Host preference and growth patterns of ivy (Hedera helix L.) in a temperate alluvial forest

(Article begins on next page)

31 January 2025

1   **Host preference and growth patterns of ivy (*Hedera helix* L.) in a temperate alluvial forest**

2

3   Daniele Castagneri [ab*], Matteo Garbarino [a], Paola Nola[b]

4

5   [a] Department of AgroSelviTer, University of Turin, I-10095 Grugliasco (TO), Italy

6   [b] Department of Earth and Environmental Sciences, University of Pavia, I-27100 Pavia (PV), Italy

7

8   [*]Corresponding author   address: via Leonardo da Vinci 44, 10095 Grugliasco (TO)

9   e-mail: daniele.castagneri@unito.it   telephone number: 00390116705549

10   fax: 00390116705546

11

12   M. Garbarino: matteo.garbarino@unito.it

13   P. Nola: paola.nola@unipv.it

14

15

16

17

18   Word count including all text (abstract, body of the text, and references): 5821

19

20   Keywords: competition, liana, plain forest, ring width

21

22

23

24

25

26

ABSTRACT

Recent studies have highlighted the role of lianas in shaping stand dynamics both in tropical and temperate forests. However, English ivy (*Hedera helix* L.), one of the most widespread liana in Europe, has received little attention. We conducted a study in the Siro Negri alluvial forest (NW Italy) to determine what factors most affected ivy distribution, and to investigate its interactions with the trees in the stand. We evaluated the influence of tree size, age, species and neighborhood crowding on ivy occurrence. In addition, growth ring widths were used to explore the development pattern of climbing stems.

Fifty-two percent of trees in our study plots carried ivy, a value comparable to liana incidence found in mature tropical forests. Tree characteristics and their spatial pattern significantly influenced ivy distribution. Preferred hosts were large, isolated trees, while the effect of tree age and species on ivy occurrence was marginal. Growth pattern analysis revealed that radial growth was positively related to the available space on the tree trunk for each ivy stem. We conclude that neighborhood crowding around trees and competition among climbing stems relying on the same trunk may reduce the colonization rate of ivy.

INTRODUCTION

Lianas are woody climbing plants that begin their life as terrestrial seedlings and later ascend to the canopy using trees as structural supports (Putz and Mooney 1991). Over the past few years their importance in forest biodiversity has been recognized (Schnitzer and Bongers 2002): they increase woody species diversity and provide food and refuge for many animal species (Emmons and Gentry 1983; Campanello et al. 2007; Page et al 2010). Lianas play a central role in forest dynamics, as they can suppress tree regeneration, and they compete with adult trees for light, water, and soil nutrients. In some cases they have been found to reduce tree growth rates and fecundity (Ladwig and Meiners 2010a; Ichihashi and Tateno 2011). Moreover, abundant lianas increase crown susceptibility to wind and, in temperate climates, to snow damage (Allen et al. 2005). Lianas can also influence forest composition, as they affect tree species differentially, modifying inter-specific relationships. Furthermore, lianas can occupy available space on the ground earlier than pioneer tree species, delaying gap colonization and forest succession (Laurence et al. 2001; Schnitzer and Bongers 2002; Toledo-Aceves and Swaine 2008).

Since lianas have such an important role in forest dynamics, research on their distribution, ecology and relationships with other plants is critical. Several studies have investigated liana dynamics at stand level, revealing that abiotic factors, forest structure and stand dynamics influence their distribution (Laurence et al. 2001; Allen et al. 2005; Londrè and Schnitzer 2006; Morrissey et al. 2009; Gianoli et al. 2010; Macía 2011; Nogueira et al. 2011). Few studies have taken an individual tree approach to tree liana-tree relationships, and there is little information on how lianas interact with their hosts, especially for temperate forests (Blick and Burns 2011; Ichihashi and Tateno 2011). As structural parasites, lianas need suitable supports to reach the canopy and maintain themselves there. As a consequence, host tree characteristics, such as size and species, influence lianas colonization patterns, growth rates, distribution and diversity (Leicht-Young et al. 2010; Nogueira et al. 2011).

79 At a global scale, lianas are widespread in tropical forests, where they represent between 10 and

80 40% of the woody species (Schnitzer and Bongers 2002), but they are even common in several

81 temperate ecosystems. In Europe, there are few autochthon liana species, and white vine (*Clematis*

82 *vitalba* L.), grapevine (*Vitis* spp.) and English ivy (*Hedera helix* L.) are the most diffuse. The genus

83 *Hedera* originated in the Tertiary, experiencing a postglacial re-colonization from the

84 Mediterranean regions. As ivy belongs to a largely tropical family (Araliaceae), it benefits from

85 warm summers, and is intolerant to cold temperatures (Metcalfe 2005). It favours nutrient-rich and

86 moist soils. Unlike many of the woody species found in southern-European plain forests, ivy is an

87 evergreen species. It presents two distinct forms: the chamephyte form at the beginning of its life,

88 with prostrate, sterile stems and palmately-lobed shade leaves that can create extensive carpets on

89 the forest floor; and the phanerophyte form when suitable supports are available and ivy stems can

90 ascend toward better light conditions. The climbing stems support reproductive shoots, with

91 unlobed oval sun leaves (Nola 1997; Garfì and Ficarrotta 2003; Metcalfe 2005). Like other lianas,

92 ivy is a serious concern for forest managers. Despite its contribution to biodiversity maintenance

93 and to nutrient cycling processes (Badre et al. 1998), ivy is often regarded as a problem, as it is

94 believed to reduce tree growth rates. Moreover, outside of its natural distribution areas, ivy is an

95 invasive species that poses a grave threat to native plants (Clarke et al. 2006; Biggerstaff and Beck

96 2007), and active management is required to control it.

97 Despite its wide home range, extending from southern Scandinavia to the Mediterranean area, few

98 studies have been conducted on ivy dynamics, and those mainly in the Rhine valley, France

99 (Trèmolières et al. 1988; Schnitzler 1995; Badre et al. 1998; Schnitzler and Heuzè 2006; Heuzè et

100 al. 2009). Research on other species can be only partially transposed to ivy, as morphological and

101 ecological features vary between liana species (Gianoli et al. 2010).

102 We conducted a study in the Siro Negri forest, one of the very few fragments in northern Italy of

103 alluvial forest, a preferential habitat for this species (Schnitzler and Heuzè 2006). Our general

104 purpose was to explore ivy dynamics on an individual tree basis. The first goal was to quantify ivy

4

105   abundance in the forest, as quantitative assessments of lianas in Europe are extremely scarce.

106   Subsequent analyses were conducted to study individual ivy-host relationships. We aimed at

107   identifying the characteristics of preferred host trees, such as size, age, species, and neighborhood

108   crowding, in order to better understand which factors affect ivy occurrence. We then explored the

109   relationships between ivy radial growth rates and host tree characteristics, to obtain information on

110   ivy development following host ascension.

111

112   **METHODS**

113

114   **Study site**

115   The study was conducted within the Siro Negri Reserve, on the southern side of the Ticino Regional

116   Park, province of Pavia, northern Italy (45°12'N, 9°03'E, 65 m a.s.l.). Mean annual rainfall is about

117   800 mm, with most precipitation in spring and autumn, and the average annual temperature is 13.6

118   °C (Pavia weather station, 10 km from the study site). The forested area, described as a *Polygonato*

119   *multiflori-Quercetum roboris* association (Sartori 1984), covers about 9 ha, and is one of very few

120   relicts of the original alluvial forest in northern Italy. The main tree species are *Acer campestre* L.,

121   *Carpinus betulus* L., *Crataegus monogyna* Jacq., *Populus alba* L., *Populus nigra* L., *Quercus robur*

122   L., *Robinia pseudacacia* L., *Ulmus minor* Mill. The forest accommodates trees of over 100 years.

123   The last important human disturbances coincide with the two world wars, when there was an

124   elevated demand for firewood (Motta et al. 2009), while the forest has been unmanaged since the

125   establishment of the reserve in 1970.

126

127   **Field sampling**

128   Two permanent plots (50 × 50 m) were established during 2005 at the south-eastern border of the

129   reserve (Motta et al. 2009). Two other permanent plots (60 × 60 m) were established at less than

130   100 m of distance in the inner part of the reserve during 2009. Trees with diameter at breast height

131   (DBH) ≥ 7.5 cm were identified, labeled with numbered plastic tags and mapped. All trees in the

132   reserve were mapped between 2009 and 2011.

133   During 2011, tagged trees in the four permanent plots (total area equal to 1.22 ha) were re-surveyed,

134   and a census of ivy was carried out. For each tree, we measured the diameter of living ivy stems ≥

135   0.5 cm at 1.3 m from the base. All the stems were measured without distinguishing between ramets

136   and genets, because it was difficult to identify their origin, and their dynamics and effects on trees

137   are comparable (Gerwing et al. 2006; Schnitzer et al. 2006; Campanello et al. 2007). The degree of

138   ivy occupancy on trees was classified according to a five class system: 0, ivy absent or below 1.3 m

139   on the tree trunk; 1, ivy present on the lower half of the trunk; 2, ivy reaching the second half of the

140   trunk, but not the crown; 3, ivy on the lower part of the principal branches; 4, ivy covering the

141   whole crown.

142

143   **Dendrochronological analysis**

144   An increment core from all the trees with DBH ≥ 10 cm and from a subsample of trees with DBH <

145   10 cm was taken at 50 cm from the tree base. In addition, an increment core was taken at 50 cm

146   from the tree base from 60 randomly chosen ivy stems in the plots. The stems were cored from side

147   to side to get a core with two radii, in order to account for possible asymmetrical growth of ivy

148   stems. In the laboratory, all the cores were fixed to wooden supports and prepared with a razor to

149   obtain an optimal surface resolution.

150   Cores from trees were used to estimate tree age. For cores that did not intersect the pith, its position

151   was estimated by means of a pith locator, and the number of missing rings was estimated (Motta

152   and Nola 2001). When it was not possible to estimate missing rings, the core was discarded.

153   Ring widths of ivy cores were measured to the nearest 0.01 mm, using LINTAB device and

154   CATRAS software (Aniol 1983). Cores with rotten wood or other irregularities were discarded.

155   Cores were also discarded when the two series of radii for each did not match (visual comparison).

156 Series from the two radii of each of the remaining 43 cores (28.3% discarded) were averaged to

157 estimate annual stem growth rate.

158

159 **Data analysis**

160 The relationships between ivy and trees were explored on an individual tree basis. Descriptors of

161 ivy, computed for each host tree, were number of stems, diameter sum, basal area, diameter of the

162 largest stem, and the degree of ivy occupancy. Tree features were diameter, age (when available),

163 and species. Also, to analyze the effects of neighborhood crowding on ivy-tree interactions, we

164 calculated the number and the sum of diameters of trees in a circle of 10 m around the tree; and the

165 neighborhood ratio calculated as the ratio between the sum of neighbors' diameters and the subject

166 tree diameter (Daniels et al. 1986; Castagneri et al. 2008). A radius of 10 m was selected because

167 the largest trees in the stand have a crown radius > 8 m, thus they compete with trees at a distance

168 of more than 8 meters.

169 Firstly, we ran all the variables in a Redundancy analysis (RDA), to order ivy attributes in relation

170 to tree and neighborhood characteristics. RDA was done on Canoco 4.0 software (Ter Braak and

171 Smilauer 1998) and the statistical significance of the relations between variables was tested by a

172 Monte Carlo test with 10,000 permutations. Next, to refine the assessment of ivy-tree interaction,

173 we performed two types of models: (1) binary logistic regression models to evaluate the

174 characteristics that determined the presence/absence of ivy on a tree, with stepwise entry of

175 predictor variables (tree characteristics and neighborhood measures); (2) General Linear Models

176 (GLMs) to determine which factors influenced ivy abundance on host trees, again, via stepwise

177 entry of predictor variables (tree characteristics and neighborhood measures). In this case, response

178 variables were number of ivy stems on the tree, sum of stem diameters, and their basal area. When

179 continuous variables were not normally distributed, a transformation was applied to improve

180 linearity of relationships. Variable collinearity and distribution of the residual were checked for

181 each model. Finally, we analyzed ivy growth rate in relation to tree characteristics, neighborhood

182 crowding and ivy abundance. Individual growth rate, which was the response variable, was

183 calculated as mean radial increment during the last 5 and 10 years, obtained from the ivy cores. All

184 models were computed using SPSS 17.0 (SPSS Inc. Chicago IL).

185

186 **RESULTS**

187

188 **Ivy distribution**

189 Ivy density in the Bosco Negri alluvial forest was 657, 346 and 225 stems per hectare considering

190 stems of respectively ≥ 0.5, 1 and 2.5 cm (three diameter thresholds commonly used in liana

191 censuses, Gerwing et al. 2006). The basal area of stems ≥ 0.5 cm was 5609 cm^2 per hectare. Of the

192 surveyed trees (n = 374), 52% hosted one or more ivy stems, although ivy was found only on the

193 tree trunk in many cases, and just 17% of the trees had ivy at crown level (classes of occupancy 3

194 and 4). Other liana species (*Clematis vitalba* L., *Vitis* spp.) occurred sporadically (0-2 individuals

195 per plot).

196 A few differences were observed between the four plots. Plot 3, characterized by low tree density

197 and large diameters, had the highest percentage of trees hosting ivy (Table 1), the largest number of

198 ivy stems larger than 0.5 cm (Fig. 1), and the largest ivy basal area (Fig. 2). Like Plot 3, Plot 4 was

199 located in the inner part of the reserve, but had a higher tree density and a lower mean diameter. It

200 had fewer ivy stems ≥ 0.5 cm, while the number of stems ≥ 2.5 cm was close to that in Plot 3. Plots

201 1 and 2, located at the forest border, had a much higher tree density. The percentage of trees hosting

202 ivy, the density of stems ≥ 1 and 2.5 cm, and ivy basal area were rather similar to those observed in

203 Plot 4, whereas the number of stems ≥ 0.5 was greater (Fig. 1).

204

205 **Ivy-tree relationships**

206 RDA highlighted the complexity of relationships between ivy and trees attributes. In the first

207 analysis (Fig. 3a) we included the descriptors of ivy, tree and neighborhood but not tree age for

208   each of the 374 sampled trees. In the second analysis (Fig. 3b) we included age as a variable. As

209   this information was not available for all the trees, the second RDA was performed on a sub-set of

210   207 samples. Relationships between variables were statistically significant ($p < 0.001$) in both the

211   RDA analyses, and the models explained 43.8% and 44.1% of variance respectively.

212   The ivy descriptors *HE_ba*, *HE_s_d*, *HE_d_M*, *HE_n* and *HE_cl* expressed liana abundance on

213   trees in different ways, and they were positively associated to each other. With regards to ivy-host

214   interactions, while tree diameter (*TR_d*) and age (*TR_age*) were positively related to ivy descriptors,

215   neighborhood crowding (expressed as neighbors number (*NE_n*), sum of diameters (*NE_s_d*), and

216   neighborhood ratio (*NE_ra*)) were negatively related to ivy abundance. In terms of species, RDA

217   showed that *Q. robur* trees were big and isolated, hosting large amounts of ivy whereas *A.*

218   *campestre* and *C. monogyna* trees were small with many neighbors, and hosted little ivy. The other

219   species were in an intermediate position. The inclusion of plot as a factor did not significantly

220   improve RDA (the variance explained by the model was 44.3%, graph not shown), suggesting that

221   the observed relationships were not influenced by site characteristics. RDA provided a general

222   pattern of ivy-host relationships. However, it was not possible to identify which tree characteristics

223   were most important in favoring ivy, as many variables correlated with each other. To discriminate

224   between these factors, several models were applied. The logistic regression model showed that the

225   presence of ivy was positively related to big tree diameters and negatively related to the number of

226   neighboring trees (Table 2), indicating that larger isolated trees were more likely to host ivy than

227   the others. Tree species increased the Nagelkerke R^2 from 0.276 to 0.303, but was not significant at

228   $p = 0.05$. Tree age was positively related to ivy, while the sum of diameters of neighbors and

229   neighborhood ratio correlated negatively, but these factors were discarded as redundant in the

230   stepwise regression. Including plot as a factor did not improve the model, indicating that the

231   observed patterns did not vary significantly between the four plots.

232   To determine which characteristics of host trees ($n = 194$) influenced the amount of ivy, we looked

233   at the number of ivy stems per tree, and their sum of diameters and basal area. These direct

measurements of ivy abundance correlated more closely to tree descriptors than diameter of the biggest stem and tree occupancy category. GLMs indicated that abundance of ivy was influenced by the same factors that determined its presence. Tree diameter was the most important feature, positively influencing ivy abundance, while the number of neighbors had a negative effect (Table 3). Tree species emerged as a significant factor only in predicting ivy stem number, with *Q. robur* and, more evidently, *C. monogyna,* hosting fewer stems that the other species. The best model performed similarly in predicting the number of ivy stems on the tree and their sum of diameters, while it explained a lower percentage of variance for ivy basal area.

Ivy growth patterns

The largest sampled ivy stem had a diameter of 14 cm at 50 cm from the base, and 53 counted rings, while the oldest one had 69 rings, and a diameter of 9.5 cm. Five stems had an estimated age > 50 years. The mean annual radial growth rate was 1.05 ($\pm$ 0.54) mm over the last five years, and 1.03 ($\pm$ 0.47) mm over the last ten years. Relationships between host tree characteristics and ivy growth were rather weak, and only host tree age was positively related to the rate of growth over the last ten years (Pearson's $r = 0.36$, $p < 0.05$, $n = 34$).

We also explored possible interactions between ivy stems growing on the same trunk. The basal area of other stems on the same host tree was negatively related to the ivy growth rate over the last five years (Pearson's $r = -0.36$, $p < 0.05$, $n = 43$) and over the last ten years ($r = -0.31$, $p < 0.05$, $n = 43$). To analyze this finding in greater detail, we tested whether ivy growth was related to the surface available on the tree trunk for each ivy stem, calculated as the ratio between the trunk circumference and the sum of ivy stems' diameters. Available space was positively correlated to the growth rate both over the last five years (Pearson's $r = 0.39$, $p < 0.01$, $n = 43$) and over the last ten years ($r = 0.40$, $p < 0.01$, $n = 43$) (Fig. 4).

260 **DISCUSSION**

261

262 **Ivy abundance**

263 An increase in the abundance and distribution of lianas has been observed both in tropical and in

264 temperate forests over recent decades, possibly due to the increase in atmospheric CO_2, warmer

265 temperatures, and increased forest fragmentation caused by disturbances and land use changes

266 (Allen et al. 2005; Londré and Schnitzer 2006; Van der Heijden and Phillips 2008). It is therefore

267 important to carry out quantitative surveys, and to monitor temporal variations in liana incidence in

268 different forest ecosystems (Ladwig and Meiners 2010b; Schnitzer and Bongers 2011). It is usually

269 assumed that lianas have higher incidence in tropical than in temperate ecosystems (Schnitzer and

270 Bongers 2002; Leicht-Young et al. 2010). However, the percentage of trees carrying ivy in the Siro

271 Negri alluvial forest (45 - 79%) was similar to those observed in many mature tropical and

272 subtropical forests (Putz 1984; Campanello et al. 2007; Nesheim and Økland 2007); while the

273 number of stems and basal area per hectare was lower than that generally found in tropical forests

274 (Schnitzer and Bongers 2002; Schnitzer et al. 2006; Van der Heijden and Phillips 2008; Madeira et

275 al. 2009; Gianoli et al. 2010). Studies in two temperate alluvial forests in the Rhine valley, France

276 (Schnitzler and Heuzé 2006), found 61.9 and 29.4 English ivy stems per hectare, both being much

277 lower than the numbers observed in the Siro Negri forest.

278 In addition to macro-ecological factors, stand density and tree size distribution can also influence

279 the quantity of liana (Van der Heijden and Phillips 2008; Madeira et al. 2009). Our survey was

280 carried out in four plots very close to each other, but differing in tree density and diameter

281 distribution. One of the plots (Plot 3) had a lower tree density compared to the others, but the

282 number of ivy stems and basal area were similar or slightly larger than in the other plots. Within the

283 same forest, patches with few but suitable supports can bear similar or larger amount of ivy than

284 patches with many less suitable trees.

285

Host preference

Lianas are structural parasites that require suitable supports to access the canopy. Tree attributes, such as species morphological features, size and age, may alter liana–host interactions, influencing liana colonization rates (Campanello et al. 2007; Blick and Burns 2011; Nogueira et al. 2011). A few recent studies, conducted both in tropical and temperate forests, indicate that the availability of suitable host trees may have more influence than climate and soil properties on vine and liana distribution (Nesheim and Økland 2007; Van der Heijden and Phillips 2008; Leicht-Young et al. 2010). In our study, we scrutinized several tree attributes, some of which have rarely been considered in previous research. The use of multiple models allowed the elimination of redundant factors, and identification of the most important ones. Larger trees were more likely to host ivy than smaller ones, and the largest host trees had the most ivy. A similar pattern has been observed in several studies on lianas conducted in various ecosystems. However, different liana species exhibit different host size preferences, depending on their climbing mechanism. Stem twiners and tendril climbers better ascend small supports, and thus are more abundant on small diameter trees. On the other hand, root climbers such as ivy adhere to trunks with adventitious roots rather than wrapping around them, and prefer to ascend trees of larger diameters and rough bark (Putz 1984; Allen et al. 1997; Schnitzler and Heuzé 2006; Yuan et al. 2009; Madeira et al. 2009; Morrissey et al. 2009; Leicht-Young et al. 2010; Blick and Burns 2011; Nogueira et al. 2011). It has been suggested that large trees have more lianas because they are, generally, older than smaller ones, meaning more colonization time for lianas (Campanello et al. 2007; Nesheim and Økland 2007; Ladwig and Meiners 2010a). However, tree age is not usually measured directly. In our study, tree age of a sub-set of trees (55% of the samples) was assessed by tree-ring analysis. This attribute turned out to be less important than diameter (it was not significant in the GLMs that included diameter as a predictor variable), indicating that tree age was of secondary importance in ivy colonization. This suggests that large trees hosted more ivy than smaller ones mainly because they provided a larger surface that could accommodate many stems.

12

312   The majority of studies analyzing liana-tree interactions have found evident species associations,

313   and some tree species seem to have a higher probability of being colonized. Trees with rougher bark

314   host more root climbers, because they provide a good surface to ascend. Moreover, crown

315   morphology also seems to affect liana-tree relationships, and trees with high stature, small leaves

316   and a light crown host more lianas, due to better light conditions (Nesheim and Økland 2007;

317   Morrissey et al. 2009). In the Siro Negri forest, *Q. robur* appeared to be preferred, and almost all

318   individuals of this species hosted ivy. However, thorough analysis revealed that ivy climbed *Q.*

319   *robur* trees because they were large and had few neighbors, whereas the effect of species *per se* was

320   negligible: when variations in size between species were excluded, different tree species were found

321   to be colonized to a similar degree by ivy. This finding, though, cannot be generalized, as the

322   species composition in the Siro Negri forest is limited to deciduous broadleaves, all characterized

323   by relatively rough bark in the adult phase: Schnitzler and Heuzè (2006) observed that ivy does in

324   fact show species preference in alluvial forests in northeastern France.

325   Using information on tree position in the stand, we analyzed the influence of neighboring trees on

326   the likelihood of a tree to carry ivy, to our knowledge an aspect never considered in previous

327   studies. Isolated trees, i.e. trees with few neighbors, were more likely to host ivy, and isolated host

328   trees had more ivy stems than host trees in crowded areas. As tree size and density are usually

329   inversely related, we checked whether the effect of neighborhood was discernible from that of tree

330   diameter. In the analyzed stand, the two parameters were slightly negatively correlated (r = -0.24).

331   However, the neighborhood ratio, expressed as the ratio between tree diameter and the sum of

332   neighbor's diameters, had a stronger (negative) relation with ivy descriptors than tree diameter

333   alone. The stepwise inclusion of neighborhood variables also enhanced the performance of all the

334   regression models. We concluded that neighborhood crowding directly influenced ivy colonization.

335   This is possibly because isolated tree trunks received more light than the others, making them more

336   attractive to light-demanding ascendant ivy stems. This finding provides an interesting contribution

337   to research on how forest structure affects lianas. Several authors report an increase in liana density

338   in disturbed areas and forest gaps, but the causes of this pattern have not yet received much

339   attention (Ladwig and Meiners 2010b; Gianoli et al. 2010). We observed that smaller numbers of

340   neighbors directly increased both tree likelihood of being colonized, and ivy abundance on host

341   trees. It is likely that the incidence of light-demanding root climbers increases when a disturbance

342   reduces the number of neighbors around surviving trees.

343

344   **Growth patterns**

345   Very little information exists on the longevity of lianas, and on what affects their growth patterns

346   (Brandes et al. 2011). In comparison to other liana species, however, relatively numerous

347   dendrochronological studies have been conducted on ivy, possibly because tree rings are more

348   evident than in many tropical liana species. The mean annual growth rate for ivy found in the Bosco

349   Negri (mean-ring width in the last five years equal to 1.05 ± 0.54 mm) and maximum age (69

350   years), were roughly comparable to those reported by other authors. Nola (1997) measured a mean

351   annual radial increment of 0.94 mm (± 0.34) and a maximum age of 68 years in southern Italy.

352   Garfì and Ficarrotta (2003) found a mean ring width of 0.86 mm (± 0.25) and maximum age of 47

353   years in Sicily. Heuzè et al. (2009) reported a mean growth rate between 0.50 mm (± 0.42) and 2.06

354   mm (± 0.67), and maximum age of 66 years in northeastern France.

355   Growth pattern analysis can provide interesting indications on liana dynamics. Unlike ivy

356   distribution, we found that ivy growth was scarcely influenced by host tree characteristics and

357   neighborhood crowding. We did, however, find a slight but significant relationship between stem

358   growth and trunk surface available for each stem. We hypothesize that when many ivy stems rely

359   on the same tree, they compete. Positive interaction between liana stems has been reported, but this

360   was related to mechanical facilitation in the colonization of trees, as older stems provided support to

361   new ones for reaching the upper canopy (Campanello et al. 2007). We are not aware of any other

362   findings on competition between lianas, and further analyses should be conducted on other species

363   to support our finding.

364

Conclusions

Ivy is an important component of temperate forests but, especially outside Europe, it is often regarded as a threat to other woody plants. Management of this species should be driven by better knowledge of its ecology. As a structural parasite, its distribution depends strongly on the availability of suitable host trees. Light-demanding climbing ivy stems ascend trees to reach better light conditions. Indeed, we observed that preferred hosts were large, isolated trees that probably receive more light than others. Tree species and tree age appeared weakly related to ivy distribution. We conclude that the climbing form of ivy can be limited by an increase in neighborhood crowding around potential host trees, i.e. by natural forest closure in the absence of disturbances. Competition between ivy stems relying on the same trunk could also limit the vertical colonization of host trees.

375

382

REFERENCES

Allen BP, Pauley EF, Sharitz RR (1997) Hurricane impacts on liana populations in an old-growth southeastern bottomland forest. J Torr Bot Soc 124:34–42

Allen BP, Sharitz RR, Goebel PC (2005) Twelve years post-hurricane liana dynamic in and old-growth southeastern floodplain forest. For Ecol Manage 218:259–269

Aniol RW (1983) Tree-ring analysis using CATRAS Dendrochronologia 1:45-53

390 Badre B, Nobelis P, Trèmoliéres M (1998) Quantitative study and modelling of the litter

391 decomposition in a European alluvial forest. Is there an influence of overstorey tree species on the

392 decomposition of ivy litter (*Hedera helix* L.)? Acta Oecol 19:491–500

393 Biggerstaff MS, Beck CW (2007) Effects of English ivy (*Hedera helix*) on seed bank formation and

394 germination. Am Mid Nat 15:250-257

395 Blick RAJ, Burns KC (2011) Liana co-occurrence patterns in a temperate rainforest. J Veg Sci

396 22:868–877

397 Brandes AFN, Lisi CS, Barros CF (2011) Dendrochronology of lianas of the Leguminosae family

398 from the Atlantic Forest, Brazil. Trees 24:1045-1060

399 Campanello PI, Garibaldi JF, Gatti MG, Goldstein G (2007) Lianas in a subtropical Atlantic Forest:

400 Host preference and tree growth. For Ecol Manage 242:250–259

401 Castagneri D, Vacchiano G, Lingua E, Motta R (2008) Analysis of intraspecific competition in two

402 subalpine Norway spruce (*Picea abies* (L.) Karst.) stands in Paneveggio (Trento, Italy). For Ecol

403 Manage 255:651–659

404 Clarke MM, Reichard SH, Hamilton CW (2006) Prevalence of different horticultural taxa of ivy

405 (*Hedera* spp., Araliaceae) in invading populations. Biol Cons 8:149-157

406 Daniels RF, Burkhart HE, Clason TR (1986) A comparison of competition measures for predicting

407 growth of loblolly pine trees. Can J For Res 16:1230–1237

408 Emmons LH, Gentry AH (1983) Tropical forest structure and the distribution of gliding and

409 prehensile tailed vertebrates. Am Nat 121:513–524

410 Garfì G, Ficarrotta S (2003) Influence of ivy (*Hedera helix* L.) on the growth of downy oak

411 (*Quercus pubescens* sl) in the Monte Carcaci Naure Reserve (central-western Sicily). Ecol Mediter

412 29:5-14

413 Gerwing JJ, Schnitzer SA, Burnham RJ, Bongres F, Chave J, DeWalt SJ et al (2006) A standard

414 protocol for liana censuses. Biotropica 38:256–261

415 Gianoli E, Saldana A, Jimènez-Castillo M, Valladares F (2010) Distribution and abundance of vines

416 along the light gradient in a southern temperate rain forest. J Veg Sci 21:66–73

417 Heuzé P, Dupoueyb J-L, Schnitzler A (2009) Radial growth response of *Hedera helix* to

418 hydrological Changes and climatic variability in the Rhine floodplain. River Res Applic 25:393–

419 404

420 Ichihashi R, Tateno M (2011) Strategies to balance between light acquisition and the risk of falls of

421 four temperate liana species: to overtop host canopies or not? J Ecol 99:1071–1080

422 Ladwig LM, Meiners SJ (2010a) Liana host preference and implications for deciduous forest

423 regeneration. J Torr Bot Soc 137:103–112

424 Ladwig LM, Meiners SJ (2010b) Spatiotemporal dynamics of lianas during 50 years of succession

425 to temperate forest. Ecology 91:671–680

426 Laurence WF, Pérez-Salicrup D, Delamônica P, Fearnside PM, D'Angelo S, Jerozolinski A, Pohl L,

427 Lovejoy TE (2001) Rain forest fragmentation and the structure of Amazonian liana communities.

428 Ecology 82 (1):105-116

429 Leicht-Young SA, Pavlovic NB, Frohnapple KJ, Grundel R (2010) Liana habitat and host

430 references in northern temperate forests. For Ecol Manage 260:1467–1477

431 Londré RA, Schnitzer SA (2006) The distribution of lianas and their change in abundance in

432 temperate forests over the past 45 years. Ecology 87:2973–2978

433 Macía MJ (2011) Spatial distribution and floristic composition of trees and lianas in different forest

434 types of an Amazonian rainforest. Plant Ecol 212:1159-1177

435 Madeira BG, Espírito-Santo MM, D'Angelo Neto S, Nunes YRF, Arturo Sánchez Azofeifa G,

436 Wilson Fernandes G, Quesada M (2009) Changes in tree and liana communities along a

437 successional gradient in a tropical dry forest in south-eastern Brazil. Plant Ecol 201:291-304

438 Metcalfe DJ (2005) Biological flora of the British Isles *Hedera helix* L. J Ecol 93:632–645

439   Morrissey RC, Gauthier MM, Kershaw JA, Jacobs DF, Seifert JR, Fischer BC (2009) Grapevine

440   (*Vitis* spp.) dynamics in association with manual tending, physiography, and host tree associations

441   in temperate deciduous forests. For Ecol Manage 257:1839-1846

442   Motta R, Nola P (2001) Growth trends and dynamics in sub-alpine forest stands in the Varaita

443   Valley (Piedmont, Italy) and their relationships with human activities and global change. J Veg Sci

444   12:219–230

445   Motta R, Nola P, Berretti R (2009) The rise and fall of the black locust (*Robinia pseudoacacia* L.)

446   in the "Siro Negri" Forest Reserve (Lombardy, Italy): lessons learned and future uncertainties. Ann

447   For Sci 66:410

448   Nesheim I, Økland RH (2007) Do vine species in neotropical forests see the forest or the trees? J

449   Veg Sci 18:395-404

450   Nogueira A, Costa FRC, Castilho CV (2011) Liana abundance patterns: the role of ecological filters

451   during development. Biotropica 43:442–449

452   Nola P (1997) Interactions between *Fagus sylvatica* L. and *Hedera helix* L. A dendroecological

453   approach. Dendrochronologia 15:23–37

454   Page NV, Qureshi Q, Rawat GS, Kushalappa CG (2010) Plant diversity in sacred forest fragments

455   of Western Ghats: a comparative study of four life forms. Plant Ecol 206:237–250

456   Putz FE, Mooney HA (1991) The biology of vines. Cambridge University Press, Cambridge

457   Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–

458   1724

459   Sartori F (1984) Les forêts alluviales de la basse vallée du Tessin (Italie du nord). In: Cramer J (ed)

460   Colloques phytosocologiques, la végétation des forêts alluviales, pp 201-216

461   Schnitzler A (1995) Community ecology of arboreal lianas in gallery forest of the Rhine valley,

462   France. Acta Oecol 16:219–236

463   Schnitzler A, Heuzé P (2006) Ivy (*Hedera helix* L.) dynamics in riverine forests: Effects of river

464   regulation and forest disturbance. For Ecol Manage 236:12-17

465   Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. Trends Ecol Evol

466   17:223–230

467   Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests:

468   emerging patterns and putative mechanisms. Ecol Lett 14:397–406

469   Schnitzer SA, DeWalt SJ, Chave J (2006) Censusing and measuring lianas: a quantitative

470   comparison of the common methods. Biotropica 38:581–591

471   Ter Braak CJF, Smilauer P (1998) CANOCO 4. Centre for Biometry, Wageningen, The

472   Netherlands

473   Toledo-Aceves T, Swaine MD (2008) Above- and below-ground competition between the liana

474   Acacia kamerunensis and tree seedlings in contrasting light environments. Plant Ecol 196:233–244

475   Trèmolières M, Carbiener R, Exinger A, Turlot JC (1988) Un exemple d'interaction non

476   compètitive entre espèces ligneuses: le cas du lierre arborescent (*Hedera helix* L.) dans la foret

477   alluviale. Acta Oecol 9:187–209

478   Van der Heijden GMF, Phillips OL (2008) What controls liana success in Neotropical forests?

479   Global Ecol Biogeogr 17:372–383

480   Yuan CM, Liu WY, Tang CQ, Li XS (2009) Species composition, diversity, and abundance of

481   lianas in different secondary and primary forests in a subtropical mountainous area, SW China. Ecol

482   Res 24:1361–1370

483

484

485

486

487

488

489

490

491 **TABLES**

492

493 **Table 1** Tree stand characteristics and percentage of trees hosting ivy in the study plots

494

Density (n/ha)	Mean diameter (cm)	Basal Area (m^2/ha)	Host trees (%)
498	26.7	28.4	48
560	28.1	34.7	45
122	46.6	20.9	79
228	30.2	18.5	55
320	33.9	24.5	52

495

496

497

498

499

500

501

502

503

504

505

506

507

508

509

510

511

512

513

514

515

516

517

518

519

520

521   **Table 2** Results of binary logistic regression to evaluate the host tree characteristics that determine

522   the presence of ivy on a tree

523

	Nagelkerke R^2	Hosmer - Lemeshow Test	Percentage Correct	Variable	Beta	Wald	p	95.0% C.I. lower	95.0% C.I. upper
Model	0.303	0.569	69.5	Diameter	0.060	15.853	**<0.001**	1.032	1.092
				Neighbors	-0.111	25.266	**<0.001**	0.857	0.934
				Species		9.582	0.088		
				Constant	-0.564	0.401	0.527		

524

525   Diameter is the diameter at breast height of the tree, neighbors is the number of trees in a circle of

526   10 m around the tree, and species is tree species. p values < 0.05 are indicated in bold

527

528

529

530

531

532

533

534

535

536

537

538

539

540

541

542

543

544

545

546

547

548

549

550

551

552

553

554

555 **Table 3** Results of General Linear Models to predict the number of ivy stems on host trees, the sum

556 of their diameters, and basal area

557

	Number of stems			Sum of diameters			Basal area		
	R^2Adj	Beta	p	R^2Adj	Beta	p	R^2Adj	Beta	p
Model	0.402		**<0.001**	0.375		**<0.001**	0.286		**<0.001**
Intercept		-0.530	0.302		-0.629	0.373		-3.451	**0.018**
Diameter		0.717	**<0.001**		0.704	**<0.001**		1.435	**<0.001**
Neighbors		-0.025	**0.008**		-0.030	**0.021**		-0.055	**0.040**
Quercus		-0.534	**0.041**		0.626	0.080		1.355	0.065
Robinia		-0.090	0.741		-0.004	0.992		0.532	0.489
Acer		-0.541	0.068		0.265	0.514		1.340	0.108
Ulmus		-0.428	0.159		-0.075	0.857		0.873	0.307
Crataegus		-0.726	**0.004**		0.112	0.742		0.893	0.204

558

559 Diameter is the diameter at breast height of the tree, neighbors is the number of trees in a circle of

560 10 m around the tree, and Quercus, Robinia, Acer, Ulmus and Crataegus are tree species. p values <

561 0.05 are indicated in bold

562

563

564

565

566

567

568

569

570

571

572

573

574

575

576

577

578

579

580

581

582

FIGURE CAPTIONS

584

585 **Fig. 1** Ivy density expressed as the number of stems per hectare ≥ 0.5, 1 and 2.5 cm in the four

586 study plots

587

588 **Fig. 2** Ivy basal area per hectare (considering stems ≥ 0.5 cm) in the four study plots

589

590 **Fig. 3** Redundancy analysis ordination biplots. In the upper RDA (Fig. 3a), all 374 trees were

591 included, and tree age was not considered. In the lower RDA (Fig. 3b), only the 207 trees for which

592 tree age was estimated were included. Full-line arrows represent the biplot scores of tree variables:

593 TR_d = tree diameter; TR_age = tree age; NE_n = number of neighbors in a circle of 10 m around

594 the tree; NE_s_d = sum of diameters of neighbors; NE_ra = neighborhood ratio. Dotted arrows

595 represent the biplot scores of ivy descriptors: *HE_n* = number of ivy stems on the tree; *HE_s_d* =

596 sum of diameters; *HE_ba* = basal area; *HE_d_M* = diameter of the biggest stem; *HE_cl* = class of

597 occupancy. The dots represent tree species: Acer, Crataegus, Quercus, Robinia, Ulmus and Others

598

599 **Fig. 4** Relationship between trunk circumference available to ivy stem (i.e. the ratio between host

600 trunk circumference and sum of ivy stem diameters) and its mean ring width over the last 5 years.

601 Both axes are log-scaled. The straight line is the linear regression fitted to the data, with confidence
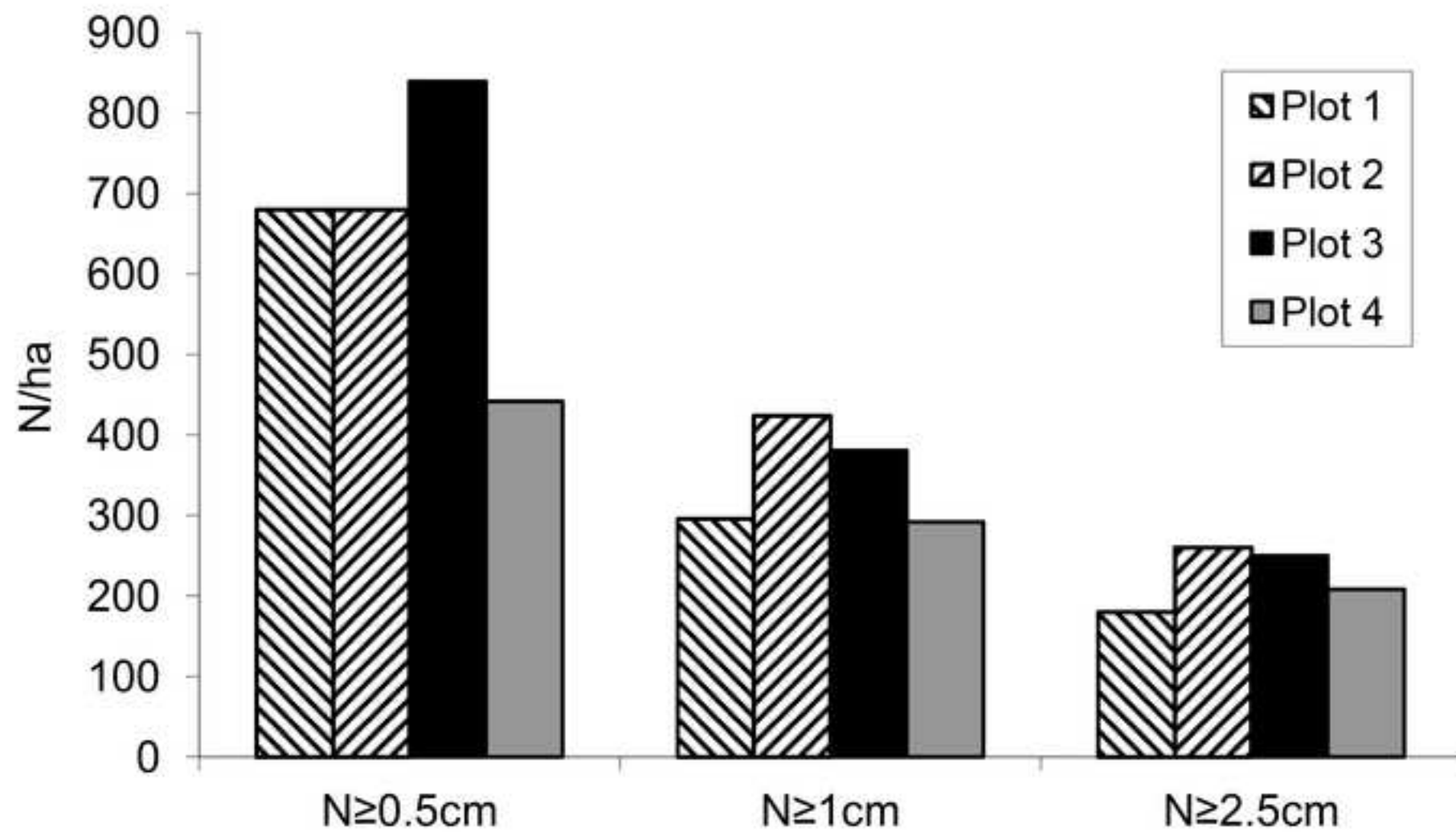
602 intervals (dotted lines)

Fig1
Click here to download high resolution image
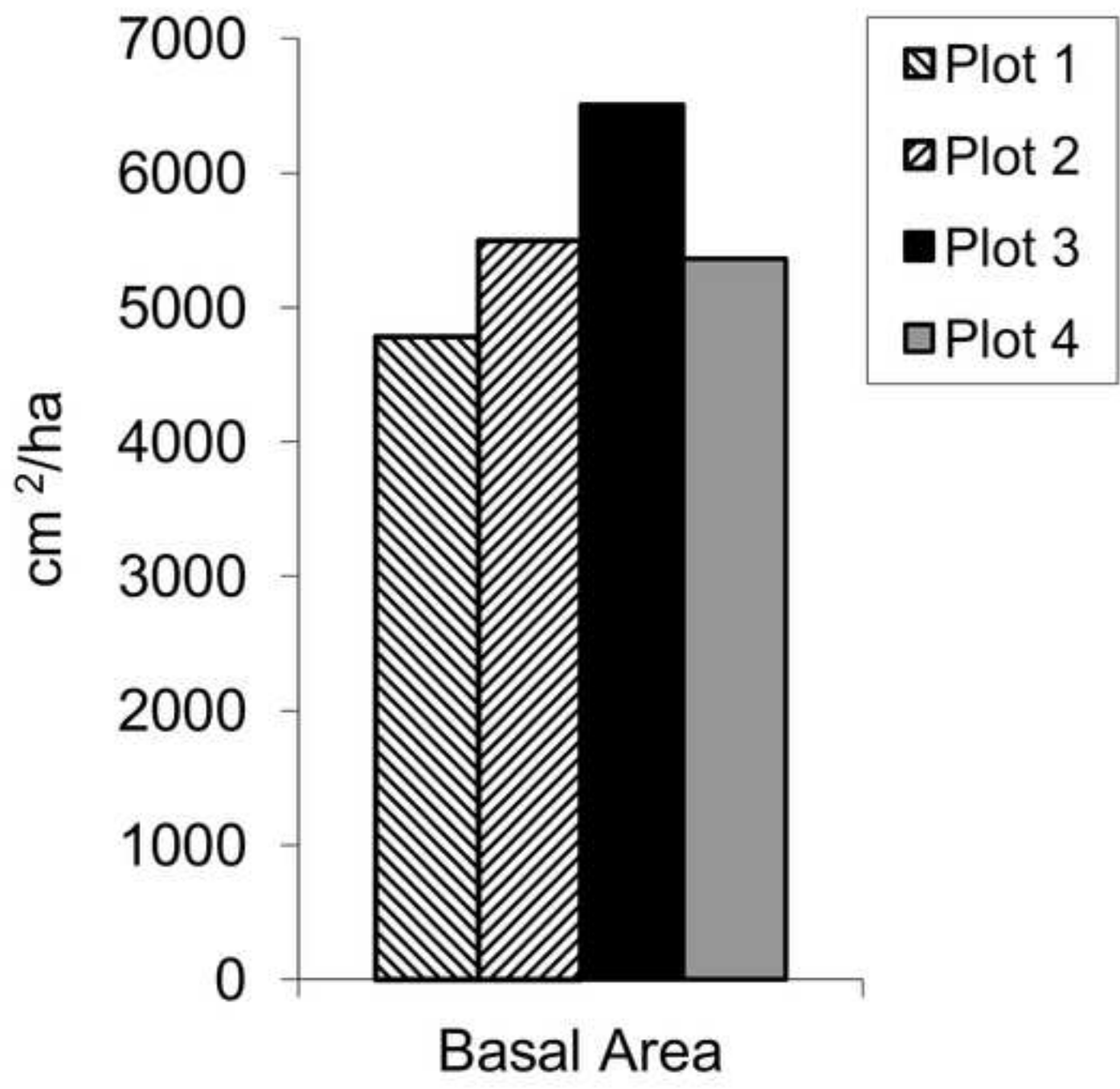
Fig2
Click here to download high resolution image

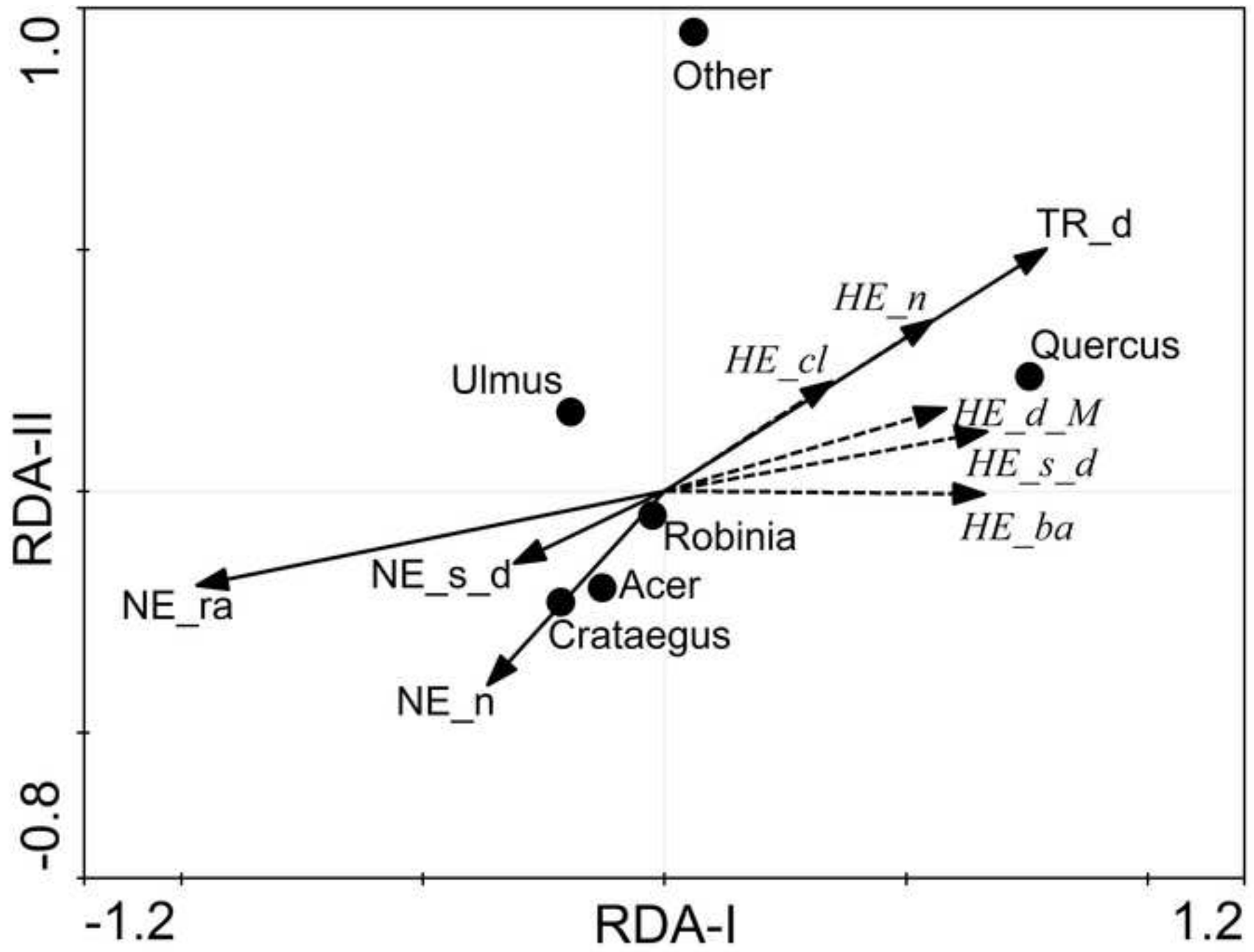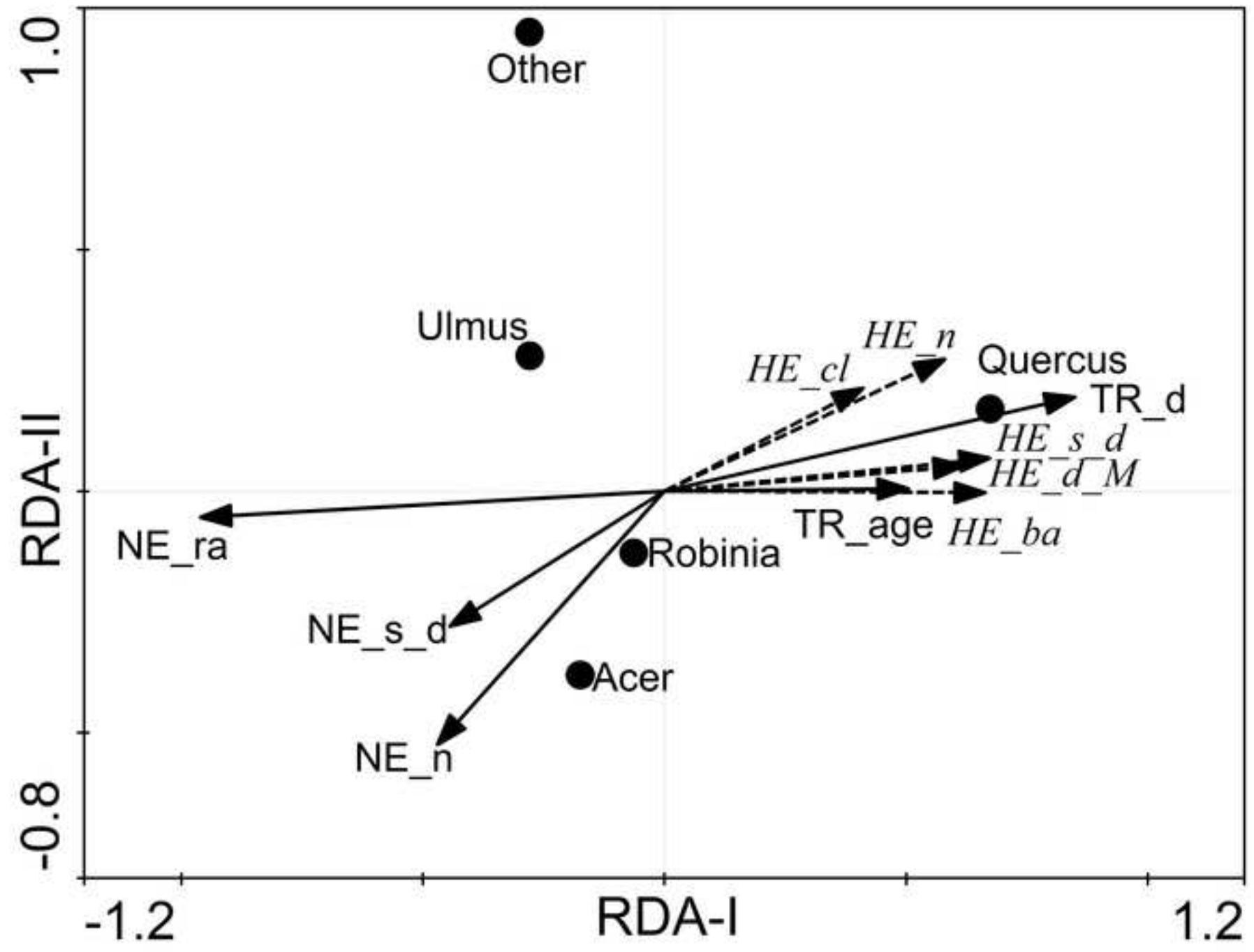Fig4
Click here to download high resolution image