


Effect of genotype on herbivory and growth rate in *Heliconia stricta* in a common garden experiment in the Amazon

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ABSTRACT

Plant genotype is known to affect plant-invertebrate interactions. However, in megadiverse tropical habitats there has been relatively little exploration of the influence of the plant genotype on plant growth and biotic interactions in an experimental setting. We set-up three adjacent plots in rainforest at the foothills of the Andes (Orellana, Ecuador), where we planted clones of 37 individual *Heliconia stricta* rhizomes collected from up to 4 km away. Each rhizome was split into at least three individual pieces, resulting in three genetically identical replicates. At least one representative of each genotype was planted in each plot. Shoot height was measured every few months. Nine months after planting, all leaves of the plants were photographed for leaf herbivory analysis. At the time of the herbivory analysis, neither shoot height nor total leaf area were more variable among than within genotypes, but the total percentage of leaf area consumed per plant varied significantly among the genotypes. Whether or not there was a significant difference in shoot height among genotypes depended on the timepoint at which the plants were measured. However, the overall growth rate over a period of 1.5 years varied significantly among the genotypes. Our results suggest that even in megadiverse systems and despite the plasticity of plant responses, plant genotype can influence growth rate and biotic interactions such as herbivory.

KEYWORDS: false-bird of paradise plant, *in-situ* experiment, genotype effects, community genetics

Efecto del genotipo sobre herbivoría y crecimiento de *Heliconia stricta* en un jardín experimental en la Amazonía

RESUMEN

El genotipo de las plantas afecta las interacciones planta-invertebrados. Sin embargo, en hábitats tropicales megadiversos se ha estudiado relativamente poco la influencia del genotipo de las plantas sobre su crecimiento y interacciones bióticas experimentalmente. Establecimos tres parcelas adyacentes en la selva tropical al pie de los Andes (Orellana, Ecuador), donde se plantaron clones de 37 rizomas individuales de *Heliconia stricta* recolectados a una distancia de hasta 4 km. Cada rizoma se dividió en al menos tres partes individuales, resultando en tres réplicas genéticamente idénticas. En cada parcela sembramos al menos un representante de cada genotipo. Medimos la altura de los brotes casi mensualmente. Nueve meses después de la siembra, se fotografiaron todas las hojas de las plantas para un análisis de herbivoría. Al tiempo del análisis de herbivoría, la altura de los brotes y el área foliar total no variaron significativamente entre genotipos comparado con entre individuos del mismo genotipo. El porcentaje total de área foliar consumida por planta varió significativamente entre genotipos. Que hubiera o no una diferencia significativa en la altura de los brotes entre los genotipos dependió del punto de tiempo en el que se midieron las plantas. Sin embargo, la tasa de crecimiento general durante un período de 1,5 años varió significativamente entre los genotipos. Nuestros resultados sugieren que, incluso en sistemas megadiversos y a pesar de la plasticidad de sus respuestas, el genotipo de las plantas puede influir en la tasa de crecimiento y las interacciones bióticas como la herbivoría.

PALABRAS CLAVE: platanillo, experimento *in-situ*, efectos genotípicos, genética de comunidades

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INTRODUCTION

Plant responses to herbivory involve direct and indirect chemical and physical defence. Physical defences can include leaf waxiness, trichomes, latex, and thorns, which directly deter herbivores (Tian *et al.* 2012). Chemical defences include toxins, as well as volatile compounds which either deter herbivores or attract their predators (Zhu-Salzman *et al.* 2008; Ninkovic and Åhman 2009; Gantner and Najda 2013). Although many of these defences are plastic and can be induced in response to an attack on the plant, many are genetically determined and vary among genotypes of the same species (Schweitzer *et al.* 2004; Bailey *et al.* 2006; Ninkovic *et al.* 2011). For example, *Arabidopsis thaliana* mutants with different levels of cuticle leaf waxiness host different bacterial communities on the leaf surface, and both constitutive and facultative trichome density in *Arabidopsis* are genetically determined (Bloomer *et al.* 2014). Herbivore-induced plant volatiles vary among genotypes of single species, such as barley (Ninkovic *et al.* 2011), and active changes in the gene expression of hormone signalling pathways control the variation in plant volatile emissions (Maffei *et al.* 2007; Mathur *et al.* 2013). These genetically-determined physical and chemical characteristics suggest that plant genetic diversity plays a role in the attraction and deterrence of herbivores, especially arthropods (Ninkovic *et al.* 2013).

Although there are many studies demonstrating a link between plant genotypic diversity and their associated invertebrate communities (e.g., Crutsinger *et al.* 2006; Bailey *et al.* 2009; Barbour *et al.* 2015; Barker *et al.* 2018; Gosney *et al.* 2021), few experimental studies have been conducted *in situ* in tropical systems (e.g., Bruna and Nogueira Ribeiro 2005; Bruna and de Andrade 2011). In tropical rainforests, both arthropods and plants are more diverse than at higher latitudes, and so the likelihood of encountering the same species twice is lower. Therefore, it is difficult to extrapolate the results of studies of relatively simple temperate systems to megadiverse tropical habitats. However, even in a megadiverse tropical system, tree genotype can affect the composition of epiphyte communities and of bark-dwelling and leaf litter arthropods (Zytynska *et al.* 2011). Similarly, epiphytic bromeliad genetic distance correlated with differences in the community of aquatic arthropods dwelling within the plant phytotelmata (Zytynska *et al.* 2012).

Commonly-known as false-birds-of-paradise plants, *Heliconia* (Heliconiaceae) are fast-growing plants mostly native to the Neotropics and members of the ginger order, Zingiberales (Monocotyledons). As well as being horticultural favourites in the Americas and introduced around the world, they are common sights in a range of megadiverse neotropical habitats, such as Amazonian rainforests in South America (Berry and Kress 1991). They provide habitat and sustenance to many animals, including invertebrates and birds. Various insect herbivores consume their seeds, leaves and flowers, including

leaf-cutter ants (Formicidae) and many species of rolled-leaf specialists like hispine beetles (Chrysomelidae) (Auerbach and Strong 1981; Seifert 1982). We used a common garden experiment to test whether the genotype of *Heliconia stricta* (J. E. Huber, 1906) is related to the level of herbivory suffered *in situ* by the plant in the rainforest, as well as whether the plant growth rate differs among genotypes. The monocotyledonous *Heliconia stricta* was chosen for its fast-growing nature, ease of obtaining genetic replicates by splitting their rhizomes, the susceptibility of their leaves to herbivory, and their common occurrence throughout our study area (X. O'Reilly-Berkeley, J.K. Rowntree, and R.F. Preziosi, pers. obs.).

MATERIAL AND METHODS

Study area

The study was carried out in San José de Payamino, Orellana, Ecuador (hereafter, Payamino), a 17000-ha patchwork of primary and secondary Amazonian rainforest on the eastern edge of the Tropical Andes Biodiversity Hotspot, within the Sumaco UNESCO Biosphere Reserve, and within the buffer zone of the Sumaco Napo-Galeras National Park core protected area (Figure 1). In some cases, rhizomes were collected from the same site, but always at least 5 m away from each other, to reduce the chance of them pertaining to the same mother plant. The experiment was set up in secondary rainforest near the Timburi Cocha Research Station (0°28'57.9"S, 77°17'05.1"W). Plant collection and planting took place in Payamino in July 2018.

Experimental design

We dug up and collected 41 rhizomes of *H. stricta* within a 4-km straight-line distance from the research station, in the forest and mostly by riverbanks (Figure 2), where plants were easily detectable and transportable by canoe. The collected rhizomes were labelled individually before returning to the research station, where each one was split into three or more pieces (Figure 3a), leaving a vertical shoot emerging from each segment. The vertical shoots were cut down to approximately 30 cm in height, following the advice of a local farmer (Oscar Aguinda, pers. comm.). The rhizome sections were labelled according to the mother plant they came from and wrapped in newspaper, before being left on the ground under banana leaves for at least five days. Planting only began once all rhizomes had been collected, sorted, and left to rest for at least five days. After this time, some samples no longer looked viable (they had rotted or turned brown) and were therefore discarded. This left us with 3-6 samples from only 37 of the 41 mother plants (118 samples in total). Following this, 37 of these rhizomes were healthy enough to plant, although some died later (see Results). Here we will consider each separate rhizome to be a separate genotype, and sections of the same rhizome to be clones.

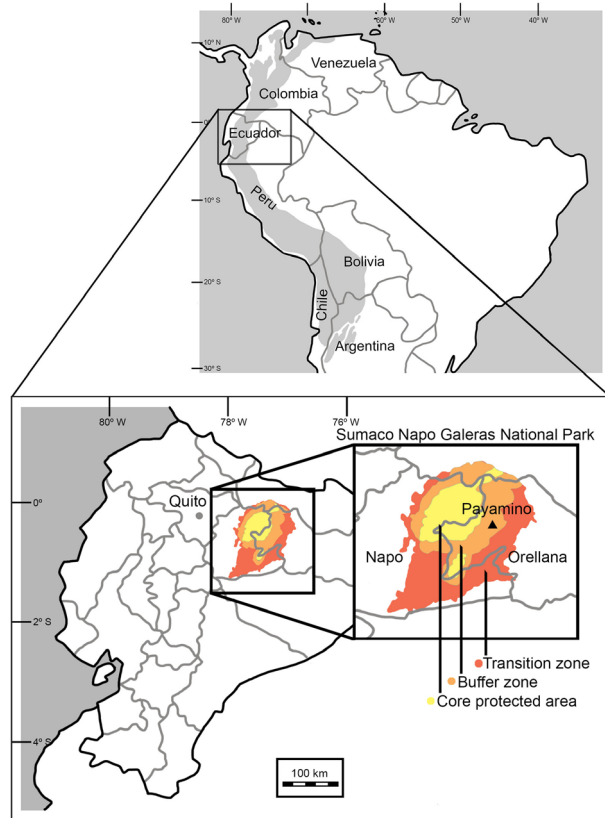


Figure 1. Location of Ecuador in South America and of the Sumaco Napo Galeras National Park in Ecuador (coloured area). The study area, San José de Payamino, is marked with a triangle within the park's buffer zone.

Three plots of approximately 5 x 50 m were set-up in secondary rainforest directly behind the research station, distanced about 40 m from each other and oriented perpendicularly to a man-made trail. The understorey in the plots was cut down in order to make way for planting. The surrounding vegetation around the plots was left intact and the soil was not cleared. The position of the rhizome samples within the plots was determined prior to planting using the randomised [*RAND()*] function in Excel, and ensuring that each plot contained at least one clone from each mother plant. The variable number of samples per mother plant resulted in an unbalanced sample distribution within plots (Plot 1 = 43, Plot 2 = 39, Plot 3 = 36). Each plot contained two rows of planted rhizomes. Each rhizome was separated from the next by two metres; the rows were staggered to ensure this equidistance between plants (Figure 3b).

Data collection

The plants were monitored over a total period of 19 months (July 2018 to February 2020). Survival rates were monitored per plot in months 2, 6, 9, 11, 12, 13, 14, 16, 18, and 19 after planting. Growth was measured in months 7, 9, 11, 12, 13, 14, 16, 18, and 19 after planting. Growth was determined by counting the number of shoots per plant, and measuring

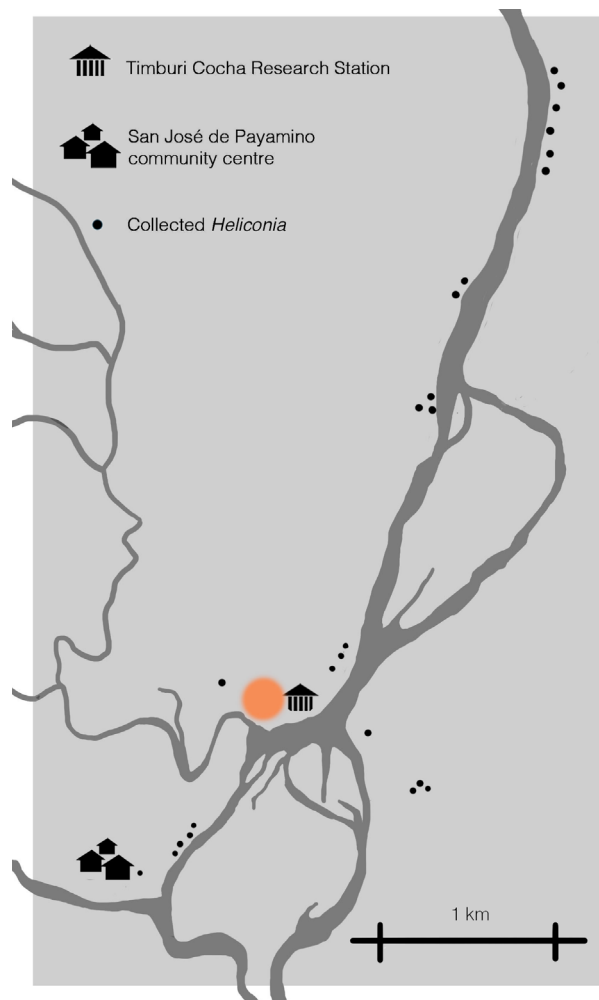


Figure 2. Distribution of the collection sites of the original *Heliconia stricta* rhizomes used in the garden experiment in the Payamino area within the Sumaco Napo Galeras National Park in Ecuador. Rhizomes were collected mostly near the riverbanks (dark grey) of the Payamino River. The experimental plots were located behind the Timburi Cocha Research Station (orange circle).

the height of the tallest and second tallest shoots from the emergence point of the shoot from the soil to the tip of the tallest leaf using a tape lineal (Figure 3c).

Nine months after planting (April 2019), every leaf of every plant was photographed individually against a white background. The leaves were not removed from the plant as the growth measurements were ongoing. After this time point, the leaves of most plants became too large and intractable to photograph, and the Covid pandemic prevented subsequent growth measurements.

Data analysis

We tested whether survival differed across the three plots at the point at which herbivory was assessed and at the end of the experiment using a chi-squared test with simulated p-values (due to the low number of dead plants).

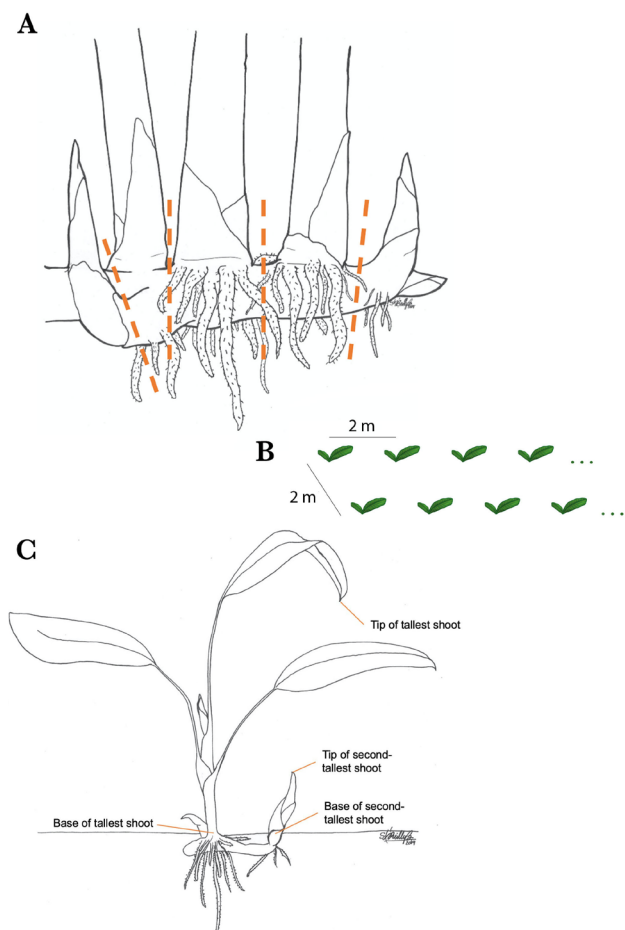


Figure 3. A – Line drawing of a *Heliconia stricta* rhizome showing the cutting plane where the rhizome was split in order to create replicates of the same genotype (dashed orange line); **B** – Arrangement of *H. stricta* rhizome sections within an experimental garden plot (two rows per plot, staggered to achieve approximately 2 m between plants); **C** – Diagram of *H. stricta* showing its above- and below-ground components. This plant is composed of two shoots connected by a single rhizome. Line drawings by X. O'Reilly-Berkeley©.

The photographs of the leaves were edited in Adobe Photoshop (CC 2017) to extract the leaves from the shadows of their background. Drops of water and wet over-exposed parts of leaves were covered so as not to be confused with eaten sections of leaf. The images were edited individually to ensure there was no automated confusion between over-exposed elements and eaten sections, or between shadows and leaf edges. Leaves were then fitted to a 4-point square scale, either of 30 cm², 60 cm², or 90 cm², depending on the size of the leaf. The consumed and remaining area of the leaf was analysed using the LeafByte (1.3.0) app (Getman-Pickering *et al.* 2020).

All statistical analyses were performed in R (4.1.1) (R Core Team 2020) using RStudio (R Core Team (R Foundation for Statistical Computing) 2021). To test whether leaf area varied among clones, the total original leaf area was analysed with

a linear mixed-effects model using the *lme4* package (Bates *et al.* 2015), with total original leaf area (maximum area prior to herbivory) and clone as fixed effects and plot as a random effect. Genotypes with only one surviving replicate were removed from the dataset, leaving 32 genotypes for herbivory analysis. Herbivory was measured as the total leaf area consumed (in absolute area, cm²), and as a percentage of the leaf area consumed relative to the original leaf area of the plant ($[\text{leaf area consumed}] / [\text{total original leaf area}] * 100$). Separate linear mixed-effects models were fitted to total leaf area and to the percentage of leaf area consumed, with plot as a random effect. Inspection of the residuals suggested a reasonable distribution of the data and transformation did not improve them, thus models used raw data. Significance values were assigned to the fixed effects of the models using the Anova function in the package *car* (Fox and Weisberg 2019) returning F statistics.

To compare growth among clones, the height of the tallest shoot was fitted to a linear mixed-effects model in *lme4* (Bates *et al.* 2015), with height and clone as fixed effects and plot as a random effect. A separate analysis was performed for every month in which growth was measured. The same analysis was undertaken for the height of the second tallest shoot of each plant. To model whether there was a difference in growth rate among clones over time, a linear mixed-effects model was used, taking into account the interaction between month and clone, with plot as a random effect. Significance values were assigned as above. This was done using the tallest shoot and the second-tallest shoot of each plant. A line plot of the evolution of the average height of the tallest shoot per genotype over time was constructed using the packages within *tidyverse* (Wickham *et al.* 2019) and *ggplot2* (Wickham 2016).

To assess whether there could be a relationship between herbivory and growth, we made a correlation analysis between the height of the tallest shoot in April 2019 (when herbivory was measured) and the percentage of consumed leaf area. The analysis was made for the overall data and then using only data from plants with less than 20% consumption, followed by only plants with more than 20% consumption.

RESULTS

Among the 41 rhizomes collected, four did not have any surviving sample after the 5-day resting period, leaving only 37 rhizomes with samples to be planted. Of these, 32 had enough replicates for herbivory analysis at month 9. A total of 34 were included in the growth-over-time analysis.

Herbivory of *H. stricta* in our plots was committed by invertebrate herbivores. We shall therefore hereafter refer to invertebrate consumption of leaves simply as herbivory, and the actors of this consumption as herbivores. At the time the leaf photographs were taken for herbivory analysis (month 9), the proportion of surviving plants was 88.3%, 87.1%, and 91.6% in Plot 1, 2 and 3, respectively, and 107 of the 118

samples planted had at least one shoot with leaves. By the end of the study (in month 19), 91 plants remained across the three plots, with survival rates of 69.7% (N = 30), 84.6% (N = 33), and 77.7% (N = 28), respectively, in Plot 1, 2 and 3. The proportion of surviving plants did not differ significantly among the plots in month 9 (chi-square = 1.324, P = 0.517) nor in month 19 (chi-square = 2.568, P = 0.259).

Neither the total original leaf area ($F_{31,68} = 0.980$, P = 0.509) nor the absolute area consumed by herbivores ($F_{31,68} = 1.171$, P = 0.287) varied significantly among genotypes (Figure 4a). However, the proportion of leaf area consumed by herbivores differed significantly among genotypes ($F_{31,68} = 1.807$, P = 0.021) (Figure 4b). In some cases there was ample variation in consumption among plots (e.g., genotype 39 lost 7.0% of leaf area in Plot 1 and 96.1% in Plot 3), while in other cases consumption was more consistent across plots (e.g., individuals of genotype 35 lost 10.0% and 3.1% of leaf area in Plot 1, 14.3% in Plot 2, and 12.8% in Plot 3 3.1%, and genotype 12 lost 6.2% and 1.6% of leaf area in Plot 1, 9.5% in Plot 2, 6.7% in Plot 3). The most leaf area lost to herbivory on an individual leaf was 100% and the most leaf area lost

over an entire plant was 96% of the original estimated total leaf area. However, 96.1% of all plants lost less than 50% of their total leaf area and 80.9% lost less than 20%.

The difference in shoot height among genotypes was variable across the measuring months (Figure 5). For example, in month 13 (August 2019), there was no significant difference among genotypes, whereas in month 7 (February 2019) and 9 (April 2019) shoot height differed significantly among genotypes. Shoot growth rate over time varied significantly among genotypes both for the tallest shoot ($F_{34,840} = 2.31$, P < 0.001) (Figure 5a) and the second-tallest shoot ($F_{34,515} = 1.78$, P = 0.005) (Figure 5b).

The height of the tallest shoot in month 9 (when herbivory was measured) and the proportion of consumed leaf area appeared to be weakly negatively correlated overall (Figure 6), although it was only marginally significant ($t = -1.978$, df = 103, P = 0.050, R = -0.191). There was no significant correlation for plants that had under 20% consumed leaf area ($t = 0.474$, df = 83, P = 0.637, R = 0.052) and plants with over 20% consumed leaf area ($t = -0.075$, df = 18, P = 0.941, R = -0.0176).

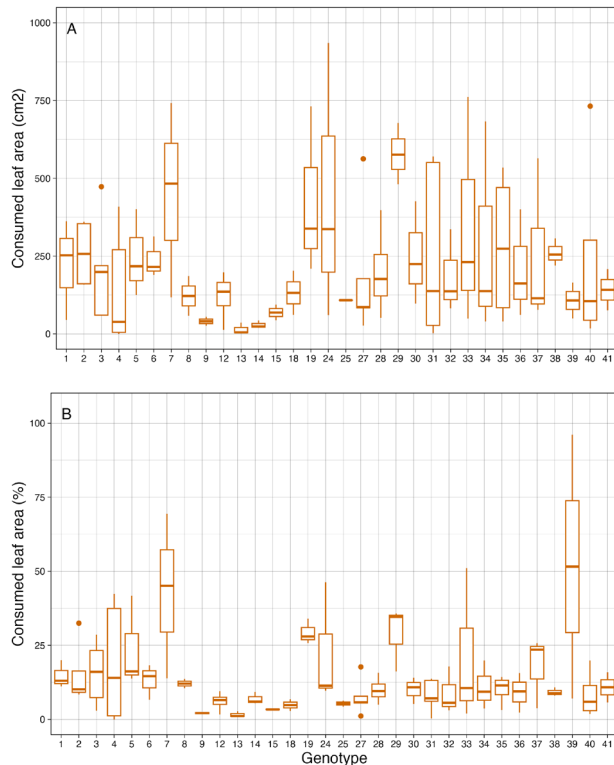


Figure 4. Consumed leaf area by herbivorous arthropods in 32 genotypes (rhizomes) of *Heliconia stricta* (2 to 6 replicates per genotype) in a common garden experiment in Amazonian Ecuador. **A** – Absolute consumed leaf area (cm²) of the tallest shoot; **B** – Proportion of consumed leaf area (%) of the tallest shoot. Genotype identification corresponds to the number given to the original rhizome in the field (1-41), but not all 41 survived to be planted. The line within the box indicates the median, the box the interquartile range, and the whiskers show the variance outside the range. Points indicate outliers.

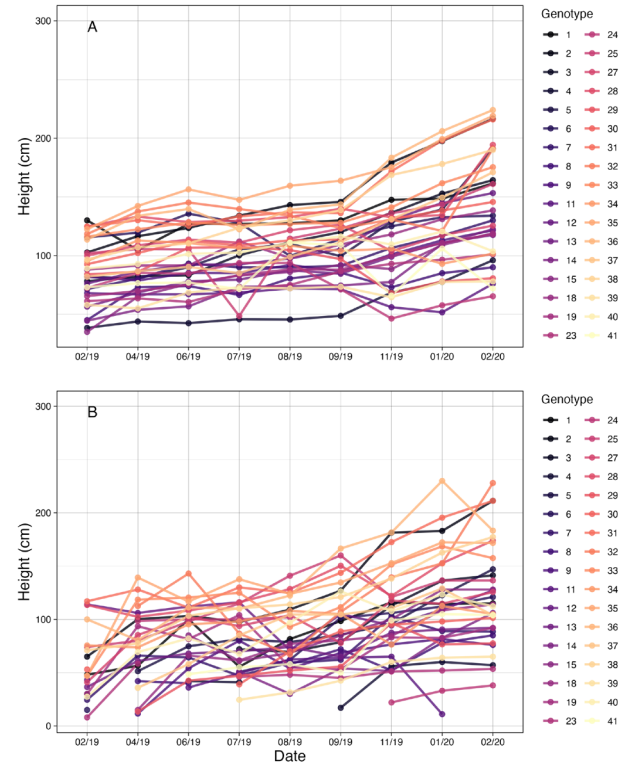


Figure 5. Evolution of shoot growth rate in 34 genotypes (rhizomes) of *Heliconia stricta* over a 19-month period (July 2018-February 2020) in a common garden experiment in Amazonian Ecuador. **A** – Growth rate of the tallest shoot; **B** – Growth rate of the second tallest shoot. Each point is the average of 2 to 6 replicates. Genotype identification corresponds to the number given to the original rhizome in the field (1-41), but not all 41 survived to be planted. Truncated lines are due to some genotypes dying out and growing new replicates at some point over the study time.

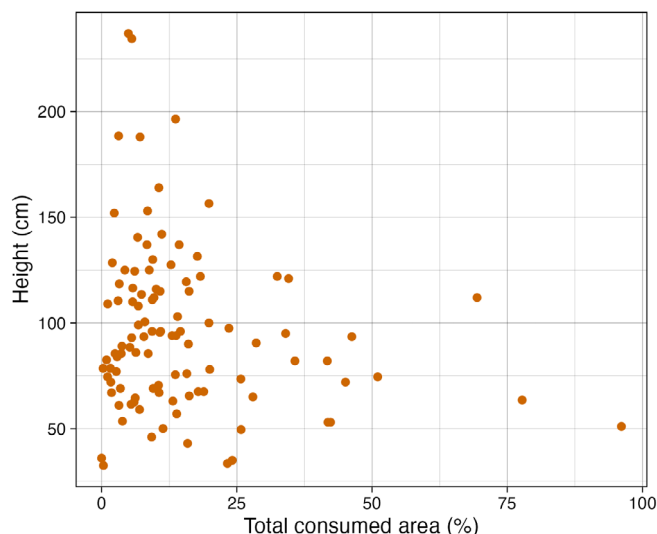


Figure 6. Correlation between the proportion of total consumed leaf area and the tallest shoot height of all surviving replicates of the 34 genotypes of *Heliconia stricta* nine months after planting in a common garden experiment in Amazonian Ecuador. Each point represents the tallest shoot of an individual.

DISCUSSION

Herbivory

We demonstrated that the level of herbivory suffered by different genotypes differed significantly, however, the effect was not uniform. Some genotypes suffered a consistently high or low level of herbivory, while other genotypes showed variation in consumed leaf area across replicates. Herbivory was committed by invertebrate herbivores, therefore – as stated in the Results section – we shall hereafter refer to invertebrate herbivores simply as herbivores and their consumption of leaves as herbivory, unless otherwise stated. The overall low herbivory rates recorded (81% plants with <20% leaf area consumed) may be due to an absence of herbivores, the inaccessibility of plants to herbivores, high levels of protection mechanisms by the plant, or less attractiveness to herbivores than other understory plants with larger leaves. As our study was carried out in a megadiverse neotropical rainforest, an absence of herbivores or inaccessibility of the plants to herbivores is implausible. The leaves of *H. stricta* are soft and bear no macroscopic physical defences, which would be obvious signs of protection. However, we did not examine the leaf phytochemistry to investigate this and, to our knowledge, the presence of chemical defense mechanisms in *H. stricta* is not known.

The phytochemical analysis of other *Heliconia* species such as *H. imbricata* and *H. latispatha* revealed an absence of common chemical deterrents of herbivory (Williams and Harborne 1977; Auerbach and Strong 1981; Gage and Strong 1981), although some components like tannins and alkaloids have been detected in *H. angustifolia* (Strong and Wang 1977; Merh and Sabnis 1986). Silicon is another known deterrent of arthropod herbivores (Reynolds *et al.*

2016), but has not been studied in relation to herbivory in *Heliconia*, although increases in silicon fertilisation are related to an increase in foliar silica (Albuquerque *et al.* 2013) and reduced fungal infection (Fortunato 2009). Although the reason for low levels of herbivory in the apparent absence of classical chemical defences is unclear (Strong 1984), it has been suggested that *Heliconia* leaves may contain low levels of available nitrogen, which could explain the slow larval development of *Heliconia* herbivores such as hispine beetles (Strong and Wang 1977; Auerbach and Strong 1981). An experiment analysing herbivory on different genotypes across plots of nitrogen and silicon treatments may reveal whether these factors deter herbivores from taking advantage of an apparently available resource.

Another anti-herbivore defence mechanism to consider is the production of volatile chemical compounds. In an olfactometer experiment, hispine beetles were able to detect the smell of plants and three out of the four beetle species showed a preference for their host plant when presented with two plant options (García-Robledo and Horvitz 2009). Although the plants tested by the latter authors were not *Heliconia*, they did include various other Zingiberales species. It may be that *Heliconia* rely on volatile chemical signals rather than chemical defences within their leaves as a mechanism of defence against herbivores or attraction of herbivore enemies. Although we did not measure any traits that may indicate this effect, there is a significant amount of literature indicating that genetically-determined traits such as volatile chemistry influence the outcome of herbivores and their predators (e.g., Ninkovic and Åhman 2009; Ninkovic *et al.* 2011), as well as evidence that polyphenolic compounds such as condensed tannins in leaves can have ecosystem effects beyond just the herbivores that consume the plants (Schweitzer *et al.* 2004,

LeRoy *et al.* 2006). The flowers of *Heliconia aemygdiana* Burle-Marx are known to emit volatile sesquiterpenes (Knudsen *et al.* 2004) and the erect inflorescence bracts of *Heliconia* are characteristically fowl-smelling (X. O'Reilly-Berkeley, pers. obs.). Chemical analysis of *Heliconia* leaves would help to establish if volatile chemicals are emitted by the vegetative parts of the plants, whether they vary among genotypes, and how invertebrate herbivores or herbivore enemies respond to them.

The size of host plants can affect the communities of arthropods associated with them (Schlinkert *et al.* 2015; Barker *et al.* 2018, Barbour *et al.* 2019). Additionally, there is often a trade-off between plant growth rate and defences against herbivores (Züst and Agrawal 2017). It would therefore be expected that plants with a faster growth rate, would suffer greater herbivory than slower growing plants. In our study, the height of the tallest shoot was weakly negatively correlated with the proportion of consumed leaf area. A high proportion of leaf area due to herbivory may simply be due to the consumption of leaves at the top of the shoot, shortening the height of plants. Because of how *Heliconia* grow, we measured the height from emergence from the soil to the tip of the tallest leaf, therefore it is possible for herbivore activity to shorten the height of the plant overall. When plants were split into those that suffered more and less than 20% leaf loss, neither group showed any relationship between height and herbivory, and plants with over 20% consumed leaf area (less than 20% of the plants) were of an intermediate size rather than particularly tall. Although measuring leaf consumption at only one time point is likely to underestimate the true level of herbivory suffered by the plants (García-Robledo 2005), the goal of this study was to ascertain whether genotypic differences existed in the extent to which plants were damaged relative to each other when growing in the same environment. Nonetheless, in order to understand the phenotypes through which the genotypic differences are manifested, it would be useful to measure herbivory more continuously and over a longer time scale, and compare it to plant traits such as leaf chemistry. We have provided a first step towards this by showing that plant genotype can play a role in biotic interactions such as herbivory in a megadiverse tropical ecosystem.

Plant growth

We found significant variation among genotypes in the evolution of the height of the tallest shoot throughout the study period. In *Heliconia acuminata* A. Rich, there was significant variation within genotypes in growth rate and above:below-soil biomass ratio in different habitats (forest edge and understory) (Bruna and de Andrade 2011). In our study, we controlled for environmental effects by having the plots in the same area of forest and separated by only 40 m from each other. There were no detectable differences

among plots in terms of survival when we conducted the herbivory analysis. Since edge effects have been demonstrated to influence *Heliconia* growth (Bruna and de Andrade 2011), we mitigated this by designing our plots longitudinally with only two plants across their width, so that all plants would experience the same edge effects.

Community genetics effects in a common garden set-up

Multiple common garden studies have shown the effects of plant genotype on associated communities. For example, differences among evening primrose genotypes could explain up to 41% of variation in associated arthropod communities, with a stronger effect on herbivores than on predators (Johnson and Agrawal 2005). Similarly, the arthropod community composition varied significantly among cottonwood tree hybrid types (Wimp *et al.* 2005) and cottonweed tree hybrids with greater genetic similarity had more similar arthropod communities – as well as chemical composition and associated arthropod communities, which also reflected in wild populations (Bangert *et al.* 2006). Common garden experiments have also demonstrated the effect of plant genotype on parasite virulence (Rowntree *et al.* 2011) and even the resistance to mammal herbivores (O'Reilly-Wapstra *et al.* 2004).

However, Tack *et al.* (2012) warn against extrapolating the effect of genotype on communities in manipulated experiments, when genotypes have been collected across large spatial scales and thus may be locally-adapted to environmental conditions (O'Reilly-Wapstra *et al.* 2004). The furthest two original rhizomes in our study were collected approximately 4 km apart, so we assume that the effect of geographical environmental variability on genotypes was negligible if at all present. Also, our experimental plots were in close proximity to each other, within the same area of forest, and so shared the same habitat and environmental conditions, although microvariations likely existed. Although the effect of genotype can be greater than the variation in microhabitat conditions (Johnson and Agrawal 2005), environmental conditions can obscure these interactions (Barbour *et al.* 2019). Future work could expand common garden experiments into other areas to test the variability in the response of genotypes concerning plant growth rate and herbivory to environmental variation. A reciprocal transplant experiment with multiple common gardens could assess the effects of local adaptation on the phenotypic expression of genotypes.

CONCLUSIONS

Genotype had a significant effect on leaf loss due to herbivory and on plant growth in *Heliconia stricta*. Contrary to what has been observed in other systems, plant size was not related to the magnitude herbivory. Even though we estimated

herbivory only punctually, we were able to detect significant differences among plant genotypes. Genotyping the *H. stricta* plants using molecular markers would allow to analyse the correlation of the genetic distance among genotypes with the degree of herbivory. Although preliminary, our study is a step towards understanding the effect of plant genotype on associated communities in a megadiverse tropical ecosystem. We recommend further exploration of the *Heliconia*-herbivore system in the context of plant traits and genotype. Future studies should assess the variability in the chemical profile of leaves among genotypes, as well as other phenotypic expressions related to plant growth and herbivory.

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