Breaching plant defence theories: growth rates of plants directly impact the evolution of consumption rates of herbivorous insects

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Independent of the nature and extent of plant defences, the growth rates of plants could solely influence the consumption rates of herbivorous insects in a manner that allows insects feeding on slower growing plants to have lower consumption rates. Further, there may be diverse links between defences and growth rates of plants that are yet to be discovered.

Insects seem to have taken to herbivory during the Devonian Period[1]. The manner in which herbivorous insects (hereafter mentioned as just insects) and plants have adapted to one another since then[2,3] has led to several patterns[4–6]. For example, insects with lower consumption rates (quantity of food consumed per unit time) seem to be associated with slower growing plant resources (late successional species, mature plant parts), and those with higher consumption rates with faster growing ones (colonizing species, young plant parts)[7–10]. This relationship between the growth rate of plants and the consumption rate of insects is currently believed to be mediated by the plant's defences against insects[7–17]. Slower growing plants appear to have higher defences and insects feeding on plants with higher defences appear to have lower consumption rates, which is said to explain the pattern. However, here I suggest that the above relationship between the growth rate of plants and the consumption rate of insects can be effected independent of plant defences.

Let us assume a situation where a plant resource is available in discrete, equal-sized perennial patches, and that an insect population feeds exclusively on this resource. Further, the insect might be assumed to first arrive at a patch, followed by feeding and breeding. Finally, considering the significant risk that is generally associated with finding new patches, individuals may be assumed to disperse in search of new patches only when they cannot be sustained by the current patch. While feeding, individuals may compete with each other for acquiring plant resources, so that they can leave behind a greater number of offsprings in the quickest time. Competition for acquiring plant resources would increase the consumption rate of the population (the consumption rate of a population would predominantly depend on the quantity of plant resources consumed by an individual in its lifetime and the growth rate of the population). Interestingly, it appears that a rise in the consumption rate is limited by a corresponding fall in the number of consumers produced, which is explained as follows. An increase in the consumption rate would result in a concurrent increase in the depletion rate of the resource. In the case of static resources, or resources that do not change their proportions with time, notwithstanding depletion rate, there would be a constant number of consumers produced at the time of resource depletion. However, plant resources are not static; they grow, and their growth can be measured in terms of the biomass cumulated over time. Therefore, an increase in the depletion rate of the resource would mean that the patch would have cumulated lesser biomass at the time of resource depletion, thus allowing a fewer number of consumers to be produced on it. In other words, an increase in the consumption rate might lead to a reduction in the number of consumers (Figure 1). This is similar to the phenomenon known as the paradox of attack rates, where mathematical models predict a reduction in the density of consumers with increasing consumption rates[18].

A decrease in the number of individuals produced on a given patch of resource can severely constrain the insect. Let us, for convenience of understanding, assume that each dispersing individual has a 10% chance to succeed in colonizing a new patch. Here, there should be at least ten dispersing individuals from a given patch, so that one of them could succeed in colonizing a new patch. Therefore, when success in colonizing new patches is a function of the number of dispersing individuals produced from a given patch (dispersal efficiency of an individual may be kept constant), it might be

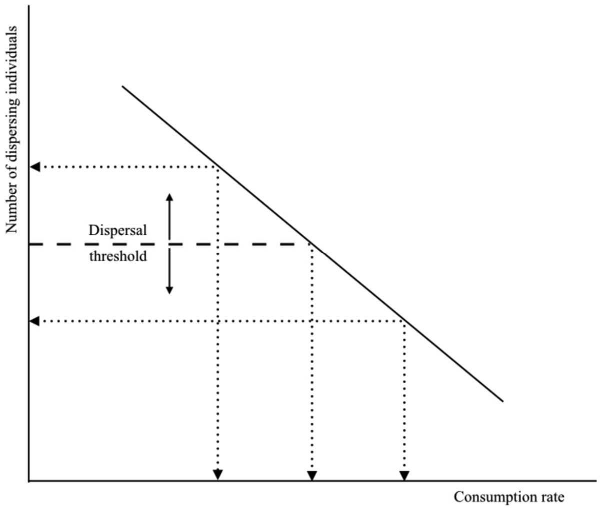

Figure 1. A hypothetical diagram depicting the inverse relationship between consumption rate of an insect population and the number of dispersing individuals produced from a given patch. Under a specific set of conditions, a minimum number of insects may be expected to disperse from a given patch of plant resource (dispersal threshold; thick dashed line). The dispersal threshold might vary along with the dynamics of the plant resource (solid arrows pointing in opposite directions).

justified to presume that the population might persist only when a certain minimum number of dispersing individuals are produced from the patch. This minimum number would set the upper limit for the consumption rate. In other words, the consumption rate might not increase beyond a certain threshold that is defined by the minimum number of dispersing individuals to be produced from a given patch (hereafter called dispersal threshold) (Figure 1).

Let us assume an insect population with two types of individuals – those with higher (*C*) and lower (*c*) consumption rates. Let us further assume the following three situations with two individuals in each. Let the first, second and third situations have both *C*, both *c* and *C*/*c* types of individuals respectively, landing on discrete, equal-sized perennial patches of resources at the same time. After landing, these individuals may be considered to feed and breed continuously, while all other factors may be kept constant. Eventually, the insects disperse when each of the patches nears exhaustion. Here, the time taken to arrive to dispersal may be the least for the first situation and maximum for the second; the third situation would occupy an intermediate position. Similarly, the number of dispersing individuals produced may be the least in the first and maximum in the second, while the third situation might continue at its previous position. Both, early dispersal and higher number of dispersing individuals confer certain advantages to the insect. However, as discussed in the preceding paragraph, the two are inversely related to each other. Therefore, the types of individuals that may prevail in a population might depend upon the dynamics of the resources. For example, it is possible to expect that *C* types can prevail when the resource becomes abundant, because increased abundance of resource would entail an increased dispersal success, which would lower the dispersal threshold. In turn, this might favour individuals with higher consumption rates. For the exactly opposite reasons, *c* types can prevail when the resource becomes scarce. Based on the above discussions, the following hypothesis has been proposed. Under a defined set of conditions, the realized consumption rate of a consumer might be the result of competition for acquiring resources, which increases the consumption rate, and the dispersal threshold, which sets the upper limit to the consumption rate. The dynamics of the resources, say, variations in their spatio-temporal patterns, might naturally select for the consumption rate (short, solid arrows in Figure 1 indicate potential shifts in the dispersal threshold, which is a reflection of the natural dynamics of the plant resources).

An extension of the proposed hypothesis suggests that the growth rate of plants might directly influence the evolution of consumption rate of insects (Figure 2). Once again, let us assume a situation where a plant resource is available in discrete, equal-sized perennial patches, and that an insect population feeds exclusively on this resource. Let us also assume an original growth rate of the resource (straight line *OA*), an original consumption rate (curved line *OA*) and a dispersal threshold (N_0) below which the insect population might be driven to extinction. Here, as the growth rate of the resource decreases (slope of straight line *OB* < straight line *OA*), keeping other things constant, the number of dispersing individuals would decrease below the dispersal threshold ($N_D < N_0$) and constrain the population. The constraint can be expected to provide greater opportunities for individuals with lower consumption rates, which would result in increasing the number of dispersing individuals while remaining with the current patch for a longer time ($T_B > T_A$). Therefore, plants with slower growth rates might tend to have individuals with lower consumption rates (curved line *OB*). On the other hand, as the growth rate of the resource increases (straight line *OC*), the number of dispersing individuals would increase above the dispersal threshold ($N_E > N_0$). Here, they may continue on the same resource for a longer period of time ($T_E > T_A$). In this situation, individuals with faster consumption rates might stand to benefit,

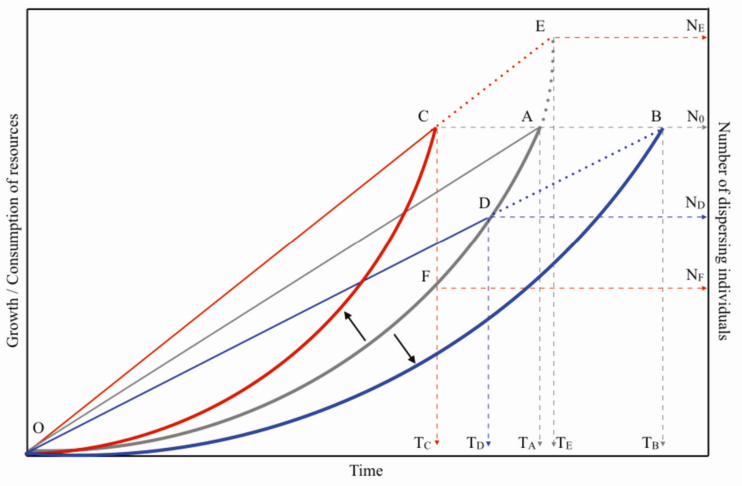

Figure 2. A hypothetical diagram showing the influence of variable growth rates of plants on the consumption rates of insects. Let us define the original growth rate of the plant resource (straight line *OA*). The consumption rate of the insect may originally be at a certain optimum (curved line *OA*), where N_0 dispersing individuals are produced in T_A time units. Let N_0 be the dispersal threshold number of individuals to be produced from a patch in the given situation. Keeping all other factors unchanged, let the growth rate of the resource be reduced in the first (straight line *OB*), and increased in the second situation (straight line *OC*). In the first case, the reduced growth rate intersects the original consumption rate at *D*, indicating that the resource is exhausted faster (T_D), thus resulting in a lower number of dispersing individuals (N_D). Going forward, natural selection might favour individuals with lower consumption rates (curved line *OB*), eventually increasing the number of dispersing individuals to N_0 in time T_B. In the second situation, the increased growth rate intersects the original consumption rate at *E*, indicating that the resource would be exhausted later (T_E) while producing a greater number of dispersing individuals (N_E). Going forward, natural selection might favour individuals with higher consumption rates (curved line *OC*), eventually decreasing the time taken (T_C) to produce N_0 dispersing individuals. In a different case, considering that fast-growing plants may be short-lived, let us add time limitation to the second situation, that the resource would be ending at T_C irrespective of herbivory. At the original rate, the actual consumption would have reached *F* when the resource would have ended, leaving behind fewer dispersing individuals (N_F). Here again, natural selection might favour individuals with higher consumption rates (curved line *OC*), eventually increasing the number of dispersing individuals to N_0, while the time remains unchanged at T_C.

which would begin to lower the number of dispersing individuals produced on the given patch. Eventually, the dispersal threshold (N_0) is reached in a shorter time ($T_C < T_A$). Therefore, plants with faster growth rates might tend to have individuals with higher consumption rates (curved line *OC*).

Let us now limit the availability of the resource to a known period of time; in other words, a patch may be unavailable after a certain time-period. Say, the faster growing resource (straight line *OC*) is unavailable after T_C (Figure 2). When all other factors are kept constant, the limited time for which the resource would be available would decrease the number of dispersing individuals ($N_F < N_0$). Going ahead, individuals with higher consumption rate would stand to gain, as this would promote competition and simultaneously result in increasing the number of dispersing individuals within the available time (reaching N_0 at time T_C). Ultimately, there may be an increase in the consumption rate of the insect population (curved line *OC*). Therefore, it is evident that slower and faster growing plant resources may favour individuals with lower and higher consumption rates respectively. In addition, plants with shorter lifespans may harbour individuals with higher consumption rates than their longer-living counterparts. Noticeably, there has been no assumption made regarding plant fitness being influenced by insects, nor regarding the influence of the chemistry of plants on insects, for arriving at the relationship that is central to this note.

While cataloguing the scientific developments in this subject of plant–insect interactions, it appears that efforts have been made to comprehend the evolution of such characters that allowed insects to successfully identify plants as resources, and walk, feed, digest, assimilate, breed, protect and depend on plants[1]. Theories suggesting insect herbivory to naturally select plants with higher defences, which is believed to have produced the present extraordinary variety of plant defences[19,20], have been investigated upon. A number of studies have scrutinized theories proposing an armsrace[2] between, and coevolution[19] of, plants and insects. Arguments against the coevolution theory, in support of the sequential evolution[21,22], also appear in the literature. However, the main idea presented here has never been proposed earlier. Along with the abilities such as walking or feeding on plants, it is logical that insects would have also adapted to the growth rate and the spatio-temporal organization of plant resources[23], even before natural selection started paving the coevolutionary paths of plants and insects. Distinct patterns, like the one discussed in the preceding paragraphs, would have emerged during the evolution of such adaptions.

The proposed hypothesis denies neither the evolution of plant defences against insects, nor the evolution of insects to a reforming plant chemistry. Alternatively, it renders a new perspective to the plant–insect interactions that allows us to view certain unexplored associations between defences and growth rates of plants. For instance, plant chemicals might not only affect insects directly, but also through altered growth rates – if producing chemicals costs plants[15], their presence would inevitably slower the plant growth rate. Unlike the direct, limiting influence of plant chemicals on the consumption rates, to which insects can evolve resistance through various mechanisms, insects cannot adjust to slow growth rates of plants, except by means of lowering their consumption rates. Thus, if the current theories are true, that plant chemicals can lower the consumption rates of insects, their impact on insects might assume permanency when the plant growth rate is slowed down too.

To summarize, specific patterns in plant–insect interactions could have been fundamentally shaped by the influence that the variable growth rates of plants and their spatio-temporal distributions may have had on the factors like competition and dispersal success in insects. The reciprocal selections between plants and insects, including the role of plant defences, may have only strengthened the underlying patterns. Thus, contrary to the contemporary belief that plant defences mediate the impacts of plant growth rate on the consumption rate of insects, it might indeed be necessary to consider that plant growth rate could mediate the effects of plant defences on the consumption rate of insects.

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1. Strong, D. R., Lawton, J. H. and Southwood, T. R. E., *Insects on Plants. Community Patterns and Mechanisms*, Blackwell Scientific, Oxford, UK, 1984.
2. Mello, M. O. and Silva-Filho, M. C., *Braz. J. Plant Physiol.*, 2002, **14**; http://dx.doi.org/10.1590/S1677-04202002000200001.
3. Wouters, F. C., Blanchette, B., Gershenzon, J. and Vassão, D. G., *Phytochem. Rev.*, 2016, **15**, 1127–1151.
4. Stamp, N. E., *Bull. Ecol. Soc. Am.*, 1996, **77**, 51–61.
5. Howe, G. A. and Jander, G., *Annu. Rev. Plant Biol.*, 2008, **59**, 41–66.
6. Strauss, S. Y. and Zangerl, A. R., *Plant–Animal Interactions: An Evolutionary Approach*, Blackwell Publishing, Oxford, UK, 2002.
7. Coley, P. D., *Nature*, 1980, **284**, 545–546.
8. Coley, P. D. and Barone, J. A., *Annu. Rev. Ecol. Syst.*, 1996, **27**, 305–335.
9. Coley, P. D., Bateman, M. L. and Kursar, T. A., *Oikos*, 2006, **115**, 219–228.
10. Brown, V. K., *Oikos*, 1985, **44**, 17–22.
11. Siemann, E., Haarstad, J. and Tilman, D., *Ecography*, 1999, **22**, 406–414.
12. Coley, P. D., Bryant, J. P. and Chapin, F. S. III., *Science*, 1985, **230**, 895–899.
13. Paul-Victor, C., Zust, T., Rees, M., Kliebenstein, D. J. and Turnbull, L. A., *New Phytol.*, 2010, **187**, 1102–1111.
14. Herms, D. A. and Mattson, W. J., *Q. Rev. Biol.*, 1992, **67**, 283–335.
15. Zust, T. and Agrawal, A. A., *Annu. Rev. Plant Biol.*, 2017, **68**: 513–534.
16. Zangerl, A. R. and Berenbaum, M. R., *Ecology*, 1993, **74**, 47–54.
17. Coley, P. D., *Oecologia*, 1988, **74**, 531–536.
18. Nilsson, K. A. and McCann, K. S., *Theor. Ecol.*, 2015, **9**, 59–71.
19. Ehrlich, P. R. and Raven, P. H., *Evolution*, 1964, **18**, 586–602.
20. Stamp, N. E., *Q. Rev. Biol.*, 2003, **78**, 23–55.
21. Jermy, T., *Am. Nat.*, 1984, **124**, 609–630.
22. Menken, S. B. J., *Entomol. Exp. Appl.*, 1996, **80**, 297-305.
23. Muralimohan, K. and Srinivasa, Y. B., *Curr. Sci.*, 2008, **94**, 876–882.

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