Tolerance to herbivory and the resource availability hypothesis

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The resource availability hypothesis (RAH), the most successful theory explaining plant defence patterns, predicts that defence investment is related to the relative growth rate (RGR) of plant species, which is associated with habitat quality. Thus, fast-growing species should show lower resistance than slow-growing species, which would lead fast growers to sustain higher herbivory rates, but the fitness consequences of herbivory would be greater for slow growers. The latter is often assumed but rarely tested. In a temperate rainforest, we tested the expected pattern of tolerance to herbivory derived from the RAH: that fast-growing species should be more tolerant than slow-growing species. We also evaluated whether other plant features covary with RGR (leaf lifespan, shade tolerance and leaf toughness) and thus could also contribute to the patterns of tolerance to herbivory. As expected, seedlings from tree species with higher RGR showed greater tolerance to herbivory. Among the three plant features included, only leaf lifespan showed a significant association with RGR, but RGR was the best predictor of tolerance. We argue that plant tolerance to herbivory must be evaluated to properly verify the assumptions of the RAH.

1. Introduction

The ubiquity of plant–herbivore interactions, which are often mediated by plant defences, has led researchers to seek general explanations. The resource availability hypothesis (RAH) [1,2] is arguably the most successful theory explaining patterns of plant defence. The RAH predicts that defence investment is closely related to the inherent relative growth rate (RGR) of plant species, which is associated with habitat quality (low/high resource availability). Ultimately, considering that defences are at the same time costly for plants and beneficial against herbivores, the cost–benefit ratio of defence investment in fast growers versus slow growers should drive their patterns of plant defence. Thus, fast-growing (gap-colonizing) species should show lower levels of defence than slow-growing (shade-tolerant) species, which would lead fast growers to sustain higher herbivory rates. However, for a given level of herbivory the fitness consequences would be greater for slow growers. A meta-analysis confirmed the main predictions of the RAH [3].

Plant defence to herbivory includes both resistance (minimize herbivore damage [4]) and tolerance (minimize the fitness consequences of herbivore damage [5]). Although the RAH focuses on plant resistance to herbivory, for the evolution of resistance strategies to occur it is also necessary to consider the impact of herbivores on plant fitness. The expected pattern of reduced resistance in fast-growing species in the RAH assumes that the fitness impact of losing plant tissue to herbivores would be low, as fast growers could replace lost tissue easily. However, tolerance is not always related to growth rate [5,6] and thus testing their relationship is critical to verify a key assumption of the RAH. Summarizing, plant tolerance to herbivory is an essential link in the RAH, but it is commonly assumed and rarely tested. In fact, the list of RAH’s predictions tested in a meta-analysis [3]...
does not include the expected tolerance pattern: that given a comparable herbivory pressure, and a common environment, fast-growing plant species should show greater survival (higher tolerance).

RGR is a main descriptor of plant species’ ecological strategies [7] and consequently plays a central role in the RAH. Several traits contribute to RGR [7–10] and there is debate on whether it is RGR itself or other plant features covarying with RGR that is actually selected in natural populations [9]. In this study, conducted in a temperate rainforest, we tested the expected pattern of tolerance to herbivory derived from the RAH: that fast-growing species should be more tolerant than slow-growing species. We also evaluated whether other plant features covary with RGR (leaf lifespan, shade tolerance and leaf toughness) and thus could also contribute to tolerance patterns. In the study forest, two patterns predicted by the RAH have been verified: fast-growing tree species sustain higher herbivory [10] and show reduced physical defences (K. Madriaza, C. Salgado-Luarte, E. Gianoli 2016, unpublished data) compared with slow-growing tree species. Therefore, if the hypothesis of greater tolerance in fast-growing species is verified there will be a full test of the RAH in the study system.

2. Material and methods

The study was carried out in an old-growth temperate rainforest at Puyehue National Park, southern Chile (40°39′ S, 72°11′ W; 350 m). Mean annual precipitation and temperature at the study site (Anticura) are 2800 mm and 9.8 °C [11]. Broad-leaf evergreen trees are the dominant species in the forest [12]. The main herbivores are beetles and snails [13].

We conducted a simulated herbivory experiment in the field with seedlings of nine tree species from seven families (60–70 seedlings per species), which span a broad shade-tolerance range (electronic supplementary material, table S1). These nine species comprise nearly two-thirds of all juveniles found in this forest [14]. Half of the seedlings were randomly assigned to receive damage (clipping with scissors 50% of total leaf area) and the remaining seedlings (control) were not damaged. Clipping was repeated every four months to maintain damage level at 50%, which corresponds to the upper damage level observed there [13]. Natural herbivores were excluded from all seedlings with pesticides (K. Madriaza, C. Salgado-Luarte, E. Gianoli 2016, unpublished data) compared with slow-growing tree species. Therefore, if the hypothesis of greater tolerance in fast-growing species is verified there will be a full test of the RAH in the study system.

Leaf toughness was measured with a penetrometer (a 600 g Pesola® scale attached to a small engine providing a constant speed). We placed the blunt rod of the scale (1.69 mm diameter) on the leaf lamina and recorded the force required to punch the leaf (kN m⁻²). We measured leaf toughness in 50 seedlings per species. Values of leaf lifespan (years) and shade tolerance (minimum light requirement) were obtained from the literature [16–18]. Mean values of the three parameters are shown in the electronic supplementary material, table S1. A multiple regression analysis evaluated the relative association of leaf toughness, leaf lifespan and shade tolerance with RGR.

3. Results

As expected, seedlings from tree species with higher RGR showed greater tolerance to experimental herbivory in the study forest ($R^2 = 0.83$, $F_{1,8} = 33.53$, $p < 0.001$, $n = 9$; regression analysis; figure 1). The multiple regression analysis showed that, among the three plant features included (leaf toughness, shade tolerance and leaf lifespan), only leaf lifespan showed a statistically significant association with RGR (table 1). Consequently, we further conducted a multiple regression analysis comparing leaf lifespan and RGR as predictors of tolerance to herbivory, but using the forward stepwise procedure to single-out the best predictor, which was RGR ($\beta \pm s.e.: 0.91 \pm 0.16$; $t_8 = 5.79$, $p = 0.0007$). The trait correlation matrix is available in the electronic supplementary material, table S2.

4. Discussion

We found that seedlings from tree species with higher RGR were more tolerant to herbivore damage in a temperate rainforest. In view of the link between RGR and resource availability [9], our results are consistent with earlier work at the study site, where seedlings of a tree species were more tolerant to herbivore damage in sun than in shade [13].

The main goal of the RAH is to explain interspecific differences in plant defence against herbivores [3]. Therefore, tolerance to herbivory, the process underlying differential survival of plant species subjected to comparable levels of damage, plays a pivotal role in the rationale of this hypothesis, as explained above. Supporting our hypothesis that tolerance to herbivory would increase with plant species
RGR was not trivial. If this pattern was not verified but the main predictions of the RAH did hold, i.e. if because of decreased resistance species with high RGR would sustain more damage, then fast-growing species would be at a competitive disadvantage and could be displaced from the local community. This conclusion could be relaxed if herbivores were not a significant selective agent, but there is evidence that herbivores select plant traits in forest communities [11,19]. In the study forest, two patterns predicted by the RAH have been verified: fast-growing tree species sustain higher herbivory [10] and show reduced physical defences (K. Madriaza, C. Salgado-Luarte, E. Gianoli 2016, unpublished data). Therefore, by supporting the hypothesis of greater tolerance in fast-growing species we gained a better understanding of the current and future ecological scenarios in this forest.

RGR, a key trait for characterizing interspecific variation in plants [7], was strongly associated with leaf lifespan, while it showed no association with leaf toughness or shade tolerance. Leaf lifespan is a major determinant of RGR and is also correlated with a number of traits at both the leaf level and the whole-plant level [20]. It has been shown that leaf toughness is associated with leaf lifespan, herbivory rate and shade tolerance [21,22]. Thus, it might be conceived that leaf lifespan could be a better predictor than RGR for these components of the RAH, and for tolerance to herbivory in particular. However, the a posteriori analysis verified that RGR was the best predictor of tolerance to herbivory. Surprisingly, we did not detect a significant association between shade tolerance and RGR, although this relationship is commonly found [23,24]. This might be explained by the low sample size (n = 9 species) because a study including 11 tree species in the same forest did find a significantly negative relationship between RGR and shade tolerance [10].

The RAH has gained a dominant position among the general theories addressing plant–herbivore interactions [3]. Here, we argue that plant tolerance to herbivory must be evaluated to properly verify the underlying assumptions of the RAH. Interestingly, a recent study advocates for the inclusion of tolerance in predictive frameworks for plant defence, but at the within-species level [25]. We call for the inclusion of tolerance to herbivory in the conceptual domain of the RAH, an addition that would further enhance the robustness and predictive power of this general hypothesis.

References


