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# Low genetic variation in tolerance to defoliation in a long-lived tropical understorey palm

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## 19 **Abstract**

20 Defoliation is a ubiquitous stressor that can strongly limit plant performance. Tolerance to defoliation  
21 is often associated with compensatory growth. Genetic variation in tolerance and compensatory growth  
22 responses, in turn, play an important role in the evolutionary adaptation of plants to changing disturbance  
23 regimes but this issue has been poorly investigated for long-lived woody species. We quantified genetic  
24 variation in plant growth and growth parameters, tolerance to defoliation and compensatory responses  
25 to defoliation for a population of the understory palm *Chamaedorea elegans*. In addition, we evaluated  
26 genetic correlations between growth and tolerance to defoliation.

27 We performed a greenhouse experiment with 731 seedlings from 47 families with twelve or more  
28 individuals of *C. elegans*. Seeds were collected in southeast Mexico within a 0.7 ha natural forest area.  
29 A two-third defoliation treatment (repeated every two months) was applied to half of the individuals to  
30 simulate leaf loss. Compensatory responses in specific leaf area, biomass allocation to leaves and growth  
31 per unit leaf area were quantified.

32 We found that growth rate was highly heritable and that plants compensated strongly for leaf loss.  
33 However, genetic variation in tolerance, compensation, and the individual compensatory responses was  
34 low. We found strong correlations between family mean growth rates in control and defoliation  
35 treatments. We did not find indications for growth-tolerance trade-offs: genetic correlation between  
36 tolerance and growth rate were not significant.

37 The low genetic variation in tolerance and compensatory responses observed here suggests a low  
38 potential for evolutionary adaptation to changes in damage or herbivory, but high ability to adapt to  
39 changes in environment that require different growth rates. The strong correlations between family mean  
40 growth rates in control and defoliation treatments suggest that performance differences among families  
41 are also maintained under stress of disturbance.

42

## 43 **Introduction**

44 Defoliation due to herbivory, pathogens, physical damage or harvesting is an ubiquitous  
45 stressor that can strongly limit individual plant performance (*i.e.* growth, reproduction and  
46 survival) as it entails a reduction in photosynthesis and resources, and thus in future growth.  
47 Performance reductions due to defoliation are often proportionately smaller than expected  
48 based on the fraction of leaf area that is being removed [1, 2] and in some cases plants even  
49 increase their performance under defoliation [3, 4]. In that sense plants can be tolerant to  
50 defoliation, and this tolerance is often associated with compensatory growth, a mechanism by  
51 which negative effects of leaf loss are mitigated [5]. There are three types of compensatory  
52 growth responses: plants can compensate for growth by allocating more new assimilates to  
53 leaves, by allocating new assimilates more efficiently to leaf area (*i.e.* by increasing specific  
54 leaf area), or by growing faster with existing leaf area (*i.e.* by increasing net assimilation rate  
55 [6]).

56 Many plant species have evolved tolerance to leaf loss [e.g. 5, 7, 8, 9], which indicates that  
57 plants have evolved compensatory growth responses. However, relatively little work has been  
58 done to study genetic variation in these compensatory growth responses [8]. Furthermore,  
59 tolerance can only evolve when there is heritable variation in compensatory mechanisms within  
60 populations [1], and thus for the underlying compensatory growth responses. Therefore, in  
61 order to estimate the magnitude of adaptation to changing defoliation regimes, estimations of  
62 genetic variation in leaf-loss tolerance and associated compensatory growth responses are  
63 critical [10].

64 Plants have to balance between investments in reserves that allow tolerance to disturbances [7,  
65 11] and growth or reproduction. This would suggest a trade-off between tolerance and  
66 performance under no disturbance [5]. However, plants can also tolerate defoliation without

67 investing in reserves: by increased photosynthetic activity due to less self-shading, or by higher  
68 stomatal conductance due to changed root-shoot ratio [7, 8]. If this is the case, growth under  
69 undamaged conditions and tolerance would be expected to be uncorrelated or even positively  
70 correlated. The trade-off between growth and tolerance is believed to be a significant factor in  
71 determining species habitat adaptation [12]. If tolerance and performance under unstressed  
72 conditions are negatively correlated, this could explain the maintenance of genetic diversity in  
73 populations with varying levels of disturbance, while a positive genetic correlation is expected  
74 to favour superior genotypes and increase variation in life histories among individuals. So far  
75 very little is known about the level of within-population genetic correlations between tolerance  
76 and performance under unstressed conditions.

77 Many studies have evaluated genetic variation in performance in short-lived species (mostly  
78 annuals and bi-annuals), and some genetic variation in tolerance and genetic correlations  
79 between performance and tolerance to leaf-loss [13]. However, for long-lived woody plant  
80 species much less is known about these issues [14]. Haukioja & Koricheva [15] argue that  
81 tolerance to defoliation might be just as important for long-lived species as it is for short-lived  
82 species, but this has not been empirically tested. Defoliation tolerance might be especially  
83 relevant for understorey species because shade tolerance is often associated with storage of  
84 reserves that allow recovery after damage [12, 16]. More information on the existence of genetic  
85 variation in performance, tolerance and genetic correlations between these two, would increase  
86 our understanding of the adaptive ability of long-lived plant populations to environmental  
87 changes.

88 In this study we analyzed the extent to which growth and tolerance to defoliation are heritable  
89 and if these two variables are genetically correlated. We did this for the long-lived, shade  
90 tolerant, tropical understorey palm *Chamaedorea elegans*. Leaf loss due to herbivory and

91 physical damage is high and an important factor limiting the performance of this species [17,  
92 18]. *C. elegans* has been shown to compensate for leaf loss, by changing net assimilation rate  
93 (NAR) and allocation of biomass to leaf mass [6]. Furthermore, the leaves of this species are a  
94 non-timber forest product, and populations of this species are under pressure due to increased  
95 harvesting activities [19].

96 Specifically, we answered the following questions for our study population:

- 97 1. Is there evidence of genetic variation in plant growth and related parameters?
- 98 2. Is there evidence of genetic variation in tolerance to defoliation (in terms of growth  
99 rate), compensatory growth, and compensatory growth responses (*i.e.* changes in net  
100 assimilation rate (NAR), specific leaf area (SLA) and biomass allocation to leaves)?
- 101 3. Are growth rate and tolerance to defoliation genetically correlated?

102 To answer these questions, we performed a greenhouse experiment with seedlings in which a  
103 defoliation treatment was applied. We choose to use seedlings because (1) tropical forest  
104 seedlings are strongly affected by damage from falling debris and herbivory [16] (2) growing  
105 seedlings from collected seeds of mother plants ensured that seedlings were half-sibs (3) using  
106 seedlings allowed to increase sample size and obtain results within 1.5 years. We estimated  
107 genetic variation in growth parameters, tolerance (in terms of growth), compensatory growth  
108 and compensatory growth responses. We used an iterative growth model [6, 20] to estimate  
109 NAR, SLA changes, and biomass allocation, which we used to calculate compensation.  
110 Furthermore, we analyzed the extent to which tolerance to defoliation and growth rate were  
111 related.

112

## 113 **Materials and methods**

## 114 **Species and site of seed collection**

115 The experiment was performed with the forest understorey palm species *Chamaedorea elegans*  
116 Mart, which naturally occurs in rainforest in Mexico, Guatemala, and Belize [21]. It is single  
117 stemmed, produces a single cluster of leaves and is dioecious. It naturally occurs mostly on  
118 karstic outcrops. Herbivory and falling canopy debris are both major causes of leaf loss in this  
119 species [6, 17]. Furthermore, leaves are harvested as a Non-Timber Forest Product (NTFP) for  
120 use in the floral industry, causing many populations to be under pressure [19, 22].

121 Seeds of *C. elegans* were collected from a natural population in south-eastern Mexico in the  
122 state of Chiapas. In October 2012, close to the Chajul Biological Station (16°06' N, 90°56' W),  
123 we set up a 0.7 ha plot, covering the majority of the karstic outcrop where the population was  
124 clustered. In this plot, we mapped and tagged all 830 undisturbed individuals with a stem length  
125 of >10 cm. From all female fruiting individuals (175 individuals in Nov-Dec 2012) within this  
126 plot seeds were collected. In addition, to assure a sufficiently large sample size, seeds were  
127 collected from 32 individuals in an 0.1 ha area connected to the main plot in which individuals  
128 with a stem length <10 cm were mapped and tagged for a similar experiment in 1997 (using the  
129 same methods as in our experiment [17]). In total 3009 seeds from 207 different mother plants  
130 were collected, with number of seeds per mother plant ranging from one to 95 seeds. Seeds  
131 were cleaned (mesocarp was removed), air-dried and weighed, and they were kept in zip-lock  
132 bags that allowed some gas exchange.

133

## 134 **Experimental setup**

135 The experiment was conducted at the Unifarm experimental facilities of Wageningen  
136 University, the Netherlands. Seeds were germinated in a growth chamber and later moved to

137 greenhouse. The experiment started for each seedling six months after germination (6 months  
138 is an age at which *C. elegans* seedlings growing under the conditions of this experiment have  
139 been depleted, S1 File). Plant size was measured non-destructively at the start of the  
140 experiment, and a 2/3 defoliation treatment was applied to half of the individuals from each  
141 family. The defoliation treatment was repeated every 8 weeks, up to the age of 12.5 months,  
142 when plant biomass and other parameters were measured destructively. Details on  
143 measurements are provided below in the Data collection and curation section. The timeframe  
144 of the experiment (*i.e.* 6.5 months) is similar to other experiments studying tolerance-  
145 performance trade-offs in seedlings of long-lived species [11, 16], and was considered to likely  
146 be long-enough to reveal differences in allocation of assimilates to storage rather than growth  
147 (one of the main mechanisms explaining growth-tolerance trade-offs) [16, 23].

## 148 **Germination and greenhouse conditions**

149 In January 2013, seeds were planted at approximately 0.5 cm depth in large trays filled with  
150 potting soil. The tray was placed in a growth chamber, where the temperature was kept constant  
151 at 30°C day and night, air humidity at 90%. Germination of individual seeds was recorded two  
152 times a week. One and a half weeks after emergence, seedlings were transplanted into small  
153 pots of 8.5 x 8.5 x 9.5 cm (l x w x h), filled with low nutrient soil (40% peat moss peat, 20%  
154 Nordic fraction 2, 20% Baltic peat agent, 20% normal garden peat, 1% pg mix, 0.2% Micromax)  
155 and moved to a greenhouse where they were placed in a cage covered with 75% shade cloth to  
156 allow for adjustment to changed climatic conditions. After one week, they were moved to a  
157 table with flood system allowing a nutrient solution to be absorbed from below into the pots  
158 (pH 5.0, EC 0.8, NPK ratio 12-14-24). Seedlings stayed on the table with flood system for the  
159 duration of the experiment (see the Experimental setup section below). To simulate forest  
160 conditions, temperature in the greenhouse was kept at a minimum day/night temperature of

161 24/22°C, air humidity at 80%, day length was reduced to a maximum of twelve hours using  
162 automatically closing black screens. Light levels were in summer months reduced using  
163 (depending on the month) either 25% or 50% shade cloth, such that plants received  
164 approximately 2 mol per day, which is the average light intensity in the forest understorey at  
165 the site where seeds were collected [24]. Monthly target shade levels were based on the 10-year  
166 monthly average light intensities recorded at the location of the greenhouses.

## 167 **Experimental design and treatment**

168 The experiment was laid out as a randomized block design with six blocks. To this end, the  
169 table was divided into six equal parts lengthwise to create the blocks. Seedlings from the same  
170 mother (half-sib families) were randomly distributed over the blocks and over position within  
171 the block. Because families differed in number of seedlings, sometimes a family was only  
172 present in one block (this was the case for families with only one seedling), and sometimes in  
173 all six (which was the case for families with at least six seedlings).

174 To assign the seedlings to control or defoliation treatments, we ranked all plants in a family  
175 according to age (*i.e.* date of emergence). We then randomly assigned a treatment (*i.e.*  
176 defoliation or control) to the oldest one, giving the other treatment to the second oldest plant  
177 and alternating in this way across the age hierarchy. Of all seedlings that were assigned to the  
178 defoliation treatment, two out of every three leaflets were cut off at six months of age. This  
179 treatment was repeated (for newly produced leaves) every eight weeks.

## 180 **Data collection and curation**

181 At six months of age, we measured seedling stem length and diameter. In addition, we measured  
182 leaf width, lamina length, rachis length, rachis diameter, leaflet width, and number of leaflets  
183 of all leaves, as well as the length of unopened leaf. With this information, seedling biomass



184 (per plant part) and leaf area of the seedlings of six months of age were estimated using an  
185 allometric model, that we constructed based on data of a destructive harvest of extra seedlings  
186 of six months of age from the same experimental conditions (see S1 File for details).

187 Surviving seedlings were destructively harvested at 12.5 months of age (1387 in total). Plants  
188 were checked for natural abscissions (which can easily be detected by the structure of the plant),  
189 but no natural abscissions were detected. Roots were carefully washed to remove all soil  
190 particles. Leaf area was measured of the second fully developed leaf (counting from the apex),  
191 using a leaf area meter (LiCor LI3100 Lincoln NE, USA). Roots, stem, rachis, undeveloped  
192 leaves, lamina of non-defoliated leaves and lamina of defoliated leaves were separated, and  
193 dried in a stove at 70°C for at least 72 hours, after which dry mass per plant part was determined.

194 Measured weights and leaf area were checked for mistakes. Mistakes included incomplete  
195 defoliation treatment, no separation of non-defoliated leaf mass at harvest, no defoliation of  
196 new leaves at harvest, and unrealistic values. Unrealistic values were defined as deviations of  
197 more than a factor of ten from the mean observed relative value compared to other plant parts  
198 (e.g. from the leaf mass/stem mass ratio). A total of 88 plants were excluded from further  
199 analysis. From the included individuals, we selected only those that belonged to families (*i.e.*  
200 were obtained from a mother palm) that contained at least 12 individuals. The selection reduced  
201 the initial number of 207 families sampled in the field to 47 families included in the analyses.  
202 Analyses were conducted on a total of 731 seedlings.

203

204 **Estimation NAR, biomass allocation to leaves, changes in SLA and**  
205 **RGR**

206 To estimate growth and several growth-related variables (net assimilation rate (NAR), fraction  
207 of newly assimilated mass that is allocated to lamina growth ( $f_{lam}$ ), fraction in daily change in  
208 mean specific leaf area ( $\gamma$ ) and relative growth rate (RGR)), we used an iterative growth model  
209 following the method of Anten & Ackerly [20]. This method of growth analysis allows more  
210 exact estimations of growth variables than either the classic or functional approaches of growth  
211 analysis [25] when a plant experiences repeated defoliation because it includes timing of leaf  
212 loss [20]. Input for this model is biomass, leaf mass, and leaf area at the beginning and end of  
213 the experiment, and leaf loss (mass and area, and time of removal) during the experiment. We,  
214 however, did not measure leaf loss directly but assumed this to be two third of existing leaf  
215 mass (*i.e.*, our defoliation treatment entailed removing two out of every three leaflets). To allow  
216 for this, we adjusted the Anten & Ackerly [20] model. A more detailed description of these  
217 methods is provided in S2 File.

218

## 219 **Estimation of tolerance and compensatory responses**

220 Tolerance and compensatory growth are both measures of plant performance under defoliation  
221 stress, compared to performance of control (non-defoliated) plants. Tolerance, the difference in  
222 fitness (or growth in our case) between individuals under defoliation stress and non-defoliated  
223 individuals [1], is the measure most widely used to make such comparisons, but it does not take  
224 into account the amount of leaf area that was removed. Compensation, the fraction of the  
225 potential loss in growth due to leaf loss that is mitigated through compensatory mechanisms,  
226 does take lost leaf area into account and some methods allow for including the time of removal  
227 as well [20]. This more functional approach allows for estimation of the underlying growth  
228 parameters (changes in NAR, SLA and biomass allocation). We analysed both, because growth

229 tolerance is a more common measure, but compensation gives more insight in the underlying  
230 mechanisms.

231 To be able to estimate genetic variation in tolerance and compensation, information on  
232 differences in tolerance within families, and therefore per individual is required. In order to be  
233 able to calculate tolerance and compensation per individual, each individual in the defoliation  
234 treatment was paired with a family member from the control treatment, based on rank order of  
235 estimated biomass at six months of age (*i.e.* seedling age at the beginning of the experiment).  
236 Pairing is a standard procedure in growth analysis [1]. Using the values of the coupled control  
237 individual, tolerance in growth rate was calculated as  $T = (G_D - G_C) / G_D$  in which T indicates  
238 tolerance, G growth, and the subscript D and C the defoliation- and control treatment  
239 respectively. For tolerance in RGR, RGR values were obtained with the iterative growth model.  
240 For tolerance in biomass growth, we calculated biomass change between 6 months and 12  
241 months of age, for which the values were obtained from direct measurements. We excluded leaf  
242 mass in this calculation.

243 We estimated compensatory growth per individual using the approach of Anten, et al. [6]. We  
244 used the coupled control family members as a null-model to be able to estimate growth rate of  
245 a hypothetical, non-compensating individual. Using the start-biomass of the defoliated  
246 individual, but the growth parameters (NAR,  $f_{lam}$ ,  $\gamma$ ) of the control individual, we calculated  
247 biomass growth rate and RGR based on the iterative growth model, for both the control and  
248 defoliation treatment. Compensation was then calculated as  $Compensation = \frac{L_{pot} - L_{real}}{L_{pot}}$  in  
249 which  $L_{pot} = C0 - D0$  and  $L_{real} = C0 - D$ .  $L_{pot}$  (the potential reduction in growth) is therefore  
250 calculated as the growth of a control individual with the null-model growth parameters (C0),  
251 minus growth of a defoliated individual with the same null-model growth parameters (D0).  $L_{real}$

252 (the realized reduction in growth) is calculated as C0 minus the actually realized growth of the  
253 defoliated individual (D).

254

## 255 **Statistical analysis**

256 To estimate genetic variation in growth parameters (NAR,  $f_{lam}$  and  $\gamma$ ), variables of biomass  
257 growth (without leaf mass) and RGR, and for tolerance and compensation, we constructed  
258 mixed effect models, in which (half-sib) family (F) was included as random factor. Seed weight  
259 (s) was included as fixed effect when its effect was significant, to correct for potential maternal  
260 effects. The resulting models were  $y_{ij} = \mu + s_j + F_i + e_{ij}$  and  $y_{ij} = \mu + F_i + e_{ij}$  with  $F_i \sim$   
261  $N(0, \sigma_F^2)$  and  $e_{ij} \sim N(0, \sigma^2)$ . From the among-family variance component ( $\sigma_F^2$ ) and the residual  
262 variance component ( $\sigma^2$ ) narrow sense heritability was estimated as  $h^2 = \frac{4\sigma_F^2}{\sigma_F^2 + \sigma^2}$ . Because  
263 mother plants were randomly pollinated, families were considered to be half-sibs in this  
264 estimation [26]. Estimates for plants that were part of the defoliation treatment were calculated  
265 separately.

266 To analyze genetic variation in response to defoliation, we constructed mixed effect models for  
267 all estimated growth parameters in which treatment (T) was included as a fixed effect, family  
268 as a random effect, as was the interaction term between treatment and family. A relatively large  
269 interaction term between defoliation treatment and family in the models of biomass growth or  
270 RGR, is an indication of genetic variation in tolerance [e.g. 27]. Likewise, a relatively large  
271 interaction term between treatment and family in the mixed models for the growth parameters  
272 NAR,  $f_{lam}$  and  $\gamma$ , are indications of genetic variation in compensatory traits. When visual  
273 inspection of the data suggested more complex variance structures, these were modeled as well,

274 and the best model was selected based on Akaike (AIC) criteria. The best model was for all  
275 tested variables the model in which separate within group variance components were estimated  
276 per treatment, which is  $y_{ijk} = \mu + T_j + s_k + F_i + F \times T_{ij} + e_{ijk}$  with  $F_i \sim N(0, \sigma_F^2)$ ,  $F \times T_{ij} \sim$   
277  $N(0, \sigma_{F \times T}^2)$  and  $e_{ijk} \sim N(0, \sigma_j^2)$ . Mixed effect models were analyzed in Genstat [28], all other  
278 analyses were performed in R [29].

279

## 280 Results

### 281 Genetic variation in growth parameters

282 We found large variation among different families in biomass growth and RGR (Fig 1). We  
283 determined within and among family variance components for biomass growth rate, RGR, and  
284 the growth parameters NAR, biomass allocation ( $f_{lam}$ ), and SLA change ( $\gamma$ ) that were estimated  
285 by the iterative growth model (Table 1). Based on the gathered variance components, we  
286 estimated narrow-sense heritability of growth rate to be relatively large for non-defoliated  
287 plants, and only slightly lower for plants that were subjected to defoliation ( $h^2$  values for  
288 biomass growth and RGR ranged from 0.41 to 0.46 for control plants and from 0.32 to 0.35 for  
289 defoliated plants, Table 1). Surprisingly, estimations of heritability of the growth parameters  
290 NAR,  $f_{lam}$ , and  $\gamma$ , were much lower, especially for the control individuals (Table 1).

291 **Fig. 1. Boxplots of biomass growth and RGR for control and defoliated seedlings of 47 families of**  
292 ***Chamaedorea elegans* from a Mexican rainforest.** Boxes are the interquartile range (IQR), black lines in the  
293 middle of boxes are medians, whiskers are the extreme data point with 1.5 x IQR. Families are ranked by increasing  
294 order of mean biomass growth. The changing rank of families between treatments is a first indication that families  
295 that grow relatively fast without the stress of defoliation do not necessarily grow relatively fast when they suffer  
296 leaf loss. The changes in rank between biomass growth rate and RGR indicate that families that grew fast in  
297 absolute terms did not necessarily grow fast in relative terms.

298 **Table 1. Estimated within- and among-family variance components and narrow-sense heritability ( $h^2$ ) for**  
 299 **several growth parameters for a population of the understory palm *Chamaedorea elegans*, for which**  
 300 **seedlings were subjected to defoliation in a greenhouse.**

	Control			Defoliation		
	$\sigma^2_F$	$\sigma^2$	$h^2$	$\sigma^2_F$	$\sigma^2$	$h^2$
<b>Biomass growth (g/6months)</b>	0.0574	0.502	0.410	0.0103	0.109	0.347
<b>RGR (g/g/day)</b>	1.65E-07	1.26E-06	0.463	1.39E-07	1.58E-06	0.324
<b>NAR</b>	6.30E-18	5.49E-10	4.66E-08	5.45E-11	9.37E-10	0.220
<b><math>f_{lam}</math></b>	3.80E-12	3.77E-03	4.04E-09	2.92E-10	8.03E-03	1.44E-07
<b><math>\gamma</math></b>	0.000220	0.00618	0.138	0.000547	0.0127	0.165

301 Biomass growth (excluding leaf mass) was determined from direct measurements. The growth parameters RGR,  
 302 NAR,  $f_{lam}$  and  $\gamma$  were estimated using an iterative growth model. Variance components were estimated from mixed-  
 303 effect models with REML estimation. RGR = Relative growth rate;  $f_{lam}$  = fraction of newly assimilated mass that  
 304 is allocated to lamina growth;  $\gamma$  = fraction in daily change in mean specific leaf area

305

## 306 **Genetic variation in tolerance, compensation, and compensatory** 307 **traits**

308 We compared family mean control and defoliation treatment values of all growth parameters  
 309 (Fig 2). Family mean biomass growth rate was as expected, lower in the defoliation treatment  
 310 for all families and for RGR in almost all families. However, all family mean values of NAR  
 311 and biomass allocation, and almost all family mean values of SLA change, were higher in the

312 defoliation treatment than in the control treatment. Therefore, all families clearly showed  
 313 compensatory responses to leaf loss by increasing their NAR and SLA, and changing their  
 314 biomass allocation.

315 **Fig. 2. Comparison of control and defoliation treatment family means of several growth parameters for**  
 316 **seedlings of the understory palm *Chamaedorea elegans*.** Biomass growth was determined from direct  
 317 measurements, the other parameters were all estimated using an iterative growth model. The dashed line  
 318 indicates a 1-to-1 relationship. Pearson correlation coefficients and associated p-values are shown. The asterisk  
 319 in panel (e) is an outlier data point; correlation coefficient and p-value without this data point are shown in  
 320 between brackets.

321 We tested whether families responded differently to defoliation, and therefore whether there  
 322 was genetic variation in response to defoliation, with a mixed effect model in which we included  
 323 the random interaction between treatment and family. This model yielded only relatively small  
 324 variance components for the interaction between treatment and family for all evaluated  
 325 parameters (Table 2). This suggests that families do not respond significantly different to leaf  
 326 loss in terms of biomass growth, RGR, NAR, allocation to leaf mass nor SLA changes.  
 327 Therefore, while families compensate strongly for leaf loss, we did not find evidence for strong  
 328 within-population genetic variation in this response.

329 **Table 2. Estimated family, family\*treatment and residual variance components for several growth**  
 330 **parameters, estimated from a greenhouse experiment that was performed with seedlings for which the seeds**  
 331 **came from a small (0.7ha) Mexican population of the understory palm *Chamaedorea elegans*.**

	$\sigma^2_F$	$\sigma^2_{F \times T}$	$\sigma^2_{Control}$	$\sigma^2_{Defoliation}$
<b>Biomass growth (g/6months)</b>	2.53	-1.44	53.91	10.69

<b>RGR (g/g/day)</b>	0.00129	0.0002	0.0127	0.0159
<b>NAR</b>	0.00242	-0.00199	0.0545	0.0983
<b>f<sub>lam</sub></b>	0.000168	-0.00018	0.00378	0.00803
<b>Γ</b>	0.00043	-0.00013	0.00613	0.0129

332 Biomass growth was determined from direct measurements, the other parameters with an iterative growth model.

333 Variance components were estimated using mixed effects models with REML estimation. RGR = Relative growth  
 334 rate; f<sub>lam</sub> = fraction of newly assimilated mass that is allocated to lamina growth; γ = fraction in daily change in  
 335 mean specific leaf area

336 To estimate genetic variation in tolerance and compensation itself, we paired defoliation  
 337 treatment individuals with control individuals from within the same family. By doing this, we  
 338 were obtaining replicated estimates of tolerance and compensation and could therefore estimate  
 339 the heritability of these parameters. Even though we found large variation between family mean  
 340 values of tolerance and compensation (e.g. family mean compensation in biomass growth  
 341 ranged from 0.16 to 1.03, i.e., 16 - ~100% of potential loss being mitigated), within-family  
 342 variance was much larger. Therefore, estimations of heritability of tolerance and compensation  
 343 were low (the highest estimated heritability was for compensation in biomass growth, which  
 344 was only 0.01, Table 3).

345 **Table 3.** Estimated within and among family variance components and heritability of tolerance to defoliation, and  
 346 compensation after repeated defoliation events in a greenhouse experiment, performed seedlings of the understory  
 347 palm *Chamaedorea elegans*. To be able to estimate tolerance and compensation, individuals from the defoliation  
 348 treatment were coupled to individuals from the control treatment based on their estimated biomass at the start of  
 349 the experiment. Compensation was calculated by using an iterative growth model that allowed estimation of a  
 350 hypothetical non-compensating individual.

	<b>Tolerance</b>			<b>Compensation</b>		
--	------------------	--	--	---------------------	--	--



	$\sigma^2_{\text{Family}}$	$\sigma^2$	$h^2$	$\sigma^2_{\text{Family}}$	$\sigma^2$	$h^2$
<b>Biomass growth (g/6months)</b>	0.00636	2.796	0.00908	0.000559	0.1820	0.0122
<b>RGR (g/g/day)</b>	1.53E-10	6.18E-02	9.90E-09	1.76E-09	5.23E-01	1.35E-08

351 Note: RGR = Relative growth rate

352

### 353 **Relation between growth and tolerance**

354 For all growth parameters, there were positive correlations between family mean control values  
 355 and family mean defoliation treatment values, indicating that growth performance was  
 356 genetically correlated between treatments (Fig 2). The correlation coefficient for biomass  
 357 growth was higher ( $r = 0.75$ ) than those for RGR, NAR and  $\gamma$  ( $r = 0.34$ ,  $r = 0.31$ , and  $r = 0.41$   
 358 respectively). Only the estimated positive correlation coefficient of  $f_{\text{fam}}$  ( $r = 0.23$ ) was not  
 359 significant. These results suggest the existence of superior genotypes that grow fast while still  
 360 being able to tolerate defoliation.

361 It is possible that even though (to some extent) the same families grew faster in both treatments,  
 362 the relative reduction in growth rate might have been larger for families that grew fast in the  
 363 control treatment. If this was the case, there would be a negative relation between tolerance or  
 364 compensation (both relative measures) and growth rate in the control treatment. To test this we  
 365 compared family mean values of tolerance and compensation, to family mean values of biomass  
 366 growth rate and RGR in the control treatment (Fig 3). This did not yield clear evidence for any  
 367 positive or negative relation between tolerance/compensation and biomass growth/RGR. The  
 368 only significant correlation that we found was between tolerance and RGR. However, this

369 relationship was heavily pulled by two outlying data points; without these outliers there was no  
370 longer a significant correlation. Therefore, we did not find evidence that would suggest costs  
371 to tolerance in terms of growth.

372 **Fig. 3. Relationships between family mean compensation (A, C), tolerance (B, D) and family mean growth**  
373 **rate.** Data were obtained from 47 half-sib families of seedlings of the understory palm *Chamaedorea elegans*, in  
374 which a defoliation treatment was applied. Compensation, RGR tolerance and RGR were estimated with an  
375 iterative growth model that takes into account timing of leaf removal (see methods). Pearson correlation  
376 coefficients and associated p-values are provided. The asterisks in panel d are two outlying data points; Pearson  
377 correlation coefficient and p-value without these data points are shown in between brackets.

378

## 379 **Discussion**

380 This study showed that genetic variation in tolerance and compensatory responses to  
381 defoliation is limited within a population of a long-lived tropical forest species. We also  
382 showed that genetic variation in growth potential was much larger than values usually  
383 detected for small populations [14, 30]. These results suggest that the studied population  
384 might have limited ability to adapt in terms of tolerance to environmental changes that entail  
385 leaf loss but does have the ability to adapt to environments that require different growth rates.  
386 Furthermore, this is one of the first studies that has analyzed genetic variation in  
387 compensatory growth responses to defoliation.

388

## 389 **Heritability of growth potential**

390 We found large within-population genetic variation in growth rate, with estimations of narrow-  
391 sense heritability ranging from 0.32 to 0.46. These estimations are higher than the estimations  
392 from the few other studies that have been performed with long-lived plant species. For example,  
393 in the shade tolerant rainforest tree *Sextonia rubra* heritability ranged from 0.23 to 0.28 for  
394 several growth-related traits [30], and between 0.20 and 0.37 in a population of *Populus*  
395 *tremuloides* [14]. The values that we found are especially high considering that the seeds used  
396 in this experiment were collected in a very small area (0.7 ha). Furthermore, the high genetic  
397 variation that we found is somewhat surprising because inbreeding in *Chamaedorea* species  
398 has been estimated to be high in several other Mexican *C. elegans* populations [31]. This  
399 suggests that heritability in growth could be higher in understory palms than in trees, but  
400 further research on multiple populations and species is necessary to determine this.

401

## 402 **Compensatory responses and heritability of tolerance to defoliation**

403 We found individuals to compensate strongly for defoliation, by increasing NAR, allocating  
404 more biomass to leaf mass, and by increasing SLA, which are similar responses that have been  
405 found in other studies [e.g. 32] including one that was also performed with *C. elegans* [albeit  
406 with adults, 6]. Mean families values of compensation varied strongly (e.g. for biomass growth  
407 between 0.16 to 1.03, i.e., the extent of compensation from about 1/8 to full compensation).  
408 However, we found only very limited evidence for genetic variation in compensatory responses  
409 and tolerance. Genetic variation in tolerance has been found for many species of annual and bi-  
410 annual plants (see e.g. [1] for a review on this), but, as Stevens, Waller & Lindroth [14] point  
411 out, much less is known about the level of genetic variation in tolerance in long-lived species.  
412 A reason for this is that resistance (e.g. chemical defenses) rather than tolerance has long been  
413 seen as a more effective measure for long-lived species to persist under the pressure of

414 herbivory, due to their different life-history traits, such as long-lived leaves [15]. However, as  
415 explained by Haukioja & Koricheva [15], tolerance could be just as important for long-lived  
416 species as for the short-lived ones, partly because herbivore attacks can never be completely  
417 avoided, and plants endure leaf losses due to chronic physical damages. Tolerance could be  
418 particularly well developed in understorey species because shade tolerance is often associated  
419 with storage of reserves that allow recovery after damage [12, 16, 23] and because understorey  
420 plants are subjected to falling canopy elements like branches, limbs and complete trees [33].  
421 Studies that have been performed on long-lived plants were all on tree species (in which part of  
422 the studies detected genetic variation in tolerance, *e.g.* [14], while others did not, *e.g.* [34]. To  
423 our knowledge, genetic variation in tolerance and compensatory responses has not been studied  
424 in natural populations of other types of long-lived plant species like lianas, ferns or palms.

425

## 426 **Relation between growth and tolerance**

427 We did not detect a genetic correlation between growth and tolerance or compensation, even  
428 though it has been shown that such correlation exists at least at the ecotype level in short-lived  
429 plants [32]. Therefore, the strong differences in growth that we detected among families cannot  
430 be explained by a growth-tolerance trade-off. In contrast, we found that ‘super-performing’  
431 families that grew relatively fast under undisturbed conditions also grew fast when exposed to  
432 defoliation. These types of superior genotypes could play a key role in population resistance  
433 when the population is being disturbed by, for example, a storm (and associated increase of  
434 falling canopy debris) or herbivore attack. Fast growers have been shown to contribute  
435 positively and disproportionately to population growth [35, 36], and our results suggest that  
436 such contribution would be maintained under disturbance. However, population growth is not  
437 only influenced by the response of individuals to disturbance in terms of growth but also by

438 their survival and ability to maintain seed production under stress. Therefore, it would be very  
439 interesting to test if fast growing adult plants have a high survival probability and are better  
440 able to maintain seed production when they suffer leaf loss, especially because *Chamaedorea*  
441 *spp.* have been shown to be relatively intolerant to leaf loss in terms of reproduction [6, 22, 37].

442 A trade-off with defoliation tolerance did not explain why genetic diversity for growth potential  
443 was high within the population that we studied. However, it is possible that there are other  
444 trade-offs with growth than the one with defoliation tolerance such as genotype x environment  
445 trade-offs (*i.e.* G x E interactions). Our study site is characterized by persistent spatial  
446 heterogeneity in environmental conditions [38]. Possibly, genotypes that grow fast in certain  
447 environmental conditions, like the greenhouse conditions in this experiment, are not the ones  
448 that would grow fast in other environments that are, for example, nutrient poor. However, it is  
449 hard to estimate how likely this is, as G x E interactions have hardly been studied in long-lived  
450 plant species, in particular, those that occur in tropical forests.

451 The current study was performed with seedlings. Possibly, our estimations of genetic variation  
452 in tolerance and compensatory growth responses could be different if the experiment had been  
453 performed with adult plants. Larger reserve storage in adult plants may lead to higher tolerance  
454 to defoliation compared to seedlings. However, compensatory responses were strong in our  
455 experiment and comparable to those reported for adults of the same species [6], suggesting that  
456 if genetic variation in these responses would be strong in our study population, this would have  
457 been expressed in our experiment.

458

## 459 **Implications**

460 The low genetic variation in compensatory responses and tolerance that we found, could have  
461 consequences for the adaptive potential of populations to environmental changes [10]. If the  
462 frequency and magnitude of leaf loss in a population persistently increases (*e.g.* due to an  
463 increase of storm frequencies, which is predicted in several climate change scenarios [39], or  
464 due to the introduction of an invasive herbivore [40]), populations with limited genetic variation  
465 in tolerance to defoliation might not be able to respond and adapt to such selective pressures.  
466 On the contrary, the high genetic variation that we estimated for growth potential, might  
467 increase the adaptability of populations if pressure for light competition changes. This could,  
468 for example, happen if canopy dynamics change due to differences in storm frequencies, or  
469 because of the introduction of a new faster-growing, light-demanding, understorey species. In  
470 this case, genotypes that allow high growth might be selected for.

471 In the above context, it is critical to obtain accurate information on genetic variation in  
472 quantitative traits present in populations in order to be able to evaluate what the effect of  
473 environmental change will be on populations [10]. Especially information on genetic variation  
474 in traits that are directly linked to individual vital rates is essential to be able to link evolutionary  
475 and demographic processes [41]. However, at this point, surprisingly little is known about this  
476 for tropical forest species. Therefore, we strongly recommend more studies that evaluate the  
477 amount of within-population genetic variation causing differences in vital rates, and the  
478 consequences of this variation for the adaptive potential of populations to changing  
479 environments.

480 Strong genetic variation in growth rate as we found in this study, can also have implications for  
481 management practices. The existence of superior individuals that grow faster while still being  
482 able to strongly compensate for leaf loss offers opportunities for increased production by  
483 artificial selection. These individuals can be used when a species is commercialized, especially

484 when this is for its leaves. In the case of *C. elegans*, leaves are harvested as a non-timber forest  
485 product (NTFP) for the floral industry, and are increasingly being planted in secondary forests  
486 for enrichment or in intercropping systems with species that provide shade [42]. This study  
487 shows that it might be beneficial to select seeds from individuals that have high growth rates,  
488 which can be easily identified for this species [35]. We believe that there are many more long-  
489 lived tropical forest species for which it could be valuable to explore this potential.

490

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500

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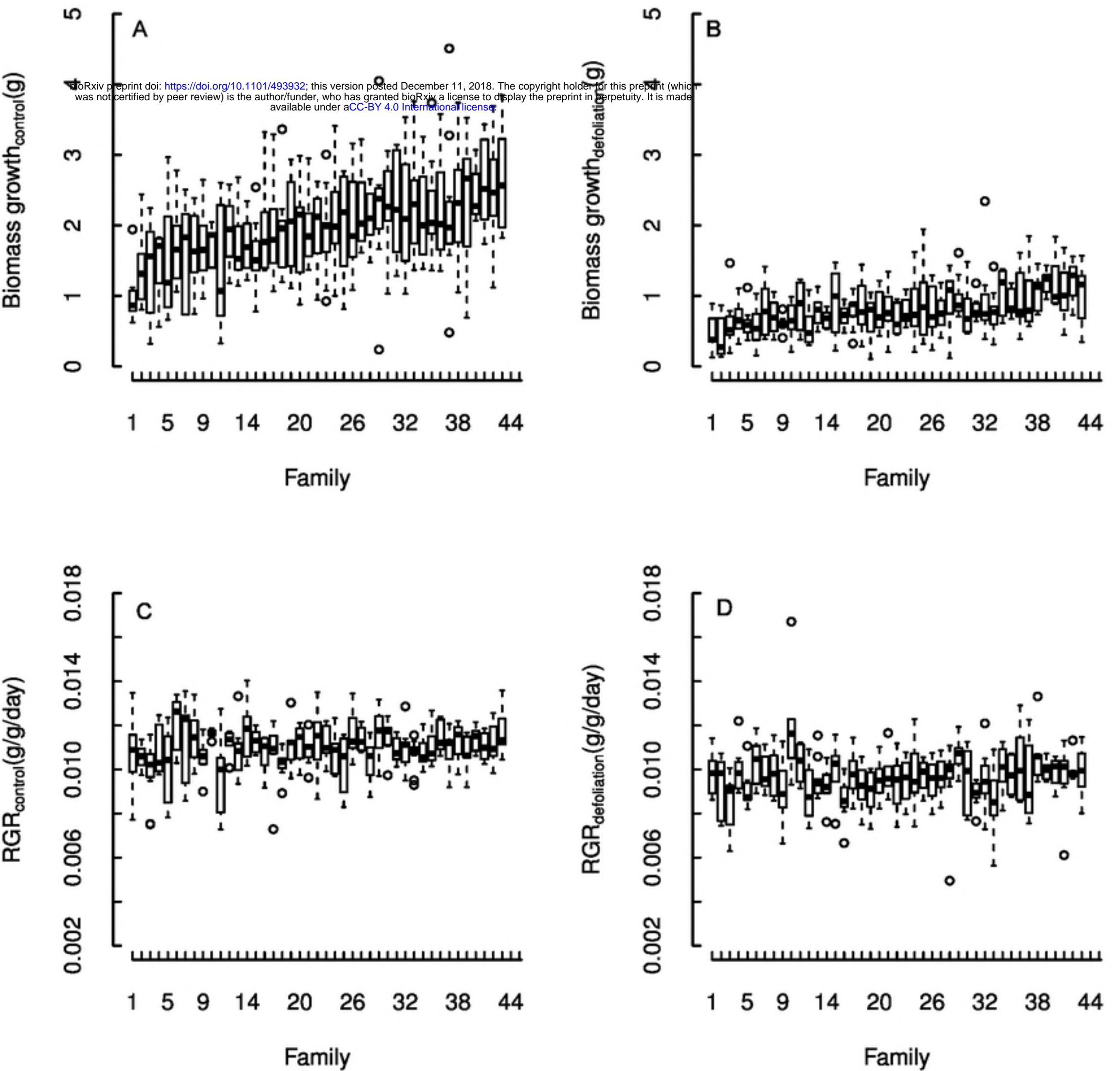
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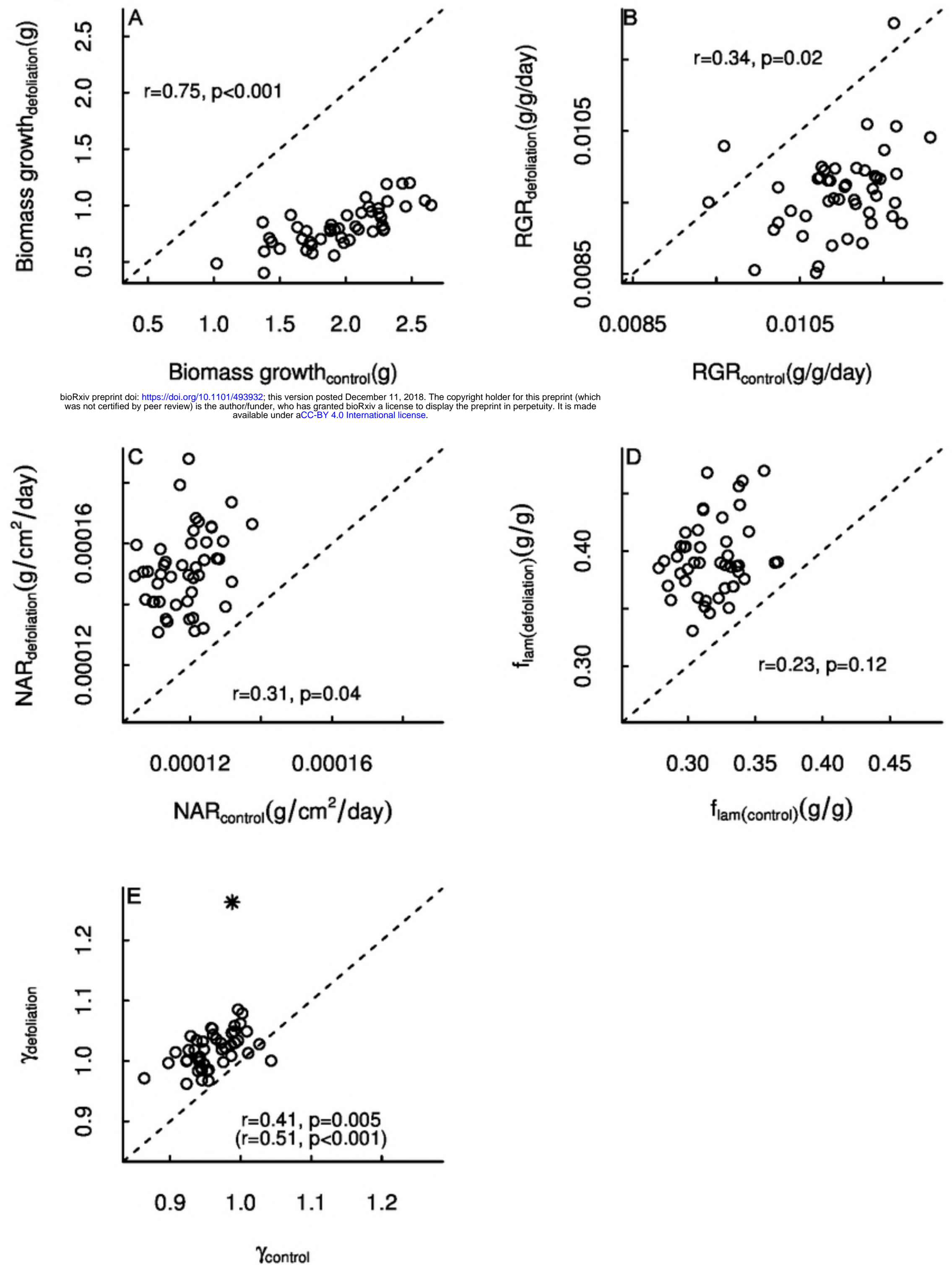
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## 600 **Supporting Information**

601 **S1 File. Allometric model.** Details on methods of the construction of an allometric model for  
602 estimation of biomass per plant part of seedlings of 6 months of age

603 **S2 File. Iterative growth model.** Details on methods of the construction and adaptation of an  
604 iterative growth model for estimation of daily individual seedling NAR,  $\text{flam}$  and  $\gamma$

**Fig.1****Figure 1**

**Fig. 2**

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**Figure 2**



Fig. 3

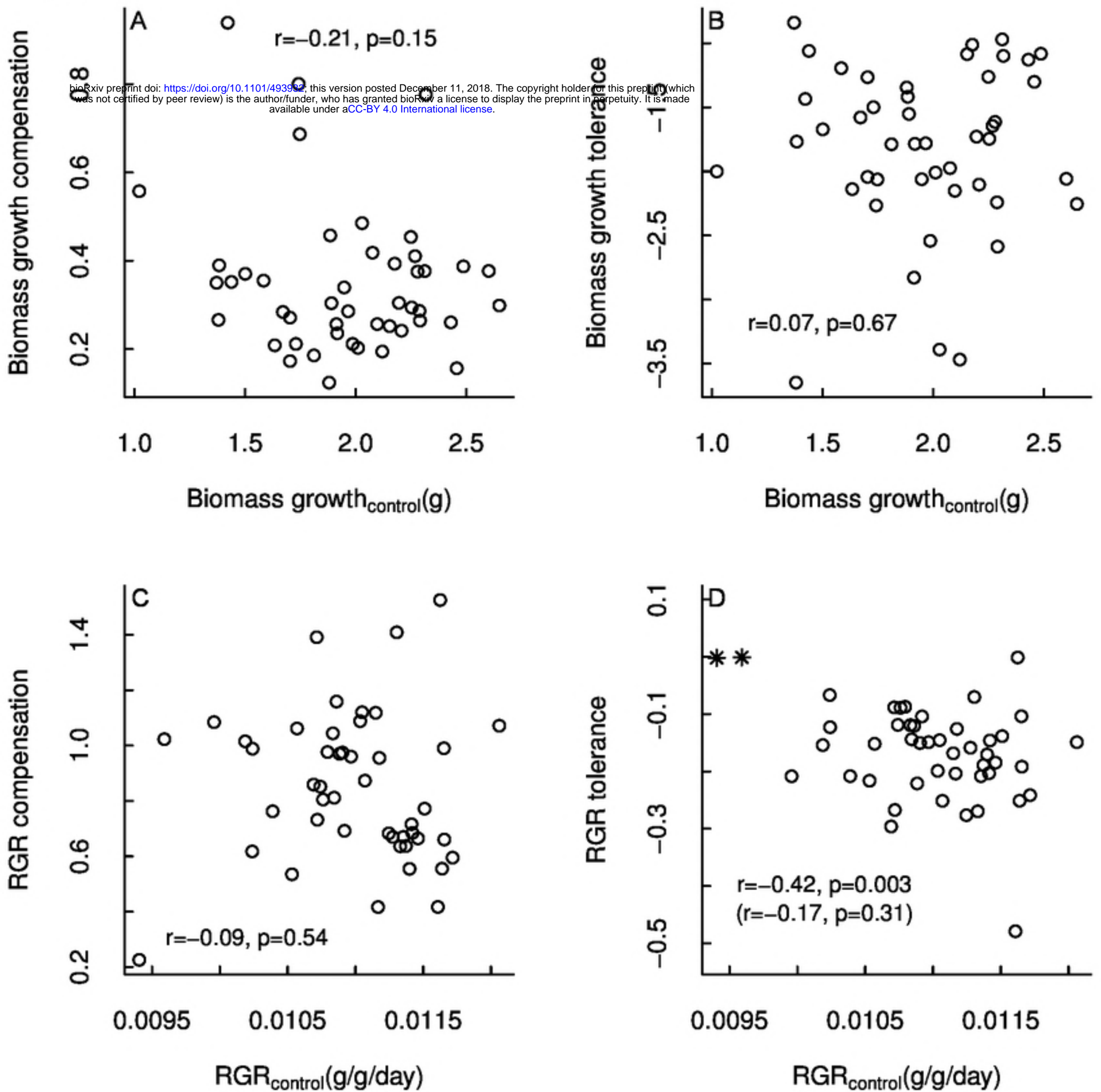


Figure 3