



Intraspecific variation in growth, defense and herbivory in *Dialium guianense* (Caesalpiniaceae) mediated by edaphic heterogeneity

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Abstract

Based on resource allocation theory, a negative correlation is predicted between resource availability and plant defense against herbivore attack. Plants growing in resource-limited environments should display lower growth and higher defense against herbivores than plants growing where resources are less limited. Interspecific comparisons generally support these predictions. We evaluated this hypothesis at the intraspecific level, for two sapling populations of the canopy tree *Dialium guianense* (Caesalpiniaceae) at the Lacandona rain forest in southeast Mexico. The two populations occur in nearby sites, adjacent to the Chajul Field Station, under the same climatic conditions and within the same vegetation type, but with considerable differences in soil quality. The Floodplain site, under the influence of the Lacantún River, has favorable conditions for plant growth, in terms of nutrient and water availability, whereas the Hills site, given its location and soil characteristics, provides more restricted conditions for plant growth. Plants in the Floodplain site had higher growth and lower concentration of phenolic compounds than plants in the Hills (a two-fold difference in leaf area production, 1.3 less total phenolics). These differences were correlated with differences in herbivore attack, as saplings from the Hills, with a higher defensive potential, had lower average levels of herbivory than Floodplain plants ($3.86\% \pm 0.80$ vs. $7.75\% \pm 1.43$ of leaf area loss). The relationship between the concentration of phenolic compounds and leaf quality for herbivores was consistent with preference assays carried out under laboratory conditions using two species of generalist herbivores, the army worm *Spodoptera fugiperda* and the native katydid *Orophus* sp. In 63.8 and 81.3% of the cases, third-instar larvae of *S. fugiperda* and adults of *Orophus*, respectively, preferred leaflets from the Floodplain plants population. Moreover, on average, the adults of *Orophus* consumed 2.9 times more leaf area from the Floodplain than from the Hills. In addition, a reciprocal transplant experiment indicated that phenotypic plasticity is likely to be the mechanism by which the plants expressed differential growth and traits affecting herbivory levels. In this experiment, growth and herbivory levels were 1.6 and 1.7 times higher, respectively, in plants transplanted into a Floodplain experimental plot than those in a Hills plot. This work contributes to our understanding of how edaphic heterogeneity can determine intraspecific variation in the relationship of plants with their herbivores and evaluates the underlying mechanisms promoting such influence.

Introduction

Several plant traits have been identified as effective defenses against herbivore attack, as they represent physical or chemical feeding impediments for plant

consumers. We know that such traits may vary significantly among (Edmunds and Alstad 1978; McKey et al. 1978; Coley 1982; Crawley 1997) and within plant species (Cates 1975; Langenheim and Stubblebine 1983; Dirzo 1984; Zangerl and Berenbaum

1990; Marquis 1992; Snyder 1992), as well as within individual plants (Karban 1989; Agrawal 1998; Kearsley and Whitham 1989). In many cases, such variation has been associated to the influence of resource availability on plant growth and production of defenses (Bryant et al. 1987; Hartley et al. 1995; Mutikainen et al. 2000), and has been considered to be relevant for the evolution of anti-herbivore defensive strategies (McKey et al. 1978; Coley et al. 1985). Thus, based on resource allocation theory (Barbour et al. 1980), a negative relationship is predicted between resource availability and a plant's investment in anti-herbivore defenses (Janzen 1974; McKey et al. 1978).

The Resource Availability/Growth Rate Hypothesis (RA/GR) (Coley et al. 1985) predicts that variation in plant defense depends on the plant's inherent growth rate. Plants with low growth rates (as determined by an adaptive response to low resource availability) should have a low capacity to compensate for the loss of tissue to herbivores and therefore should allocate more resources to defenses. In contrast, plants with higher inherent growth rates and higher leaf turnover rates should display a greater capacity to replace tissue lost to herbivory instead of investing in defenses (Coley et al. 1985). Even if the RA/GR hypothesis was originally conceived to analyze interspecific variation, the contrast between populations in which a genetic component may be involved (e.g., population differentiation) permit to invoke this hypothesis for analyses of intraspecific variation, given the fact that the latter can be an initial step for species differentiation. Therefore, under those circumstances the underlying mechanisms of the RA/GR hypothesis can be invoked to explain such intraspecific variation (Lerdau and Coley 2002; Messina et al. 2002). On the other hand, when intraspecific variation is not explained by genetic differentiation but by phenotypic variation, the tradition has been to explain such variation in the context of plasticity, along the lines of the Carbon/Nutrients Balance Hypothesis (Bryant et al. 1983). This hypothesis suggests that when growth is limited by resource availability, the Carbon/Nutrients ratio in the plant is modified and, as a consequence, resources acquired in excess are shunted into the production of secondary metabolites. Thus, if the intake of nutrients is restricted, plants are predicted to allocate the excess of carbon into carbon-based defenses. In contrast, if growth is limited by light, plants are expected to allocate any nitrogen in excess into nitrogen-based compounds (Bryant et al. 1983). However, several authors have pointed out to a number of limi-

tations of this hypothesis, including the lack of consideration of the differential energetic costs among types of metabolites, the assumption that growth always takes priority over secondary metabolism, and the lack of consideration of the role of genotype in determining chemical phenotype in plants, among others (Hamilton et al. 2001). Therefore this hypothesis remains highly controversial (see Koricheva 2002; Lerdau and Coley 2002; Nitao et al. 2002; Stamp 2003).

Most efforts directed to evaluate the negative relationship between growth and defense have compared interspecific differences in defensive patterns (McKey et al. 1978; Coley 1982; Bryant et al. 1989; Louda and Collinge 1992; and see Herms and Mattson 1992), or differences among plants from the same species under controlled experimental conditions (Bryant et al. 1987; Chapin 1991; Hartley et al. 1995; Koricheva et al. 1998; Mutikainen et al. 2000). In contrast, studies of plant defensive patterns associated to differences in plant growth and its impacts on herbivory regimes and herbivore response, as promoted by intraspecific variation in natural systems are scarce (see Cates 1975; Dirzo and Harper 1982; Jing and Coley 1990; Sork et al. 1993; Glawe et al. 2003). Other studies have found evidence of intraspecific and seasonal variation in defenses (Arnold et al. 1995; Folgarait and Davidson 1995; Suomela et al. 1995; Nurmi et al. 1996; Darrow and Bowers 1997; Laitinen et al. 2000; Glynn et al. 2003; Taylor et al. 2003), providing potentially valuable systems to study the ecological and evolutionary consequences of such intraspecific variation in defenses.

There are two recognized mechanisms responsible for the existence of intraspecific variation in plant traits, including defense: phenotypic plasticity and genetic differentiation among populations. Phenotypic plastic responses are changes in the expression of traits associated to variation in the environment (Stearns 1989). On the other hand, genetic differentiation is promoted when the influence of inheritable traits on each genotype's fitness varies in heterogeneous environments (Harper 1977; Hartl and Clark 1999). Both mechanisms have relevant ecological and evolutionary consequences when plants are exposed to environmental heterogeneity, since they influence the range of ecological conditions in which the species' genetic pool may succeed (Stearns 1989). The relative importance of these mechanisms to explain intraspecific variation in defensive traits has been

poorly explored in tropical ecosystems and this is particularly so in the case of tropical trees.

A common source of environmental heterogeneity in tropical ecosystems is the spatial variation in soil characteristics (e.g., Clark and Clark 1999). This provides an opportunity to study the impact of nutrient availability on resource allocation patterns and its consequences on plant-herbivore relationships. In order to test whether edaphic heterogeneity leads to differences in growth and defense and if this, in turn, affects plant-herbivore interactions, we studied two adjacent sapling populations of *Dialium guianense* (Aublet) Sandw, occurring in sites with contrasting soil conditions in a Mexican tropical rain forest. We first evaluated growth and total phenolics production in saplings from both populations. We then examined if herbivory and foliage palatability were correlated with differences in growth and defense. Finally, to evaluate indicators of the possible mechanisms promoting such variation (*i.e.*, phenotypic plasticity or genetic differentiation), we conducted a reciprocal transplant experiment in which plants from the two populations were transplanted into their own and the other's environment.

Methods

Study System

This study was carried out in the Chajul Field Station (CFS), located in the Montes Azules Biosphere Reserve, Selva Lacandona region, in Southeast Mexico. This area has a warm, humid climate with 3850 mm of annual rainfall, and a mean annual temperature of 22 °C. The predominant vegetation is tropical rain forest represented by canopy trees such as *Dialium guianense*, *Brosimum alicastrum* Sw, *Vatairea lundellii* (Standley) Killipex Record, *Terminalia amazonia* (Gmelin) Exell, *Swietenia macrophylla* G. King, and *Ceiba pentandra* (L.) Gaertn. (Dirzo 1991; Mendoza and Dirzo 1999). The region of the CFS has considerable edaphic heterogeneity that promotes the establishment of several subtypes of vegetation within the area surrounding the field station and under the same climatic regime, ranging from flooded evergreen forest to semideciduous forest.

We selected two areas of the CFS with contrasting soil conditions, one adjacent to the Lacantún river (Floodplain) and the other one located in an area of small hills, approximately 15 km away from the first

Table 1. Edaphic characteristics of both sites of study in the Chajul Field Station (Data kindly provided by Dr. C. Siebe).

Edaphic characteristics	Floodplain	Hills
C/N	14.8	12
P Reserves (mg/Kg)	1270	115
% Total N	1.09	0.55
% Al	0	5.8
pH	6.68	4.64
% organic matter	27.8	11.4
Texture		
% sand	15.6	66.1
% loam	45.2	10.9
% clay	39.2	23

site (Hills). The soils of the Floodplain site are considerably richer in the availability of phosphorous, nitrogen, and organic matter, compared with the soils of the Hills site, which in turn are sandier, contain higher aluminum concentration and are more acid (Table 1). Thus, soils from the Floodplain are more suitable for plant growth than those from the Hills (except for plants adapted to soils with nutrient limitation). A previous study showed that these two sites (and specifically the plots we studied) do not differ in availability and heterogeneity of light in the understory, as analyzed by hemispheric photographs (F. Carrillo, unpublished data). *D. guianense* (Caesalpiniaceae), a codominant canopy tree of this rain forest occurs in both sites. Reproductive trees can reach 45 m high and measure up to 1.5 m in diameter at breast height or above the prominent buttresses. *D. guianense* is considered to be a slow-growing species (Pennington and Sarukhán 1998). The compound leaves (with three, five or seven leaflets) of this species show evidence of herbivory by Lepidoptera larvae in the study site (R. Dirzo and R. Frías, unpublished data). Given the prevalence of this species and the availability and abundance of saplings in the understory of both sites, we considered it to be a good candidate to test the influence of edaphic heterogeneity on patterns of resource allocation and herbivory, and to carry out reciprocal transplants (see below).

To assess the effect of heterogeneity in soil quality on resource allocation in *Dialium guianense* saplings, we evaluated two plant variables, growth and production of total phenolics.

Growth

Plant growth was measured on 20 saplings (20-40 cm height) randomly selected from each site. We recorded height increment and leaflet area produced in a 174-day period during 1998. Increment in height was measured by subtracting the initial height from the final measured height. Leaflet area production was calculated, for each plant, from a regression between leaflet length and leaflet area. We carried out this regression by using 98 undamaged leaflets randomly selected from both populations. Leaflet area was measured with a leaf area meter (DeltaT Devices, Cambridge, England). The resulting regression was highly significant [$\ln(\text{leaflet area}) = 0.1912 + 1.716 \ln(\text{leaflet length})$, $R^2 = 0.91$, $P < 0.001$]. Total leaflet area production of the 20 saplings was estimated by multiplying the number of leaflets produced in this period by mean leaflet area of 10 randomly selected leaflets from each plant. Differences in growth of both populations were examined using MANOVA, including total leaf area produced and increment in height as response variables, and the initial number of leaflets (measured at the beginning of the study, February, 1998) as a covariate. However, since this covariate was non-significant in the model, it was excluded from further analyses. To evaluate the contribution of each growth variable to the overall effect in the MANOVA model, subsequent univariate ANOVAs were performed for each variable.

Secondary metabolites

Concentration of total phenolics was determined twice using the Folin-Denis method (Waterman and Mole 1994). Fully expanded leaves were collected from 25 saplings of each population in May 1998 and in October 2001. In 1998, leaf samples were dried at 40 °C for 24 hours while in 2001 leaves were immediately frozen in liquid nitrogen after collection, and then freeze-dried in the laboratory. In 1998 we calculated the concentration of phenolics using tannic acid (Sigma Chemical Co., St. Louis Missouri USA), while in 2001 we used purified *D. guianensis* tannins as a standard.

Concentration of total phenolics was expressed as the percentage of dry mass tannic acid and *D. guianense* phenolic equivalents, respectively. In 1998 we were not able to estimate the contents of these metabolites on a per-plant basis, since we combined foliage of the saplings of each population in order to

have sufficient dry biomass to run the assays. In contrast, in 2001 we were able to use a microscale modification of the Folin-Denis method (Waterman and Mole 1994) and therefore we did not require large amounts of biomass, and samples were analyzed individually for each plant. Differences between populations were statistically compared using ANOVA.

Herbivory

To assess the ecological consequences of variation in plant resource allocation to defense, we recorded natural levels of herbivory in plants from both populations. Herbivory was measured in June and September of 1998 in 20 plants randomly selected from each population. Percentage of leaf area consumed was estimated in ten randomly selected leaflets/plant, using six visual damage categories corresponding to a specific range of consumed leaflet area (0=0%, 1=1-6%, 2=6-12%, 3=12-25%, 4=25-50%, 5=50-100%; Dirzo and Domínguez 1995). The reason for using these categories is that low levels of damage were the most frequent, therefore requiring narrower ranges of damage per category. In contrast, high levels of damage were very rare and therefore could be lumped into broader range categories. Percentage of leaf area lost to herbivores (H) was calculated using the formula: $H = (C_i * n_i) / N$, where C_i corresponds to the percentage midpoint of each category (i.e., $C_1 = 3.5$, $C_2 = 9.0$, $C_3 = 18.5$, $C_4 = 35.5$, and $C_5 = 75\%$, respectively), n_i is the number of leaflets in the i_{th} category of damage, and N is the total number of leaflets (modified from Dirzo and Domínguez 1995). We evaluated differences in herbivory between populations with a repeated measures ANOVA (Sokal and Rohlf 1981).

Preference and palatability assays

To determine whether differences in the foliage of both populations could influence natural levels of herbivory, we conducted cafeteria-type bioassays (see Dirzo 1980) with two generalist herbivores in 1998 and in 2001. We evaluated the palatability of foliage from both populations by quantifying the amount of area eaten by herbivores when exposed to both types of foliage. In 1998, we used third-instar larvae ($n=43$) of the generalist herbivore *Spodoptera fugiperda* (Lepidoptera: Noctuidae), a known crop pest. In 2001 we used adult individuals of a common native katydid, *Orophus* sp. ($n=16$) observed to be

capable of feeding on a variety of plant species. In the case of the army worm, prior to their use in the bioassays, herbivores were fed *ad libitum* with a mixture of corn, bean, soy, and sorghum as a standard diet (F. Meraz, pers. comm.). Twelve hours before the beginning of the experiment, larvae were starved to standardize their appetite and to ensure feeding. In the case of the katydid, freshly collected animals from the field were fed with lettuce for 6 h and then starved for 5 h. We placed one larva or one katydid in the center of a Petri dish containing one fresh leaflet from each population. Leaflets for this experiment were standardized by size, so that available leaf area to each herbivore was the same for both types of plants. Leaflets were collected from randomly selected saplings from both populations in June 1998 and May 2001. Humidity was maintained during the assays with a moist cotton-ball placed in the Petri dish. After 21 and 15 h, when most of the larvae and the katydid, respectively, had eaten a visible amount of one or both leaflets, we measured the amount of tissue eaten with a transparent grid (1 mm²). Differences in palatability of the foliage from the two populations were assessed by comparing the amount of leaflet area eaten with a Wilcoxon paired test.

Reciprocal transplant experiment

To explore the possible mechanisms promoting intraspecific differences in growth and defense between populations, we conducted a reciprocal transplant experiment. Experimental plots (8 × 5 m) were established at both sites, by transplanting 20 intact saplings from each population in August 1997. Plants were placed randomly 1 m apart from each other in both experimental plots. Following an acclimation period of five months, we measured plant growth (new leaves produced) during the next 174 days (February to September 1998). In April 1999 we assessed herbivory of all mature leaflets of the surviving plants, by estimating herbivory as previously described. In order to determine the mechanism by which variation in resource allocation occurs in *D. guianense*, we analyzed the data obtained for both variables (growth and herbivory) by a two-way ANOVA. In this model, we considered site of origin of each population, transplant site, and their interaction as the possible factors promoting variation in growth and herbivory. Significant effects of transplant site would suggest that plant phenotypic plasticity could be the mechanism promoting intraspecific vari-

ation in the response variables. A significant effect of population origin, or the interaction term, would suggest that differences between populations are more likely to be promoted by genetic differentiation for resource allocation patterns.

Statistical analyses

One important caveat to bear in mind for the statistical analyses is that we only used two sites for the comparisons and this may lead to some kind of pseudoreplication. However, we were not able to replicate sites of the two types of edaphic conditions without involving other additional variables (aspect, microclimatic regime, vegetation structure and composition, elevation, etc.) that might have obscured the contrast in soil conditions. Prior to the application of all parametric statistical analyses we normalized the data and tested for heterogeneity of variances. In all cases, normality was met after the appropriate transformations (growth data were *ln* transformed and herbivory data were *arc-sine* square root transformed; Shapiro's test, $P > 0.19$ in all cases). Likewise, all variances were homogeneous (Bartlett's test, $P > 0.09$ in all cases). All statistical analyses were carried out with JMP for Windows (1995), except for MANOVA, which was performed with the GLM procedure of SAS (SAS Institute 1989). Unless otherwise indicated, reported data are means ± standard errors.

Results

Growth

The overall effect of site on growth variables was significant (Wilks' $\lambda_{(2, 33)} = 0.82$, $P = 0.03$). The plants of the Floodplain site grew significantly more during the 174-day period in terms of leaflet area produced (Figure 1A). The final difference in photosynthetic area was nearly two-fold (14.51 ± 4.09 cm² for the Floodplain and 7.02 ± 1.28 cm² for the Hills site; $F_{(1, 36)} = 4.40$, $P = 0.045$). Increment in height over the study period, in contrast, was not significantly different between Floodplain (3.32 ± 0.52 cm) and Hills (3.63 ± 0.59 cm) plants ($F_{(1, 36)} = 0.16$, $P = 0.69$; Figure 1B).

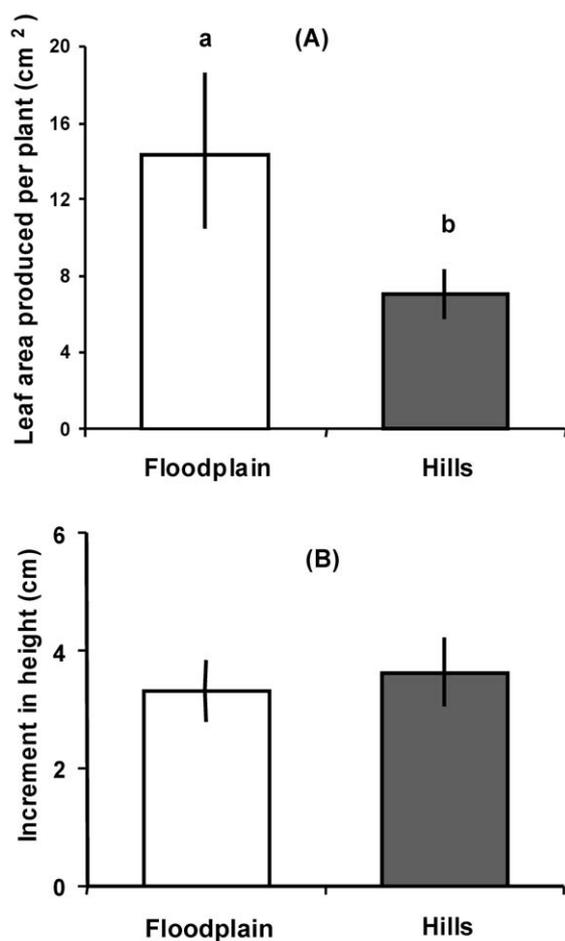


Figure 1. Growth of *D. guianense* plants expressed as the mean \pm standard error of leaflet area (A) and height (B) of plants during a period of 174 days. $N = 19$ plants from each population. Untransformed data are shown and different letters indicate statistically significant differences.

Secondary metabolites

Concentration of total phenolics in 1998 was 1.30 times higher in the plants growing in the Hills (1.197 mg/g) than in the Floodplain (0.921 mg/g). Likewise, in 2001, concentration of total phenolics was 1.15 times higher in plants growing in the hills (1.90 ± 0.09 mg/g) than plants from the Floodplain (1.64 ± 0.1 mg/g), representing 9.24 and 8.06% dry mass *D. guianense* tannin equivalents. However, this difference was only marginally significant ($F = 3.47$, $P = 0.07$).

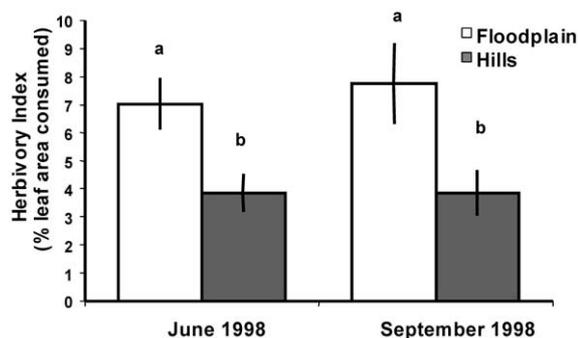


Figure 2. Herbivory Index (mean \pm SE) estimated in plants from the Floodplain and the Hills in June ($n=18$ Floodplain plants and $n=16$, Hills plants) and in September ($n=17$ Floodplain plants and $n=14$, Hills plants), 1998. Different letters indicate statistically significant differences ($P < 0.01$).

Herbivory

Herbivore attack was higher in plants growing in the Floodplain than in plants growing in the Hills in June ($7.02 \pm 0.93\%$, and $3.87 \pm 0.80\%$, respectively) and September ($7.75 \pm 0.93\%$, and $3.86 \pm 0.80\%$, respectively) 1998 (Figure 2). The repeated measures ANOVA indicated that site of origin was highly significant ($F = 7.46$, $P = 0.01$) while within-subject factors were not statistically significant (recording time, $F = 0.619$, $P = 0.43$; interaction term, $F = 0.005$, $P = 0.942$).

Preference and palatability assays

In 63.8 and 81.3% of the cases, *S. fugiperda* and *Orophus* sp., respectively, preferred the Floodplain leaflets over the Hills leaflets, suggesting some preference for the Floodplain foliage. The median consumption of foliage by *S. fugiperda* was 1.55 times higher in the case of Floodplain leaflets, compared to leaflets from Hills plants (121 vs. 78 mm²), but this difference was only marginally significant ($Z = 138.5$, $P = 0.09$). This tendency was more evident in the case of *Orophus* sp. (Figure 3). These insects consumed 1.89 times more area from Floodplain leaflets than from Hills leaflets and this difference was highly significant ($Z = 3.12$, $P = 0.002$). This supports the suggestion that Floodplain foliage has a higher quality as food for herbivores.

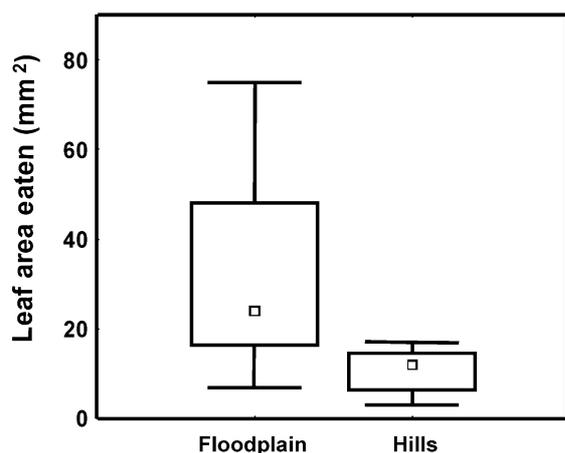


Figure 3. Leaf area eaten of leaflets of *D. guianense* from two populations by adults of *Orophus* sp. (Orthoptera: Tettigonidae). The data show the median, 25-75% quartiles and range from 16 replicates.

Reciprocal transplant experiment

Plants displayed a significantly higher leaf production in the Floodplain plot (2.24 ± 0.24) than in the Hills plot (1.35 ± 0.15) (Figure 4A, Table 2). This result was independent of the population's origin, which did not yield significant differences in either transplant site (Table 2).

Significant differences in herbivory also were found in the reciprocal transplant experiment, suggesting a strong influence of soil heterogeneity in plant traits that influence herbivore attack. Plants from both populations exhibited a significantly higher level of herbivory when grown in the Floodplain (15.45 ± 1.2) than in the Hills (6.69 ± 1.06 ; Figure 4B). There was no significant effect of the population's origin or the interaction term (Table 2) for either variables.

Discussion

For the present discussion it is important to bear in mind that our results are based on the comparison of only two sites, given the difficulty of replicating without introducing additional uncontrolled variables. Therefore, our conclusions may be only applicable to the specific locations we studied. However, our results may reflect a situation of wider applicability to the understanding of plant-herbivore interactions in heterogeneous environments, as we discuss below.

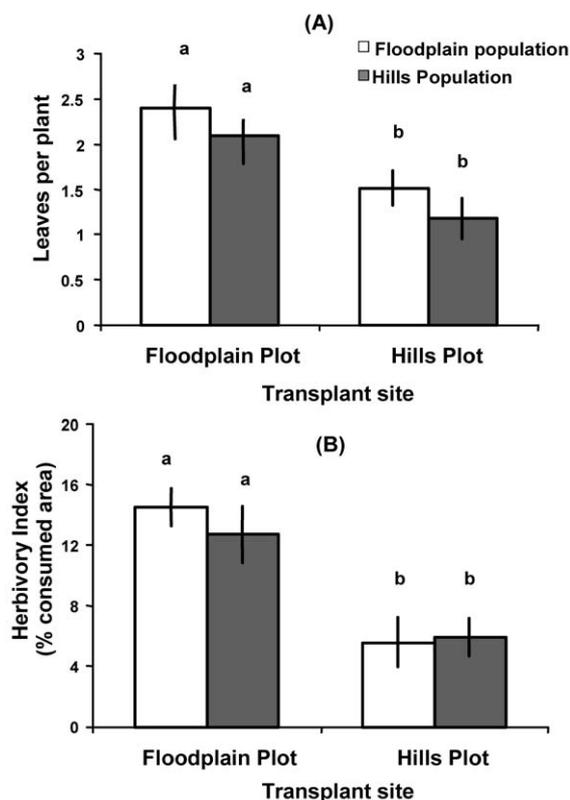


Figure 4. A) Growth displayed by the plants from each population in the reciprocal transplant experiment, in terms of the leaves (mean \pm standard error) produced during a period of 174 days. Different letters indicate statistically significant differences ($P=0.003$). B) Herbivory incidence on the plants from each population in the reciprocal transplant experiment, expressed by the mean \pm standard error of the herbivory index per plant estimated on April 1999. Different letters indicate statistically significant differences ($P < 0.0001$).

Edaphic variation between Floodplain and Hills influenced both growth and secondary metabolite production in the two populations. In accordance with the patterns found in other studies (McKey et al. 1978; Bryant et al. 1987; Reichardt et al. 1991), phenolic compounds production was negatively related to soil resource availability and plant growth. Moreover, herbivory levels and the results of acceptability assays suggest differences in resource allocation to growth and defense which have the potential to alter herbivore-plant interactions, as a result of the modification of foliage quality for herbivores.

Differences observed in plant growth from both populations could be related to the differences detected in some important nutrients, such as phosphorous and nitrogen, commonly limiting for plants

Table 2. Two-way ANOVA of the mean number of leaves produced per plant and herbivory index per plant estimated on plants from both populations in the reciprocal transplant experiment.

Source	Leaf production (June 1998)			Herbivory (April 1999)		
	DF	MS	F	DF	MS	F
Transplant Site	1	13.72	9.35*	1	1094.63	32.18**
Origin of Population	1	2.29	1.56	1	0.811	0.024
Transplant * Origin	1	0.001	0.00	1	22.06	0.65
Error	68	99.78		51	34.02	

*P < 0.001, **P < 0.0001

in the tropics. Moreover, soil texture could also be influencing water availability for the plants in both populations, limiting growth rates in the Hills population more than in the Floodplain population. The difference in total leaflet area produced between the plants of the two populations was two-fold, and even though this implies a difference of only a few leaves, such difference may be biologically important. In tropical understory plants in which leaf production rates are typically very low, a difference of one or few leaves may bring about important consequences for plant performance and survival (see examples in Dirzo 1984). Furthermore, the growth displayed by *D. guianense* is within the range typically reported for tropical tree saplings (Coley and Barone 1996; Clark and Clark 1985).

Although the results obtained in this work are consistent with other studies that have demonstrated an increase in phenolic compounds concentration when plants grow under conditions of low water or low nutrient availability (McKey et al. 1978; Koricheva et al. 1998; Mutikainen et al. 2000), it has been argued that such differences may lead to erroneous conclusions regarding resource allocation to defense. In particular, reduced phenolics concentrations in plants growing in resource-rich conditions may simply reflect a dilution of the same amount of such compounds in plants with larger biomass and not an indication of reduction in phenolic compounds production (Koricheva 1999). Nevertheless such a dilution effect may not be responsible for the differences we observed, because our study was based on a comparison of plants of the same size category.

Phenolic compounds have been suggested to have a defensive function in plants since they have the ability to reduce the digestibility of photosynthetic tissue (McKey et al. 1978; Rhoades 1979, but see Ayres et al. 1997). Given the differences found in the concentration of this type of defensive compounds

between the two populations of *D. guianense*, we expected to observe an increase in damage at the high nutrient site, where the plants presumably produced less anti-herbivore defense.

Plants from the two populations showed a marked contrast in the levels of natural herbivory. In two recording dates during 1998 damage was greater in plants from the Floodplain. We believe that these differences could be promoted by variation in foliage quality between sites as a consequence of soil heterogeneity. Similar results of differences in herbivory associated to environmental variation have been found in other systems (see Coley and Barone 1996). The significant differences we found in herbivory between plant populations, together with the results found in the chemical and palatability analyses, provide insights into how environmental heterogeneity, through differential resource allocation, may influence plant-herbivore interactions.

Despite the consistency of the results we cannot discard that the differences in herbivory in the field could also be due to variation in herbivore community composition or abundances between sites (see Cates 1975). Yet, even if such differences in herbivore communities existed, they could still be interpreted as a consequence of differences in the quality of tissue of the plants from each site. This is an aspect that warrants further investigation. Nevertheless, the fact that in the bioassays herbivores showed significant preferences for the Floodplain foliage is compatible with the tendencies observed in the field. Therefore, we suggest that independent from the herbivore community composition or abundance at each site, the foliage of *D. guianense* has intrinsic, site-related traits that modify its quality as food for herbivores.

Even though we found differences in concentrations of phenolic compounds with defensive potential in the foliage of *D. guianense*, and they are negatively associated with the incidence of herbivory observed

in the field, the influence of other defensive traits, including different secondary compounds, nitrogen and water content in leaves, cannot be ruled out.

When selective pressures such as nutrient availability or herbivory vary in space, the environmental range that a plant species may occupy depends on the degree of genetic differentiation or phenotypic plasticity of the populations, coupled to the spatial heterogeneity (Harper 1977). *D. guianense* is a codominant species of the Lacandona rain forest and grows under diverse soil conditions (Pennington and Sarukhán 1998). Such wide environmental range might be due to a genetic system based on the expression of plastic responses in its resource allocation patterns, or on the expression of fixed genetic differences under different environments. Our reciprocal transplant experiment revealed that growth, expressed as the number of leaves per plant, and those plant traits influencing herbivore damage, had a plastic response to changes in soil conditions. Furthermore, there was no effect of the site of population origin, or of the interaction between transplant site and population of origin, providing evidence that the higher growth in the Floodplain plot is coupled with the greater herbivory in the same site. This supports the suggested relationship of lower allocation to defense in the nutrient-rich site (Mutikainen et al. 2000). Thus, we propose that phenotypic plasticity in *D. guianense*, rather than genetic differentiation, is likely to be the underlying mechanism by which the observed variation in resource allocation to growth and defense is promoted. This finding may be expected given the fact that the two study sites are only 15 km apart and thus gene flow (via pollination and dispersal) may prevent genetic differentiation. Clearly this is an aspect that warrants further investigation.

The present study contributes to our understanding of the patterns by which soil heterogeneity can modify resource allocation to growth and defense in plants, and how these modifications can influence plant-herbivore interactions. Furthermore, this study suggests that phenotypic plasticity can be an important source of variation leading to such responses of plants in edaphically heterogeneous tropical ecosystems.

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