

## EVOLUTIONARY ECOLOGY OF PLANT DEFENCES

**The resource availability hypothesis revisited:  
a meta-analysis**María-José Endara<sup>\*1,2</sup> and Phyllis D. Coley<sup>1,3</sup>

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**Summary**

1. Several theories have provided a framework for understanding variation in plant defence against herbivores. Among them, the plant apparency theory and the resource availability hypothesis (RAH) have aimed to explain the patterns of defence investment and the selective pressures that have led to the variety of defensive strategies across species. Here we provide a historical review of both theories, present evidence that shaped their development and contrast their predictions.

2. We present the results of a meta-analysis of the utility of the RAH 25 years after it was proposed and compare it to apparency theory. We performed a meta-analysis of 50 studies that have examined plant growth, defences and herbivory in relation to resource availability across latitude and ontogeny. Specifically, we tested four predictions that follow the RAH: (i) species adapted to resource-rich environments have intrinsically faster growth rates than species adapted to resource-poor environments; (ii) fast-growing species have shorter leaf lifetimes than slow-growing species; (iii) fast-growing species have lower amounts of constitutive defences than slow-growing species; and (iv) fast-growing species support higher herbivory rates than slow-growing species.

3. Our results confirm the predictions that species adapted to resource-poor environments grow inherently more slowly, invest more in constitutive defences and support lower herbivory than species from more productive habitats. Our data also showed that variation in growth rate among species better explains the differences in herbivory than variation in apparency, suggesting that the evolution of different defensive strategies across species is resource, rather than herbivore driven. We also found that the application of this theory appears robust across latitude and ontogeny, as the magnitude of the effect sizes for most of the predictions did not vary significantly between ecosystems or across ontogenetic stages.

4. We conclude that the RAH has served as a valid framework for investigating the patterns of plant defences and that its applicability is quite general.

**Key-words:** habitat resources, herbivory, meta-analysis, plant apparency, plant defences, plant defence theory, plant growth, resource availability hypothesis

**Introduction**

Because plants and herbivores constitute over half of the macroscopic diversity on earth, their interactions play a fundamental role in biodiversity and ecosystem function. For example, the diversity of plant species coexisting at a single site may frequently be shaped by the negative density- and distance-dependent effects of herbivores (Janzen 1970;

Connell 1971). Additionally, the evolutionary trajectory of both plant and herbivore traits is driven by the ‘arms race’ where plants are under continual selection to optimize defence investments and herbivores respond with counter adaptations to detoxify or avoid the defences (Ehrlich & Raven 1964; Thompson 1988). In this paper, we provide some historical context for the development of theories that have aimed to explain the patterns of defence investment and the selective pressures that have led to the variety of defensive strategies across species. We focus on two main

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theories, plant apparency theory (Feeny 1976) and the resource availability hypothesis (Coley, Bryant & Chapin 1985), present evidence that shaped their development and contrast their predictions. We then present results from a meta-analysis of studies examining interspecific variation in defence to assess the utility of these theories.

Although plants were credited with having effective anti-herbivore defences as early as 1888 (Stahl), it was not until Dethier's (1954) and Fraenkel's (1959) papers that the significance of plant secondary metabolites was widely appreciated. Since then, the details of myriad defensive traits and the concept of bottom-up control of herbivores have permeated the literature (Ehrlich & Raven 1964; Whittaker & Feeny 1971; Levin 1976; Haukioja 1980; Lindroth & Batzli 1984; Power 1992). While the concept of plant defences was embraced, the puzzle remained as to why the amount and type of defence differed so much among species. Fundamental to explaining interspecific variation in defences is, understanding the costs and benefits of defensive traits. The costs of defence have been extensively studied, and although they have occasionally been difficult to quantify, many examples of direct, indirect and ecological costs have been documented (Simms 1992; Koricheva 2002; Strauss *et al.* 2002). The benefits of reduced herbivory, while not universal, have also been shown (Marquis 1984; Belsky 1986). Most of the synthetic theories addressing interspecific differences in defence assume that selection has optimized investments, such that the benefits outweigh the costs (Feeny 1976; Grime 1977; McKey 1979; Rhoades 1979; Coley, Bryant & Chapin 1985; Crawley 1985). In the next section we focus on two of these theories, apparency theory and the resource availability hypothesis that sought explanations for why species differed in their investment in defences. We start with a historical review of the theories and the evidence that shaped their development.

### Apparency theory

The first major attempt to identify interspecific patterns of plant defences and to infer the processes responsible was apparency theory (Feeny 1976). A similar idea was simultaneously presented by Rhoades & Cates (1976). This theory revolutionized the field, as it shifted the focus from cataloguing the array of defensive traits, to asking *why* species differed in defences. The theory not only identified patterns of defences but suggested that the apparency of species to herbivores was the cause. Feeny posited that species that were long-lived would be apparent or 'bound to be found' by both generalist and specialist herbivores and therefore would be under strong selection for effective defences against both. The high investments in secondary metabolites, such as tannins in oaks, were consistent with this. Tannins were thought to reduce digestibility of leaves by binding with proteins, a mechanism of action that would be difficult for herbivores to circumvent. Feeny referred to these types of defences as 'quantitative' because the greater the investment, the more effective they would be. Furthermore, he posited that they

would present an effective defence against all herbivores, both specialists and generalists. In contrast, he suggested that unapparent species were short-lived and ephemeral in time and space, and because of this unpredictability, it would be difficult for herbivores to specialize on them. Thus, unapparent species could evade specialists and would only need defences that were effective against generalists. Using herbaceous crucifers as an example, he called these 'qualitative' defences. Qualitative defences of apparent plants were typically present in low concentrations and were low molecular weight molecules such as sinigrins and alkaloids. They were thought to act on specific animal targets and present significant barriers to generalists and non-adapted insects. Although Feeny hypothesized that it would be possible for herbivores to evolve counter adaptations to qualitative defences, the opportunity for specialization would not arise because unapparent plants were ephemeral and unreliable food sources. Unapparent plants would therefore escape from specialists and have qualitative defences against generalists. Apparent plants would have quantitative defences that would be effective against both generalists and specialists. Thus, the apparency of plants would determine if they were attacked by specialist herbivores or not, and the herbivores in turn would determine which defences, quantitative or qualitative, were optimal. Because of the elegance of apparency theory and the plausible fit with nature, the theory was rapidly accepted and profoundly shaped the field. It has been cited 1400 times and established the paradigm against which subsequent theoretical and empirical work has been judged.

### Resource availability hypothesis

The resource availability hypothesis (RAH), also called the growth rate hypothesis (Coley 1987; Stamp 2003), accepted Feeny's premise that long-lived species (apparent) invested heavily in defences and short-lived species (unapparent) did not, but presented an alternative explanation of the mechanism. Coley, Bryant & Chapin (1985) proposed that the observed range of defence investment was not due to differences among species in apparency, but to differences among species in the cost/benefit ratio of defences. They argued that the costs and benefits of investing in defence depended on the inherent growth rate of the species. In a fast-growing species, the opportunity cost of investing in defence would be high, as reallocating resources from photosynthetic leaves would have a much bigger negative impact on a fast grower compared to a slow grower. However, for fast growers, the negative impact of losing leaf area would be low, as they could more quickly replace lost leaves and a given amount of damage would represent a smaller percentage of their annual growth. Furthermore, the RAH postulated that herbivore pressure was a characteristic of the environment, rather than of a species' apparency, and that even if the *risk* of herbivory were uniform across species, selection could favour different levels of defence in species with different inherent growth rates. This is because the inherent growth rate determines the opportunity cost of defence and the impact of herbivory.

The quantitative expression of these thoughts led to the model:  $dC/dt = G \times C \times (1 - kD^\alpha) - (H - mD^\beta)$ . Here, the realized growth of a plant ( $dC/dt$ ) depends on the inherent growth rate  $G$  ( $\text{g g}^{-1}\text{day}^{-1}$ ) times the plant biomass at time zero ( $C$  g) minus investments in defence ( $1 - kD^\alpha$ ) and losses to herbivores ( $H - mD^\beta$ ). The inherent growth rate ( $G$ ) of a species is determined by the resource levels of the habitat to which it is adapted, regardless of herbivore pressure. For example, species from nutrient-poor or low-light habitats grow slowly, even if moved to better conditions because the best adaptation to a low-resource environment is to have a low demand for resources (Grime 1977; Chapin 1980).  $D$  ( $\text{g g}^{-1}$ ) is the defence investment expressed as a proportion of plant biomass, because this reflects allocation by the plant and impact on herbivores. The growth reduction due to defences ( $1 - kD^\alpha$ ) reflects the amount of investment and the opportunity costs, where  $k$  ( $\text{g day}^{-1}$ ) and  $\alpha$  are constants that relate an investment in defence ( $D$ ) to a reduction in growth. The rate of herbivory  $H$  ( $\text{g day}^{-1}$ ) drops as defences increase ( $mD^\beta$ ), where  $m$  ( $\text{g day}^{-1}$ ) and  $\beta$  are constants that determine the shape of the defence-effectiveness curve. In the simplest model, the maximum possible rate of herbivory ( $H$ ) is held constant, although this can be changed to reflect differences across habitats. However, even holding maximum herbivory constant, and by changing only the inherent growth rate, we shift the level of defence that maximizes the realized growth (Fig. 1). Thus, for fast-growing species the optimal defence level is low, even though this leads to high rates of herbivory. For slow-growing species, the optimal defence level is high, even though this cost further reduces the realized growth rate.

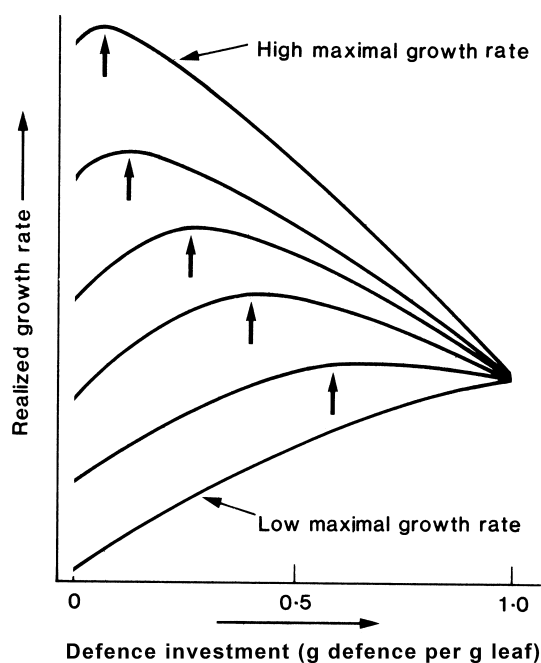


Fig. 1. Effects of defence investment on realized growth. Each curve represents a plant species with a different maximal inherent growth rate. Levels of defence that maximize growth are indicated by arrows. From Coley, Bryant & Chapin (1985).

The RAH was inspired by independent research in rain forests in Panama and boreal forests in Alaska. Coley (1983) undertook to test apparency theory in the tropical rain forest, where the high species diversity allowed replicates of 41 species. She classified gap-requiring trees as unapparent since they were short-lived and only occurred in light gaps. Shade-tolerant trees were spread throughout the forest in both gaps and understorey, were long-lived and were considered apparent. As predicted by apparency theory, the pioneers invested less in defences, however, they did not escape damage, but on average had six times the rates of herbivory as compared to shade-tolerant species even though all plants were measured in the same gap habitats. Furthermore, there was no difference in the variance of herbivory for gap and shade species, although the variance should have been higher for gap species if some individuals were escaping discovery by specialist herbivores and others were found and heavily eaten. Thus apparency did not seem to explain the differences in defence strategies. Instead, there was a strong correlation between investment in defences and the amount of herbivory ( $r^2 = -0.52$ ,  $P < 0.001$ ) confirming that defences did reduce herbivory and that plants benefited in proportion to their investment. There was also a strong negative relationship between the growth rate of a species and the investment in defences ( $r^2 = -0.69$ ,  $P < 0.01$ ) suggesting that differences in growth rates might be important determinants of defence costs and benefits. These results paralleled those found by Bryant and Chapin in the boreal forest with hares browsing on dormant twigs (Bryant & Kuropat 1980; Bryant, Chapin & Klein 1983). Again apparency did not seem to differ among species but there were strong correlations between plant growth rate and both defence investment and herbivory. The strikingly similar patterns observed in these two very different ecosystems inspired the collaboration that led to the RAH.

### Other theories

In this paper we focus on theories aimed at explaining differences among species in defences. Both apparency theory and the RAH have proposed possible reasons selection may have led to a range of optimal defences across species. Elements of the RAH have also been developed previously by Janzen (1974), Grime (1977, 2001) and Mattson (1980). Alternative approaches suggest that interspecific differences could arise due to variation in the extent of sexual reproduction (Levin 1975; Johnson, Smith & Rausher 2009) or to selection for escalation during radiations in tightly co-evolved systems (Farrell, Dussourd & Mitter 1991; Agrawal & Fishbein 2008). In addition, there are other influential theories that have been effective in helping us to understand defence differences among individuals within a species. Although these differences can arise through divergent selection, they are more frequently the result of plastic responses within a species to environmental gradients. Most notable are the carbon-nutrient balance hypothesis (Bryant, Chapin & Klein 1983) and the growth-differentiation balance hypothesis (Herms & Mattson 1992). Plants can also respond to herbivory by

inducing production of defences (Karban & Myers 1989; Karban 2011). Another strategy is to tolerate herbivore damage by storing sufficient resources to allow regrowth (Strauss & Agrawal 1999). We do not discuss these ideas, as the goal of this paper is to review theories whose main objective was to understand interspecific differences in constitutive defences.

However, it is worth noting that there is much confusion in the literature regarding the predictions of some of the above mentioned theories and the circumstances under which they are applicable (Stamp 2003). In our literature review, it was common to find studies claiming they supported the RAH when they did not, and others refuting the theory when their results were in agreement. The RAH was also frequently invoked when comparing phenotypic responses of plants to different environments, even though the RAH explicitly refers to optimal levels of defence that have evolved in species adapted to different environments. Although phenotypic plasticity theoretically could mirror adaptations seen across species, they often do not, but instead seem to reflect imbalances in allocation. The carbon-nutrient balance hypothesis (CNB), which was designed to explain these phenotypic shifts in defences, does not assume optimality and therefore makes different predictions than the RAH (Bryant, Chapin & Klein 1983). Conversely, the growth-differentiation balance hypothesis (GDBH), as elaborated by Herms & Mattson (1992), does assume that phenotypic variation in secondary metabolism represents adaptive plasticity consistent with predictions of optimal defence theory (see also Glynn *et al.* 2007). Furthermore, we found that the CNB hypothesis was often misused to explain interspecific differences, as did Stamp (2003) for GDBH. Bryant, Chapin & Klein (1983) and Herms & Mattson (1992) addressed both phenotypic and evolutionary responses of plants to resource availability, which no doubt has contributed to this confusion.

### Contrasting plant apparency and RAH

Because the theories of resource availability and apparency are not mutually exclusive and in some cases make similar predictions, in the next section of the paper we examine the generality and utility of the RAH 25 years after it was proposed and, compare it to apparency theory. We examined interspecific patterns of growth, defence and herbivory by means of meta-analyses based on 50 studies published between 1985 and 2010 and conducted on > 600 different plant species (see references of studies included in Appendix S1, Supporting information). Specifically, we performed separate meta-analyses for each of the four predictions from the RAH: (i) species adapted to resource-rich environments have intrinsically faster growth rates than species adapted to resource-poor environments; (ii) fast-growing species have shorter leaf lifetimes than slow-growing species; (iii) fast-growing species have lower amounts of constitutive defences than slow-growing species; and (iv) fast-growing species support higher herbivory rates than slow-growing species. We examine these predictions across latitude and ontogeny. We selected for relevant studies using Web of Knowledge, Google

Scholar and Web of Science, searching for the terms 'plant' and 'herbiv\*' and 'defens\*' and 'resource\*' (or 'light' or 'nutrient\*') and 'growth'. Other relevant studies were found by searching the reference section in the articles retrieved from the term searches. We restricted our analyses to studies that examined *interspecific* differences in plant species within a site or between sites differing in their degree of resource availability. Thus, studies that compared growth, defences or herbivory in the same plant species in different resource environments were not considered. For a complete description of our inclusion criteria see methods in Appendix S2 (Supporting information). For the last two meta-analyses (predictions 3 and 4 from the RAH), the articles were grouped into two types: studies that compared investment in plant defences, herbivory and growth between two or more *different* species within a site, and those that compared two or more *different* species growing in sites with divergent resource levels (light and nutrients, see Appendix S3, Supporting information for further categorization of studies included in these meta-analyses). In the original articles, the habitats in which the studies were conducted were usually classified as either resource-poor environments or resource-rich environments based on the levels of nutrient availability or of light availability. All the meta-analyses were conducted with the program MetaWin version 2.1.5 (Rosenberg, Adams & Gurevitch 2000), and using the mixed effects model (Gurevitch & Hedges 1993; see Appendix S2, Supporting information for a complete description of materials and methods and Appendix S3, Supporting information for effect sizes).

### Results

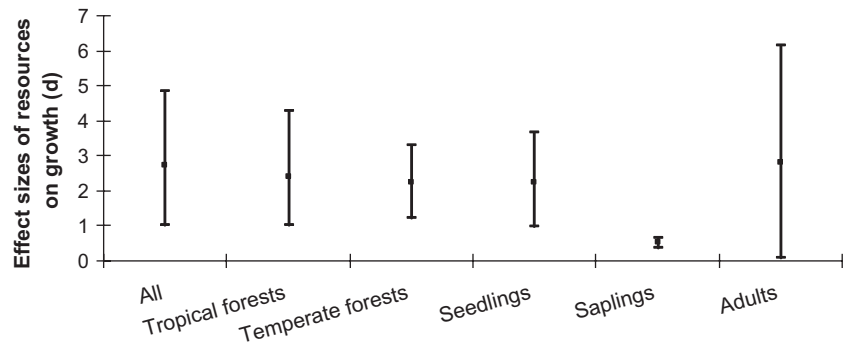
The results that follow are based primarily on studies of woody terrestrial species. Although we did not specifically exclude studies of herbaceous plants, or of marine and aquatic plants, most of these studies evaluated intraspecific differences in growth, defences and herbivory, and as such, did not meet our inclusion criteria (see Appendix S2, Supporting information).

#### PREDICTION 1: SPECIES ADAPTED TO RESOURCE-RICH ENVIRONMENTS HAVE INTRINSICALLY FASTER GROWTH RATES THAN SPECIES ADAPTED TO RESOURCE-POOR ENVIRONMENTS

Overall, we found that species from resource-rich environments grew faster than those from resource-poor environments ( $d = 2.75$ , 95% CI = 1.01–4.85,  $n = 24$ ,  $n_{fs} = 232$ ; Fig. 2; Table 1 in Appendix S3, Supporting information). We did not find significant variation among studies conducted in tropical forests vs. temperate forests ( $Q_B = 0.6$ , d.f. = 1,  $P = 0.59$ ), nor among ontogenic stages ( $Q_B = 7.07$ , d.f. = 2,  $P = 0.33$ ). However, we found that the magnitude of the effect was significantly different among the different growth traits ( $Q_B = 16.35$ ,  $P = 0.04$ ). The lower variance was found among those studies that reported growth rate and height. When only these studies were analysed, the results



**Fig. 2.** Mean and 95% confidence intervals for the effect sizes of resources on plant growth measures (weighted standardized mean, Hedges'  $d$ ): for all studies ( $n = 24$ ) and for studies conducted only in tropical forests ( $n = 17$ ), in temperate forests ( $n = 6$ ), with seedlings ( $n = 9$ ), with saplings ( $n = 5$ ), and with adults ( $n = 8$ ).



were similar to those obtained from the whole data set ( $d = 1.22$ , 95% CI = 0.17–2.14,  $n = 17$ ,  $n_{fs} = 36.6$ ).

#### PREDICTION 2: FAST-GROWING SPECIES HAVE SHORTER LEAF LIFETIMES THAN SLOW-GROWING SPECIES

We found a strong and negative effect of growth rate on leaf lifetime ( $z = -1.78$ , 95% CI =  $-2.55$  to  $-1.06$ ,  $n = 10$ ,  $n_{fs} = 110$ ; Fig. 3; Table 2 in Appendix S3, Supporting information), confirming the prediction that slow-growing species have longer leaf lifetimes than fast-growing species. We were unable to compare the magnitude of the effect between habitats with different resources, different ecosystems or ontogenic stages because most studies included in our meta-analysis were conducted with species in the same site, in tropical forests and with adult individuals (Appendix S2, Supporting information).

#### PREDICTION 3: FAST-GROWING SPECIES HAVE LOWER INVESTMENTS IN CONSTITUTIVE DEFENCES THAN SLOW-GROWING SPECIES

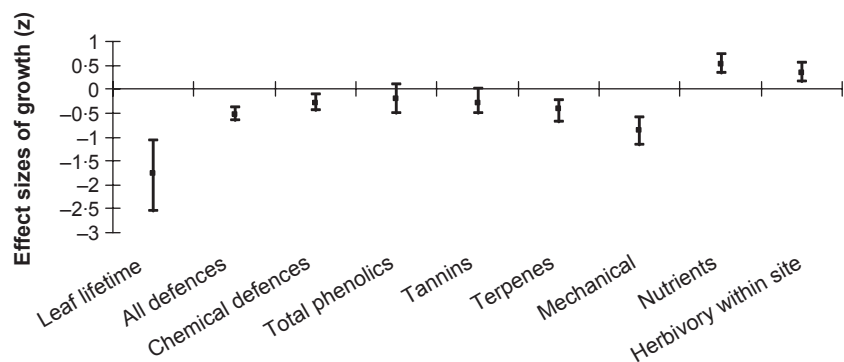
To test this prediction we conducted two analyses. We analysed growth effects on defences for fast- and slow-growing species in the same habitat to control, at least in part, for differences in the expression of defences across species caused by varied environments. We also compared growth effects between two or more different species in different habitats, which would include plasticity as well as evolved differences for constitutive defences (see meth-

ods in Appendix S2, Supporting information). The studies only reported quantitative results for phenolic compounds and terpenes, but not for other classes of chemical defences (see Table 3 in Appendix S3, Supporting information).

#### Effect of plant growth on investment in plant defences between species within a site

As predicted by the RAH, when all types of defences were considered together (chemical and mechanical), fast-growing species invested less in constitutive defences than slow-growing species ( $z = -0.52$ , 95% CI =  $-0.66$  to  $-0.38$ ,  $n = 57$ ,  $n_{fs} = 1824.6$ ; Fig. 3). This effect was more pronounced for seedlings and saplings than for adults as differences between seedlings and saplings ( $-0.61$  vs.  $-0.59$ ) were virtually non-existent ( $-0.18$ ;  $Q_B = 9.36$ , d.f. = 2,  $P = 0.04$ ), and also for studies conducted in tropical ( $-0.62$ ) vs. temperate ( $-0.3$ ) forests ( $Q_B = 6.44$ , d.f. = 2,  $P = 0.04$ ). The result was also significant when considering only chemical defences ( $z = -0.3$ , 95% CI =  $-0.45$  to  $-0.12$ ,  $n = 23$ ,  $n_{fs} = 139.6$ ; Fig. 3). The same pattern was maintained for the effect of growth on investment in terpenes ( $z = -0.43$ , 95% CI =  $-0.7$  to  $-0.23$ ,  $n = 4$ ,  $n_{fs} = 105.7$ ; Fig. 3) and total phenolics and tannins, although it was not significant for the last two. We also found that fast-growing species invested less in mechanical defences ( $z = -0.85$ , 95% CI =  $-1.2$  to  $-0.59$ ,  $n = 25$ ,  $n_{fs} = 584.2$ ; Fig. 3), and the magnitude of the effect was significantly higher in seedlings ( $-1.67$ ) vs. saplings ( $-0.64$ ) and adults ( $-0.33$ ;  $Q_B = 26.29$ , d.f. = 2,  $P = 0.004$ ). Our meta-analysis also confirmed that fast-growing species had higher leaf

**Fig. 3.** Mean effect sizes ( $z$ ) and 95% confidence intervals for growth rate effects on investment in plant defences and herbivory between species within a site. The dependent variables include: leaf lifetime ( $n = 10$ ), all constitutive defences ( $n = 57$ ), all chemical defences ( $n = 23$ ), total phenolics ( $n = 6$ ), tannins (hydrolysable and condensed;  $n = 12$ ), terpenes ( $n = 4$  records from one study by Fine, Mesones & Coley 2004), mechanical defences ( $n = 6$ ), nutrient content ( $n = 25$ ) and herbivory ( $n = 16$ ).



nutrient content ( $z = 0.51$ , 95% CI = 0.33–0.72,  $n = 6$ ,  $n_{fs} = 42.5$ ; Fig. 3).

#### Effect of plant growth on investment in defences between species in habitats with different nutrient availability

Our meta-analyses showed that studies comparing investment in defences between two or more different species from habitats with different levels of nutrients had contradictory results compared to within site comparisons. In these studies, there were no differences between fast-growing and slow-growing species in defence investment when all defences were combined (chemical and mechanical). We found the same result when all chemical defences were combined into one response variable (total phenolics, hydrolysable tannins and condensed tannins), or individually for tannins and leaf toughness (Fig. 4). There were not enough studies to compare trichomes. However, fast-growing species invested more in total phenolics ( $z = 0.85$ , 95% CI = 0.04–1.41,  $n = 8$ ,  $n_{fs} = 0$ ; Fig. 4). We did not find differences in the effect of growth on defences between studies conducted in tropical vs. temperate forests, nor among studies performed with seedlings or saplings or adult individuals. Since only one of our selected studies compared nutrient content in leaves between species from habitats with different nutrient levels we did not conduct a meta-analysis for this trait (Appendix S1, Supporting information).

#### Effect of plant growth on investment in defences between species in habitats with different light availability

Although in general slow-growing species invested more in defences than fast-growing species, this difference was not sig-

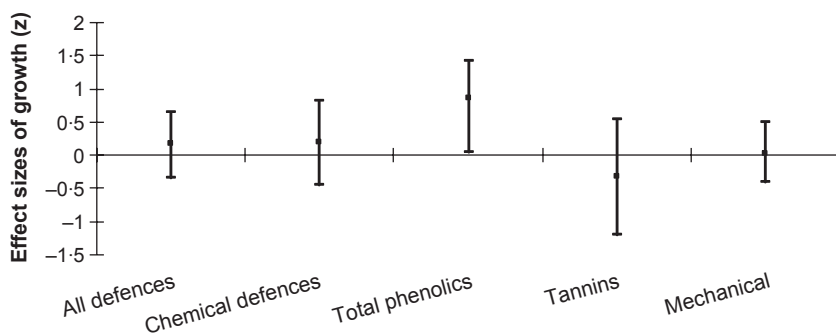
nificant when comparing different species from habitats with different levels of light (95% CI = –0.35 to 0.64; Fig. 5). Individually, we found a significant negative effect of growth on mechanical defences (only leaf toughness, as there were not enough studies comparing production of trichomes) ( $z = -0.82$ , 95% CI = –1.42 to –0.13,  $n = 8$ ,  $n_{fs} = 18.8$ ) but not on other defences. There were no differences in studies conducted in different ecosystems and with different ontogenetic stages.

#### PREDICTION 4: FAST-GROWING SPECIES SUPPORT HIGHER HERBIVORY RATES THAN SLOW-GROWING SPECIES

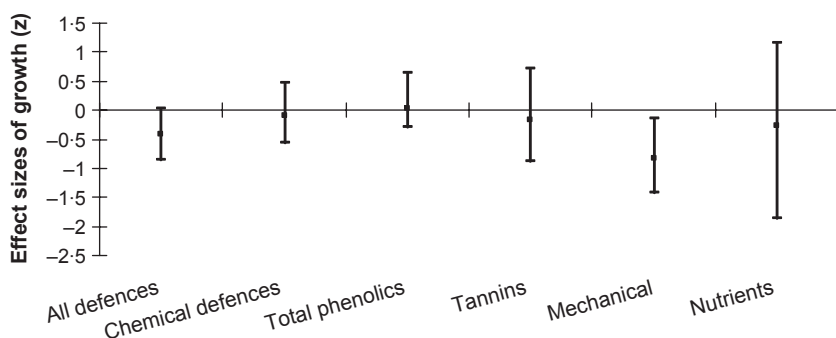
When comparing different species within the same site, we found that fast-growing species suffered higher herbivory compared to slow-growing species ( $z = 0.35$ , 95% CI = 0.15–0.55,  $n = 16$ ,  $n_{fs} = 27.4$ ; Fig. 3; Table 4 in Appendix S3, Supporting information). In contrast, the comparison across sites includes not only differences among species in their growth rate, but also differences among sites in overall herbivore pressure. In this comparison, herbivory for fast growers in resource-rich sites was higher than for slow growers at resource-poor sites, but the effect was not significantly different from zero ( $z = 0.29$ , 95% CI = –0.18 to 0.68,  $n = 29$ ,  $n_{fs} = 0$ ).

## Discussion

The goal of both apparency theory and the RAH has been to provide a theoretical framework that adequately explains the interspecific variation in plant defensive strategies. The RAH relates the evolution of defences to interspecific differences in



**Fig. 4.** Mean effect sizes ( $z$ ) and 95% confidence intervals for growth rate effects on investment in plant defences between species in habitats with different nutrient availability. Dependent variables include: all defences ( $n = 24$ ), chemical defences ( $n = 18$ ), total phenolics ( $n = 8$ ), tannins ( $n = 10$ ) and mechanical defences ( $n = 6$ ).



**Fig. 5.** Mean effect sizes ( $z$ ) and 95% confidence intervals for growth rate effects on investment in plant defences between species in habitats with different light availability. Dependent variables include: all defences ( $n = 17$ ), chemical defences ( $n = 9$ ), total phenolics ( $n = 4$ ), tannins ( $n = 5$ ), mechanical defences ( $n = 8$ ) and nutrient content ( $n = 2$ ).

inherent growth rate, whereas apparency theory assumes that defences are related to a species' predictability to herbivores. Although the theories have different assumptions regarding the reasons leading to defence differences, some of the predictions are similar. For example, both theories agree that long-lived, slow-growing species (apparent species) should invest more in defences than short-lived, fast-growing species (unapparent species). However, a fundamental difference between the theories is their contrasting predictions for the amount of herbivory. The RAH predicts that fast-growing species should suffer greater herbivore damage, while apparency theory predicts similar losses for apparent and unapparent species. In the discussion that follows, we examine results for defence and herbivory, as these apply to both theories. We also examine two predictions that apply only to the RAH, that resources affect growth and that growth affects leaf lifetimes.

#### PREDICTION 1: RESOURCE EFFECTS ON PLANT GROWTH RATE

Our meta-analysis suggests that, in agreement with the RAH, plant species from resource-rich environments had higher growth rates than species from resource-poor environments (Fig. 2). These patterns hold across different ecosystems and ontogenetic stages, as we did not find significant differences between studies conducted in tropical forests vs. temperate forests and in seedlings, saplings and adults. It is less certain whether these patterns will also hold for herbaceous species since all the studies included in our meta-analysis were based on woody species. However, a similar association between resources and inherent growth was found in a meta-analytical study performed with temperate herbs (Taub 2007). Our results are consistent with the well-established fact that species growth rates vary with fertility levels (Grime 2001) and light requirements (Swaine & Whitmore 1988). High rates of growth are hallmark characteristics of plant species adapted to high-resource environments (Grime 1979; Chapin 1980; Lambers & Poorter 1992). In contrast, species adapted to low-resource environments grow slowly and retain their growth habit even under high-resource conditions (Grime 2001).

#### PREDICTION 2: GROWTH RATE EFFECTS ON LEAF LIFETIME

As predicted, slow-growing species have leaves with significantly longer leaf lifetimes than fast-growing species. Long-lived leaves minimize nutrient losses (Aerts 1995) and constitute an essential adaptation of slow-growing species to habitats with low-resource availability (Grime 1977). The relationship between growth rate and leaf life span was the foundation for suggesting that qualitative defences, because of a higher maintenance cost, would be favoured in leaves with short life spans, and quantitative defences, with high initial costs but low maintenance costs, would be favoured in leaves with long life spans (Coley 1987).

#### PREDICTION 3: GROWTH RATE EFFECTS ON DEFENCES

Both theories predicted greater investment in defence for slow-growing species, but for different reasons. The RAH predicts that for slow-growing species the opportunity cost of defence will be low and the negative impact of herbivory high. Therefore, slow growers should exhibit higher investments in constitutive defences (Coley 1987). Apparency theory predicted that apparent plants would need effective defences against both specialists and generalists. The results from our meta-analysis found that, when considering only the studies that compared defence investment across species in the same habitat, there was a significant negative effect of growth rate on overall defence investment. This result was also maintained when considering chemical and mechanical defences independently (Fig. 3). Moreover, this pattern appears robust, as the direction of the growth effect on defences was the same when comparing different latitudes and ontogenetic stages.

Although defences were universally higher in slow growers, our meta-analysis showed that defence differences between fast and slow growers were significantly greater in tropical ecosystems. Possible explanations for this pattern might lie in the fact that, in the tropics, there is a higher absolute investment in defences (Coley & Aide 1991), a higher variance in defensive compounds (Gauld & Gaston 1994), and a greater range of plant growth rates (Van Zandt 2007). Greater amounts and ranges could facilitate detection of differences. Similarly, there was a negative effect of growth on overall defences for all ontogenetic stages, but the magnitude of this effect was significantly higher for seedlings. The reason for this is unclear, however, again, it may be easier to detect differences in defences if seedlings invest more than other age classes because of the potentially devastating effects of herbivory (Barton & Koricheva 2010; but see Boege & Marquis 2005).

However, when analysing the studies comparing two or more different species from different sites, we did not find a significant effect of growth rate on overall defences. This was consistent whether habitats differed with respect to nutrients or light. We interpret this as resulting from a combination of phenotypic responses of plants to short-term changes in resources with selection for different defence strategies in different habitats. Thus, these results can be better explained by integrating both the RAH and the carbon-nutrient balance hypothesis (CNB; Bryant, Chapin & Klein 1983; Dyer & Coley 2002; Stamp 2003). The CNB hypothesis suggests that when resources are in excess of what can be used for growth, they will be invested in defences. Accordingly, under high light where carbon is in excess relative to nutrients, this theory predicts higher amounts of carbon-based defences, whereas the RAH predicts lower defences for species adapted to this low-resource condition. Because of these counterbalancing influences, we would expect no significant effect of plant growth on defences, and this is what we found in our meta-analysis for studies comparing species from sites with different levels of light. In another study, Baldwin & Schultz (1988)

also found no significant differences in phenol investment when comparing species of the genus *Piper* from gaps and understorey. For mechanical defences, the CNB theory does not have a prediction, while the RAH predicts lower mechanical defences for species adapted to high-light levels. Again, our results were consistent with this, as leaves of slow-growing species were significantly tougher.

In contrast to the defence comparisons across light gradients, which were consistent with the combined effects of RAH and CNB theories, results from habitats with different nutrient levels were confusing. Under high nutrient levels, both the CNB hypothesis and the RAH predict lower carbon-based defences, however, we found a non-significant opposite trend. Another meta-analysis (Koricheva 1998) also found a weak but negative effect of fertilization on carbon-based defences. Although Herms & Mattson (1992) proposed a model that integrates genetic and phenotypic plasticity, the predictions are nonlinear and complex, making it difficult or impossible to capture secondary metabolic responses to variation in resource availability (Stamp 2003). Thus, when comparisons are made within a site, there is a clear negative relationship between plant growth and defence following the RAH, however, when confounding effects of environmental plasticity are included (Figs 4 and 5), particularly those associated with nutrient gradients, it is obvious that our understanding is incomplete.

The RAH also predicts higher inducible defences in fast-growing species. This is because the opportunity cost of defence is higher for fast growers, and because fast growers may more often occur under conditions that favour induction, such as predictable, but periodic herbivore attack (Karban 2011). Although we did not analyse this prediction, supporting evidence has been found. In a literature review of 68 studies, Nykanen & Koricheva (2004) found that the production of phenolics and protein-precipitation capacity of tannins increased in fast-growing species after herbivore damage more than in slow-growing species. Van Zandt (2007) found a similar result in an experimental study with nine species of temperate herbaceous plants.

#### PLANT DEFENCES: UNANSWERED QUESTIONS

A pattern first identified by Feeny was that unapparent plants invested in qualitative defences and apparent plants in quantitative defences. Although this observation has been fairly well supported, the reasons why are still unclear. A quantitative review of defensive classes in different plant guilds corroborated this idea by finding that fast-growing plants (apparent plants) are most often defended with quantitative, dose-dependent defences and slow-growing plants (unapparent plants) with qualitative defences (T. Massad & L. Dyer, pers. comm.). Feeny suggested it was because quantitative defences worked against all herbivores, while qualitative defences worked only against generalists and non-adapted specialists. However, the fact that the herbivores attacking apparent and unapparent plants are a similar mix of specialists and generalists (Futuyma & Gould 1979), and that quantitative and qual-

itative defences do not have different effects on generalists vs. specialists herbivores (Smilanich 2008; Carmona, Lajeunesse & Johnson 2011; T. Massad & L. Dyer, pers. comm.) brings this explanation into question. Another criticism of apparency theory, though one that we do not view as a fatal attack, is that the primary function of tannins may not be to bind proteins and reduce digestion (Bernays 1981). Instead, more recent evidence shows that oxidation of hydrolysable tannins forms reactive oxygen species, which can overwhelm the antioxidant defences of herbivorous insects and damage midgut tissues (Martin, Martin & Bernays 1987; Appel 1993; Summers & Felton 1994; Salminen & Karonen, 2011). Nonetheless, this could be considered a quantitative defence as higher concentrations of hydrolysable tannins will lead to greater levels of oxidative stress.

The RAH proposed that leaf lifetime, which is related to plant growth rates, is the key factor directing selection for the type of defence. They argued that qualitative defences, in addition to being present in low concentrations, are low molecular weight molecules with high turnover or maintenance rates. In contrast, quantitative defences such as condensed tannins, would require a considerable initial investment since they are present at high concentrations, but because they do not turnover, there would be no subsequent maintenance costs. Thus, for species with short-leaf lifetimes, it would be more cost effective to invest in qualitative compounds, whereas for long-lived leaves, the cumulative cost would be lower for quantitative compounds. However, this argument rests on differences in turnover rates for qualitative and quantitative compounds, an assumption that also has been challenged (Mihaliak, Gershenzon & Croteau 1991; Baldwin & Ohnmeiss 1994; van Dam *et al.* 1995; Salminen & Karonen 2011). Thus, the underlying factors favouring compounds along the quantitative/qualitative continuum remain to be determined.

#### PREDICTION 4: GROWTH RATE EFFECTS ON HERBIVORY

One of the key differences between the RAH and apparency theory is related to the predicted herbivore damage. Apparency theory (Feeny 1976; Rhoades & Cates 1976) predicts similar rates of damage. Unapparent plants escape from specialists and have secondary metabolites that are effective against generalists, whereas, apparent plants have metabolites that are effective against both specialists and generalists. In contrast, RAH predicts that fast-growing species will support higher levels of herbivory than slow-growing species because they are less defended. Our results support the last prediction, since we found a negative and significant effect size of growth rate on herbivory when analysing studies comparing species with different growth rates within the same habitat. Thus, unapparent plant species (fast-growing species according to the RAH) did not escape from herbivory, but had significantly higher levels than apparent species (slow-growing species according to the RAH). Therefore, variation in growth rate among species explains better the differences in



herbivory than variation in apparency. We found similar trends in the meta-analyses for studies comparing herbivory and growth rate between species growing in sites with different level of resources. This comparison not only takes into account differences in growth rates, but also differences between sites in overall herbivore pressure. A negative effect size of growth suggested that fast-growing species from resource-rich habitats suffered higher herbivory than slow-growing species from resource-poor habitats. However, the greater variance and absence of significance is consistent with herbivore pressure varying among habitats.

In addition to high herbivory on unapparent, fast-growing species, there is no evidence that they are attacked more by specialists than ephemeral species (Futuyma & Gould 1979; Cates 1980; Basset 1992), a key element of apparency theory posited to drive selection for different defence strategies. The host-finding abilities of insect herbivores are sufficiently good that escape from discovery does not appear to occur, except perhaps for extremely ephemeral species or tissues. Thus the patterns of defence first described by Feeny may not be adequately explained by a plant's apparency, as this does not lead to differential attack by specialist vs. generalist herbivores.

## Conclusions

Both apparency theory and the RAH have provided testable hypotheses for investigating interspecific variation in patterns of plant defences and have stimulated a multitude of studies. Both have been extremely influential and are widely cited (1400 and 1600 citations respectively). Our evaluation of the generality of the RAH 25 years after its first publication shows strong support for the basic tenets linking resources, plant growth, defence and herbivory. It has been suggested that the predictive power of the RAH is mostly supported in tropical forests, with mixed support in temperate forests (Van Zandt 2007). Although we found a higher mean effect size for all our predictions in the tropics, this difference was significant for only one of the predictions. Therefore, we suggest that the applicability of the RAH is general. In addition, because of its simplicity and wide application, the RAH has provided a coherent framework for the generation of new ideas about plant – insect interactions. For example, it has been proposed that resource availability and enemy release may interact in plant invasions (Blumenthal 2006).

More recent approaches in understanding the origin and maintenance of plant defences are often framed in an explicit phylogenetic context. Other approaches of promise ask mechanistic questions regarding the macroevolutionary trends in plant defences, and how selection by herbivores could influence both the speed and direction of selection. Furthermore, how could these interactions be shaped across species ranges and depend on the mosaic of other interacting species? And finally, can plant – herbivore interactions promote plant diversity by promoting rates of speciation or slowing extinction? New phylogenetic and molecular techniques as well as new theoretical approaches in studying plant – herbivore interactions should further enhance our understanding of

these fundamentally important interactions across evolution-ary and ecological time-scales.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Studies included in the meta-analyses.

**Appendix S2.** Materials and methods.

**Appendix S3.** Meta-analysis records.

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