1 **Tropical forest lianas have greater non-structural carbohydrate concentrations in**

2 **the stem xylem than trees**

3 Caroline Signori-Müller[1,2,3,*], David Galbraith[3], Julia Valentim Tavares[4,3], Simone

4 Matias Reis[5,6,7], Francisco Carvalho Diniz[3], Martin Gilpin[3], Beatriz Schwantes

5 Marimon[5,6], Geertje M. F. van der Heijden[8], Camila Borges[5,6], Bruno Barçante Ladvocat

6 Cintra[9,3], Sarah Mião[2], Paulo S. Morandi[5,6], Alex Nina[10], Carlos A. Salas Yupayccana[10],

7 Manuel J. Marca Zevallos[11,10], Eric G. Cosio[10], Ben Hur Marimon Junior[5,6], Abel

8 Monteagudo Mendoza[11,12], Oliver Phillips[3], Norma Salinas[7,10], Rodolfo Vasquez[12],

9 Maurizio Mencuccini[13,14] and Rafael S. Oliveira[15]

10

11 [1]College of Life and Environmental Sciences, University of Exeter, Exeter, UK

12 [2]Department of Plant Biology, Institute of Biology, Programa de Pós Graduação em

13 Biologia Vegetal, University of Campinas, Campinas, Brazil

14 [3]School of Geography, University of Leeds, Leeds, UK

15 [4]Department of Ecology and Genetics - Uppsala University, Sweden

16 [5]Programa de Pós-Graduação da Rede de Biodiversidade e Biotecnologia da Amazônia

17 Legal (BIONORTE), UFAM–UNEMAT, Nova Xavantina, Brazil

18 [6]Laboratório de Ecologia Vegetal, Universidade do Estado de Mato Grosso, Nova

19 Xavantina, Brazil

20

21

22   [7]School of Geography and the Environment, Environmental Change Institute, University

23   of Oxford, Oxford, UK

24   [8]School of Geography, University of Nottingham, Nottingham, UK

25   [9] School of Geography, Earth and Environmental Sciences, University of Birmingham

26   [10]Pontificia Universidad Católica del Perú, Lima, Peru

27   [11]Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru

28   [12] Jardín Botánico de Missouri, Cusco, Peru

29   [13]CREAF, Campus UAB, Cerdanyola del Vallés, Spain

30   [14]ICREA, Barcelona, Spain

31   [15] Department of Plant Biology, Institute of Biology, University of Campinas, Campinas,

32   Brazil

33   [*] Correspondence author: c.signori-muller@exeter.ac.uk

Abstract

Lianas (woody vines) are important components of tropical forests and are known to compete with host trees for resources, decrease tree growth and increase tree mortality. Given the observed increases in liana abundance in some forests and their impacts on forest function, an integrated understanding of carbon dynamics of lianas and liana-infested host trees is critical for improved prediction of tropical forest responses to climate change. Non-structural carbohydrates (NSC) are the main substrate for plant metabolism (e.g., growth, respiration), and have been implicated in enabling tree survival under environmental stress, but little is known of how they vary among life-forms or of how liana infestation impacts host tree NSC. We quantified stem total NSC (NSC) concentrations and its fractions (starch and soluble sugars) in trees without liana infestation, trees with more than 50% of the canopy covered by lianas, and the lianas infesting those trees. We hypothesized that i) liana infestation depletes NSC storage in host trees by reducing carbon assimilation due to competition for resources; ii) trees and lianas, which greatly differ in functional traits related to water transport and carbon uptake, would also have large differences in NSC storage, and that As water availability has a significant role in NSC dynamics of Amazonian tree species, we tested these hypotheses within a moist site in western Amazonia and a drier forest site in southern Amazonia. We did not find any difference in NSC, starch or soluble sugar concentrations between infested and non-infested trees, in either site. This result suggests that negative liana impact on trees may be mediated through mechanisms other than depletion of host tree NSC concentrations. We found lianas have higher stem NSC and starch than trees in both sites. The consistent differences in starch concentrations, a long term NSC reserve, between life forms across sites reflect differences in carbon gain and use of lianas and trees. Soluble sugar concentrations were higher in lianas than in trees in the moist site but indistinguishable between life forms in the dry site. The lack of difference in soluble sugars between trees and lianas in the dry site emphasize the importance of this NSC fraction for plant metabolism of plants occurring in water limited environments.

Abstract in Portuguese and Spanish are available in the supplementary material.

Keywords: starch, soluble sugars, liana infestation, host-tree

Introduction

66

67   Lianas (woody vines) are important components in forests worldwide, especially

68 lowland tropical forests (Gentry 1991) where they constitute up to 40% of woody stems

69 and up to 35% of woody species richness (Schnitzer and Bongers 2011). Liana abundance

70 and biomass are increasing throughout the Neotropics, with potentially profound

71 implications for the future of tropical forest carbon balance (Phillips et al. 2002, Schnitzer

72 et al. 2021). Lianas are non-self-standing plants that reach the forest canopy by using host

73 tree stems or other established lianas as support, and can compete with trees through local

74 light monopolization, affecting host tree carbon sequestration and growth (Schnitzer and

75 Bongers 2002, Avalos et al. 2007, Paul and Yavitt 2011, van der Heijden et al. 2013,

76 2015, García León et al. 2017). Lianas have developed root and vascular systems that

77 may effectively compete with trees for water and nutrients (Pérez-Salicrup and Barker

78 2000, Andrade et al. 2005, Meunier et al. 2021). Furthermore, lianas can cause direct

79 mechanical damage to host trees, causing changes in leaf and branch area index (Schnitzer

80 and Bongers 2002, Reis et al. 2020), factors that could also limit carbon gain. Not

81 surprisingly, liana presence is associated with major decreases in tree productivity,

82 reproduction, biomass accumulation and biomass carbon stocks across tropical forests

83 (Durán and Gianoli 2013, van der Heijden et al. 2015, García León et al. 2017).

84   In the tropics, liana abundance increases towards areas with lower mean annual

85 precipitation and longer dry seasons. Trees, in contrast, , follow the opposite pattern with

86 greater abundance in less seasonal areas (Gentry 1991, DeWalt et al. 2010, Esquivel-

87 Muelbert et al. 2017, Parolari et al. 2020). The growth advantage lianas have over trees

88 particularly in areas with high climatic seasonality (Schnitzer and van der Heijden 2019),

89 are suggested to be driven by their more efficient strategy to capture dry season

4

90 precipitation (De Deurwaerder et al. 2018), and their efficient hydraulic system, with

91 some studies also suggesting lianas also have a safe hydraulic system (Carvalho et al.

92 2015, Chen et al. 2017, van der Sande et al. 2019). These set of characteristics may allow

93 lianas to absorb and transport more water and potentially enhance their growth rates

94 without risks for their hydraulic system. The enhanced capacity lianas have in keeping

95 water transport efficient and possibly also safety without restricting growth during the

96 dry season, may be related to the amount and efficiency in use of their carbon stores (i.e.,

97 non-structural carbohydrates)(Schnitzer and van der Heijden 2019). Non-structural

98 carbohydrates (NSC) are the primary products of photosynthesis, providing plants with

99 the necessary energy for growth and survival (O'Brien et al. 2014, Hartmann and

100 Trumbore 2016). The NSC also play a key role mediating plant responses to abiotic

101 stresses, as they contribute to the regulation of osmotic potential and provide energy for

102 active water transport, thereby contributing to a healthier water balance in plants (Myers

103 and Kitajima 2007, Dietze et al. 2014, Dickman et al. 2015, Thalmann and Santelia 2017).

104 The two main NSC fractions are the soluble sugars (glucose, fructose, sucrose, etc) which

105 are the main substrate for plant metabolism (e.g., growth, respiration), and starch, a long-

106 term reserve that can be converted to soluble sugars when carbon demand surpasses

107 supply (Rosa et al. 2009, Krasensky and Jonak 2012, MacNeill et al. 2017, Thalmann and

108 Santelia 2017). Although the use of stored NSC has been hypothesised to be involved in

109 the higher capacity lianas have to grow during the dry season compared to trees (Schnitzer

110 and van der Heijden 2019), to our knowledge there is no study that explores the

111 differences in NSC concentrations in co-occurring trees and lianas (Schnitzer 2018,

112 Schnitzer and van der Heijden 2019).

113 Liana infestation can hinder tree growth, fecundity, and survival (Schnitzer et al.

114 2005, Ingwell et al. 2010, van der Heijden et al. 2015, García León et al. 2017, McDowell

5

115   et al. 2018, Reis et al. 2020). Shading caused by lianas over tree canopies can lead to a

116   reduction in the amount of light intercepted by trees, resulting in a decrease in carbon

117   assimilation (Godoy-Veiga et al. 2018). Meanwhile, belowground lianas compete

118   strongly with trees belowground for water and nutrients (Pérez-Salicrup 2001, Andrade

119   et al. 2005, Meunier et al. 2021). The negative response to liana infestation, observed in

120   tree growth rates, fecundity, and survival, may reflect carbon limitation resulting from

121   decreased carbon gain in host trees caused by above and belowground competition. Such

122   limitation in carbon gain could lead to reduction in NSC reserves in trees, that in turn can

123   reduce tree growth and limit its ability to deal with environmental stressors (e.g.,

124   drought). Nevertheless, to our knowledge there is no empirical evidence that liana

125   infestation can cause reduction in NSC reserves in long-term storage organs (e.g., stem)

126   of host trees. Given the increase in liana abundance in some tropical areas (Phillips et al.

127   2002, Schnitzer et al. 2021), it is essential to provide a mechanistic explanation of their

128   impact on tree function, which will enable estimates of future changes in species

129   composition and carbon stocks in tropical forests.

130   It has been demonstrated that in Amazonian forests the NSC concentrations in tree

131   species can vary along climatic gradients (Signori-Müller et al. 2021), with higher

132   proportion of soluble sugars in species occurring in drier areas (precipitation < 2000

133   mm/year). The concentration of NSC in Amazonian species can also vary depending on

134   plant life history strategy (i.e., fast vs. slow growing species), with slow-growing species

135   presenting higher starch storage and less seasonal variation of NSC than fast-growing

136   species(Herrera-Ramirez et al. 2021, Signori-Müller et al. 2022). The position of a species

137   along the fast–slow growth continuum may have important implication in plant capacity

138   to deal with stressors, for example Visser et al. (2018) showed that in tropical tree species,

139   liana infestation has stronger negative effects on growth and survival of fast-growing

6

140 species than in slow-growing species. Fast-growing species, which have lower NSC

141 concentrations than slow-growing species (Herrera-Ramirez et al. 2021, Signori-Müller

142 et al. 2022), may be more vulnerable to liana infestation due to impairment between

143 carbon assimilation and demand for metabolism maintenance. None of these studies,

144 however, have investigated the NSC storage in plants with different life forms (lianas vs

145 trees) and on the impact of liana infestation on NSC reserves of host trees. To address

146 this knowledge gap, we sampled trees infested by lianas, the lianas infesting those trees,

147 and non-infested trees in two Amazon locations with contrasting mean annual

148 precipitation and dry season length. We quantified starch and soluble sugars, which

149 comprise the most significant portions of NSC reserves in most trees (Martínez-Vilalta et

150 al. 2016). We hypothesized that 1) liana infestation negatively impact on the NSC

151 reserves of host-trees, with stronger impact in fast-growing species (Visser et al. 2018).

152 Additionally, we expected trees infested by lianas to have lower NSC concentrations than

153 non-infested trees in the dry site, where trees are less adapted to shading (Medina-Vega,

154 Bongers, Schnitzer, et al. 2021) and where the forest may already be at their physiological

155 limit (Tavares et al. 2023); 2) co-occurring lianas and tress will have different NSC

156 concentrations per gram of dry wood, with lianas having higher stem NSC concentrations

157 compared to trees in both, the dry and moist site. It because lianas have better capacity

158 to intercept light than trees, which can reflect in enhanced carbon gain leading to higher

159 stem NSC concentration on a dry mass basis in wood , with accentuated differences in

160 the dry site(Medina-Vega, Bongers, Schnitzer, et al. 2021, Medina-Vega et al. 2022).

161 **Material and methods**

162 *Site description and species selection*

163 We performed our sampling in two forests in the Amazon with contrasting

7

164 precipitation regimes. One of the sites is in the Western Amazon, in the Tambopata

165 National Reserve, Puerto Maldonado, Madre de Dios, Peru (12°49'S, 69°16'W),

166 hereafter referred to as the moist site. In this site mean annual precipitation is ≈2450

167 mm/year, with a three-month dry season (rainfall < 100 mm; Sombroek 2001) extending

168 from June to August (Fick and Hijmans 2017). The other chosen site is an ecotonal forest

169 located at the dry fringe of the Amazon basin, in a permanent plot in Fazenda Vera Cruz,

170 Nova Xavantina, Mato Grosso, Brazil (14°49' S, 52°9' W), hereafter referred as the dry

171 site. In this site mean annual precipitation is ~1500 mm and the dry season can last up to

172 six months (Marimon et al. 2010). We selected these sites due to the markedly differences

173 in climatic conditions and consequently species composition and likely functional

174 strategies to identify the difference in NSC storage of co-occurring trees and lianas living

175 in contrasting environments.

176 Studies with seedlings and adult trees have shown that the stem represents one of

177 the major storage organs for NSC (Poorter and Kitajima 2007, Martínez-Vilalta et al.

178 2016) therefore due to financial constraints to sample and perform chemical analysis we

179 focus our study on the xylem stem of trees and lianas. In both sites, sampling occurred

180 during the wet season, taking place in January 2017 in the moist site and in December

181 2017 in the dry site. Although stems have smaller diurnal variation in NSC concentrations

182 compared to canopy organs (Tixier et al. 2018), we standardized the sampling time to be

183 between 08:30 and 11:00 a.m. In the field and during the transport to the laboratory,

184 samples were kept on ice. Upon arrival at the laboratory, we microwaved the samples for

185 90 s at 700 W to stop enzymatic processes and oven-dried at ~60°C for at least 48 hr or

186 until they were completely dry.

187 In each site we sampled trees infested by lianas, the lianas infesting the trees and

8

188   non-infested trees. We selected the trees based on the liana Crown Occupancy Index

189   (COI, percentage of the canopy covered by lianas, Schnitzer et al. 2005) and tree diameter

190   at breast high (DBH). Here, we considered infested those trees with COI = 3 or 4, meaning

191   that liana cover was more than 50% or 75% of tree canopy cover, respectively. All lianas

192   with DBH ≥ 5 cm infesting the trees were then sampled too. Non-infested trees are those

193   with COI = 0, meaning that there were no liana infesting the tree canopy.

194   In both sites, wherever possible, we sampled individuals with a similar diameter

195   for the trees of the same species, resulting in no difference in diameter between infested

196   and non-infested trees in both sites (Fig. 1S). Both in the moist and dry site we selected

197   late-successional canopy species for NSC sampling. In the moist site all sampled trees

198   had a DBH ≥ 20 cm. This is a hyperdiverse forest making it challenging to find many

199   infested and non-infested individuals of the same species. We selected those tree species

200   that are representative of the community and which we could find at least three infested

201   and non-infested individuals (Table 1), the sampled species represent ≈24% of the total

202   plot basal area. In the moist site we sampled 59 individual trees (30 non-infested, 29

203   infested) from 10 species, and 55 lianas with DBH ≥ 5 that were infesting those trees.

204   From the 10 species we sampled in the moist site eight are evergreen, one is deciduous

205   (*Pouteria torta*), and one is a semi-deciduous species (*Cedrelinga cateniformis*). For

206   Amazonian species wood density and tree size are good proxies for life-history strategies

207   (Coelho de Souza et al. 2016).In the moist site, species span a wide range across the fast–

208   slow continuum of growth, with species with wood density as low as 0.38 g/cm^3 to up to

209   0.87 g/cm^3 (Chave et al. 2009, Zanne et al. 2009).

210   In the dry site, due to the smaller tree sizes, sampling was performed on trees with

211   diameter ≥ 10 cm. However, preference was given to larger individuals whenever

9

212   possible. In the dry site, we sampled individuals from four species from a mixed plot

213   where these species accounted for ≈61% of the total plot basal area (Soares Jancoski et

214   al. 2022), and one species, *Brosimum rubescens*, from a plot where it is the

215   monodominant species and accounts for ≈70% of the total plot basal area. For the dry site

216   we sampled in total 71 trees (31 non-infested trees, 40 infested trees) and 37 lianas with

217   DBH ≥ 5 cm infesting those trees. In the dry site four out five species are evergreen, and

218   one is a brevi-deciduous (*Mabea fistulifera*). Species sampled in this site have high wood

219   density, varying between 0.61 to 0.80 g/cm^3 (Soares Jancoski et al. 2022). Due to the

220   difficulty in accessing leaf and fertile material, lianas were not identified on any of the

221   sites.

222   We collected stem samples for both trees and lianas at 1.20 m above the ground

223   using a 4.3 mm increment borer (Haglöf Company Group, Sweden). To quantify the

224   stored NSC concentration and not transient sugars we removed the bark and phloem and

225   then obtained the stem xylem cores of lianas and trees. As tree species vary in their growth

226   rates, we use a proportion of the sampled core that should roughly represent the last five

227   years of growth increment. This is because liana infestation status (COI) changes over

228   time and we established five years as the minimum period over which COI measured

229   during our field campaign could reasonably be expected to apply. Establishing a fixed

230   window for analysis based on five years of growth should also reduce the bias caused by

231   trees growing under different environmental conditions. To estimate the proportion of the

232   core to use in the NSC analyses we calculated the growth rate of each species using

233   inventory data from TAM-05, TAM-07, VCR-01 and VCR-02 plots (Lopez-Gonzalez et

234   al. 2011, ForestPlot.net et al. 2021). When possible, we used the growth rate of the

235   sampled individual trees to estimate the amount of material for NSC analysis. When this

236   was not possible, we used the mean growth rate calculated for the species across all

10

237   individuals of the species occurring in the plot. It is worth noting that the sampled infested

238   and non-infested trees did not differ in growth rate, likely due to a temporal mismatch

239   between the growth data at our disposal and the liana infestation data (data not presented).

240   This result may reflect the small number of individuals of each species, and the fact that

241   for some of them it was not possible to obtain the mean growth rate. Lianas have a small

242   stem diameter increment (Putz 1990, Restom and Nepstad 2004), and therefore, we

243   standardize the amount of material used to 1.5 cm long cores (excluding bark and phloem)

244   to ensure that we had enough liana material for the NSC analysis.

245   *Non-structural carbohydrates quantification*

246   Before the NSC quantification we ground the samples to a fine powder

247   (GenoGrinder®, USA). Non-structural carbohydrates are defined here as free, low

248   molecular weight sugars (glucose, fructose, sucrose, etc) plus starch. NSC was analysed

249   as described in Hoch et al. (2002) with minor modifications (Rowland et al. 2015,

250   Signori-Müller et al. 2021, 2022). First, we diluted 15 mg of the ground plant material

251   with 1.6 ml of distilled water and then incubated in a water bath at 90–100°C for 60 min

252   to solubilize sugars. We then took an aliquot of 700 μl from each sample and used the

253   remaining aliquot volume (900 μl) to determine soluble sugar concentrations using

254   invertase from *Saccharomyces cerevisiae* (Sigma-Aldrich, USA) to break down sucrose

255   and fructose to glucose. Additionally, for both reaction routines, we used GAHK

256   (Glucose Assay Hexokinase Kit – Sigma-Aldrich, USA) together with phosphoglucose

257   isomerase from *Saccharomyces cerevisiae* (Sigma-Aldrich, USA). The concentration of

258   free glucose was measured photometrically in a 96-well microplate spectrophotometer at

259   340 mm (EPOCH – Biotek Instruments INC, USA). The 700 μl aliquot that we initially

260   separated was incubated overnight to react with amyloglucosidase from *Aspergillus niger*

11

261   (Sigma-Aldrich, USA) to break down the total NSC to glucose. Thereafter total glucose

262   (corresponding to NSC) was determined as described above and starch was calculated as

263   total NSC minus soluble sugars. All NSC values are expressed in mg/g dry mass.

264   *Statistical analysis*

265   We performed all statistical analysis using R software (R Core Team 2018,

266   version 4.2.3). Preliminary tests included: analysis of normality (Shapiro–Wilk), and

267   homogeneity of variances (Flinger–Killeen) for each NSC fraction (NSC, starch and

268   soluble sugars). As NSC, starch and soluble sugars were not normally distributed, we

269   used non-parametric analyses or log1p transformed the data.

270   To conduct a paired analysis to test differences in median stem NSC, starch and

271   soluble sugars between infested and non-infested trees we averaged the concentration per

272   species and used the Paired Samples Wilcoxon Test. We also tested the effect of

273   infestation at species level for species where $n \geq 3$ (Tab. 1) using a t-test, following log1p

274   transformation of NSC data. We investigated whether infestation influences NSC

275   concentration of trees depending on the leaf habit. Due to the small number of species

276   that are not evergreen (Tab. 1), we used the individual value of each sampled tree and

277   grouped deciduous and semi-deciduous species into a single group. Analysis was

278   conducted independently for each site and NSC fraction using Wilcoxon Tests.

279   As species with different life strategies may differ in their response to liana

280   infestation (Visser et al. 2018), we tested how the NSC varied depending on the level of

281   infestation (COI) interacting with species wood density, a trait established as a good

282   proxy to identify the position of species across the fast-slow continuum of growth for

283   Amazonian species (Kitajima and Poorter 2008, Coelho de Souza et al. 2016). We

12

284   perform the analysis separately from each site and each NSC fraction using the *lmer*

285   function from lme4 package (Bates et al. 2007), for this analysis we used the individual

286   log1p transformed NSC, starch and soluble sugars concentration for each tree and species

287   as random effect. Wood density data from the dry site is from (Soares Jancoski et al.

288   2022) and from the moist site from (Zanne et al. 2009), diameter was measured in situ in

289   the sampled trees at 130 cm above the ground.

290   To compare the NSC concentration of trees and lianas we used Wilcoxon rank

291   sum test. Analysis was performed using the individual NSC concentration of each

292   individual tree and liana, for each NSC fraction and site. As lianas were not identified it

293   was not possible to carry out analysis that control for the lack of independence between

294   observations within species. For all analyses, we assumed a significance level of 0.05.

295   **Results**

296   *Infested vs non-infested trees*

297   Our results demonstrate that NSC concentrations in stem xylem are similar in

298   infested (Median±SE; 30.8 ± 1.73 mg/g) and non-infested trees (28.4 ± 1.43 mg/g; $p >$

299   0.05; Paired Samples Wilcoxon Test; Fig. 2S). Furthermore, these results remain

300   consistent across both the dry and moist sites (Fig. 1). Infested and non-infested trees

301   have similar starch (infested: 16.0 ± 1.92 mg/g; non-infested: 1.32 ± 1.31 mg/g) and

302   soluble sugars (infested: 7.67 ± 1.35 mg/g; non-infested: 7.88 ± 0.75 mg/g) concentration

303   (Fig 2S), with results consistent for the dry and moist sites (Fig. 1). At species level (Fig.

304   2), only *Pouteria torta*, from the moist site, showed statistically significant differences in

305   stem starch concentration between infested (17.8 ± 2.17 mg/g) and non-infested trees

306   (34.7 ± 1.55, p <0.05), all other species from both sites had similar stem NSC, starch and

13

307   soluble sugars concentrations between infested and non-infested trees. There were also

308   no significant differences observed between infested and non-infested trees when we

309   examined deciduous and evergreen species separately (Fig. 3S).

310   We fitted Linear Mixed-Effects Models to predict NSC, starch and soluble sugar

311   concentration with infestation level and wood density as predictors and found that overall,

312   the explanatory power of these models was low, especially at the dry site (Table 2 and3).

313   Interaction between infestation level (COI), and wood density did not explain the variance

314   in any NSC fraction in both dry and moist sites (Fig. 4S). Only wood density alone in the

315   moist site has a statistically significant and positive relationship on stem NSC and starch

316   concentration (Fig. 3; Table 2-3).

317   *Trees vs. lianas*

318   Due to the lack of differences in NSC, starch and soluble sugar concentrations

319   between infested and non-infested trees we grouped them to compare to lianas.

320   Lianas have higher stem NSC concentrations than trees (Fig. 4) both in the dry

321   (liana: 59.1 ± 6.15 mg/g; tree: 34.2 ± 3.69 mg/g; $p < 0.001$) and moist site (liana: $59.5 \pm$

322   6.15 mg/g; tree: 24.8 ± 4.43 mg/g; $p < 0.001$). Stem starch concentrations were higher in

323   lianas than in trees (Fig. 4), both in the dry (liana: 47.2 ± 5.56 mg/g; tree: 16 ± 3.30 mg/g;

324     $p < 0.001$; Wilcoxon rank sum test) and moist site (liana: 44 ± 6.69 mg/g; tree: $17.9 \pm$

325   4.33; $p < 0.001$). In the moist site, stem soluble sugar concentrations were higher in lianas

326   (17.6 ± 1.31 mg/g; $p < 0.001$) than in trees (6.25 ± 0.73 mg/g; Fig. 4), while in the dry

327   site both life forms have similar stem soluble sugar concentrations (liana: 11.5 ± 1.24

328   mg/g; tree: 12.6 ± 1.83 mg/g; $p = 0.92$). Lianas had similar NSC, starch and soluble sugar

329   concentrations in both sites (Fig. 6S), while trees only differed among sites with respect

14

330   to soluble sugar concentrations, which was higher in the dry site (Fig. 6S)

331   The proportion of total NSC allocated to soluble sugars (SS:NSC) was similar

332   between lianas (30.0 ± 2.67) and trees (29.3 ± 2.75) in the moist site (p = 0.60; Wilcoxon

333   rank sum test), but not in the dry site (Fig. 5), where we find trees have higher SS:NSC

334   (49.1 ± 3.73) than lianas (30.9 ± 3.16; p = 0.005). Intersite comparisons show that lianas

335   have similar SS:NSC among sites (p > 0.05), while for trees the higher SS:NSC are found

336   in the dry site (p < 0.001; Fig. 6S).

337   **Discussion**

338   Despite its role in plant fitness, to our knowledge, this is the first study to

339   investigate differences in NSC concentrations of trees and lianas, and the effect of liana

340   infestation on tree NSC concentrations. The hypothesis that lianas have higher xylem

341   stem NSC than trees was confirmed by our results (Fig. 2). However, our hypothesis that

342   major differences in NSC concentration between trees and lianas would occur in the dry

343   site was not confirmed by our results. In fact, in the dry site, soluble sugar concentrations

344   in tree stem xylem were indistinguishable to those from lianas, while starch and total NSC

345   were higher in lianas than in trees in both sites (Fig. 4). Despite the negative impact of

346   liana infestation on host trees (Schnitzer et al. 2005, 2014, van der Heijden et al. 2013,

347   2015, Reis et al. 2020), our results do not support the hypothesis that liana infestation can

348   lead to changes in stem NSC concentration of Amazonian trees (Fig. 1).

349   *Infested vs non-infested trees*

350   Liana presence may prevent trees from experiencing the expected maximum

351   growth capacity throughout their lifetime (Godoy-Veiga et al. 2018), with more

352   pronounced negative effect in fast-growing species than in slow-growing species (Visser

15

353 et al. 2018). Despite that we found no difference in stem NSC, starch and soluble sugar

354 concentration of infested and non-infested trees regardless of tree life-history strategy

355 (Tab. 1-2, Fig. 3, Fig. 4S). The fitted linear models only showed a significant relationship

356 between NSC and starch with wood density in the moist site (Fig. 3), and it was

357 independent of infestation or tree size. These results are in line with previous studies with

358 Amazonian species, which showed that across the fast-slow continuum of life story

359 strategies, stem starch is positively related with wood density (Herrera-Ramírez et al.

360 2021, Signori-Müller et al. 2022). The lack of relationship between starch and wood

361 density in the dry site may reflect the fact that only species with high wood density were

362 sampled there. Reis et al. (2020) showed that in the southern Amazonia, where our dry

363 site is located, slow-growing, dense-wooded species are more susceptible to liana

364 infestation than fast-growing species, elucidating the absence of species with low wood

365 density in our data set. Considering the many impacts lianas have on trees performance

366 and community structure the results we found are surprising. (Ingwell et al. 2010, García

367 León et al. 2017, Reis et al. 2020).

368   Although lianas can exert mechanical damage on host trees, causing changes in

369 leaf and branch area index (Schnitzer and Bongers 2002, Reis et al. 2020) the mechanical

370 stress they induce on host trees does not affect stem NSC concentrations (Fig. 1).

371 Rademacher et al. (2021), manipulated phloem transport in a conifer species through

372 compressing the stem, and found that although compression affects wood formation it

373 does not affect the NSC reserves. Investigating the impact of liana infestation on water

374 status of trees species in a forest close to our dry site, in southeast Amazon, Beú (2019)

375 found infested and non-infested trees have similar pre-dawn and mid-day water potential

376 across seasons. Based on our findings of no difference in NSC concentrations between

377 infested and non-infested trees, we hypothesise that the much-reported impacts of lianas

16

378 on forest dynamics (reduced growth, increased mortality) (Ingwell et al. 2010, van der

379 Heijden et al. 2015, Reis et al. 2020, 2022), may be mediated primarily by the weakening

380 of tree structure..

381

382 *Tree vs lianas*

383   Parenchymatic cells constitute a major NSC storage compartment in plants

384 (Plavcová and Jansen 2015), and have been reported to be found in lianas in amounts

385 about twice as high as in angiosperm trees (Morris et al. 2016). We find the stem xylem

386 NSC concentrations in lianas are the double of that in trees. This may be driven by a

387 greater parenchyma fraction in stem xylem of lianas relative to trees and not necessarily

388 by greater NSC concentrations per unit of parenchyma.

389   Trees can have access to NSC pools integrating carbon accumulated over more

390 than a decade (Vargas et al. 2009, Muhr et al. 2018). Despite the ability of trees to use

391 old, stored carbon, some NSC accumulated in woody tissues may become sequestered,

392 and therefore not available for future use, representing a metabolic dead end, with the

393 carbon no longer physiologically active and so not affecting metabolism (Millard et al.,

394 2007). Maximum ages of accessible carbon reserves could be affected by the time that

395 sapwood is alive and functional before it undergoes heartwood transformation (Muhr et

396 al. 2018). Average sapwood lifespans for tropical tree species can vary between 5.7 and

397 88.6 years with an average of 29.78 years (van der Sande et al. 2015). In the trees, we

398 quantified the NSC concentration in a portion of the xylem that represent the increment

399 of the last five years (see methods), which likely encompasses the functional portion of

400 the xylem. For lianas, we standardized the length of the xylem segment we used for

17

401   analysis to 1.5 cm, which may represent growth increments of > 10 years (considering

402   stem increment of 1.4 mm/year presented by Putz 1990 and Restom and Nepstad 2004).

403   Information about liana sapwood lifespan is missing, however it is known that they have

404   a high sapwood to heartwood ratio (Tyree and Ewers 1996), therefore for the purposes of

405   this study we assume the xylem portion we analysed for lianas is active and reserves in

406   this portion accessible to be used. To understand the liana dynamics and its increase in

407   abundance in some areas, we must comprehend its carbon metabolism, including the

408   dynamics of NSC, which remains unexplored compared to the water relations (i.e.,

409   hydraulic traits). Future studies should prioritize investigating the life span of liana xylem

410   and the extent to which lianas can utilize stored (NSC) that are several years old and in

411   which temporal scale it occurs (seasonally vs extreme events) (Carbone et al. 2007,

412   Vargas et al. 2009).

413   A recent study conducted in a tropical forest in Panama showed that lianas have

414   the ability to maintain higher growth rates during dry season and the authors speculate

415   this may occur through the maintenance of high water potential or by relying on stored

416   NSC (Schnitzer and van der Heijden 2019). Starch, which we found concentrations in

417   lianas to be higher than in trees in both sites, is a long term NSC fraction that can be

418   remobilized to fulfil plant needs for carbon when demand is higher than assimilation

419   (MacNeill et al. 2017). Through analysis of scanning electron photomicrographs of liana

420   xylem, Masrahi (2014) found a dense accumulation of starch grains on ray parenchyma

421   cells near vessel groups of lianas from a very dry area (precipitation 150 mm/year). We

422   speculate that by relying on the structural investment of trees for mechanical support,

423   lianas can allocate a high proportion of the assimilated carbon into reserves. By being

424   hydrolysed into soluble sugars, starch can support growth, enhance water flow by raising

425   vessel osmotic pressure to regulate conductance and reduce the risk of embolism entering

18

426   the vessels (Thalmann and Santelia 2017, Tomasella et al. 2017). High concentrations of

427   starch allied to parenchyma cells in contact with vessels could enable lianas to have easy

428   access and use of the NSC reserves, increasing hydraulic efficiency without

429   compromising safety (Secchi et al. 2017), promoting growth during period of carbon

430   limitation and fuelling liana reproductive events and leaf flush (Olson 2003, Schnitzer

431   and van der Heijden 2019).

432   In this study differences between trees and lianas were overall consistent in both

433   dry and moist sites, while other studies found co-occurring trees and lianas differ more in

434   drier than in wetter sites in functional traits related to water transport, (Medina-Vega,

435   Bongers, Poorter, et al. 2021, Smith-Martin et al. 2022). The only similarity observed in

436   stem NSC concentration between the different life forms was found in the soluble sugars

437   fraction in the dry forest (Fig. 4). Although absolute stem soluble sugar concentration of

438   both life-forms was similar in the dry site, the proportion of the total NSC allocated to

439   soluble sugars (SS:NSC) was higher for trees than for lianas (Fig. 5). A study considering

440   leaves and branches of Amazonian tree species, also found higher SS:NSC in more dry

441   and seasonal sites (Signori-Müller et al. 2021). Together these results reinforce the idea

442   that soluble sugars cannot be drawn below a certain threshold (Sala et al. 2012) due to its

443   immediate role in the maintenance of plant metabolism (e.g., growth, respiration,

444   osmoregulation, embolism repair, etc. Rosa et al. 2009, Krasensky and Jonak 2012,

445   MacNeill et al. 2017, Thalmann and Santelia 2017). Based on the higher starch

446   concentrations in lianas than in trees, lianas could have more carbon to fulfil their soluble

447   sugar requirements than trees, in both dry and moist sites. The increase in liana abundance

448   towards areas that are experiencing reduction in water availability and increasing

449   seasonality, especially in the Neotropics (Phillips et al. 2002, Laurance et al. 2014,

450   Marimon et al. 2020), may be the result of a well-adjusted hydraulic system and carbon

19

451 metabolism (McDowell 2011).

452 **Conclusion**

453 In Amazonian tree species, high starch concentration in stem xylem is linked to
454 high wood density and low mortality rates (Herrera-Ramirez et al. 2021, Signori-Müller
455 et al. 2022). For lianas, it is unknown whether starch or soluble sugar concentrations are
456 related to plant life-history traits and whether the seasonal dynamics are similar to those
457 in trees. An increasing number of experimental studies with mature trees, seedlings and
458 shrubs shows that under stressful conditions plants with higher NSC concentrations can
459 cope better with stressors (e.g., drought, canopy damage), hence increasing survival rates
460 (e.g., O'Brien et al. 2014, Shibata et al. 2016, Tomasella et al. 2017, Gessler and
461 Grossiord 2019, Guo et al. 2020). Non-structural carbohydrates may play a similar role
462 in liana response to stressors as it does in plants with other life forms, even favouring
463 liana growth in periods that trees would prioritize the maintenance of storage (Schnitzer
464 and van der Heijden 2019, Chuste et al. 2019). The high starch concentration in lianas
465 compared to trees, point to differences in carbon gain (Cai et al. 2009) and possibly in
466 carbon storage and use. To be able to predict changes in forest composition and carbon
467 accumulation, we need to understand the mechanisms linked to liana ability to increase
468 in abundance in areas where seasonality in precipitation is increasing. An underrate but
469 key component to understand it can be related to how liana use its carbon reserves and
470 how well coordinated it is with their hydraulic system. Despite their significance, lianas
471 are persistently understudied and even a basic understanding of NSC dynamics remains
472 elusive (Zotz et al. 2006, Slot et al. 2014).

473 We do not rule out the hypothesis that liana infestation may impact the NSC
474 dynamics of host trees. To better understand if it is the case, future studies should

20

475 investigate for example if there are differences in NSC concentrations of infested and

476 non-infested trees also during the dry season, when water transport and carbon

477 assimilation are potentially compromised (Wagner et al. 2016). Leaves and branches,

478 which have more dynamic NSC pools should also be considered (Würth et al. 2005,

479 Signori-Müller et al. 2022). It may be that the canopy organs may have more carbon

480 imbalance due to liana infestation than the stem xylem, which can serve as a long-term

481 storage organ thus less affected if storage is prioritized over growth (Herrera-Ramírez et

482 al. 2021, Signori-Müller et al. 2022).

21

Authors' contributions

C.S.-M., R.S.O., D.G. and M.M. conceived the research ideas. C.S.-M. led the data analysis and writing of the manuscript. C.S.-M. and J.V.T. led the field sampling for the moist site; C.S.-M., S.M.R. and B.S.M. led the field sampling for the dry site. C.S.-M., J.V.T., F.C.D., M.G., A.N., C.A.S.Y. and M.J.M.Z collected samples in the moist site. S.M.R, C.B. and P.S.M. collected samples in the dry site. C.S.-M., M.G., S.M. and B.B.L.C. took part on sample preparing and analysis. G.M.F.v.d.H. provided the crown occupancy index for the moist site. B.S.M. provided the crown occupancy index for the dry site. R.B., E.G.C., B.S.M., B.H.M.J., A.M.M., O.P., N.S. and R.V. lead the ForestPlots.net field expeditions for data collection for inventory. All authors contributed to the drafts and gave the final approval for publication.

Acknowledgments

22

507 authors' view, and the European Commission/Agency is not responsible for any use that

508 may be made of the information it contains. This paper is an outcome of ForestPlots.net

509 approved Research Project #18. The authors especially thank: Vanessa Hilares and the

510 Asociación para la Investigación y Desarrollo Integral (AIDER) for field campaign

511 support; Hugo Ninantay and Alex Ninantay for sample collection; Fernanda Piccolo for

512 laboratory support; and Adriane Esquivel-Muelbert for comments on an early version of

513 this manuscript.

514 **Data availability**

515 The stem non-structural carbohydrate concentration data for trees and lianas are available

516 as data packages via ForestPlots.net (available after manuscript acceptance). The

517 inventory data to estimate species growth rate at the study site are from the RAINFOR

518 network, available upon request at ForestPlots.net (Lopez-Gonzalez et al. 2011,

519 ForestPlot.net et al. 2021). Wood density from species occurring in the dry site are from

520 Soares Jancoski et al. (2022), for species in the moist site, we used mean species wood

521 density for the Amazon Basin from Chave et al. (2009), Zanne et al. (2009).

522 **Conflict of interest**

523 The authors declare that there are no conflicts of interest.

524 **References**
525 Andrade JL, Meinzer FC, Goldstein G, Schnitzer SA (2005) Water uptake and transport
526   in lianas and co-occurring trees of a seasonally dry tropical forest. Trees - Struct
527   Funct 19:282–289.
528 Avalos G, Mulkey SS, Kitajima K, Wright SJ (2007) Colonization strategies of two
529   liana species in a tropical dry forest canopy. Biotropica 39:393–399.
530 Bates D, Sarkar D, Bates MD, Matrix L (2007) The lme4 Package. October 2:1–6.
531   http://postgresql.mirrorservice.org/sites/lib.stat.cmu.edu/R/CRAN/doc/packages/l
532   me4.pdf
533 Beú RG (2019) Como as lianas afetam árvores de um cerradão na transição Amazônia-
534   Cerrado? Universidade do Estado de Mato Grosso.
535   http://portal.unemat.br/media/files/raiane-beu-ppgec-dissertacao-2017.pdf
536 Cai ZQ, Schnitzer SA, Bongers F (2009) Seasonal differences in leaf-level physiology
537   give lianas a competitive advantage over trees in a tropical seasonal forest.
538   Oecologia 161:25–33.

23

539   Carbone MS, Czimczik CI, McDuffee KE, Trumbore SE (2007) Allocation and
540   residence time of photosynthetic products in a boreal forest using a low-level 14C
541   pulse-chase labeling technique. Glob Chang Biol 13:466–477.

542   Carvalho ECD, Martins FR, Soares AA, Oliveira RS, Muniz CR, Araújo FS (2015)
543   Hydraulic architecture of lianas in a semiarid climate: Efficiency or safety? Acta
544   Bot Brasilica 29:198–206.

545   Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a
546   worldwide wood economics spectrum. Ecol Lett 12:351–366.

547   Chen YJ, Schnitzer SA, Zhang YJ, Fan ZX, Goldstein G, Tomlinson KW, Lin H, Zhang
548   JL, Cao KF (2017) Physiological regulation and efficient xylem water transport
549   regulate diurnal water and carbon balances of tropical lianas. Funct Ecol 31:306–
550   317.

551   Chuste P-A, Maillard P, Bréda N, Levillain J, Thirion E, Wortemann R, Massonnet C
552   (2019) Sacrificing growth and maintaining a dynamic carbohydrate storage are key
553   processes for promoting beech survival under prolonged drought conditions. Trees
554   34:381–394. https://doi.org/10.1007/s00468-019-01923-5

555   Coelho de Souza F, Dexter KG, Phillips OL, Brienen RJW, Chave J, Galbraith DR,
556   Lopez Gonzalez G, Monteagudo Mendoza A, Pennington RT, Poorter L, Alexiades
557   M, Álvarez-Dávila E, Andrade A, Aragão LEOC, Araujo-Murakami A, Arets
558   EJMM, Aymard C GA, Baraloto C, Barroso JG, Bonal D, Boot RGA, Camargo
559   JLC, Comiskey JA, Valverde FC, de Camargo PB, Di Fiore A, Elias F, Erwin TL,
560   Feldpausch TR, Ferreira L, Fyllas NM, Gloor E, Herault B, Herrera R, Higuchi N,
561   Honorio Coronado EN, Killeen TJ, Laurance WF, Laurance S, Lloyd J, Lovejoy
562   TE, Malhi Y, Maracahipes L, Marimon BS, Marimon-Junior BH, Mendoza C,
563   Morandi P, Neill DA, Vargas PN, Oliveira EA, Lenza E, Palacios WA, Peñuela-
564   Mora MC, Pipoly JJ, Pitman NCA, Prieto A, Quesada CA, Ramirez-Angulo H,
565   Rudas A, Ruokolainen K, Salomão RP, Silveira M, Stropp J, ter Steege H,
566   Thomas-Caesar R, van der Hout P, van der Heijden GMF, van der Meer PJ,
567   Vasquez R V., Vieira SA, Vilanova E, Vos VA, Wang O, Young KR, Zagt RJ,
568   Baker TR (2016) Evolutionary heritage influences Amazon tree ecology. Proc R
569   Soc B Biol Sci 283:20161587.
570   http://rspb.royalsocietypublishing.org/lookup/doi/10.1098/rspb.2016.1587

571   De Deurwaerder H, Hervé-Fernández P, Stahl C, Burban B, Petronelli P, Hoffman B,
572   Bonal D, Boeckx P, Verbeeck H (2018) Liana and tree below-ground water
573   competition—evidence for water resource partitioning during the dry season. Tree
574   Physiol:1071–1083. https://academic.oup.com/treephys/advance-
575   article/doi/10.1093/treephys/tpy002/4917324

576   DeWalt SJ, Schnitzer SA, Chave J, Bongers F, Burnham RJ, Cai Z, Chuyong G, Clark
577   DB, Ewango CEN, Gerwing JJ, Gortaire E, Hart T, Ibarra-Manríquez G, Ickes K,
578   Kenfack D, Macía MJ, Makana JR, Martínez-Ramos M, Mascaro J, Moses S,
579   Muller-Landau HC, Parren MPE, Parthasarathy N, Pérez-Salicrup DR, Putz FE,
580   Romero-Saltos H, Thomas D (2010) Annual Rainfall and Seasonality Predict Pan-
581   tropical Patterns of Liana Density and Basal Area. Biotropica 42:309–317.

582   Dickman LT, Mcdowell NG, Sevanto S, Pangle RE, Pockman WT (2015) Carbohydrate
583   dynamics and mortality in a piñon-juniper woodland under three future
584   precipitation scenarios. Plant, Cell Environ 38:729–739.

585   Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas
586   R (2014) Nonstructural Carbon in Woody Plants. Annu Rev Plant Biol 65:667–
587   687. http://www.annualreviews.org/doi/10.1146/annurev-arplant-050213-040054

588   Durán SM, Gianoli E (2013) Carbon stocks in tropical forests decrease with liana

24

589   density. Biol Lett 9:3–6.

590 Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, ter Steege H, Lopez-Gonzalez
591   G, Monteagudo Mendoza A, Brienen R, Feldpausch TR, Pitman N, Alonso A, van
592   der Heijden G, Peña-Claros M, Ahuite M, Alexiaides M, Álvarez Dávila E,
593   Murakami AA, Arroyo L, Aulestia M, Balslev H, Barroso J, Boot R, Cano A,
594   Chama Moscoso V, Comiskey JA, Cornejo F, Dallmeier F, Daly DC, Dávila N,
595   Duivenvoorden JF, Duque Montoya AJ, Erwin T, Di Fiore A, Fredericksen T,
596   Fuentes A, García-Villacorta R, Gonzales T, Guevara Andino JE, Honorio
597   Coronado EN, Huamantupa-Chuquimaco I, Killeen TJ, Malhi Y, Mendoza C,
598   Mogollón H, Jørgensen PM, Montero JC, Mostacedo B, Nauray W, Neill D,
599   Vargas PN, Palacios S, Palacios Cuenca W, Pallqui Camacho NC, Peacock J,
600   Phillips JF, Pickavance G, Quesada CA, Ramírez-Angulo H, Restrepo Z, Reynel
601   Rodriguez C, Paredes MR, Sierra R, Silveira M, Stevenson P, Stropp J, Terborgh J,
602   Tirado M, Toledo M, Torres-Lezama A, Umaña MN, Urrego LE, Vasquez
603   Martinez R, Gamarra LV, Vela CIA, Vilanova Torre E, Vos V, von Hildebrand P,
604   Vriesendorp C, Wang O, Young KR, Zartman CE, Phillips OL (2017) Seasonal
605   drought limits tree species across the Neotropics. Ecography (Cop) 40:618–629.

606 Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces
607   for global land areas. Int J Climatol 37:4302–4315.

608 Forest P net, Blundo C, Carilla J, Grau R, Malizia A, Malizia L, Osinaga-Acosta O,
609   Bird M, Bradford M, Catchpole D, Ford A, Graham A, Hilbert D, Kemp J,
610   Laurance S, Laurance W, Ishida FY, Marshall A, Waite C, Woell H, Bastin JF,
611   Bauters M, Beeckman H, Boeckx P, Bogaert J, De Canniere C, de Haulleville T,
612   Doucet JL, Hardy O, Hubau W, Kearsley E, Verbeeck H, Vleminckx J, Brewer
613   SW, Alarcón A, Araujo-Murakami A, Arets E, Arroyo L, Chavez E, Fredericksen
614   T, Villaroel RG, Sibauty GG, Killeen T, Licona JC, Lleigue J, Mendoza C,
615   Murakami S, Gutierrez AP, Pardo G, Peña-Claros M, Poorter L, Toledo M, Cayo
616   JV, Viscarra LJ, Vos V, Ahumada J, Almeida E, Almeida J, de Oliveira EA, da
617   Cruz WA, de Oliveira AA, Carvalho FA, Obermuller FA, Andrade A, Carvalho
618   FA, Vieira SA, Aquino AC, Aragão L, Araújo AC, Assis MA, Gomes JAMA,
619   Baccaro F, de Camargo PB, Barni P, Barroso J, Bernacci LC, Bordin K, de
620   Medeiros MB, Broggio I, Camargo JL, Cardoso D, Carniello MA, Rochelle ALC,
621   Castilho C, Castro AAJF, Castro W, Ribeiro SC, Costa F, de Oliveira RC,
622   Coutinho I, Cunha J, da Costa L, da Costa Ferreira L, da Costa Silva R, da Graça
623   Zacarias Simbine M, de Andrade Kamimura V, de Lima HC, de Oliveira Melo L,
624   de Queiroz L, de Sousa Lima JR, do Espírito Santo M, Domingues T, dos Santos
625   Prestes NC, Carneiro SES, Elias F, Eliseu G, Emilio T, Farrapo CL, Fernandes L,
626   Ferreira G, Ferreira J, Ferreira L, Ferreira S, Simon MF, Freitas MA, García QS,
627   Manzatto AG, Graça P, Guilherme F, Hase E, Higuchi N, Iguatemy M, Barbosa
628   RI, Jaramillo M, Joly C, Klipel J, do Amaral IL, Levis C, Lima AS, Dan ML,
629   Lopes A, Madeiros H, Magnusson WE, dos Santos RM, Marimon B, Junior BHM,
630   Grillo RMM, Martinelli L, Reis SM, Medeiros S, Meira-Junior M, Metzker T,
631   Morandi P, do Nascimento NM, Moura M, Müller SC, Nagy L, Nascimento H,
632   Nascimento M, Lima AN, de Araújo RO, Silva JO, Pansonato M, Sabino GP, de
633   Abreu KMP, Rodrigues PJFP, Piedade M, Rodrigues D, Rodrigues Pinto JR,
634   Quesada C, Ramos E, Ramos R, Rodrigues P, de Sousa TR, Salomão R, Santana F,
635   Scaranello M, Bergamin RS, Schietti J, Schöngart J, Schwartz G, Silva N, Silveira
636   M, Seixas CS, Simbine M, Souza AC, Souza P, Souza R, Sposito T, Junior ES, do
637   Vale JD, Vieira ICG, Villela D, Vital M, Xaud H, Zanini K, Zartman CE, Ideris
638   NKH, Metali F binti H, Salim KA, Saparudin MS, Serudin RM, Sukri RS, Begne

25

639   S, Chuyong G, Djuikouo MN, Gonmadje C, Simo-Droissart M, Sonké B,
640   Taedoumg H, Zemagho L, Thomas S, Baya F, Saiz G, Espejo JS, Chen D,
641   Hamilton A, Li Y, Luo T, Niu S, Xu H, Zhou Z, Álvarez-Dávila E, Escobar JCA,
642   Arellano-Peña H, Duarte JC, Calderón J, Bravo LMC, Cuadrado B, Cuadros H,
643   Duque A, Duque LF, Espinosa SM, Franke-Ante R, García H, Gómez A,
644   González-M. R, Idárraga-Piedrahíta Á, Jimenez E, Jurado R, Oviedo WL, López-
645   Camacho R, Cruz OAM, Polo IM, Paky E, Pérez K, Pijachi A, Pizano C, Prieto A,
646   Ramos L, Correa ZR, Richardson J, Rodríguez E, Rodriguez M. GM, Rudas A,
647   Stevenson P, Chudomelová M, Dancak M, Hédl R, Lhota S, Svatek M, Mukinzi J,
648   Ewango C, Hart T, Yakusu EK, Lisingo J, Makana JR, Mbayu F, Toirambe B,
649   Mukendi JT, Kvist L, Nebel G, Báez S, Céron C, Griffith DM, Andino JEG, Neill
650   D, Palacios W, Peñuela-Mora MC, Rivas-Torres G, Villa G, Demissie S, Gole T,
651   Gonfa T, Ruokolainen K, Baisie M, Bénédet F, Betian W, Bezard V, Bonal D,
652   Chave J, Droissart V, Gourlet-Fleury S, Hladik A, Labrière N, Naisso P, Réjou-
653   Méchain M, Sist P, Blanc L, Burban B, Derroire G, Dourdain A, Stahl C, Bengone
654   NN, Chezeaux E, Ondo FE, Medjibe V, Mihindou V, White L, Culmsee H, Rangel
655   CD, Horna V, Wittmann F, Adu-Bredu S, Affum-Baffoe K, Foli E, Balinga M,
656   Roopsind A, Singh J, Thomas R, Zagt R, Murthy IK, Kartawinata K, Mirmanto E,
657   Priyadi H, Samsoedin I, Sunderland T, Yassir I, Rovero F, Vinceti B, Hérault B,
658   Aiba SI, Kitayama K, Daniels A, Tuagben D, Woods JT, Fitriadi M, Karolus A,
659   Khoon KL, Majalap N, Maycock C, Nilus R, Tan S, Sitoe A, Coronado G. I, Ojo
660   L, de Assis R, Poulsen AD, Sheil D, Pezo KA, Verde HB, Moscoso VC, Oroche
661   JCC, Valverde FC, Medina MC, Cardozo ND, de Rutte Corzo J, del Aguila
662   Pasquel J, Llampazo GF, Freitas L, Cabrera DG, Villacorta RG, Cabrera KG, Soria
663   DG, Saboya LG, Rios JMG, Pizango GH, Coronado EH, Huamantupa-
664   Chuquimaco I, Huasco WH, Aedo YTH, Peña JLM, Mendoza AM, Rodriguez
665   VM, Vargas PN, Ramos SCP, Camacho NP, Cruz AP, Arevalo FR, Huaymacari
666   JR, Rodriguez CR, Paredes MAR, Bayona LR, del Pilar Rojas Gonzales R, Peña
667   MER, Revilla NS, Shareva YCS, Trujillo RT, Gamarra LV, Martinez RV, Arenas
668   JV, Amani C, Ifo SA, Bocko Y, Boundja P, Ekoungoulou R, Hockemba M, Nzala
669   D, Fofanah A, Taylor D, Bañares-de Dios G, Cayuela L, la Cerda ÍG de, Macía M,
670   Stropp J, Playfair M, Wortel V, Gardner T, Muscarella R, Rutishauser E, Chao KJ,
671   Munishi P, Bánki O, Bongers F, Boot R, Fredriksson G, Reitsma J, ter Steege H,
672   van Andel T, van de Meer P, van der Hout P, van Nieuwstadt M, van Ulft B,
673   Veenendaal E, Vernimmen R, Zuidema P, Zwerts J, Akite P, Bitariho R, Chapman
674   C, Gerald E, Leal M, Mucunguzi P, Abernethy K, Alexiades M, Baker TR, Banda
675   K, Banin L, Barlow J, Bennett A, Berenguer E, Berry N, Bird NM, Blackburn GA,
676   Brearley F, Brienen R, Burslem D, Carvalho L, Cho P, Coelho F, Collins M,
677   Coomes D, Cuni-Sanchez A, Dargie G, Dexter K, Disney M, Draper F, Duan M,
678   Esquivel-Muelbert A, Ewers R, Fadrique B, Fauset S, Feldpausch TR, França F,
679   Galbraith D, Gilpin M, Gloor E, Grace J, Hamer K, Harris D, Jeffery K, Jucker T,
680   Kalamandeen M, Klitgaard B, Levesley A, Lewis SL, Lindsell J, Lopez-Gonzalez
681   G, Lovett J, Malhi Y, Marthews T, McIntosh E, Melgaço K, Milliken W, Mitchard
682   E, Moonlight P, Moore S, Morel A, Peacock J, Peh KSH, Pendry C, Pennington
683   RT, de Oliveira Pereira L, Peres C, Phillips OL, Pickavance G, Pugh T, Qie L,
684   Riutta T, Roucoux K, Ryan C, Sarkinen T, Valeria CS, Spracklen D, Stas S,
685   Sullivan M, Swaine M, Talbot J, Taplin J, van der Heijden G, Vedovato L,
686   Willcock S, Williams M, Alves L, Loayza PA, Arellano G, Asa C, Ashton P,
687   Asner G, Brncic T, Brown F, Burnham R, Clark C, Comiskey J, Damasco G,
688   Davies S, Di Fiore T, Erwin T, Farfan-Rios W, Hall J, Kenfack D, Lovejoy T,

26

689   Martin R, Montiel OM, Pipoly J, Pitman N, Poulsen J, Primack R, Silman M,
690   Steininger M, Swamy V, Terborgh J, Thomas D, Umunay P, Uriarte M, Torre EV,
691   Wang O, Young K, Aymard C. GA, Hernández L, Fernández RH, Ramírez-Angulo
692   H, Salcedo P, Sanoja E, Serrano J, Torres-Lezama A, Le TC, Le TT, Tran HD
693   (2021) Taking the pulse of Earth's tropical forests using networks of highly
694   distributed plots. Biol Conserv 260

695   García León MM, Martínez Izquierdo L, Mello FNA, Powers JS, Schnitzer SA (2017)
696   Lianas reduce community-level canopy tree reproduction in a Panamanian forest. J
697   Ecol:1–9.

698   Gentry AH (1991) The distribution and evolution of climbing plants. Biol vines
699   Cambridge:3–49.

700   Gessler A, Grossiord C (2019) Coordinating supply and demand: plant carbon
701   allocation strategy ensuring survival in the long run. New Phytol 222:5–7.

702   Godoy-Veiga M, Gregório V, Philipp C, Stefan P, Dieter K (2018) Shadows of the edge
703   effects for tropical emergent trees : the impact of lianas on the growth of
704   Aspidosperma polyneuron. Trees 32:1073–1082. http://dx.doi.org/10.1007/s00468-
705   018-1696-x

706   Guo JS, Gear L, Hultine KR, Koch GW, Ogle K (2020) Non-structural carbohydrate
707   dynamics associated with antecedent stem water potential and air temperature in a
708   dominant desert shrub. Plant Cell Environ:1–17.
709   https://onlinelibrary.wiley.com/doi/abs/10.1111/pce.13749

710   Hartmann H, Trumbore S (2016) Understanding the roles of nonstructural
711   carbohydrates in forest trees–from what we can measure to what we want to know.
712   New Phytol 211:386–403.

713   van der Heijden GMF, Powers JS, Schnitzer SA (2015) Lianas reduce carbon
714   accumulation and storage in tropical forests. Proc Natl Acad Sci 112:13267–
715   13271. http://www.pnas.org/lookup/doi/10.1073/pnas.1504869112

716   van der Heijden GMFF, Schnitzer S a, Powers JS, Phillips OL (2013) Liana Impacts on
717   Carbon Cycling, Storage and Sequestration in Tropical Forests. 45:682–692.

718   Herrera-Ramirez D, Sierra CA, Römermann C, Muhr J, Trumbore S, Silvério D, Brando
719   PM, Hartman H (2021) Starch and lipid storage strategies in tropical trees relate to
720   growth and mortality. New Phytol

721   Hoch G, Popp M, Korner C (2002) Altitudinal increase of mobile carbon pools in Pinus
722   cembra suggests sink limitation of growth at the Swiss treeline. Oikos 98:361–374.
723   http://doi.wiley.com/10.1034/j.1600-0706.2002.980301.x

724   Ingwell LL, Joseph Wright S, Becklund KK, Hubbell SP, Schnitzer SA (2010) The
725   impact of lianas on 10 years of tree growth and mortality on Barro Colorado
726   Island, Panama. J Ecol 98:879–887.

727   Kitajima K, Poorter L (2008) Functional basis for resource niche partitioning by tropical
728   trees. In: Carson WP, Schnitzer SA (eds) Tropical forest community ecology.
729   Blackwell Science, pp 160–181.
730   http://www.biology.ufl.edu/COURSES/pcb5356/2010Spring/Kitajima/KitajimaPo
731   orter2008.pdf

732   Krasensky J, Jonak C (2012) Drought, salt, and temperature stress-induced metabolic
733   rearrangements and regulatory networks. J Exp Bot 63:1593–1608.

734   Laurance WF, Andrade AS, Magrach A, Camargo JLC, Valsko JJ, Campbell M,
735   Fearnside PM, Edwards W, Lovejoy TE, Laurance SG (2014) Long-term changes
736   in liana abundance and forest dynamics in undisturbed Amazonian forests. Ecology
737   95:1604–1611.

738   Lopez-Gonzalez G, Lewis SL, Burkitt M, Phillips OL (2011) ForestPlots.net: A web

27

739   application and research tool to manage and analyse tropical forest plot data. J Veg
740   Sci 22:610–613.
741 MacNeill GJ, Mehrpouyan S, Minow MAA, Patterson JA, Tetlow IJ, Emes MJ (2017)
742   Starch as a source, starch as a sink: the bifunctional role of starch in carbon
743   allocation. J Exp Bot 68:4433–4453.
744   http://academic.oup.com/jxb/article/doi/10.1093/jxb/erx291/4103066/Starch-as-a-
745   source-starch-as-a-sink-the
746 Marimon BS, Felfili JM, Lima EDS, Duarte WMG, Marimon-Júnior BH (2010)
747   Environmental determinants for natural regeneration of gallery forest at the
748   Cerrado/Amazonia boundaries in Brazil. Acta Amaz 40:107–118.
749   http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0044-
750   59672010000100014&lng=en&tlng=en
751 Marimon BS, Oliveira-Santos C, Marimon-Junior BH, Elias F, de Oliveira EA, Morandi
752   PS, Nayane NCC do., Mariano LH, Pereira OR, Feldpausch TR, Phillips OL
753   (2020) Drought generates large, long-term changes in tree and liana regeneration in
754   a monodominant Amazon forest. Plant Ecol 8. https://doi.org/10.1007/s11258-020-
755   01047-8
756 Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F
757   (2016) Dynamics of non-structural carbohydrates in terrestrial plants: A global
758   synthesis. Ecol Monogr 86:495–516. http://doi.wiley.com/10.1002/ecm.1231 (14
759   August 2019, date last accessed).
760 Masrahi YS (2014) Ecological significance of wood anatomy in two lianas from arid
761   southwestern Saudi Arabia. Saudi J Biol Sci 21:334–341.
762   http://dx.doi.org/10.1016/j.sjbs.2013.11.005
763 McDowell NG (2011) Mechanisms Linking Drought, Hydraulics, Carbon Metabolism,
764   and Vegetation Mortality. Plant Physiol 155:1051–1059.
765   http://www.plantphysiol.org/cgi/doi/10.1104/pp.110.170704
766 McDowell N, Allen CD, Anderson-Teixeira K, Brando P, Brienen R, Chambers J,
767   Christoffersen B, Davies S, Doughty C, Duque A, Espirito-Santo F, Fisher R,
768   Fontes CG, Galbraith D, Goodsman D, Grossiord C, Hartmann H, Holm J, Johnson
769   DJ, Kassim AR, Keller M, Koven C, Kueppers L, Kumagai T, Malhi Y, McMahon
770   SM, Mencuccini M, Meir P, Moorcroft P, Muller-Landau HC, Phillips OL, Powell
771   T, Sierra CA, Sperry J, Warren J, Xu C, Xu X (2018) Drivers and mechanisms of
772   tree mortality in moist tropical forests. New Phytol 219:851–869.
773 Medina-Vega JA, Bongers F, Poorter L, Schnitzer SA, Sterck FJ (2021) Lianas have
774   more acquisitive traits than trees in a dry but not in a wet forest. J Ecol:1–18.
775 Medina-Vega JA, Bongers F, Schnitzer SA, Sterck FJ (2021) Lianas explore the forest
776   canopy more effectively than trees under drier conditions. Funct Ecol 35:318–329.
777 Medina-Vega JA, Wright SJ, Bongers F, Schnitzer SA, Sterck FJ (2022) Vegetative
778   phenologies of lianas and trees in two Neotropical forests with contrasting rainfall
779   regimes. New Phytol 235:457–471.
780 Meunier F, Verbeeck H, Cowdery B, Schnitzer SA, Powers CMSJS, Xu X, Slot M,
781   Deurwaerder HPT De, Detto M, Bonal D, Longo M, Santiago LS, Dietze M (2021)
782   Unraveling the relative role of light and water competition between lianas and trees
783   in tropical forests : A vegetation model analysis. :519–540.
784 Morris H, Plavcová L, Cvecko P, Fichtler E, Gillingham MAF, Martínez-Cabrera HI,
785   Mcglinn DJ, Wheeler E, Zheng J, Ziemińska K, Jansen S (2016) A global analysis
786   of parenchyma tissue fractions in secondary xylem of seed plants. New Phytol
787   209:1553–1565.
788 Muhr J, Trumbore S, Higuchi N, Kunert N (2018) Living on borrowed time -

789   Amazonian trees use decade-old storage carbon to survive for months after
790   complete stem girdling. New Phytol 220:111–120.
791   http://doi.wiley.com/10.1111/nph.15302
792 Myers JA, Kitajima K (2007) Carbohydrate storage enhances seedling shade and stress
793   tolerance in a neotropical forest. J Ecol 95:383–395.
794 O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A (2014) Drought survival of
795   tropical tree seedlings enhanced by non-structural carbohydrate levels. Nat Clim
796   Chang 4:710–714.
797 Olson ME (2003) Stem and leaf anatomy of the arborescent Cucurbitaceae
798   Dendrosicyos socotrana with comments on the evolution of pachycauls from
799   lianas. Plant Syst Evol 239:199–214.
800 Parolari AJ, Paul K, Griffing A, Condit R, Perez R, Aguilar S, Schnitzer SA (2020)
801   Liana abundance and diversity increase with rainfall seasonality along a
802   precipitation gradient in Panama. Ecography (Cop) 43:25–33.
803 Paul GS, Yavitt JB (2011) Tropical Vine Growth and the Effects on Forest Succession:
804   A Review of the Ecology and Management of Tropical Climbing Plants. Bot Rev
805   77:11–30.
806 Pérez-Salicrup DR (2001) Effect of liana cutting on tree regeneration in a liana forest in
807   Amazonian Bolivia. Ecology 82:389–396.
808 Pérez-Salicrup DR, Barker MG (2000) Effect of liana cutting on water potential and
809   growth of adult Senna multijuga (Caesalpinioideae) trees in a Bolivian tropical
810   forest. 124:469–475.
811 Phillips OL, Vésquez Martínez R, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y,
812   Monteagudo Mendoza A, Neill D, Núñez Vargas P, Alexiades M, Cerón C, Di
813   Flore A, Erwin T, Jardim A, Palacios W, Saldias M, Vinceti B (2002) Increasing
814   dominance of large lianas in Amazonian forests. Nature 418:770–774.
815 Plavcová L, Jansen S (2015) The Role of Xylem Parenchyma in the Storage and
816   Utilization of Nonstructural Carbohydrates. Funct Ecol Xylem Anat:1–281.
817 Poorter L, Kitajima K (2007) Carbohydrate Storage and Light Requirements of Tropical
818   Moist and Dry Forest Tree Species. Ecology 88:1000–1011.
819 Putz FE (1990) Liana Stem Diameter Growth and Mortality Rates on Barro Colorado
820   Island, Panama. Biotropica 22:103.
821 Rademacher T, Fonti P, Fonti M V, Basler D, Seyednasrollah B, Richardson AD,
822   Lemoine JM, Chen Y, Friend AD, Eckes-shephard AH (2021) Manipulating
823   phloem transport affects wood formation but not local nonstructural carbon
824   reserves in an evergreen conifer. :2506–2521.
825 Reis SM, Marimon BS, Esquivel-Muelbert A, Marimon BH, Morandi PS, Elias F, de
826   Oliveira EA, Galbraith D, Feldpausch TR, Menor IO, Malhi Y, Phillips OL (2022)
827   Climate and crown damage drive tree mortality in southern Amazonian edge
828   forests. J Ecol 110:876–888.
829 Reis SM, Marimon BS, Morandi PS, Elias F, Esquivel-Muelbert A, Marimon Junior
830   BH, Fauset S, de Oliveira EA, van der Heijden GMF, Galbraith D, Feldpausch TR,
831   Phillips OL (2020) Causes and consequences of liana infestation in southern
832   Amazonia. J Ecol 108:2184–2197.
833 Restom TG, Nepstad DC (2004) Seedling growth dynamics of a deeply rooting liana in
834   a secondary forest in eastern Amazonia. For Ecol Manage 190:109–118.
835 Rosa M, Prado C, Podazza G, Interdonato R, González JA, Hilal M, Prado FE (2009)
836   Soluble sugars-metabolism, sensing and abiotic stress a complex network in the
837   life of plants. Plant Signal Behav 4:388–393.
838 Rowland L, Da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR,

29

839   Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS, Ferreira L V., Malhi Y,
840   Grace J, Mencuccini M, Meir P (2015) Death from drought in tropical forests is
841   triggered by hydraulics not carbon starvation. Nature 528:119–122.
842   http://dx.doi.org/10.1038/nature15539
843   Sala A, Woodruff DR, Meinzer FC (2012) Carbon dynamics in trees: Feast or famine?
844   Tree Physiol 32:764–775.
845   van der Sande MT, Poorter L, Schnitzer SA, Engelbrecht BMJ, Markesteijn L (2019)
846   The hydraulic efficiency–safety trade-off differs between lianas and trees. Ecology
847   100
848   van der Sande MT, Zuidema PA, Sterck F (2015) Explaining biomass growth of
849   tropical canopy trees: the importance of sapwood. Oecologia 177:1145–1155.
850   Schnitzer SA (2018) Tansley review Testing ecological theory with lianas. New Phytol
851   220:266–380.
852   Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. Trends
853   Ecol Evol 17:223–230.
854   Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical
855   forests: Emerging patterns and putative mechanisms. Ecol Lett 14:397–406.
856   Schnitzer SA, DeFilippis DM, Visser M, Estrada-Villegas S, Rivera-Camaña R, Bernal
857   B, Peréz S, Valdéz A, Valdéz S, Aguilar A, Dalling JW, Broadbent EN, Almeyda
858   Zambrano AM, Hubbell SP, Garcia-Leon M (2021) Local canopy disturbance as
859   an explanation for long-term increases in liana abundance. Ecol Lett 24:2635–
860   2647.
861   Schnitzer SA, van der Heijden GMF (2019) Lianas have a seasonal growth advantage
862   over co-occurring trees. Ecology 100:1–12.
863   Schnitzer SA, Van Der Heijden G, Mascaro J, Carson WP (2014) Lianas in gaps reduce
864   carbon accumulation in a tropical forest. Ecology 95:3008–3017.
865   Schnitzer SA, Kuzee ME, Bongers F (2005) Disentangling above- and below-ground
866   competition between lianas and trees in a tropical forest. J Ecol 93:1115–1125.
867   Secchi F, Pagliarani C, Zwieniecki MA (2017) The functional role of xylem
868   parenchyma cells and aquaporins during recovery from severe water stress. Plant
869   Cell Environ 40:858–871.
870   Shibata R, Kurokawa H, Shibata M, Tanaka H, Iida S, Masaki T, Nakashizuka T (2016)
871   Relationships between resprouting ability, species traits and resource allocation
872   patterns in woody species in a temperate forest. Funct Ecol 30:1205–1215.
873   Signori-Müller C, Oliveira RS, Barros FDV, Tavares JV, Gilpin M, Diniz FC, Zevallos
874   MJM, Yupayccana CAS, Acosta M, Bacca J, Chino RSC, Cuellar GMA, Cumapa
875   ERM, Martinez F, Mullisaca FMP, Nina A, Sanchez JMB, da Silva LF, Tello L,
876   Tintaya JS, Ugarteche MTM, Baker TR, Bittencourt PRL, Borma LS, Brum M,
877   Castro W, Coronado ENH, Cosio EG, Feldpausch TR, Fonseca L d'Agosto M,
878   Gloor E, Llampazo GF, Malhi Y, Mendoza AM, Moscoso VC, Araujo-Murakami
879   A, Phillips OL, Salinas N, Silveira M, Talbot J, Vasquez R, Mencuccini M,
880   Galbraith D (2021) Non-structural carbohydrates mediate seasonal water stress
881   across Amazon forests. Nat Commun 12:2310. http://dx.doi.org/10.1038/s41467-
882   021-22378-8
883   Signori-Müller C, Oliveira RS, Valentim Tavares J, Carvalho Diniz F, Gilpin M, de V.
884   Barros F, Marca Zevallos MJ, Salas Yupayccana CA, Nina A, Brum M, Baker TR,
885   Cosio EG, Malhi Y, Monteagudo Mendoza A, Phillips OL, Rowland L, Salinas N,
886   Vasquez R, Mencuccini M, Galbraith D (2022) Variation of non-structural
887   carbohydrates across the fast–slow continuum in Amazon Forest canopy trees.
888   Funct Ecol 36:341–355.

889 Signori-Müller C, Oliveira RS, Valentim Tavares J, Carvalho Diniz F, Gilpin M, de V.
890   Barros F, Marca Zevallos MJ, Salas Yupayccana CA, Nina A, Brum M, Baker TR,
891   Cosio EG, Malhi Y, Monteagudo Mendoza A, Phillips OL, Rowland L, Salinas N,
892   Vasquez R, Mencuccini M, Galbraith D (2022) Variation of non-structural
893   carbohydrates across the fast–slow continuum in Amazon Forest canopy trees.
894   Funct Ecol 36:341–355. https://onlinelibrary.wiley.com/doi/full/10.1111/1365-
895   2435.13971 (3 January 2022, date last accessed).
896 Slot M, Rey-Sánchez C, Gerber S, Lichstein JW, Winter K, Kitajima K (2014) Thermal
897   acclimation of leaf respiration of tropical trees and lianas: response to experimental
898   canopy warming, and consequences for tropical forest carbon balance. Glob Chang
899   Biol 20:2915–2926. http://doi.wiley.com/10.1111/gcb.12563
900 Smith-Martin CM, Jansen S, Brodribb TJ, Medina-Vega JA, Lucani C, Huppenberger
901   A, Powers JS (2022) Lianas and Trees From a Seasonally Dry and a Wet Tropical
902   Forest Did Not Differ in Embolism Resistance but Did Differ in Xylem
903   Anatomical Traits in the Dry Forest. Front For Glob Chang 5:1–14.
904 Soares Jancoski H, Schwantes Marimon B, C. Scalon M, de V. Barros F, Marimon-
905   Junior BH, Carvalho E, S. Oliveira R, Oliveras Menor I (2022) Distinct leaf water
906   potential regulation of tree species and vegetation types across the Cerrado–
907   Amazonia transition. Biotropica 54:431–443.
908 Sombroek W (2001) Spatial and Temporal Patterns of Amazon Rainfall. AMBIO A J
909   Hum Environ 30:388–396.
910 Tavares JV, Oliveira RS, Mencuccini M, Signori-Müller C, Pereira L, Diniz FC, Gilpin
911   M, Marca Zevallos MJ, Salas Yupayccana CA, Acosta M, Pérez Mullisaca FM,
912   Barros F de V., Bittencourt P, Jancoski H, Scalon MC, Marimon BS, Oliveras
913   Menor I, Marimon BH, Fancourt M, Chambers-Ostler A, Esquivel-Muelbert A,
914   Rowland L, Meir P, Lola da Costa AC, Nina A, Sanchez JMB, Tintaya JS, Chino
915   RSC, Baca J, Fernandes L, Cumapa ERM, Santos JAR, Teixeira R, Tello L,
916   Ugarteche MTM, Cuellar GA, Martinez F, Araujo-Murakami A, Almeida E, da
917   Cruz WJA, del Aguila Pasquel J, Aragão L, Baker TR, de Camargo PB, Brienen R,
918   Castro W, Ribeiro SC, Coelho de Souza F, Cosio EG, Davila Cardozo N, da Costa
919   Silva R, Disney M, Espejo JS, Feldpausch TR, Ferreira L, Giacomin L, Higuchi N,
920   Hirota M, Honorio E, Huaraca Huasco W, Lewis S, Flores Llampazo G, Malhi Y,
921   Monteagudo Mendoza A, Morandi P, Chama Moscoso V, Muscarella R, Penha D,
922   Rocha MC, Rodrigues G, Ruschel AR, Salinas N, Schlickmann M, Silveira M,
923   Talbot J, Vásquez R, Vedovato L, Vieira SA, Phillips OL, Gloor E, Galbraith DR
924   (2023) Basin-wide variation in tree hydraulic safety margins predicts the carbon
925   balance of Amazon forests. Nature 617:111–117.
926 Thalmann M, Santelia D (2017) Starch as a determinant of plant fitness under abiotic
927   stress. New Phytol 214:943–951.
928 Tixier A, Orozco J, Amico Roxas A, Earles JM, Zwieniecki MA (2018) Diurnal
929   variation in non-structural carbohydrate storage in trees: remobilization and
930   vertical mixing. Plant Physiol:pp.00923.2018.
931   http://www.plantphysiol.org/lookup/doi/10.1104/pp.18.00923
932 Tomasella M, Häberle KH, Nardini A, Hesse B, Machlet A, Matyssek R (2017) Post-
933   drought hydraulic recovery is accompanied by non-structural carbohydrate
934   depletion in the stem wood of Norway spruce saplings. Sci Rep 7:1–13.
935 Tyree MT, Ewers FW (1996) Hydraulic Architecture of Woody Tropical Plants. In:
936   Mulkey SS, Chazdon RL, Smith AP (eds) Tropical Forest Plant Ecophysiology.
937   Chapman & Hall, New York, pp 217–243.
938 Vargas R, Trumbore SE, Allen MF (2009) Evidence of old carbon used to grow new

939   fine roots in a tropical forest. New Phytol 182:710–718.

940 Visser MD, Jongejans E, Wright SJ, Schnitzer SA, Muller-landau HC, Kroon H De,
941   Comita LS, Hubbell SP (2018) Tree species vary widely in their tolerance for liana
942   infestation : A case study of differential host response to generalist parasites. :781–
943   794.

944 Wagner FH, Hérault B, Bonal D, Stahl C, Anderson LO, Baker TR, Becker GS,
945   Beeckman H, Souza DB, Botosso PC, David MJ, Bowman S, Bräuning A, Brede
946   B, Brown FI, Camarero JJ, Chagas K, Chave J, Chidumayo EN, Clark DA, Regina
947   F, Costa C, Couralet C, Henrique P, Dalitz H, De VR, Eloisa J, Milani DF,
948   Oliveira EC De, Arruda LDS (2016) Climate seasonality limits leaf carbon
949   assimilation and wood productivity in tropical forests. :2537–2562.

950 Würth MKR, Peláez-Riedl S, Wright SJ, Körner C (2005) Non-structural carbohydrate
951   pools in a tropical forest. Oecologia 143:11–24.

952 Zanne AE, Lopez-Gonzalez G, Coomes DA, Ilic J, Jansen S, Lewis SL, Swenson NG,
953   Wiemann MC, Chave J (2009) Data from: Towards a worldwide wood economics
954   spectrum. Glob Chang Biol

955 Zotz G, Cueni N, Körner C, Institut B, Basel DU, Basel C- (2006) In situ growth
956   stimulation of a temperate zone liana (Hedera helix) in elevated CO 2. :763–769.

957
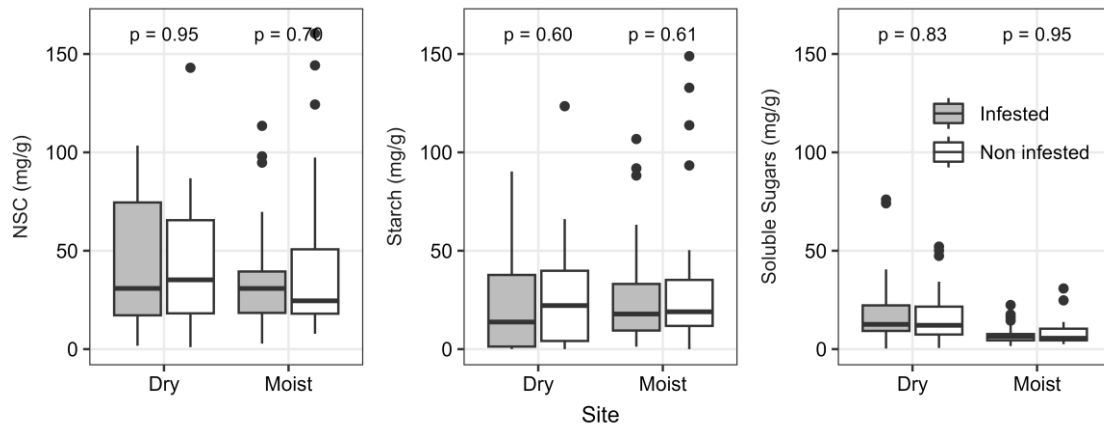
958
959 **Figure 1** – Concentrations of stem non-structural carbohydrates (NSC), starch and
960 soluble sugars in co-occurring trees species with liana infestation ≥ 50% (grey) and in
961 trees without liana infestation (white). For figure and analysis, we used the mean
962 concentration per species. Differences between groups were tested using Paired Samples
963 Wilcoxon Test. Data are present for the dry and moist site. Dry site: infested n = 40, non-
964 infested n = 31; Moist site: infested n = 29, non-infested n = 30. Each box encompasses
965 the 25th to 75th percentiles; the median is indicated by the horizontal line within each
966 box while external horizontal lines indicate the 10th and 90th percentiles; dots indicate
967 outlier.

968

969

970
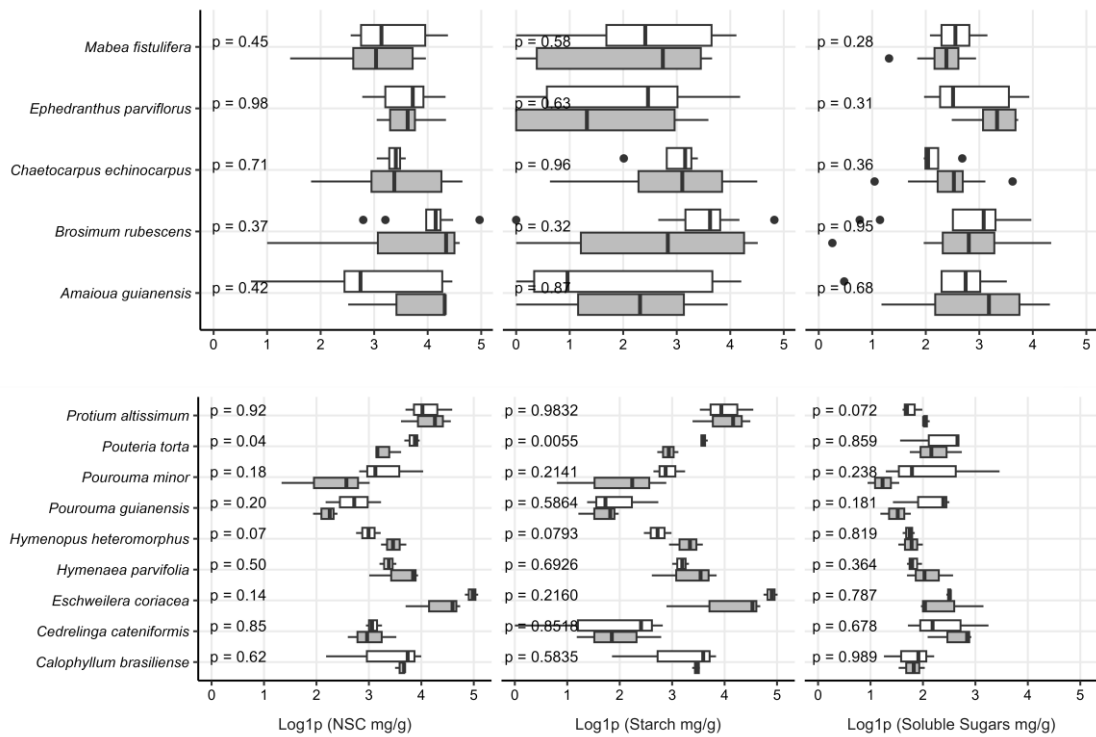
Figure 2 – Concentrations of stem non-structural carbohydrates (NSC), starch and soluble sugars from trees infested by lianas (grey) and non-infested trees (white). Data are present for the dry site (top panels) and moist site (bottom panels). *Micropholis guyanensis* was excluded due to small sample size (n <3). Data was log1p transformed and differences between groups was tested using T-Test. Each box encompasses the 25th to 75th percentiles; the median is indicated by the horizontal line with each box while external horizontal lines indicate the 10th and 90th percentiles.

978

979
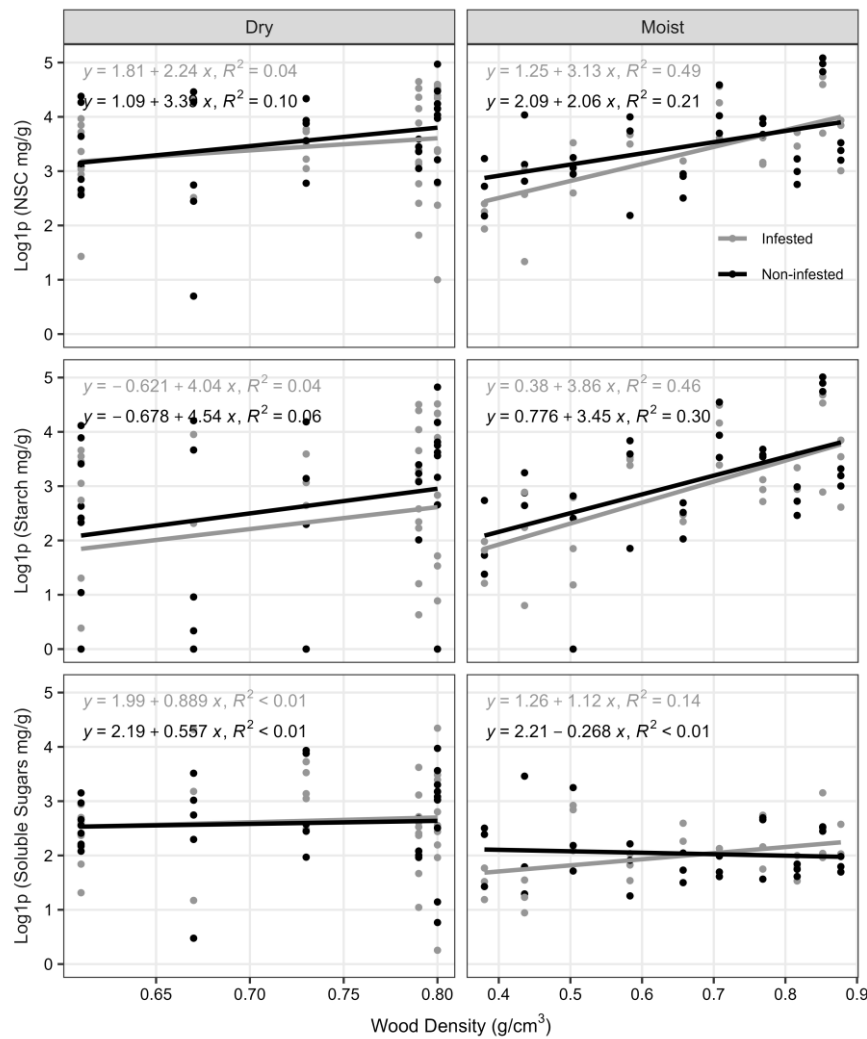
980

981 **Figure 3** – Relationship between stem non-structural carbohydrates (NSC), starch and
982 soluble sugars (mg/g) with wood density (g/cm^3). Mean wood density per species in the
983 dry site (n = 5 species) are from Soares Jancoski et al. (2022) and for the species in moist
984 site (n = 10 species) we used the basin mean from Zanne et al. (2009). The R^2 values
985 were calculated using ordinary linear regression, NSC concentration and its fraction were
986 log1p transformed before analysis. Gray colour represent infested trees and black colour
987 non-infested trees.

988

989

990
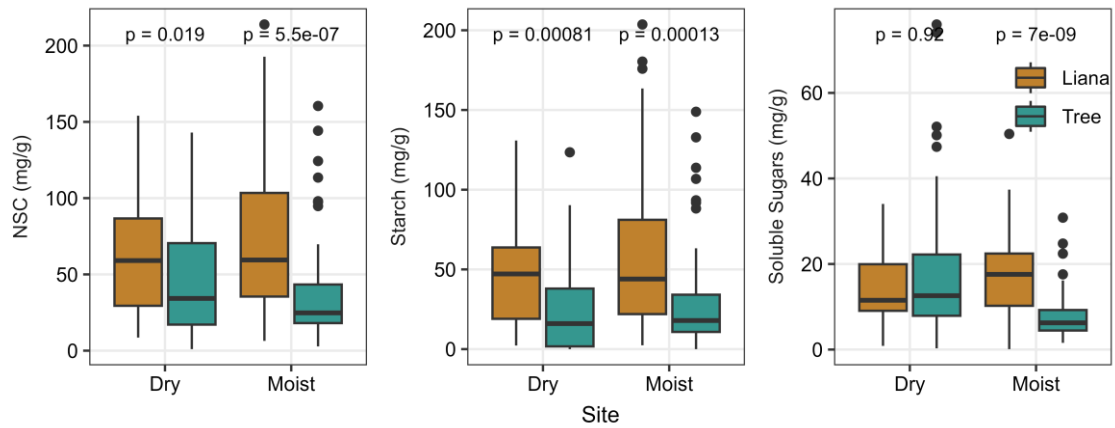
Figure 4 – Concentrations of stem non-structural carbohydrates (NSC), starch and soluble sugars in co-occurring lianas (purple), and trees (green). Data are present for the dry and moist site. To test for differences between life form within site we used Wilcoxon rank sum test. Dry site: liana n = 37, tree n = 71; Moist site: liana n = 73, tree = 59 individuals. Each box encompasses the 25th to 75th percentiles; the median is indicated by the horizontal line with each box while external horizontal lines indicate the 10th and 90th percentiles; dots indicate outliers.

998

999
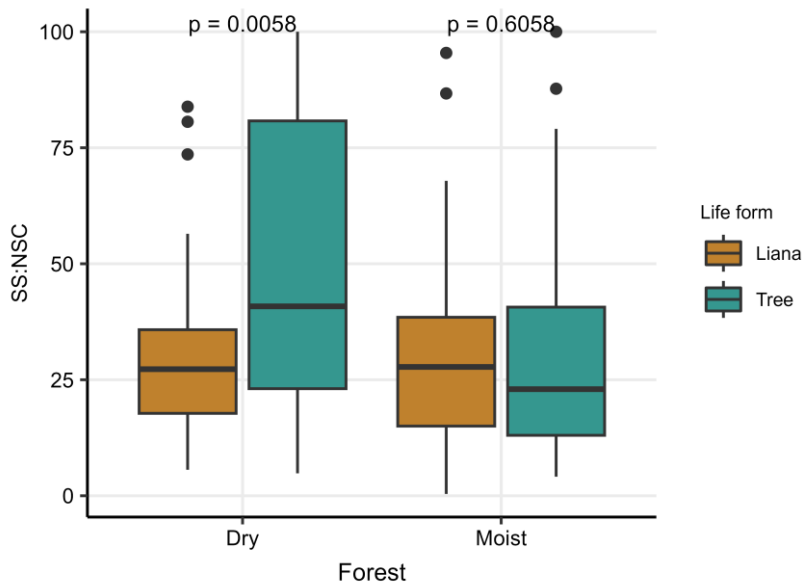
1000

Figure 5 – Comparison of proportion of NSC in the form of soluble sugars (SS:NSC) in
stems of co-occurring lianas (brown), and trees (green). Data are present for the dry and
moist site. To test for differences between life-form within site we used Wilcoxon rank
sum test. Dry site: liana n = 37, tree n = 71; Moist site: liana n = 73, tree = 59 individuals.
Each box encompasses the 25th to 75th percentiles; the median is indicated by the
horizontal line with each box while external horizontal lines indicate the 10th and 90th
percentiles; dots indicate outliers.

1008

1009

1010

37

1011

1012 **Table 1 –** Collected species and number of infested and non-infested trees, in the dry and
1013 in the moist site.

Species	Site	*n*	WD*	Phenology
Amaioua guianensis	Dry	Infested = 3 Non-infested = 5	0.67	Evergreen
Brosimum rubescens	Dry	Infested = 11 Non-infested = 9	0.80	Evergreen
Chaetocarpus echinocarpus	Dry	Infested = 11 Non-infested = 4	0.79	Evergreen
Ephedranthus parviflorus	Dry	Infested = 6 Non-infested = 6	0.72	Evergreen
Mabea fistulifera	Dry	Infested = 9 Non-infested = 7	0.61	Brevi-deciduous
Calophyllum brasiliense	Moist	Infested = 3 Non-infested = 3	0.58	Evergreen
Cedrelinga cateniformis	Moist	Infested = 3 Non-infested = 3	0.50	Semi-deciduous
Eschweilera coriacea	Moist	Infested = 3 Non-infested = 3	0.85	Evergreen
Hymenaea parvifolia	Moist	Infested = 3 Non-infested = 3	0.87	Evergreen
*Hymenopus heteromorphus***	Moist	Infested = 3 Non-infested = 3	0.81	Evergreen
Micropholis guyanensis	Moist	Infested = 2 Non-infested = 3	0.65	Evergreen
Pourouma guianensis	Moist	Infested = 3 Non-infested = 3	0.38	Evergreen
Pourouma minor	Moist	Infested = 3 Non-infested = 3	0.43	Evergreen
Pouteria torta	Moist	Infested = 3 Non-infested = 3	0.76	Deciduous
*Protium altissimum****	Moist	Infested = 3	0.70	Evergreen

38

		Non-infested = 3		

1014   *WD: wood density (g/cm3); **Former *Licania heteromorpha;* *** Former *Tetragastris*
1015   *altissima*

1016 **Table 2** – Linear Mixed-Effects Models results to predicting non-structural carbohydrate, starch, and soluble sugars with Crown Occupancy

1017 Index (COI) and Wood Density (WD) in the dry site.

	log1p (NSC)			log1p (Starch)			log1p (Soluble Sugars)		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	1.46	-1.44 – 4.35	0.319	-0.62	-5.83 – 4.58	0.812	2.44	-0.90 – 5.77	0.149
COI	0.03	-1.04 – 1.11	0.952	0.03	-1.87 – 1.94	0.972	-0.25	-1.28 – 0.78	0.623
WD	2.85	-1.16 – 6.86	0.161	4.39	-2.82 – 11.60	0.228	0.19	-4.43 – 4.82	0.933
COI × WD	-0.07	-1.56 – 1.41	0.923	-0.13	-2.76 – 2.50	0.922	0.37	-1.05 – 1.79	0.603
Random Effects									
σ^2	0.77			2.42			0.70		
τ_{00}	0.00 Species			0.01 Species			0.05 Species		
ICC				0.00			0.07		
N	5 Species			5 Species			5 Species		
Observations	71			71			71		
Marginal R^2 / Conditional R^2	0.055 / NA*			0.043 / 0.047			0.013 / 0.080		

1018
1019
1021
1022
1023
1024
1025

1026 *Not estimated because variance estimates for random effect is nearly zero.

40

1027   **Table 3** – Linear Mixed-Effects Models results to predicting non-structural carbohydrate, starch, and soluble sugars with Crown Occupancy

1028   Index (COI) and Wood Density (WD) in the wet site. Bolt values represent significative relationships.

1029

Predictors	log1p (NSC)			log1p (Starch)			log1p (Soluble Sugars)		
	Estimates	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	2.06	0.72 – 3.39	**0.003**	0.73	-0.98 – 2.43	0.396	2.18	1.27 – 3.10	**<0.001**
COI	-0.24	-0.55 – 0.06	0.110	-0.10	-0.51 – 0.31	0.629	-0.27	-0.58 – 0.03	0.075
WD	2.14	0.17 – 4.10	**0.033**	3.55	1.04 – 6.05	**0.006**	-0.19	-1.53 – 1.16	0.781
COI × WD	0.29	-0.15 – 0.72	0.194	0.08	-0.52 – 0.68	0.795	0.37	-0.06 – 0.81	0.093
Random Effects									
σ^2	0.23			0.43			0.23		
τ_{00}	0.19 Species			0.30 Species			0.05 Species		
ICC	0.46			0.41			0.18		
N	10 Species			10 Species			10 Species		
Observations	59			59			59		
Marginal R^2 / Conditional R^2	0.332 / 0.637			0.352 / 0.616			0.062 / 0.230		

41