Tradeoffs associated with constitutive and induced plant resistance against herbivory

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Several prominent hypotheses have been posed to explain the immense variability among plant species in defense against herbivores. A major concept in the evolutionary ecology of plant defenses is that tradeoffs of defense strategies are likely to generate and maintain species diversity. In particular, tradeoffs between constitutive and induced resistance and tradeoffs relating these strategies to growth and competitive ability have been predicted. We performed three independent experiments on 58 plant species from 15 different plant families to address these hypotheses in a phylogenetic framework. Because evolutionary tradeoffs may be altered by human-imposed artificial selection, we used 18 wild plant species and 40 cultivated garden-plant species. Across all 58 plant species, we demonstrate a tradeoff between constitutive and induced resistance, which was robust to phylogenetic effects of the species. Moreover, the tradeoff was driven by wild species and was not evident for cultivated species. In addition, we demonstrate that more competitive species—not fast growing ones—had lower constitutive but higher induced resistance. Thus, our multispecies experiments indicate that the competition–defense tradeoff holds for constitutive resistance and is complemented by a positive relationship of competitive ability with induced resistance. We conclude that the studied genetically determined tradeoffs are indeed likely to play an important role in shaping the high diversity observed among plant species in resistance against herbivores and in life history traits.

Given that green plants are the ultimate source of energy for most other organisms, it is not surprising that plants evolved a variety of resistance strategies, which can be constitutively expressed or induced after damage (1). Although herbivory selects for enhanced plant resistance, plants vary greatly in their resistance, both among species (2) and among genotypes within species (3). This indicates that being well defended may not always be the best strategy—most likely because allocation to resistance may physiologically constrain other investments (reviewed in refs. 4 and 5) and because constraints on resource allocation may produce negative genetic correlations between resistance mechanisms and other life-history traits (6–8). The current assumption in evolutionary ecology is that such tradeoffs contribute to the generation and maintenance of species diversity (8).

Several hypotheses on tradeoffs associated with constitutive and induced resistance have been formulated. Among the most fundamental ones is the long-predicted tradeoff between constitutive and induced resistance itself (6, 9). This hypothesis is derived from the idea that resistance is costly and that a species already well defended by high constitutive resistance will benefit only negligibly by further induced resistance (1, 10). However, general empirical evidence for this predicted tradeoff is still ambiguous (11), largely because most studies considered only single or very few species. Moreover, some studies reporting a tradeoff between constitutive and induced resistance were apparently compromised by spurious correlations due to including the same data for calculating constitutive and induced resistance (12). In addition, most studies that did not find such a tradeoff compared cultivated plant species or genotypes that had been subjected to artificial selection. In cultivated plants the selection pressures maintaining a tradeoff might be alleviated because nonnative cultivated plants might have escaped natural enemies (e.g., refs. 13 and 14), are artificially protected from enemies, or might have undergone artificial breeding that changed or broke up tradeoffs. As a consequence, those cultivated species might be relieved from evolutionary forces that shape tradeoffs in nature (15). However, to date no study has explicitly tested whether tradeoffs differ between cultivated and wild species.

Another fundamental hypothesis is the growth-rate or resource-availability hypothesis (16). It predicts that slow-growing plant species, which typically evolved in resource-limited environments, are less able to replace lost tissue than fast-growing plant species from more productive and competitive environments and should therefore invest in constitutive rather than induced resistance. As a corollary, induced resistance is expected to be higher in fast-growing and more competitive species. Several studies tested for correlations between constitutive resistance and growth, but to date only one study tested whether both constitutive and induced resistance are correlated with growth in the predicted manner (17). Moreover, although it is frequently assumed that fast growth is equivalent to high competitive ability (13), no study has explicitly tested whether competitive ability—rather than growth—of plant species trades off with constitutive resistance and whether competitive plants therefore might have evolved the strategy of induced resistance.

To address the generality of the relationships among constitutive and induced resistance, growth rate, and competitive ability, we took a comparative experimental approach. We performed three independent experiments to assess several important plant traits of 58 plant species from 15 different plant families. In the first experiment, we assessed constitutive and induced resistance to the bioassay caterpillar Spodoptera littoralis, whose feeding response, although possibly not representative for all herbivores, is considered to be a good approximation of plant resistance against generalist herbivores (17); in the second one growth rate; and in the third one competitive ability. To test whether evolutionarily important tradeoffs have disappeared in cultivated species, we compared cultivated horticultural plants (40 species) with wild plant species (18 species). Correcting for phylogenetic relatedness among species, we addressed the following specific questions. (i) Is there a tradeoff between constitutive and induced resistance among our study species, and if so, does it differ between wild and cultivated species? (ii) How are constitutive and induced resistance related to growth rate and competitive ability of wild and cultivated plant species?
Results

Phylogenetic Signal. We found a significant phylogenetic signal for relative growth rate ($K = 0.453$, $n = 51$, $P = 0.002$) and competitive ability ($K = 0.289$, $n = 53$, $P = 0.044$), indicating that part of their variation was predicted by evolutionary relationships among species. However, we found no significant phylogenetic signal for constitutive ($K = 0.268$, $n = 58$, $P = 0.068$) or induced resistance ($K = 0.163$, $n = 58$, $P = 0.787$).

Tradeoff Between Constitutive and Induced Resistance. Across all 58 plant species, induced and constitutive resistance were negatively correlated with each other [correction for spurious correlation (12); observed correlation = $-0.451$, one-sided $P = 0.031$]. This tradeoff was also significant when we corrected for phylogeny (estimate $\pm$ SEM = $-0.249 \pm 0.058$, $P < 0.001$), indicating the robustness of our result. Interestingly, this tradeoff was significant among wild plant species [correction for spurious correlation (12); observed correlation = $-0.696$, one-sided $P = 0.016$] but was not evident among cultivated plant species (observed correlation = $-0.309$, one-sided $P = 0.208$). This strongly suggests that the tradeoff has been lost for species under cultivation. This was also reflected in a significant interaction of species status (wild vs. cultivated) with constitutive resistance using induced resistance as dependent variable, both in a phylogenetically uncorrected (estimate = $-0.249 \pm 0.099$, $P = 0.015$; Fig. 1 and Table S1) and a phylogenetically corrected analysis (estimate $\pm$ SEM = $-0.288 \pm 0.092$, $P = 0.003$; Table S1).

Relationship of Resistance with Relative Growth Rate. Cultivated species seemed to follow the predictions of the growth-rate hypothesis—species with higher constitutive resistance had lower growth rates—but this was not significant (accounting for phylogeny and analyzed separately for cultivated plants: estimate $\pm$ SEM = $-0.045 \pm 0.040$, $P = 0.289$; Fig. 2 and Table S2). On the other hand, wild plant species with higher constitutive resistance tended to have higher instead of lower relative growth rates (accounting for phylogeny and analyzed separately for wild plants: estimate $\pm$ SEM = $0.113 \pm 0.052$, $P = 0.051$; Fig. 2 and Table S2). These different patterns for cultivated and wild plant species were reflected in a significant constitutive resistance $\times$ species status interaction using relative growth rate as dependent variable (accounting for phylogeny: estimate $\pm$ SEM = $0.162 \pm 0.055$, $P = 0.005$; Table S1). Consequently, across all species, constitutive resistance was not significantly related to relative growth rate (Table 1).

Relationship of Resistance with Competitive Ability. Although it is frequently assumed that fast growth is equivalent to competitive ability, relative growth rate was not significantly positively correlated with competitive ability across all study species (accounting for phylogeny; Fig. 2 and Table 1). This marginally significant correlation did not differ between wild and cultivated plant species (induced resistance $\times$ species status interaction using relative growth rate as dependent variable: estimate $\pm$ SEM = $-0.123 \pm 0.133$, $P = 0.362$; Table S1). Overall, our results do not support the predictions of the growth-rate hypothesis.

Across all study species, induced resistance was not positively, as expected, but slightly negatively correlated with relative growth rate (accounting for phylogeny; Fig. 2 and Table 1). This marginally significant correlation did not differ between wild and cultivated plant species (induced resistance $\times$ species status interaction using relative growth rate as dependent variable: estimate $\pm$ SEM = $-0.004 \pm 0.009$) but followed a humped relationship, with highest competitive ability at intermediate growth rates (accounting for phylogeny: estimate for the quadratic term of growth rate $\pm$ SEM = $-0.263 \pm 0.131$, $P = 0.049$). This relationship did not differ between wild and cultivated plant species [nonsignificant (relative growth rate)$^2 \times$ species status interaction using competitive ability as dependent variable: estimate $\pm$ SEM = $-0.222 \pm 0.333$].

Species with higher competitive ability had significantly lower constitutive resistance and significantly higher induced resistance (accounting for phylogeny; Fig. 2 and Table 1). These relationships did not differ between wild and cultivated plant species (constitutive resistance $\times$ species status interaction using competitive ability as dependent variable: estimate $\pm$ SEM = $-0.715 \pm 0.834$, $P = 0.016$; Fig. 2 and Table S2).
Table 1. Correlations between species traits assessed with GLS regression models

<table>
<thead>
<tr>
<th>Y variable</th>
<th>X variable</th>
<th>n</th>
<th>Coefficient ± SEM</th>
<th>Phylogenetic correction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Induced resistance</td>
<td>Constitutive resistance</td>
<td>58</td>
<td>-0.249 ± 0.058****</td>
<td>No</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>Constitutive resistance</td>
<td>51</td>
<td>-0.006 ± 0.034</td>
<td>Yes</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>Induced resistance</td>
<td>51</td>
<td>-0.113 ± 0.064*</td>
<td>Yes</td>
</tr>
<tr>
<td>Competitive ability</td>
<td>Constitutive resistance</td>
<td>53</td>
<td>-0.972 ± 0.465**</td>
<td>Yes</td>
</tr>
<tr>
<td>Competitive ability</td>
<td>Induced resistance</td>
<td>53</td>
<td>2.930 ± 0.850***</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Correlations are either raw or phylogenetically corrected, depending on the presence of a phylogenetic signal in at least one of the correlated variables. Shown are regression coefficients ± SEs (SEM).

P = 0.396; induced resistance × species status interaction using competitive ability as dependent variable: estimate ± SEM = 0.857 ± 1.796, P = 0.635; Table S1). These results indicate a genetically determined tradeoff between competitive ability and constitutive resistance, which for good competitors is counterbalanced by their high ability to induce resistance.

Discussion
Tradeoff Between Constitutive and Induced Resistance. Different types and strategies of resistance, large variation among species in the degree of resistance, and their potential consequences for the evolution of other plant traits have inspired biologists for decades. We demonstrated the long-predicted tradeoff between constitutive and induced resistance (6, 9) using a large taxonomically diverse number of herbaceous plant species. As hypothesized, the tradeoff between constitutive and induced resistance was significant among wild species but not among cultivated species. Concordantly, most previous studies that did not find a tradeoff between constitutive and induced resistance used genotypes or varieties of cultivated crop species (6, 18–21). The presence of the tradeoff in wild plant species and its absence in cultivated plant species indicates that evolutionary rather than physiological forces cause the tradeoff in nature. This clearly calls for using wild species when addressing natural evolutionary patterns in life-history traits and shows the advantage of using cultivated plant species as controls.

Two previous studies found a positive, instead of a negative, correlation between components of constitutive and induced resistance (2, 22). Possibly, this apparent contradiction with our results reflects that those studies looked at single defensive compounds rather than at an integrative measure of plant resistance obtained, for example, by using generalist bioassay caterpillars. This explanation would be in line with recent claims that, although the univariate tradeoff model may not hold for individual elements (e.g., lignin, condensed tannins), which reduce the digestibility of the plants for generalist and specialist herbivores (28). Therefore, one hypothesis might be that in natural habitats, to be able to grow and defend, there is selection in fast-growing plants toward qualitative rather than quantitative compounds. In cultivated garden plants, which during their breeding programs are frequently protected from herbivores and usually do not experience nutrient deficiency, selection for qualitative compounds might be relaxed. The relation of growth and resistance in those plant species might rather follow physiological constraints, as predicted by the growth-rate hypothesis. For these reasons, our results are in line with recent suggestions that fast growth and constitutive resistance are not necessarily alternative strategies (27, 29, 30).

Surprisingly few studies assessed the association between induced resistance and growth rate across multiple species. Karban and Baldwin (1) reported in a review that slow-growing species frequently have the ability to induce resistance, but that it tends to be stronger in species categorized as fast growers. In a comparative experiment with 18 species (17), plant species from a low-resource and stressful environment produced less biomass and had lower induced but higher constitutive resistance (e.g., lignin, condensed tannins), which reduce the digestibility of the plants for generalist and specialist herbivores (28). Therefore, one hypothesis might be that in natural habitats, to be able to grow and defend, there is selection in fast-growing plants toward qualitative rather than quantitative compounds. In addition, it is assumed that fast-growing species, if they have any antiherbivore resistance at all, accumulate low concentrations of highly potent, qualitative compounds (e.g., alkaloids, cardenolides, glucosinolates), which are mainly effective against specialist herbivores, such as our bioassay caterpillar. Slow-growing species instead are assumed to accumulate mainly qualitative compounds (e.g., lignin, condensed tannins), which reduce the digestibility of the plants for generalist and specialist herbivores (28). Therefore, one hypothesis might be that in natural habitats, to be able to grow and defend, there is selection in fast-growing plants toward qualitative rather than quantitative compounds. In cultivated garden plants, which during their breeding programs are frequently protected from herbivores and usually do not experience nutrient deficiency, selection for qualitative compounds might be relaxed. The relation of growth and resistance in those plant species might rather follow physiological constraints, as predicted by the growth-rate hypothesis. For these reasons, our results are in line with recent suggestions that fast growth and constitutive resistance are not necessarily alternative strategies (27, 29, 30).

Constitutive and Induced Resistance in Relation to Relative Growth Rate. Several previous studies reported a tradeoff between constitutive resistance and growth rate, which supports the growth-rate or resource-availability hypothesis (e.g., refs. 16, 17, and 25), and its universality has been claimed (26). Cultivated plant species in our study showed a trend to follow the predictions of the growth-rate hypothesis, with slow-growing species having more constitutive resistance than fast-growing species. Interestingly, however, we found the opposite for wild plant species. Moreover, rather than a positive association between induced resistance and relative growth rate, we found a marginally significant negative one. Our results therefore indicate that there is no universal support for a tradeoff between constitutive resistance and growth rate or for a corresponding positive association between induced resistance and growth rate.

It has been suggested that the tradeoff between growth and constitutive resistance should not hold if resistance is provided by low-cost, qualitative compounds (27). In addition, it is assumed that fast-growing species, if they have any antiherbivore resistance at all, accumulate low concentrations of highly potent, qualitative compounds (e.g., alkaloids, cardenolides, glucosinolates), which are mainly effective against generalist herbivores, such as our bioassay caterpillar. Slow-growing species instead are assumed to accumulate mainly qualitative compounds (e.g., lignin, condensed tannins), which reduce the digestibility of the plants for generalist and specialist herbivores (28). Therefore, one hypothesis might be that in natural habitats, to be able to grow and defend, there is selection in fast-growing plants toward qualitative rather than quantitative compounds. In cultivated garden plants, which during their breeding programs are frequently protected from herbivores and usually do not experience nutrient deficiency, selection for qualitative compounds might be relaxed. The relation of growth and resistance in those plant species might rather follow physiological constraints, as predicted by the growth-rate hypothesis. For these reasons, our results are in line with recent suggestions that fast growth and constitutive resistance are not necessarily alternative strategies (27, 29, 30).

Constitutive and Induced Resistance in Relation to Competitive Ability. Competition and herbivory are among the most important ecological forces affecting plant evolution (9). It is assumed that increased constitutive resistance compromises the competitive ability of plants (33), resulting in a competition–constitutive resistance tradeoff. Compared with constitutive resistance, in-
duced resistance might be more valuable for plants faced with strong competition: in the absence of enemies more resources can be allocated to competitive ability, because the plant only induces defense when attacked. Consequently, plants can be constitutively more defended at the same time, when necessary. Indeed, among both wild and cultivated plant species, the more competitive ones had lower constitutive resistance and higher abilities to induce resistance.

A positive relationship between induced resistance and competitive ability has been addressed in very few previous studies. Cipollini (34) found that mutants of Arabidopsis thaliana lacking the ability to induce resistance are poorer competitors than the wild type, and he suggested that pathways essential to produce induced resistance also mediate some plant responses to competitors. Kong et al. (35) demonstrated that herbivore-inducible compounds in Ageratum conyzoides can possess allelopathic potential and directly suppress the growth of neighboring plants. We did not aim at disentangling whether more-competitive plant species are better competitors because (i) they induce resistance and directly or indirectly affect their neighbors, as described above (34, 35), or (ii) because low constitutive resistance combined with the ability to induce resistance is selectively favored in competitive environments on the basis of cost-effectiveness. However, our study shows not only that the competition-defense tradeoff is holding for constitutive resistance, but also that it is consistently higher in more competitive plant species. Therefore, we had both wild and cultivated species in almost all families. Because we wanted wild plant species to be representative of wild genotypes, we obtained them from Swiss seed suppliers providing these species for restoration projects and ecological compensation areas (UFA Samen, Wyss Samen und Pflanzen, and Samen-Steffen). Seeds of cultivated species were instead obtained mainly from nurseries (B & T World Seeds, Thompson & Morgan, and Wyss Samen und Pflanzen) and are likely to have undergone intense breeding. In three experiments, we assessed, respectively, herbivore resistance, growth rate, and competitive ability of all plant species. Because of low germination rates for some species, we used 51 wild and 40 cultivated species; Table S3). Because species did not germinate simultaneously, they differed in starting times. Two weeks after germination, we harvested six offspring per plant species and determined total dry weight as initial size measure. For each species, we then transplanted six additional offspring individually into 1-L pots filled with a 1:1 mixture of sand and plain field soil. Six weeks after germination of each species, we harvested the plants and again determined total dry weight. From these data, we calculated the relative growth rate (RGR) of each species (44):

\[ RGR = \frac{\ln(\text{weight}_2) - \ln(\text{weight}_1)}{\text{day}_2 - \text{day}_1} \]

Assessment of Competitive Ability. For the determination of competitive ability, it was important that the experiment started simultaneously for all species. Therefore, we germinated the plant species sequentially between March and June 2009, starting with the species having the longest and ending with the ones having the shortest time to germination. Because of low germination rates for some species, this experiment included 51 of the 58 species for which we had assessed resistance to herbivory (13 wild and 38 cultivated species; Table S3). Because species did not germinate simultaneously, they differed in starting times. Two weeks after germination, we harvested six offspring per plant species and determined total dry weight as initial size measure. For each species, we then transplanted six additional offspring individually into 1-L pots filled with a 1:1 mixture of sand and plain field soil. Around eight of the 16 seedlings, we planted a circle of 10 competitors instead obtained mainly from nurseries (B & T World Seeds, Thompson & Morgan, and Wyss Samen und Pflanzen) and are likely to have undergone intense breeding. In three experiments, we assessed, respectively, herbivore resistance, growth rate, and competitive ability of all plant species. Because of low germination rates for some species, we used 51–58 of the 77 species in these experiments (Table S3). Most of the species with low germination rates were wild plant species, which led to an imbalance between the number of wild and cultivated plant species.

Assessment of Constitutive and Induced Resistance to Herbivory. Herbivore species. As bioassay herbivore for the assessment of constitutive and induced resistance, we used larvae of the Egyptian cotton leafworm Spodoptera littoralis (Lepidoptera: Noctuidae), which are known to feed on plants of at least 40 plant families (38). The extreme polyphagy of S. littoralis makes it an excellent bioassay species for comparing leaf palatability across plant species from different families (e.g., refs. 37–40), and its feeding response and performance are used as integrative and functionally relevant measures of plant resistance (15). Another advantage of S. littoralis for the present study is that it is native to (sub)tropical Africa and therefore unlikely to result in a coevolutionary history with any of our study species. Therefore, it is unlikely that S. littoralis would have had an a priori biased preference for wild or cultivated species. Caterpillars for our experiments originated from a laboratory stock (Institute of Cell Biology, Bern, Switzerland) bred on a bean-based artificial diet to avoid adaptation of the insects to any of our study species.

Experiment and Design. In August 2008, seeds of our plant species were germinated in trays filled with potting soil. For 18 wild and 40 cultivated species with sufficient numbers of seedlings (Table S3), we planted 10 seedlings into 1-L pots with potting soil (totaling 580 plants) and placed them in a greenhouse (15 °C night, 28 °C day, and a constant day length of 14 h). All plants were watered as needed. Because the species did not germinate simultaneously, the experiment was performed over a period of 4 mo until all 58 species had been tested. Confluent wild and cultivated species were tested at the same time.

After 8 wk of growth, we enclosed all 580 plants individually into perforated polyester bags. To induce possible resistance mechanisms in half of the plants of each species, we allowed two third- to fourth-instar caterpillars (hereafter called induction caterpillars) of S. littoralis to feed on these plants for 1 d. Directly after removal of the induction caterpillars, we added one of the 16 seedlings of S. littoralis to each caterpillar cage, either the induced or noninduced plants—and allowed them to feed for 5 d. We assessed the increase in biomass of the bioassay caterpillars by recording fresh mass of the caterpillars before and after feeding (41).

For each plant species the effect of induction on final caterpillar mass was assessed by means of an analysis of covariance with type I sums of squares after considering effects of initial caterpillar mass as covariate (42, 43). The resulting adjusted final mass therefore represents caterpillar growth during the experiment. As a measure of constitutive resistance, we used mean adjusted final mass of caterpillars feeding on undamaged plants per plant species. Induced resistance was assessed as adjusted mass of caterpillars feeding on damaged plants minus the adjusted mass of caterpillars feeding on nondamaged plants (see refs. 12 and 40). Because large increases in caterpillar mass indicate low resistance of the plants, we multiplied caterpillar mass and the differences in caterpillar mass, respectively, with −1 for easier visualization (i.e., high values correspond to high resistance).

Assessment of Relative Growth Rate. To determine relative growth rate, we germinated species as before, in May 2008. Because of low germination rates of some species, this experiment included 51 of the 58 species for which we had assessed resistance to herbivory (13 wild and 38 cultivated species; Table S3). Because species did not germinate simultaneously, they differed in starting times. Two weeks after germination, we harvested six offspring per plant species and determined total dry weight as initial size measure. For each species, we then transplanted six additional offspring individually into 1-L pots filled with a 1:1 mixture of sand and plain field soil. Six weeks after germination of each species, we harvested the plants and again determined total dry weight. From these data, we calculated the relative growth rate (RGR) of each species (44):

\[ RGR = \frac{\ln(\text{weight}_2) - \ln(\text{weight}_1)}{\text{day}_2 - \text{day}_1} \]
We thank Bill Morris for conducting the statistical analysis of different species. It is necessary to consider their phylogenetic relationship, because closely related species are likely to be phenotypically more similar than others. Therefore, we constructed a phylogenetic tree of all our species (SI Methods and Fig. S1). We tested for a phylogenetic signal for each measured variable using statistics on a random walk model of phenotypic evolution (46).

Raw and phylogenetically corrected correlations were estimated among species traits. We used generalized least squares (GLS), implemented in R (47) with and without correcting for phylogeny (Table S4), because this allowed us to consider multiple factors and interaction models. The GLS method codes the phylogeny as a variance—covariance matrix to account for the relatedness among species. Because this method corrects the dependent variable for phylogeny, we always used the variable with the phylogenetic signal as the dependent variable (48). To test whether relationships between two variables depended on phylogeny, we calculated the log-response ratio for each species (45) as:

$$\ln R_i = -\ln(M_{\text{controll}}) - \ln(M_{\text{treatment}}).$$

### Statistical Analysis

When analyzing characteristics of different species, it is necessary to consider their phylogenetic relationship, because closely related species are likely to be phenotypically more similar than others. Therefore, we constructed a phylogenetic tree of all our species (SI Methods and Fig. S1). We tested for a phylogenetic signal for each measured variable using statistics on a random walk model of phenotypic evolution (46).

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### Acknowledgments

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