary to make even qualitative predictions about the direction of evolution of antiherbivore defence investment as a function of resource availability and maximum growth rate.

In an influential paper Coley et al. (1985) proposed resource availability in the environment as the major determinant of both the amount and type of plant antiherbivore defence. Low resource availability would favour plants with inherently slow growth rates, which in turn would favour large investments in defence. Their hypothesis was attractive because it seemed to explain patterns of plant defence and herbivory in a wide range of ecosystems. It hinged, however, on a very simple theoretical argument with a number of simplifying assumptions. Subsequent authors (de Jong 1995, Yamamura and Tsuji 1995) relaxed some of these assumptions and predicted that Coley et al.'s (1985) pattern should hold most of the time. But all these theoretical treatments preserved one critical implicit assumption in Coley et al.'s (1985) original argument, namely, that the amount of available resources is con-

stant and unaffected by plants. This implicit assumption of a constant environment led Coley et al. (1985) and de Jong (1995) to measure fitness by what they called the plant 'realised' growth rate, but which is really a potential growth rate at the plant population level, similar to the intrinsic rate of natural increase, r , in the logistic equation, because it ignores plant competition mediated by resource consumption.

This fitness measure makes sense for pioneer species colonising temporary environments but is inappropriate for species competing for limited resources in 'climax' environments. Whenever plants have accumulated enough biomass to affect the amount of resources in their environment, they compete for that resource which is limiting, and their growth hinges on their ability to tolerate low concentrations of that resource. If the environment is homogeneous, fitness is then determined by the ability to deplete the limiting resource (Tilman 1982). If the environment is spatially structured, fitness is determined by the basic reproductive rate (Loreau 1998a). Here we present a simple model of evolution of plant allocation to antiherbivore defence in a system incorporating plant-resource dynamics, and show that taking plant resource competition into account leads to very different predictions than those from the classical resource availability hypothesis. We show that the common argument used in favour of the resource availability hypothesis — herbivory is more costly in resource-poor environments because the lost biomass is more costly to replace — is incorrect, because it is the balance between the cost of herbivory and the cost of defence investment that determines the optimal investment, and this does not necessarily change with resource availability.

We begin with an explicit model of plant resource allocation that is based on the same assumptions as, and simplifies into a dynamical model of plant growth equivalent to, de Jong's (1995), but with an explicit dependence on resource concentration. This model is

useful to make clear how the simplified model incorporates resource allocation and to define various quantities of interest to our later discussion of plant fitness measures. Assume that plant growth is limited by a single resource such as soil nitrogen, and biomass is measured accordingly as the standing stock of that resource in the plant population. Define P as the total plant biomass, which divides into two components, G , the part of biomass that is mobilised for growth, and R , the part of biomass that is mobilised for the production of defences. A fraction δ of the amount of resource consumed for primary production is constantly allocated to defence, the remainder, $1 - \delta$, being allocated to growth; δ represents defence investment. Finally, define u_M as the maximum rate of resource uptake by plants; $f(N)$ as the plant functional response to resource concentration, N , where $f(N)$ is a monotonic increasing function of N and is scaled so that $0 \leq f(N) \leq 1$; $h(R/P)$ as the rate of herbivory, which is a monotonic decreasing function of the proportion of biomass mobilised for defence; and b as the loss rate of biomass. The dynamical equations for the two plant biomass compartments are then:

$$\frac{dG}{dt} = u_M f(N) G (1 - \delta) - h(R/P) G - bG \quad (1a)$$

$$\frac{dR}{dt} = u_M f(N) G \delta - h(R/P) R - bR \quad (1b)$$

This model can be rewritten conveniently in terms of two new variables that change on different time scales: total plant biomass, $P = G + R$, and the fraction of biomass mobilised for defence, $r = R/P$. Taking the time derivatives of these new variables and using (1), we obtain:

$$\frac{dP}{dt} = u_M f(N) P (1 - r) - h(r) P - bP \quad (2a)$$

$$\frac{dr}{dt} = u_M f(N) (1 - r) \delta - h(r) P \quad (2b)$$

Now we make the simplifying but reasonable assumption that the distribution of resource in the two biomass compartments is achieved on a physiological time scale that is much faster than the population dynamical time scale governing plant biomass. This means that r can be regarded as being at its steady-state value, r^* , on the population dynamical time scale. Setting the time derivative equal to zero in (2.b), this steady-state value is found to be simply $r^* = \delta$. We are then left with the following equation for the dynamics of plant biomass:

$$\frac{dP}{dt} = [u_M f(N) (1 - \delta) - h(\delta) - b] P \quad (3)$$

This equation is formally very similar to de Jong's (1995), but its interpretation is very different on one critical aspect. Whereas previous authors (Coley et al. 1985, Herms and Mattson 1992, Yamamura and Tsuji 1995, de Jong 1995) considered the growth of an isolated individual plant, we regard eq. (3) as a description of the dynamics of a species' total plant biomass on a given area. In the long term, plant biomass will reach a steady state such that the time derivative in eq. (3) vanishes. At this steady state, plants will control resource concentration at a level N^* set by eq. (3):

$$N^* = f^{-1} \left[\frac{h(\delta) + b}{u_M (1 - \delta)} \right] \quad (4)$$

where f^{-1} denotes the inverse of function f .

A well-known result from competition theory is that the plant type with the lowest N^* outcompetes all other types in a homogeneous environment because, when it is established, all other types have a negative population growth rate (Tilman 1982, Grover 1997). Therefore in such a steady-state system the appropriate measure of fitness is no longer the potential individual growth rate but N^* instead (or, more exactly, its inverse). The optimal allocation to defence, $\hat{\delta}$, will be the value of δ that minimises N^* , i.e., that is the solution of:

$$\frac{dN^*}{d\delta} = 0 \quad (5)$$

(It is easily verified that this extreme is indeed a minimum by noting that $dN^*/d\delta$ is necessarily positive at $\delta = 1$.) Using (4), this equation reduces to:

$$h'(\hat{\delta}) (1 - \hat{\delta}) - h(\hat{\delta}) + b = 0 \quad (6)$$

where $h'(\hat{\delta})$ is the derivative of h with respect to δ evaluated at $\hat{\delta}$.

Eq. (6) depends only on the herbivory function h and the loss rate b , but is independent of u_M , the maximum rate of resource uptake, which may be regarded as a measure of the maximum growth rate. It is also independent of any conceivable measure of resource availability. As a result, the optimal defence investment, which is the solution of this equation, is also independent of the maximum growth rate and resource availability. Clearly, the resource availability hypothesis fails to predict evolution in a steady-state, homogeneous system.

This conclusion is explained easily. Competition is governed by the ability to deplete the limiting resource at steady state, and this in turn is entirely determined by the balance between the production of new plant biomass and its loss through herbivory or other processes (eq. 4). A common argument used in favour of the resource availability hypothesis is that herbivory is more costly in resource-poor environments because the

lost biomass is more costly to replace. But this argument ignores the fact that investment in defence is also costly; it is the balance between the two costs that determines the optimal investment, and this does not change with resource availability in a homogeneous environment.

This conclusion is quite general; it does not depend on either the plant functional response, $f(N)$, the functional form of the rate of herbivory, $h(\delta)$, or the dynamical equation for resource concentration, N . At this point, however, it is useful to be more specific to proceed further in the analysis.

- (1) We assume a classical type-2 or Michaelis-Menten functional response with half-saturation constant K .
- (2) We choose a herbivory function of the form:

$$h(\delta) = \frac{h_M}{1 + \gamma\delta} \quad (7)$$

where h_M is the maximum rate of herbivory, and γ is a coefficient that measures the sensitivity of herbivory to defence investment. This form has the same properties as those used by Yamamura and Tsuji (1995) and de Jong (1995), but is much simpler to handle.

- (3) We assume that the limiting resource is a soil nutrient renewed by a constant input I into the system and subject to losses from the system at a rate q . The model then reads:

$$\frac{dP}{dt} = P \left[\frac{u_M N}{K + N} (1 - \delta) - \frac{h_M}{b} \right] \quad (8a)$$

$$\frac{dN}{dt} = I - qN - \frac{u_M N P}{K + N} (1 - \delta) \quad (8b)$$

This model does not explicitly consider nutrient recycling by plants and herbivores (which can be thought of as being here absorbed into the input term I) and herbivore population dynamics, but these complications are not necessary for the present purpose. A more elaborated model will be presented elsewhere (de Mazancourt, Loreau and Dieckmann, unpubl.).

It is easy to show that the dynamics of this model system leads to a stable steady state. An explicit solution for optimal defence investment can then be found by applying eq. (6) to this model:

$$\hat{\delta} = \frac{-(b + h_M) + \sqrt{h_M(b + b\gamma + h_M)}}{b\gamma} \quad (9)$$

Complete tolerance to herbivory ($\hat{\delta} \leq 0$) is selected when:

$$\gamma \leq 1 + b/h_M \quad (10)$$

Thus, the sensitivity of herbivory to defence investment, γ , has to be greater than this threshold value for some

level of defence to be selected. The optimal defence allocation can then be shown to peak at an intermediate value of γ and to increase with the maximum rate of herbivory, h_M , as illustrated in Fig. 1. Note that it is always moderate; it can be proved never to exceed 0.5.

The above results hinge on the assumption that the environment is homogeneous and plants have unrestricted access to the limiting resource, so that competition is governed by the ' N^* rule' (Tilman 1982, Grover 1997). But plants usually have only local access to resources such as soil nutrients (Huston and DeAngelis 1994, Loreau 1998b), a likely situation in poor environments in particular, where plants are spaced apart. To what extent are our results likely to be affected by spatial heterogeneity? A homogeneous environment may be viewed as one extreme in the range of possibility, the other extreme being a perfectly structured environment in which each plant occupies an isolated site (Loreau 1998a). Examining this other extreme is a convenient way to answer this question.

To that end we continue to use model (8), but now as a description of plant-nutrient dynamics within a site. We assume that a local steady state is attained relatively rapidly, and competition obeys a 'competitive lottery' for vacant sites. In such a system fitness is determined by the basic reproductive rate (Loreau 1998a). Since the release of vacant sites through mortality is here the same for all plants, fitness is governed simply by the ability to produce propagules that establish successfully in vacant sites. Since our objective here is to assess the robustness of the results rather than the outcome of a particular case, we examine four possible scenarios: we assume that plant fitness is measured by either (1) total biomass, (2) the part of biomass that is mobilised for growth, (3) total productivity, or (4) the part of productivity that is allocated to growth. The justification for these scenar-

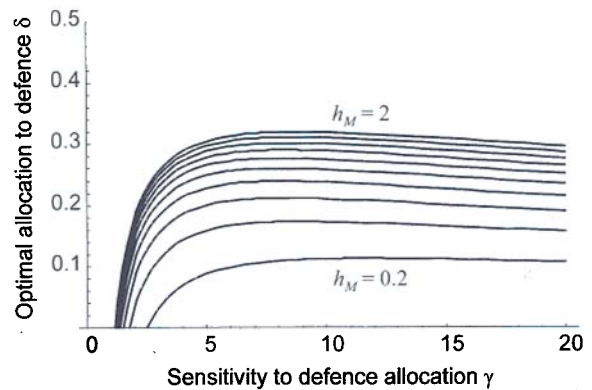


Fig. 1. Optimal allocation to defence, $\hat{\delta}$, as a function of sensitivity of herbivory to defence allocation, γ , for different values of the maximum rate of herbivory, h_M , in a homogeneous environment where competition is governed by a ' N^* rule'. Parameter $b = 0.3$. Curves from bottom to top: $h_M = 0.2, 0.4, 0.6, 0.8, 1, 1.2, 1.4, 1.6, 1.8$ and 2 , respectively.

ios is the following. On the one hand, plant biomass may be correlated with the plant nutrient stock that can be re-allocated to seed production. This hypothesis is likely for annual plants. On the other hand, plant productivity is proportional to the amount of nutrient absorbed per unit time and may be correlated with seed production. This hypothesis is likely for perennial plants, and corresponds to physiological models of plant resource allocation (Mole 1994). All the above scenarios would ultimately result in a correlation between plant biomass and seed production, as is often found in the field (Aarssen and Taylor 1992), because biomass is generally correlated with productivity. Therefore it is difficult to decide exactly what variable determines fitness on the basis on existing data (de Mazancourt and Loreau, 2000).

1. Fitness measured by total biomass

At steady state, the local plant biomass and nutrient stock are, respectively, from eqs (8):

$$P^* = \frac{(I - qN^*)(1 + \gamma\delta)}{h_M + b(1 + \gamma\delta)} \quad (11a)$$

$$N^* = \frac{K[h_M + b(1 + \gamma\delta)]}{u_M(1 - \delta)(1 + \gamma\delta) - [h_M + b(1 + \gamma\delta)]} \quad (11b)$$

The optimal defence investment is now that which maximises P^* , i.e., which is the solution of:

$$\frac{dP^*}{d\delta} = 0 \quad (12)$$

This equation is too complicated to provide an analytical solution for $\hat{\delta}$, but an insight into its properties can be obtained by expressing $dP^*/d\delta$ in the following form:

$$\frac{dP^*}{d\delta} = \frac{(I - qN^*)\gamma h_M - q(1 + \gamma\delta)[h_M + b(1 + \gamma\delta)](dN^*/d\delta)}{[h_M + b(1 + \gamma\delta)]^2} \quad (13)$$

This shows that increasing the nutrient input or supply, I , tends to make $dP^*/d\delta$ positive, hence to select for a higher defence investment. Nutrient supply is the parameter that is closest to what was meant by the imprecise notion of 'resource availability' used by previous authors, because it governs the flow of resources taken up by the plant, i.e., plant productivity. Thus, in this case, increasing resource supply has an effect exactly opposite to that predicted by the resource availability hypothesis.

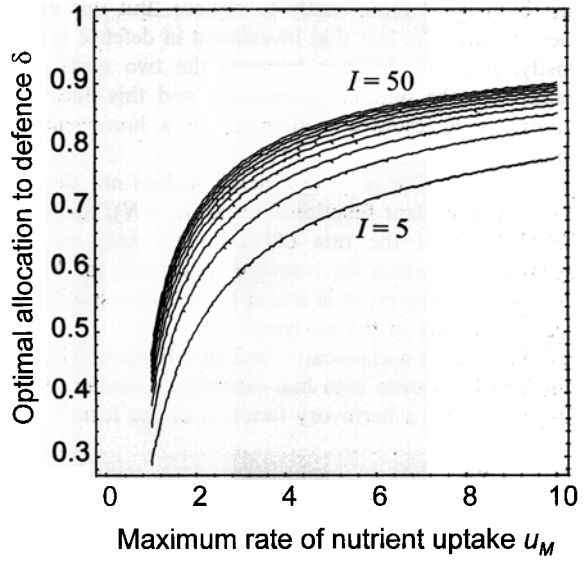


Fig. 2. Optimal allocation to defence, $\hat{\delta}$, as a function of maximum rate of nutrient uptake, u_M , for different values of nutrient supply, I , in a heterogeneous environment where fitness is determined by total biomass. Curves are not shown for $\hat{\delta}$ and u_M values that do not allow a feasible steady state. Parameter values: $b = 0.3$; $K = 20$; $h_M = 0.6$, $\gamma = 9$; $q = 0.05$. Curves from bottom to top: $I = 5, 10, 15, 20, 25, 30, 35, 40, 45$ and 50 , respectively.

The same is true for the maximum growth rate as measured by u_M . It is easily seen from eq. (11.b) that N^* tends to zero as u_M becomes large, and it can be shown that $dN^*/d\delta$ also tends to zero as u_M becomes large. This tends to make $dP^*/d\delta$ positive. Thus, increasing the maximum growth rate also tends to select for a higher defence investment, in contradiction with the resource availability hypothesis. These qualitative results are confirmed by a numerical analysis of optimal defense investment in Fig. 2.

2. Fitness measured by growth biomass

Plant growth biomass at steady state is:

$$G^* = P^*(1 - \delta) = \left(\frac{K + N^*}{u_M} \right) \left(\frac{I}{N^*} - q \right) \quad (14)$$

$$\frac{dG^*}{d\delta} = - \left(\frac{KI + qN^{*2}}{u_M N^{*2}} \right) \left(\frac{dN^*}{d\delta} \right) \quad (15)$$

Thus, $dG^*/d\delta$ has the inverse sign of $dN^*/d\delta$. The optimal defence investment is exactly the same as in a homogeneous environment; it is not affected by either the nutrient supply or the maximum resource uptake rate.

3. Fitness measured by total productivity

Plant productivity is determined by the flow of nutrient taken up by the plant, which, at steady state, is simply:

$$\Phi^* = I - qN^* \quad (16)$$

$$\frac{d\Phi^*}{d\delta} = -q \left(\frac{dN^*}{d\delta} \right) \quad (17)$$

Again $d\Phi^*/d\delta$ has the inverse sign of $dN^*/d\delta$, and the optimal defence investment is the same as in a homogeneous environment; it is not affected by either the nutrient supply or the maximum resource uptake rate.

4. Fitness measured by growth productivity

Plant growth productivity at steady state is:

$$\Phi_G^* = (I - qN^*)(1 - \delta) \quad (18)$$

$$\frac{d\Phi_G^*}{d\delta} = q(1 - \delta) \left(\frac{dN^*}{d\delta} \right) - (I - qN^*) \quad (19)$$

By the same line of reasoning as in case 1 (fitness measured by total biomass), it is easily seen that increasing either I or u_M tends to make $d\Phi_G^*/d\delta$ negative, hence to select for a lower defence investment. In this case, increased resource supply and maximum growth rate favour tolerance to herbivory, in agreement with the resource availability hypothesis. These qualitative results are confirmed by a numerical analysis of optimal defence investment in Fig. 3.

In conclusion, it is abundantly clear from our analysis that the effects of resource supply and maximum growth rate on the optimal defence investment are strongly dependent upon the criterion that determines fitness. The resource availability hypothesis is based on the assumption that fitness is determined by the potential growth rate, hence, implicitly, on the assumption of unlimited growth in a transient environment where plants do not deplete resources through their consumption. In an environment where plants have accumulated enough biomass to affect the amount of available resources, fitness is determined by the ability to deplete the limiting resource if the environment is homogeneous or by other traits correlated with biomass or productivity if the environment is spatially structured. In this case, resource supply and maximum growth rate may either increase, decrease, or in most cases not affect at all, optimal defence investment. Much more detailed data about what determines fitness in 'climax' environments would be necessary to make even qualitative predictions about the direction of evolution of antiherbivore defence investment as a function of resource availability and maximum growth rate.

One limitation of our analysis, however, is that it concerns steady states. It is conceivable that the resource availability hypothesis might still apply to early successional species, which experience a fast-changing environment, whereas the present model should hold for late successional species. The problem with the resource availability hypothesis, however, is that the empirical patterns it seeks to explain involved successional gradients (Cates and Oriens 1975, Bryant et al. 1983) or late successional species (Coley et al. 1985, Bryant 1987). It is also conceivable that plants from extremely poor environments are adapted to exploiting occasional pulses of nutrient enrichment (Campbell and Grime 1989), a scenario that we have not considered here. It remains to be seen, however, whether this could alter any of our conclusions for that particular kind of plants. The results of a recent experiment in which both herbivory and soil fertility were manipulated (Fraser and Grime in press) rather support our conclusions. In this experiment, the highest plant benefit from antiherbivore defence was found at the highest soil fertility, which, if anything, suggests a stronger selective pressure for defence investment at a higher nutrient availability, in contradiction with the resource availability hypothesis.

Given the weak theoretical foundations on which it rests, why has the resource availability hypothesis been considered to receive so much support from empirical patterns (Cates and Oriens 1975, Bryant et al. 1983,

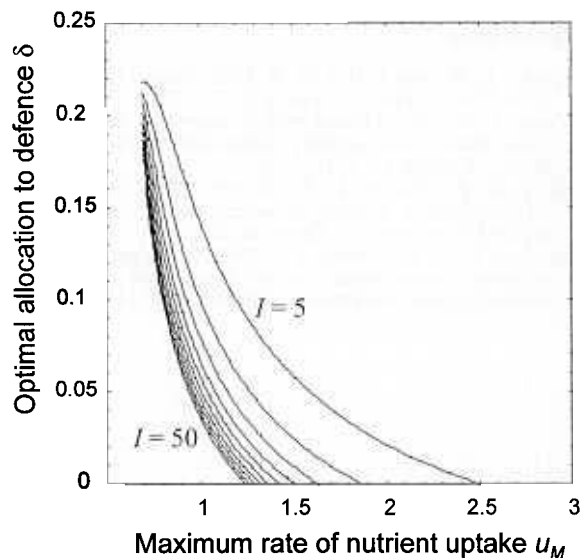


Fig. 3. Optimal allocation to defence, $\hat{\delta}$, as a function of maximum rate of nutrient uptake, u_M , for different values of nutrient supply, I , in a heterogeneous environment where fitness is determined by growth productivity. Curves are not shown for low u_M values that do not allow a feasible steady state. Parameter values: $b = 0.3$; $K = 20$; $h_M = 0.6$; $\gamma = 9$; $q = 0.05$. Curves from top to bottom: $I = 5, 10, 15, 20, 25, 30, 35, 40, 45$ and 50 , respectively.

Coley 1986, 1988, Coley et al. 1985)? We suggest that it has not been sufficiently contrasted against alternative hypotheses. Plant maximum growth rate is not the only factor that changes between nutrient-poor and nutrient-rich environments, and the observed patterns are likely to be explained by other factors. In particular, they can also be explained by the carbon/nutrient balance hypothesis (Bryant et al. 1983), which has since been encompassed in the broader framework of the growth-differentiation balance hypothesis (Herms and Mattson 1992, Tuomi 1992). This hypothesis assumes that cell growth and differentiation have competing demands on photosynthates in a plant, and growth is more limited than photosynthesis and differentiation in nutrient- or water-stressed environments. It predicts that more photosynthates are available for the production of carbon-based secondary metabolites in nutrient-poor environments. Thus it provides a more convincing explanation for the empirical patterns than does the resource availability hypothesis (Bryant 1987, Koricheva et al. 1998), although it still needs further refinements (Tuomi 1992, Herms and Mattson 1994, Lerdau et al. 1994, 1995, Koricheva et al. 1998).

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