

Vegetative regeneration of beech coppices for biomass in Piedmont, NW Italy

Giorgio Vacchiano^{1*}, Roberta Berretti¹, Pierpaolo Brenta², Fabio Meloni¹, Renzo Motta¹, Antonio Nosenzo¹, Pier Giorgio Terzuolo²

1 University of Turin, DISAFA. Largo Braccini 2, 10095 Grugliasco (TO), Italy

2 Istituto per le Piante da Legno e l'Ambiente IPLA S.p.A. Corso Casale 476, 10132 Torino, Italy

* corresponding author. giorgio.vacchiano@unito.it, tel +39 011 6705536, fax +39 011 6705556

Abstract

Interest in coppices is growing due to the need to replace fossil fuels with renewable energy sources. In Italy, beech covers one million hectares, half of which originated by coppicing. This study tested which factors drive the presence and growth of beech resprouts, with a focus on fertility, cutting intensity, age, and size at time of coppicing.

We analyzed 509 stools in 24 stands coppiced between 1 and 26 years before sampling. We fitted Generalized Linear Mixed Models of the probability of sprouting and height of the tallest resprout for each stool as a function of elevation, slope, aspect, bedrock, precipitation, temperature, age at coppicing, time since coppicing, residual shoot density, the sum, average and coefficient of variation of the diameter of cut shoots, and type of stool treatment.

Of all harvested stools, 249 (49%) had sprouted with an average of 7.6 resprouts per stool. Height of the tallest resprout on each stool ranged from 3 to 800 cm, mainly as a function of time since coppicing.

Resprout mortality was on average 1.4% per plot. Sprouting decreased with decreasing site fertility, increasing precipitation, and increasing size of cut stems. Leaving one or more shoots on the stool after felling produced a high proportion of sprouting stools (82%).

Although based on a limited sample, our quantitative analysis of the driving factors of sprouting in beech can be used to support silvicultural decisions in over-mature beech coppices, and to optimize trade-offs between ecosystem services such as biomass production, biodiversity, and hydro-geologic protection.

Keywords: biomass, *Fagus sylvatica* L., forest management, sprouting

Highlights:

- Forest coppicing allow to replace fossil fuels with renewable energy sources
- We tested which factors drive the probability and vigor of beech sprouting in the Italian Alps
- Sprouting decreased with poor soils, higher precipitation and increasing stool size
- When one or more shoots were left, 82% of the stools sprouted
- This evidence can be used to sustainably manage beech coppices for biomass

1. Introduction

Coppicing is a silvicultural treatment that takes advantage of the ability of broadleaves to reproduce clonally [1]. When a stem or root is damaged by natural disturbance or cut, changes in hormonal controls prompt root collar buds to generate a new resprout [2]. Such ability varies among species [3] and can be maintained indefinitely or lost with ageing [4].

Since regeneration by coppicing is relatively easy to obtain, and usually grows faster than seedlings thanks to the reserves stored in the root systems of the living stools [5], coppicing has been one of the most common forms of forest management, mostly preferred when seed regeneration is impractical for time, money, or site constraints, and to obtain a fast and steady production of firewood or charcoal [6].

To compensate for the progressive exhaustion of root reserves and consequent mortality of whole stools, and to mitigate the loss of soil and nutrients, clearcut coppicing has often been replaced by sheltered coppicing [7], selection coppicing [8], or maintained under a seed-regenerated overstory.

In Europe, coppicing has historically been more common in southern and eastern countries, e.g., Italy, Spain, Bulgaria, or Serbia, but has recently declined due to depopulation of rural areas and the spreading of fossil fuels, leading to an increase of stored or neglected coppices [9]. To avoid growth stagnation and mechanical instability, steer the forest towards a more "natural" structure, and promote the harvest of larger and more valuable timber, many administrations subsidized the conversion of stored coppices to high forest [1,10,11], while most private-owned coppices were neglected. In recent years, however, the interest in coppices has been rekindled due to the need to replace fossil fuels with renewable energy sources [12-14]. Above being a source of bioenergy, coppices can sustain effectively other ecosystem services such as biodiversity conservation [15-18, but see also 19], protection from natural hazards [20], provision of non-wood forest products [21], or climate change resilience [22].

The key factor in successful coppice management restoration, whether for nature conservation or for economic reasons, is the permanence of the capacity of trees to sprout from their stool. However, there is still very little quantitative information on sprouting ability and its drivers in the main European tree

69 species. For some of them, sprouting success is known to be limited when coppicing is carried out on
1
70² older stems [8,23,24]. Beech (*Fagus sylvatica* L.), one of the most widespread and commercially
3
71⁴ important forest trees in Europe, is one of such species. In non-managed stands dominated by species of
5
72⁷ the genus *Fagus*, the incidence of clonal reproduction is often greater where disturbances are more
8
73⁹ severe [25]. Studies on such survival benefits of sprouting in natural systems exist [15,26], but research
10
74¹³ exploring the contribution of vegetative reproduction in managed stands are still scarce.

15
75¹⁶ Beech coppices are widespread in Southern European mountains, and have been used extensively to
17
76¹⁹ provide firewood and charcoal. However, beech has been showed as one of the weakest sprouters among
19
77²¹ temperate broadleaves, especially when the temporal span of such sprouting ability is concerned [27]. In
21
78²⁴ Italy, beech covers more than one million hectares (10% of total forest cover), half of which originated
24
79²⁶ by coppicing [28]. In Alpine regions such as Piedmont (NW Italy) the share of coppices among beech
26
80²⁸ forests reaches 90%. Here, the recent regional Forest Management Act prohibited coppicing beech
28
81³¹ stands older than 40 years. To support decisions on the ecological and economic sustainability of
31
82³³ maintaining coppicing, and to test legal disposition against ecological evidence, we carried out an
33
83³⁴ analysis of vegetative regeneration of beech coppices in Piedmont. The aim was to test which factors
34
84³⁶ ensure a successful sprouting of beech stools, with a specific attention on fertility, cutting intensity, age
36
85³⁸ and size at the time of coppicing.
38
86⁴¹

87 2. Material and methods

88
89⁴⁸ We analyzed 24 beech coppice stands in 13 municipalities of Piedmont (Fig. 1). Stands were within an
48
90⁵⁰ elevation range of 850-1350 m a.s.l.; mean annual temperature and precipitation ranged from 6.4 to 11.0
50
91⁵² °C and from 1120 to 2315 mm, respectively (interpolated weather station data for the period 1951-86
52
92⁵⁴ [29]). At all sites, soil water regime was classified as udic; soil type and soil nutrient supply were note
54
93⁵⁵ measured directly, but site fertility was described by a dummy variable ranging from 1 (poor) to 4 (very
55
94⁵⁷

93 good), following a region-wide forest cover type classification [30]. All stands had been coppiced
1
94² between 1 and 26 years before sampling. Data on tree density before and after coppicing were available
3
95⁴ from local forest management records; in absence of any other information, we assumed that all stems
4
96⁵ had originated as shoots in the original stands. Harvest intensity was defined as the relative change in the
6
97⁷ number of shoots before and immediately after coppicing (Table 1). Coppicing was carried out as either
8
98⁹ clearcut (one site, harvest intensity =100%), coppice-with-standards (72-95%, 15 sites), or conversion to
9
99¹⁰ high forest (61-82%, 8 sites); no selective coppices were present.
11
100¹¹
12
101¹²
13
102¹³
14
103¹⁴
15
104¹⁵
16
105¹⁶
17
106¹⁷
18
107¹⁸
19
108¹⁹
20
109²⁰
21
110²¹
22
111²²
23
112²³
24
113²⁴
25
114²⁵
26
115²⁶
27
116²⁷
28
117²⁸
29
118²⁹
30
119³⁰
31
120³¹
32
121³²
33
122³³
34
123³⁴
35
124³⁵
36
125³⁶
37
126³⁷
38
127³⁸
39
128³⁹
40
129⁴⁰
41
130⁴¹
42
131⁴²
43
132⁴³
44
133⁴⁴
45
134⁴⁵
46
135⁴⁶
47
136⁴⁷
48
137⁴⁸
49
138⁴⁹
50
139⁵⁰
51
140⁵¹
52
141⁵²
53
142⁵³
54
143⁵⁴
55
144⁵⁵
56
145⁵⁶
57
146⁵⁷
58
147⁵⁸
59
148⁵⁹
60
149⁶⁰
61
150⁶¹
62
151⁶²
63
152⁶³
64
153⁶⁴
65

[Figure 1 here]

154 Stands ranged in size from 0.8 to 4.2 ha, as a result of the extreme fragmentation of privately owned
155
156 forests such as beech coppices in Northern Italy. In each stand we established a circular sampling plot
157
158 (radius = 8-14 m, proportional to tree density) centered on randomly extracted coordinates within the
159
160 stands (making sure that the whole plot area was contained within the stand limits). In each plot we
161
162 recorded slope, aspect, and visually estimated canopy cover. For each stool in the plot, we counted all
163
164 cut and uncut shoots, and all live and dead resprouts (i.e., shoots that we could confidently classify as
165
166 having sprouted after the cut), and measured their diameter at stump height, origin (root or stem
167
168 sprouting), and height (Table 1). We estimated the age of the stand at the time of coppicing by averaging
169
170 tree ring counts from 3-5 exposed stools per plot. We also estimated the age of the resprouts by
171
172 averaging the ring counts from 3-5 increment cores taken from each resprout diameter class.
173
174 We defined as “sprouting” all stools with at least a living resprout at the time of survey, and computed
175
176 resprout mortality as the relative frequency of dead over all resprouts. These figures include mortality
177
178 due to all causes (e.g., competition or natural disturbance), but do not account for resprouts that have
179
180 died and fallen from the stool. The frequency of sprouting stools is therefore a conservative estimate.
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200

117 We fitted Generalized Linear Mixed Models (GLMMs) of the probability of sprouting (0 or 1, n = 509
118 stools) and height of the tallest resprout (n = 249 stools with live resprouts), which has been often found
119 to correlate with future resprout survival [31]. GLMMs allowed us to accommodate non-independent
120 observations (random variable =plot), non-normality and heterogeneity of the response, by using a
121 binomial and lognormal distribution to model the probability of sprouting and the height of the tallest
122 resprout, respectively. Independent variables included slope, bedrock (granite/acidic or limestone),
123 annual precipitation, mean annual temperature, age at coppicing, time since coppicing, the mean and
124 coefficient of variation of the diameter of cut shoots, and type of stool treatment (total or partial cut)
125 (Table 1). Predictors were filtered for collinearity using variance inflation factors (VIF) thresholds
126 (predictors were excluded if VIF >4). All models were optimized including only significant predictors
127 and successfully scrutinized for overdispersion, normality of random factors, and residual patterns.
128 Goodness-of-fit was assessed by the marginal (fixed factors) and conditional (fixed and random factors)
129 coefficient of determination R^2 for GLMMs [32,33], computed by the function *r.squaredGLMM* in the
130 *MuMIn* package for R [34].

3. Results

131 The stands were coppiced at an age of 35 to 55 years (25th, 50th, 75th percentiles: 40 – 45 – 50 years,
132 respectively). Average shoot density before coppicing was in a range of 969-3550 trees ha⁻² (1524 –
133 2134 – 2383), and harvest intensity was in a range of 61-100% (70% – 79% – 90%). Of all 509
134 harvested stools, 249 (49%) had sprouted a total of 2163 new resprouts (range: 0-100% of sprouting in
135 each plot), with an average of 7.6 resprouts per stool (range: 0.3 - 18.4). Only 5% of them sprouted from
136 roots. Six out of 24 plots experienced resprout mortality (average: 1.4%, range: 1-17%). Except for one
137 recently treated plot where no resprouts existed yet at the time of sampling, the height of the tallest
138 resprout in the plot was significantly correlated with time since coppicing (Pearson's $R = 0.66$, $p < 0.001$).
139 The average age of resprouts was also correlated to time since coppicing ($R = 0.86$, $p < 0.001$) but the two

142 variables did not match perfectly, with a difference of 0-13 years between time since coppicing and
143 average age of resprouts. Current canopy cover ranged from 20 to 100% (average: 55%, correlation with
144 time since coppicing: $R = 0.58$, $p = 0.003$), and tended to saturate after about 15 years from coppicing.
145 (Fig. 2).

146 At the plot level, both the proportion of sprouting stools and maximum resprout height were weakly
147 correlated to decreasing residual shoot density ($R = -0.45$ and -0.33 , $p = 0.03$ and 0.14 , respectively)
148 (Fig. 3). The low significance of the correlation between height and residual density has to do with the
149 fact that age since coppicing is not factored in the analysis, indicating the need for a multiple regression
150 approach. At the stool level, both the number of resprouts per stool and height of tallest resprout
151 decreased with decreasing site fertility (Fig. 4), although the robustness of the correlation is somehow
152 limited by the categorical classification of fertility. However, since fertility and bedrock were highly
153 collinear ($R = 0.85$), we decided to use only the second variable in GLMMs.

154 [Figure 2 here]

155 [Figure 3 here]

156 [Figure 4 here]

157 The model for probability of sprouting explained 41.2% of the total variance in the data (marginal R^2 :
158 26.4% from fixed factors only; dispersion parameter = 0.86). The significant variables were
159 presence/absence of shoots left alive on the stool, mean diameter of cut shoots, age at the time of
160 coppicing, and precipitation (Table 2). Sprouting decreased with increasing size of cut shoots (80% of
161 the those > 40 cm in diameter did not resprout) and increasing precipitation, and increased with
162 increasing age at time of coppicing (Fig. 5); the presence of live shoots on the stool improved the
163 probability of sprouting by 20-25% (Fig. 6). When one or more stools were left on the stool after felling,
164 82% of the stools sprouted.

167
1
168²
3
169⁴
5
6
170⁷
8
171⁹
10
172¹¹
13
173¹⁴
15
174¹⁶
17
175¹⁸
19
20
21
176²²
23
177²⁴
25
178²⁶
27
28
179²⁹
30
180³¹
32
33
181³⁴
35
182³⁶
37
38
183³⁹
40
184⁴¹
42
185⁴³
44
45
186⁴⁶
47
187⁴⁸
49
50
188⁵¹
52
189⁵³
54
55
190⁵⁶
57
191⁵⁸
59
60
61
62
63
64
65

[Table 2 here]

[Figure 5 here]

[Figure 6 here]

The model for height of tallest resprout explained 88.9% of the total variance (marginal R^2 : 62.2%). The significant variables were annual precipitation, bedrock, and time since coppicing (Table 3). Age at time of coppicing was, as expected, the dominant driver of maximum resprout height (Fig. 7). However, height also decreased significantly with increasing annual precipitation, and on acidic bedrocks (Fig. 8).

[Table 3 here]

[Figure 7 here]

[Figure 8 here]

4. Discussion

Knowledge about coppicing of European beech stands has a long history in both textbook and operational silviculture [35]. The two main results reported in this paper are not new to the forester community, i.e., that larger shoots are less successful in sprouting due to faster desiccation of the cut stem, and that leaving a shoot on the stool acting as sap sucker keeps the stool tissues vital. However, such knowledge got somewhat obsolete in last decades and very few peer reviewed contributions exist on the topic. Having such popular knowledge confirmed and detailed by the main quantitative results of this paper is of high interest for managers.

Despite the limited sample size and the use of some non-quantitative or partially subjective measurement due to data limitations (e.g., bedrock, fertility, canopy cover), some clear trends emerged.

In managed stands from this study, beech sprouting was influenced by stem diameter, age at the time of

192 coppicing, presence of uncut shoots, time since coppicing, annual precipitation and bedrock. The effect
1
193 of size at the time of coppicing has been documented by previous studies [4,36]; small stools are
2
3
4
194 younger and their resprouts may be more vigorous [37]. This is consistent with anecdotal knowledge of
5
6
195 European foresters [38] and with studies from other species of the *Fagaceae* family, e.g., on North
7
8
196 American oaks, showing a decline in the number of resprouts and a lower height growth with increasing
9
10
197 diameter at the time of coppicing [39,40]. Such behavior may be related to failure of hidden epicormic
11
12
198 buds to develop into new resprouts due to the increasing physical resistance of the bark as diameter
13
14
199 increases with age [41].
15
16

200 All other things being equal, age of the shoot at the time of coppicing had a positive effect at the
17
18
201 individual level, but a negative effect at the stand level; if mean age was <40 years, on average 70% of
19
20
202 stools sprouted, but only 50% if mean age was >50 years. Other European species show a positive effect
21
22
203 of age at time of coppicing on sprouting, e.g., hornbeam [42], as young resprouts can benefit from the
23
24
204 mature root system of a parent tree [43]. The ability of stools to sprout at a later age is the main obstacle
25
26
205 for coppice restoration, as many coppice stands have been either neglected, or converted to high forest
27
28
206 several decades ago. These results are generally consistent with provisions by regional forest regulations
29
30
207 that, in many Italian regions, forbid coppicing of beech beyond 40 years of age.
31
32
33

208 In our study, more productive sites – those with limestone bedrock rather than acidic – were associated
34
35
209 to an increased probability of sprouting, other factors being equal. Relative to the overall figure (70%),
36
37
210 stands on the most fertile sites (eutrophic beech forest cover type) showed a much higher proportion of
38
39
211 sprouting stools at age <40 years (91%). This suggests the relevance of resource allocation mechanisms,
40
41
212 as abundant non-structural carbohydrates can be preferentially allocated to bud growth rather than shoot
42
43
213 biomass [44], but data on this trait are largely lacking [45].
44
45
46
47
48
49
50

214 Regarding the role of climate, high precipitation and moisture may cause the bark to partly fall off from
51
52
215 the stool in shade-tolerant species characterized by a thin bark such as beech, consequently killing or
53
54
216 damaging the buds [31]; in sites where annual precipitation was higher than 1500 mm we observed total
55
56
57
58
59
60
61
62
63
64
65

217 decay of stools as soon as eight years after cutting.

218³ Finally, a very strong effect on sprouting probability was played by the presence of one or more uncut
219⁵ shoots on the stool. This has the advantage of slowing down stool decay and avoid drying out of the cut
220⁸ surface. All else being equal, stools with uncut shoots (even if these had poor growth and form) showed
221¹⁰ a higher probability of sprouting, a higher number of resprouts and a better average resprout growth.

222¹² This result is consistent with earlier evidence from selection coppices, where the number and growth of
223¹⁴ resprouts after a rotation of 20 years was higher than in clearcut coppices or coppices with standards of
224¹⁵ the same age [8]. We therefore suggest that sprouting ability can be improved by retaining at least one
225¹⁷ shoot per stool uncut, especially when restoring coppice in unfavorable situations (poor fertility or late
226¹⁹ age).

227²⁰ Similar variables appeared to influence the growth of resprouts after the cut. Beyond the obvious
228²² influence of time since coppicing, height of the tallest resprout was positively influenced by nutrient
229²⁴ availability (limestone bedrock), and negatively by precipitation. Warmer aspect (south-facing) were
230²⁶ expected to improve resprout growth, especially due to the sensitivity of young resprouts to late frost,
231²⁸ but the effect was not significant (albeit positive).

232³⁰ Another driver of resprout growth was residual shoot density. At the stand level, shading from
233³² increasing stand density markedly affected stool sprouting and growth of the resprouts: the average
234³⁴ proportion of sprouting stools was 69% when residual shoot density was <400 trees per hectare, but only
235³⁶ 32% above that threshold (Fig. 3). Trees that are, or have to be, left standing as a seed source to
236³⁸ compensate for stool exhaustion, also limit the amount of light that reaches the forest floor, and may
237⁴⁰ therefore either favor or hinder the regeneration depending on their density [41].

238⁴² This work, albeit conducted on a limited sample size, confirmed that increasing age and size at the time
239⁴⁴ of coppicing are associated to a decline in sprouting ability of European beech. Over-mature coppices
240⁴⁶ suffer from detrimental physiological changes, a reduction in re-sprouting ability, and increased

241 mechanical failure that substantially decreases their longevity [46]. The recommended maximum age for
1
242 coppicing beech is 40 years. However, leaving one shoot uncut on the stool significantly improves
2
3
4
243 sprouting. All else being equal, residual shoot density, site fertility and climate were also found to play
5
6
244 an important role.
7
8
9

245 10 11 12 13 246 **5. Conclusions** 14 15

247 We showed how beech sprouting in the western Italian Alps decreases with poor soils, higher
16
17
18
248 precipitation, and increasing stool size and age. An effective measure to preserve vegetative regeneration
19
20
249 (82% of cases) is to leave one or more shoots uncut.
21
22

23
24
250 Such evidence can support silvicultural decisions in overmature beech coppices, which still represent
25
26
251 present an unsolved silvicultural dilemma. When the choice must be made between abandonment, active
27
28
252 conversion into high forest, mixed regeneration systems [47], or restoration of clearcut or selection
29
30
253 coppicing, forest managers should carefully examine stand age, climate, soil, and site characteristics.
31
32
33

34
254 Old coppices on poor soils and humid climates exhibit a poor sprouting capacity, and are the first
35
36
255 candidates for conversion to high forest. On the other hand, coppices on more fertile soils that have not
37
38
256 yet reached 40-50 years of age can be targeted for a continuation or restoration of vegetative
39
40
257 regeneration aimed at the provision of sustainable energy wood, provided that one or more live shoots
41
42
258 are left on the stool.
43
44
45

46
47
259 In a warming world, over-mature and neglected coppices are also more vulnerable to climatic stress and
48
49
260 xylem cavitation [48,49]. Therefore, restoration of coppices has the potential to increase forest resilience
50
51
261 in all broadleaves forests at risk from e.g. drought or pests – that put especially large, old trees at risk of
52
53
262 death faster than they can be replaced by seed regeneration – and still sustain key ecosystem services
54
55
263 such as biodiversity, biomass production, and hydrogeologic protection.
56
57
58
59
60
61
62
63
64
65

264
1
265²
3
266⁴
5
267⁸
8
268⁹
10
269¹³
13
270¹⁴
15
271¹⁶
16
272¹⁷
17
273¹⁹
20
274²¹
21
275²²
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Acknowledgments

The authors support the campaign #ricercaprecaria for the full implementation of the European Charter for Researchers and the acknowledgement of all researchers as workers, and the Change.org petition “Salviamo la ricerca italiana” (<https://www.change.org/p/salviamo-la-ricerca-italiana>) for the increase of research funding in Italy to the levels requested by the EU Lisbon strategy.

Conflict of interest

The authors declare no conflict of interest and compliance with the current laws of the country in which field measurement were performed.

276 **References**

- 1
2
277
3
278 [1] Buckley GP. Ecology and management of coppice woodlands. London, UK: Chapman & Hall; 1992.
4
5
279 [2] Vesk PA. Plant size and resprouting ability: trading tolerance and avoidance of damage?. J Ecol
6
7
280 2006;94(5):1027–1034.
8
9
281 [3] Matula R, Svátek M, Kůrová J, Úradníček L, Kadavý J, Kneifl M. The sprouting ability of the main
10
11
282 tree species in Central European coppices: implications for coppice restoration. Eur J For Res
12
13
283 2012;131:1501-1511.
14
15
284 [4] Del Tredici P. Sprouting in temperate trees: a morphological and ecological review. Bot Rev
16
17
285 2001;67(2):121-140.
18
19
286 [5] Zhu WZ, Xiang JS, Wang SG, Li, MH. Resprouting ability and mobile carbohydrate reserves in an
20
21
287 oak shrubland decline with increasing elevation on the eastern edge of the Qinghai–Tibet Plateau. For
22
23
288 Ecol Manag 2012; 278(8):118–126.
24
25
289 [6] Vacchiano G, Garbarino M, Lingua E, Motta R. Ecology of mountain forest ecosystems in the Italian
26
27
290 Apennines. For Ecol Manag 2017;in press.DOI 10.1016/j.foreco.2016.10.33
28
29
291 [7] Stewart PJ. Coppice with standards: a system for the future. Commonw For Rev 1980;59:149-154.
30
31
292 [8] Coppini M, Hermanin L. Restoration of selective beech coppices: a case study in the Apennines
32
33
293 (Italy). For Ecol Manag 2007;249(1):18-27.
34
35
294 [9] Amorini E, Fabbio G, Bertini G. Stand dynamics of a beech coppice beyond the rotation age and
36
37
295 under conversion into high forest. Ann Silv Res 2010;36:151-172.
38
39
296 [10] Ciancio O, Corona P, Lamonaca A, Portoghesi L, Travaglini D. Conversion of clearcut beech
40
41
297 coppices into high forests with continuous cover: A case study in central Italy. For Ecol Manag 2006;
42
43
298 224(3):235-240.
44
45
299 [11] Mattioli W, Ferrari B, Giuliarelli D, Mancini LD, Portoghesi L, Corona P. Conversion of mountain
46
47
300 beech coppices into high forest: an example for ecological intensification. Environ
48
49
301 Manag 2015;56(5):1159-1169.
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

- 302 [12] Hall JP. Sustainable production of forest biomass for energy. For Chron 2002; 78(3):391–396.
1
- 303² [13] Jansen P, Kuiper L. Double green energy from traditional coppice stands in the Netherlands.
3
304⁴ Biomass Bioenerg 2004;26(4):401–402.
5
6
- 305⁷ [14] McKenney DW, Yemshanov D, Fraleigh S, Allen D, Preto F. An economic assessment of the use
8
306⁹ of short-rotation coppice woody biomass to heat greenhouses in southern Canada. Biomass Bioenerg
10
307¹¹ 2011;35(1):374–384.
12
13
- 308¹⁴ [15] Vacik H, Zlatanov T, Trajkov P, Dekaniæ S. Role of coppice forests in maintaining forest
15
309¹⁶ biodiversity. Silva Balc 2009;10(1):35–45.
17
18
- 310¹⁹ [16] Negro M, Vacchiano G, Berretti R, Chamberlain DE, Palestrini C, Motta R, et al. Effects of forest
20
311²¹ management on ground beetle diversity in alpine beech (*Fagus sylvatica* L.) stands. For Ecol Manag
22
312²³ 2014;328:300-309.
24
25
- 313²⁶ [17] Müllerová J, Hédl R, Szabó P. Coppice abandonment and its implications for species diversity in
26
314²⁷ forest vegetation. For Ecol Manag 2015;343:88-100.
28
29
- 315³¹ [18] Kirby KJ, Buckley GP, Mills J. Biodiversity implications of coppice decline, transformations to
30
316³² high forest and coppice restoration in British woodland. Folia Geobotanica 2017;in press.
33
317³⁴ doi:10.1007/s12224-016-9252-1.
35
36
- 318³⁶ [19] Vacchiano G, Meloni F, Ferrarato M, Freppaz M, Chiaretta G, Motta R, Lonati M. Frequent
37
319³⁸ coppicing deteriorates the conservation status of black alder forests in the Po plain (northern Italy). For
39
320⁴⁰ Ecol Manage 2016; 382: 31-38
41
42
- 321⁴³ [20] Jancke O, Dorren LK, Berger F, Fuhr M, Köhl M. Implications of coppice stand characteristics on
43
322⁴⁴ the rockfall protection function. For Eco Manag 2009;259(1):124-131.
45
46
- 323⁴⁷ [21] Kobayashi T, Kitahara M, Ohkubo T, Aizawa M. Relationships between the age of northern Kantou
47
324⁴⁸ plain (central Japan) coppice woods used for production of Japanese forest mushroom logs and butterfly
48
325⁴⁹ assemblage structure. Biodivers Conserv 2010;19(8):2147-2166.
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

326 [22] Gavinet J, Prévosto B, Fernandez C. Introducing resprouters to enhance Mediterranean forest
327 resilience: importance of functional traits to select species according to a gradient of pine density. J Appl
328 Ecol 2016;in press. doi:10.1111/1365-2664.12716.

329 [23] Atwood CJ, Fox TR, Loftis DL. Effects of alternative silviculture on stump sprouting in the
330 southern Appalachians. For Ecol Manag 2009;257(4):1305–1313

331 [24] Harmer R, Howe J. The silviculture and management of coppice woodlands. Edinburgh, UK: The
332 Forestry Commission;2003.

333 [25] Morris AB, Small RL, Cruzan MB. Variation in frequency of clonal reproduction among
334 populations of *Fagus grandifolia* Ehrh. in response to disturbance. Castanea 2004;69(1):38-51.

335 [26] Zywiec M, Holeksa J. Sprouting extends the lifespan of tree species in a seedling bank: 12-year
336 study. For Ecol Manag 2012;284:205–212.

337 [27] Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, et al. Resprouting as a key
338 functional trait: how buds, protection and resources drive persistence after fire. New Phytol
339 2013;197:19–35.

340 [28] Nocentini S. Structure and management of beech (*Fagus sylvatica* L.) forests in Italy. iForest -
341 Biogeosciences and Forestry 2009;2:105-113.

342 [29] Biancotti A, Bellardone G, Bovo S, Cagnazzi B, Giacomelli L, Marchisio C. Distribuzione
343 regionale di piogge e temperature. Torino, IT: Regione Piemonte e Università degli Studi di Torino;
344 1998.

345 [30] Camerano P, Gottero F, Terzuolo P, Varese P. Tipi forestali del Piemonte. Torino, IT: Regione
346 Piemonte; 2008.

347 [31] Leonardsson J, Götmark F. Differential survival and growth of stumps in 14 woody species after
348 conservation thinning in mixed oak-rich temperate forests. Eur J For Res 2015;134(1):199-209.

349 [32] Nakagawa S, Schielzeth H. A general and simple method for obtaining R^2 from Generalized Linear
350 Mixed-effects Models. Methods Ecol Evol 2013;4:133–142.

- 351 [33] Johnson PCD. Extension of Nakagawa & Schielzeth's R^2 _GLMM to random slopes
1
352 models. *Methods Ecol Evol* 2014;5:44-946.
3
4
353 [34] Bartoń K. MuMIn: Multi-Model Inference. R package version 1.15.6. 2016. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
6
354 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn).
8
355 [35] Buckley GP, Mills J. Coppice silviculture: from the Mesolithic to the 21st century. In: Kirby K,
10
356 Watkins C (eds). *Europe's Changing Woods and Forests*. Oxfordshire: CABI Publishing; 2002; 77-92.
13
357 [36] Vesik PA, Westoby M. Sprouting ability across diverse disturbances and vegetation types
14
358 worldwide. *J Ecol* 2004;92(2):310–320.
16
359 [37] Harrington CA. Factors influencing initial sprouting of red alder. *Can J For Res* 1984;14:357–361.
18
360 [38] Burley J, Evans J, Youngquist J. *Encyclopedia of forest sciences*. Amsterdam: Elsevier;2004.
21
361 [39] Weigel DR, Peng CYJ. Predicting stump sprouting and competitive success of five oak species in
23
362 southern Indiana. *Can J For Res* 2002;32(4):703-712.
25
363 [40] Sands BA, Abrams MD. Effects of stump diameter on sprout number and size for three oak species
26
364 in a Pennsylvania clearcut. *North J Appl For* 2009;26(3):122–125.
28
365 [41] Wilson BF. Red maple stump sprouts: development the first year. Harvard Forest Paper No. 18.
30
366 Petersham, MA: Harvard University;1968.
32
367 [42] Matula R, Svátek M, Kůrová J, Úradníček L, Kadavý J, Kneifl M. The sprouting ability of the main
34
368 tree species in Central European coppices: implications for coppice restoration. *Eur J For Res* 2012;
36
369 131(5):1501-1511.
38
370 [43] Johnson PS, Shifley SR, Rogers R. *The ecology and silviculture of oaks*. New York: CABI
40
371 Publishing;2002.
42
372 [44] Clarke PJ, Lawes MJ, Midgley JJ. Resprouting as a key functional trait in woody plants—
44
373 challenges to developing new organizing principles. *New Phytol* 2010;188(3): 651–654.
46
374 [45] Bond WJ, Midgley JJ. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol*
48
375 *Evol* 1001;16(1):45–51.
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

376 [46] Sjölund MJ, Jump AS. The benefits and hazards of exploiting vegetative regeneration for forest
 1 conservation management in a warming world. *Forestry* 2013;86:503-513.

377²
 3

378⁴ [47] Motta R, Berretti R, Dotta A, Motta Fre V, Terzuolo P. Il governo misto. *Sherwood - Foreste ed*
 6 *Alberi Oggi* 2015;211:9-13.

379⁸

380⁹ [48] Corcuera L, Camarero JJ, Sisò S, Gil-Pelegrin E. Radial-growth and wood-anatomical changes in
 10 overaged *Quercus pyrenaica* coppice stands: functional responses in a new Mediterranean landscape.
 11 *Trees* 2006;20:91–98.

382¹³

383¹⁴ [49] Di Filippo A, Alessandrini A, Biondi F, Blasi S, Portoghesi L, Piovesan G. Climate change and oak
 16 growth decline: dendroecology and stand productivity of a Turkey oak (*Quercus cerris* L.) old stored
 18 coppice in central Italy. *Ann For Sci* 2010;67:706-706.

385²¹
 22
 23
 24
 25
 26
 27
 28
 29
 30
 31
 32
 33
 34
 35
 36
 37
 38
 39
 40
 41
 42
 43
 44
 45
 46
 47
 48
 49
 50
 51
 52
 53
 54
 55
 56
 57
 58
 59
 60
 61
 62
 63
 64
 65

Figure captions

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Fig. 1 – Distribution of beech in Piedmont, Italy (blue) and beech coppice stands analyzed by this study (red dots)

Fig. 2 – Mean resprout age, maximum resprout height, and current canopy cover as a function of time since coppicing

Fig. 3 - Relationship between residual shoot density and (a) proportion of sprouting stools or (b) maximum resprout height in each plot (n =24)

Fig. 4 - Relationship between site fertility and number of resprouts per stool (a) (n =509) or maximum resprout height (b) (n =249)

Fig. 5 – Marginal effects of significant predictors in the GLMM for the probability of sprouting (binomial regression with log link); in each panel, all other predictors were kept at their mean level

Fig. 6 - Predicted probability of sprouting as a function of mean cut diameter with or without uncut shoots, conditioned on fixed and random effects. Dots represent observed data. Precipitation and age at time of coppicing were set at the average value for all plots

Fig. 7 – Marginal effects of significant predictors in the GLMM for maximum resprout height (lognormal regression with identity link); in each panel, all other predictors were kept at their mean level

1
2 Fig. 8 - Predicted maximum resprout height as a function of time since coppicing and
3
4 bedrock, conditioned on fixed and random effects. Dots represent observed data.
5
6

7 Precipitation was set at the average value for all plots
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Tables

Table 1 – Definition and units of variables used in this study

Variable (units)	Description
<i>Descriptive</i>	
Tree density before coppicing (ha ⁻¹)	From local forest management records
Harvest intensity (%)	100 – (Residual shoot density / Tree density before coppicing)
Resprouts (ha ⁻¹)	Shoots that we could confidently classify as having sprouted after the cut
Number of stools (ha ⁻¹)	Only including those that were cut
Proportion of sprouting stools (%)	Stools with live or dead resprouts / Number of stools (per plot)
Number of resprouts per stool (-)	Resprouts / Number of stools
Residual shoot density (ha ⁻¹)	From local forest management records; includes all shoots but no resprouts
Fertility (ordinal 1 to 4)	From forest cover type map
Resprout diameter (cm)	Measured at stump height
Resprout origin (binary)	Root or shoot
Resprout height (cm)	Measured from stump height
Resprout status (binary)	Dead or alive
Mean resprout age (years)	Average of ring counts from 3-5 increment cores taken from each resprout diameter class
Resprout mortality rate (%)	Relative frequency of dead resprouts (e.g., by competition or natural disturbance), not including those that had died and fallen from the stool
<i>GLMMs - Dependent</i>	
Probability of sprouting (0-1)	On each stool
Height of the tallest resprout (cm)	On each stool
<i>GLMMs - Independent</i>	
Age at time of coppicing (years)	Average of tree ring counts from 3-5 exposed stools per plot
Time since coppicing (years)	From documental records
Bedrock (categorical)	Limestone or granite
Annual precipitation (mm)	From regional climate database
Mean annual temperature (°C)	From regional climate database
Type of stool treatment (binary)	Total or partial cut
Sum of the diameter of cut shoots (cm)	
Average diameter of cut shoots (cm)	
Coefficient of variation of the diameter of cut shoots (0-1)	

Table 2 - GLMM for probability of sprouting - summary of standardized coefficients.

Dispersion =0.86. Marginal R^2 : 0.264. Conditional R^2 : 0.412. St.dev. of random effects: 1.09.

N =479 after deletion of missing cases

	β	Std. Error	p-value
intercept	-0.57	0.29	0.047
Type of stool treatment: partial	1.86	0.35	<0.001
average cut diameter	-0.37	0.15	0.012
age at coppicing	0.75	0.29	0.009
precipitation	-1.01	0.28	<0.001

Table 3 - GLMM for height of tallest resprout - summary of standardized regression

coefficients. Marginal R^2 : 0.622. Conditional R^2 : 0.888. St.dev. of random effects: 0.66. N

=242 after deletion of missing cases.

	β	Std. Error	p-value
intercept	3.89	0.23	<0.001
time since coppicing	1.03	0.17	<0.001
precipitation	-0.40	0.21	0.071
bedrock: limestone	0.93	0.43	0.046

Figure 1
[Click here to download high resolution image](#)

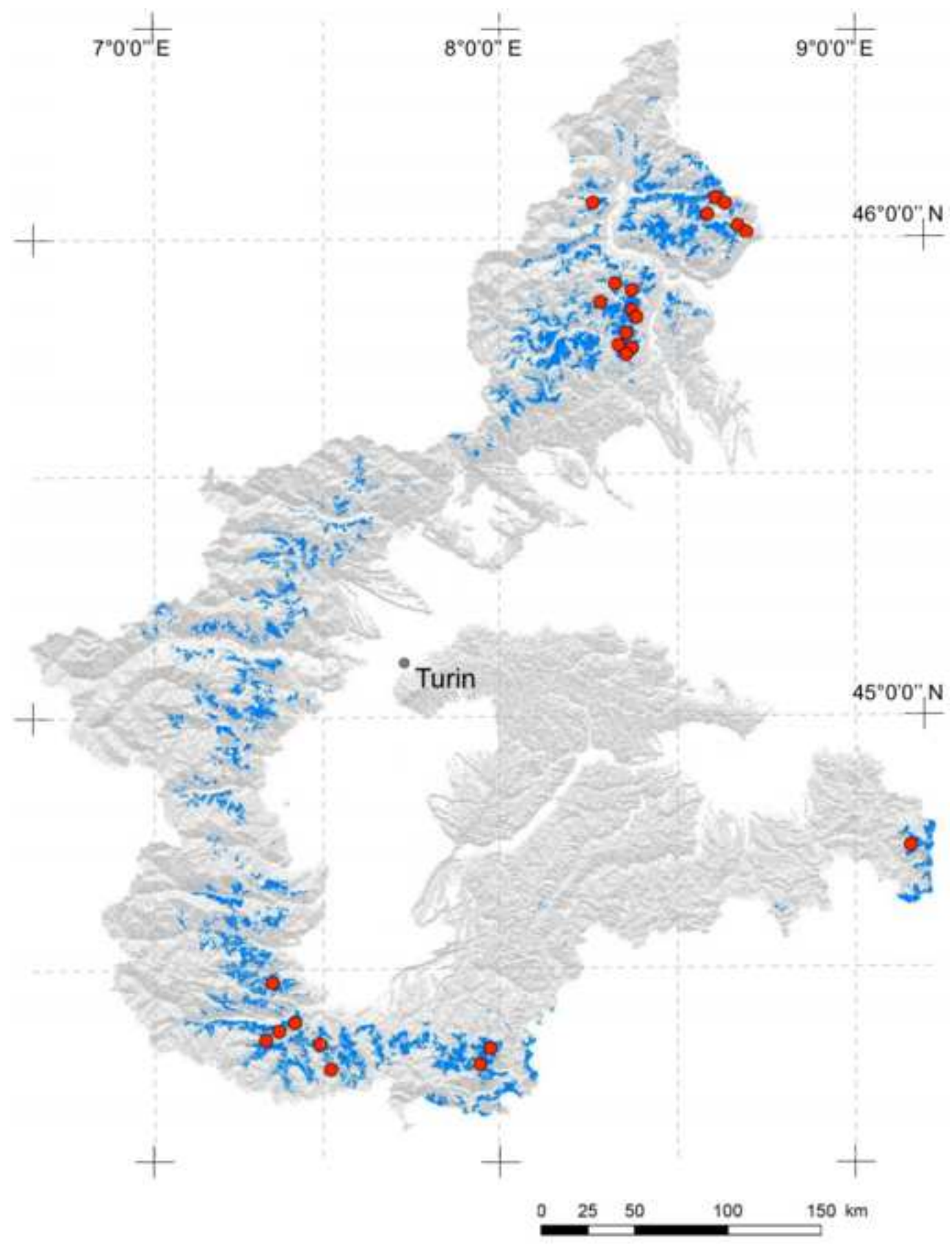


Figure 2

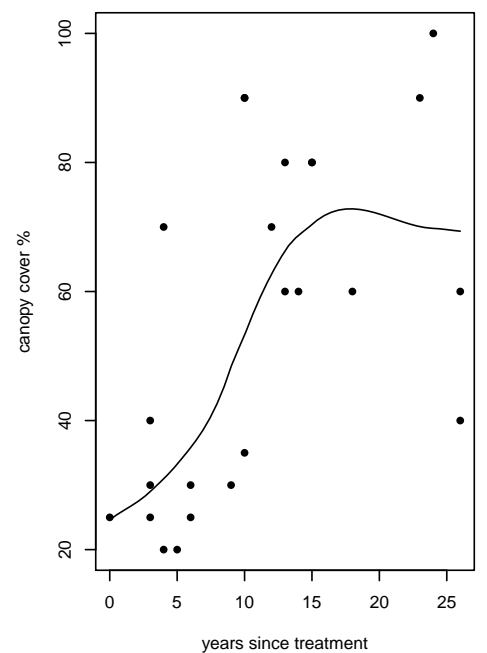
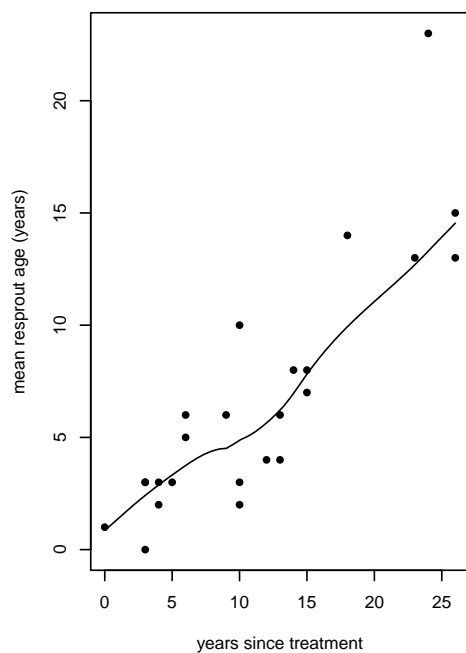
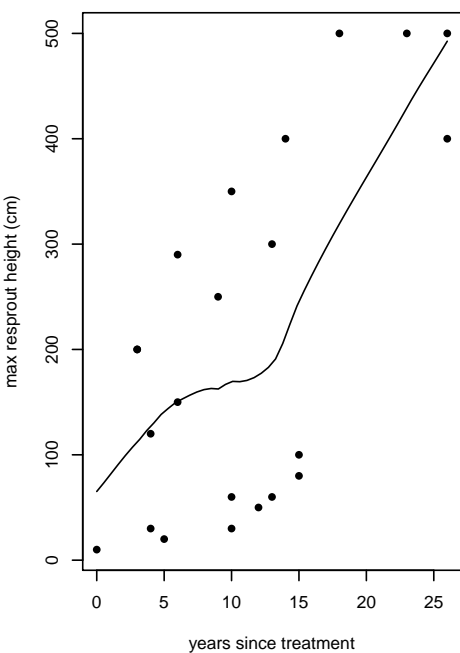


Figure 3

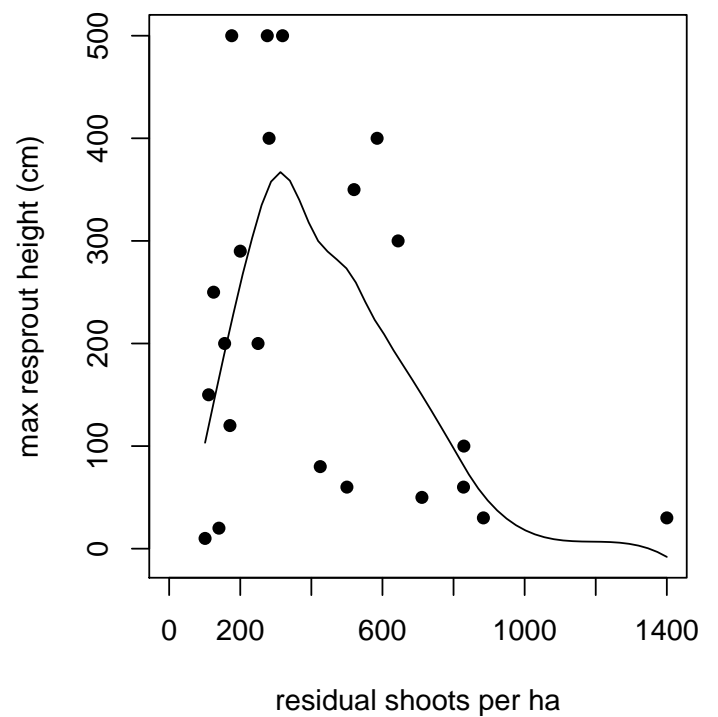
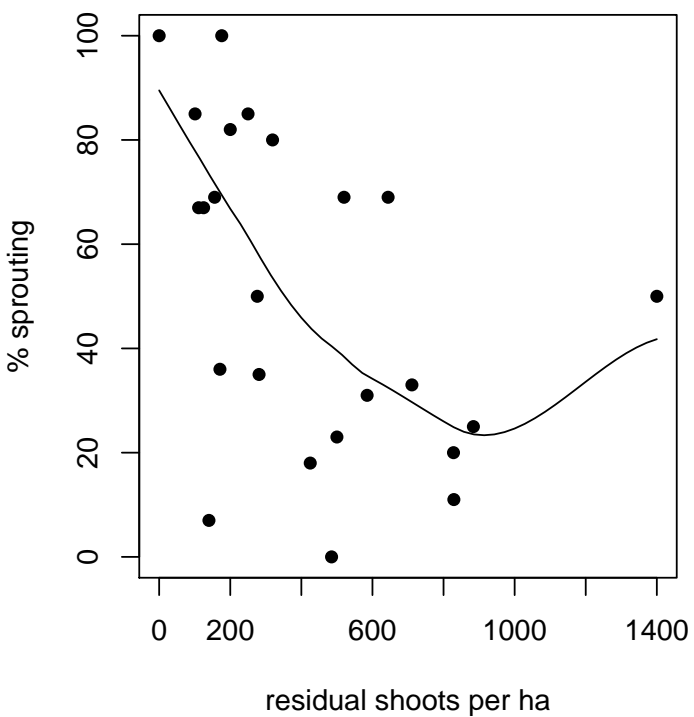


Figure 4a
[Click here to download high resolution image](#)

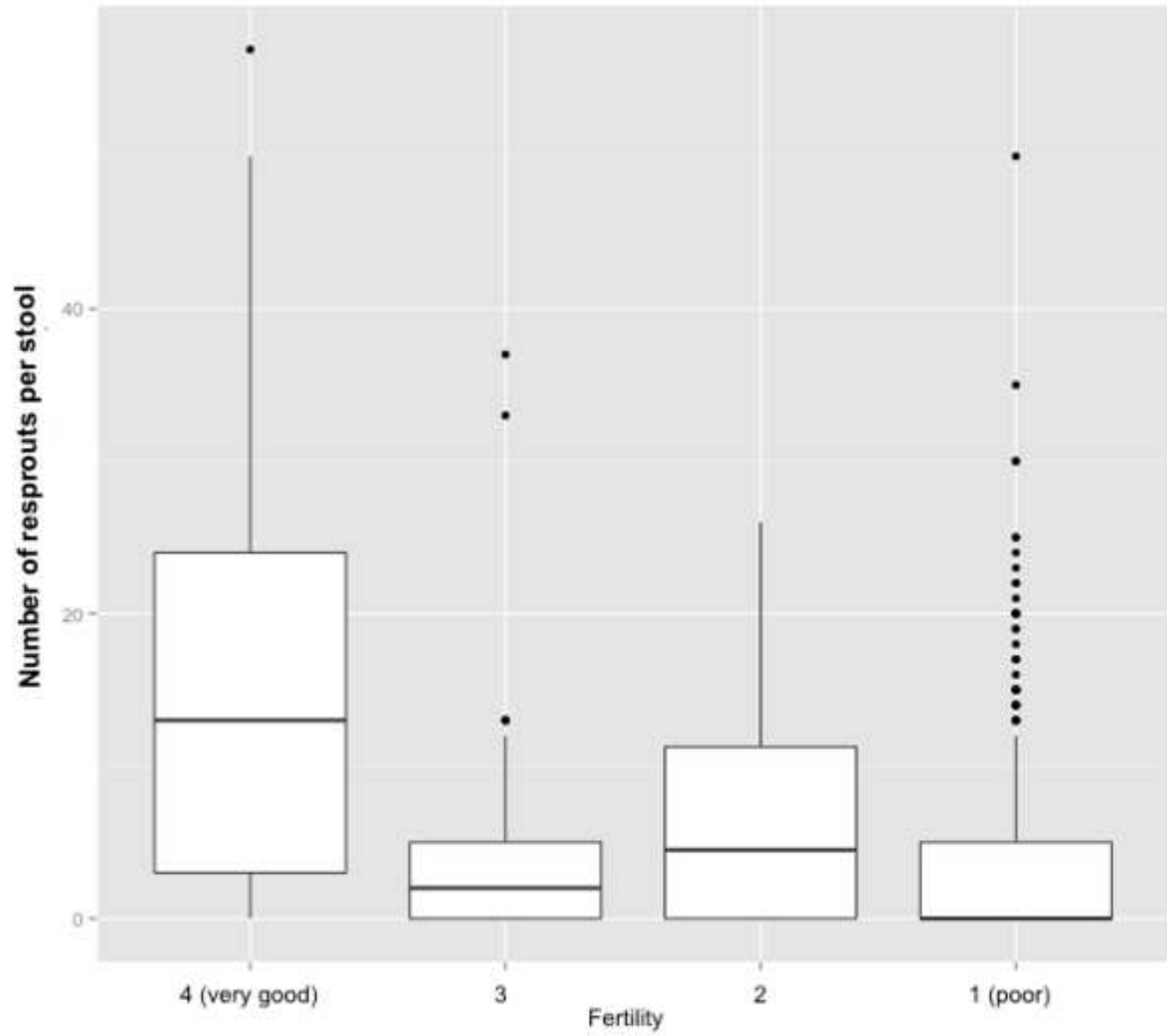


Figure 4b
[Click here to download high resolution image](#)

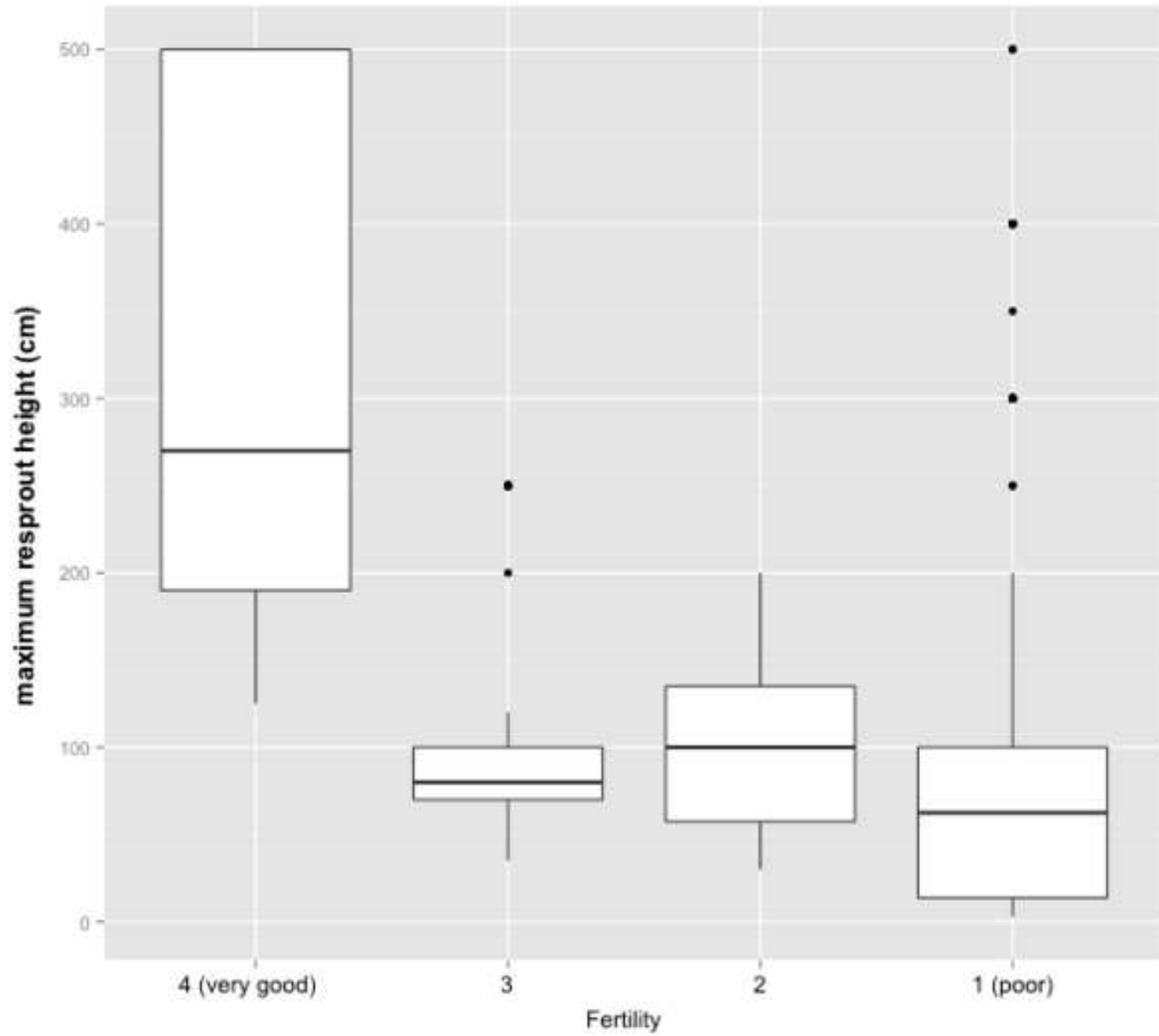


Figure 5
[Click here to download high resolution image](#)

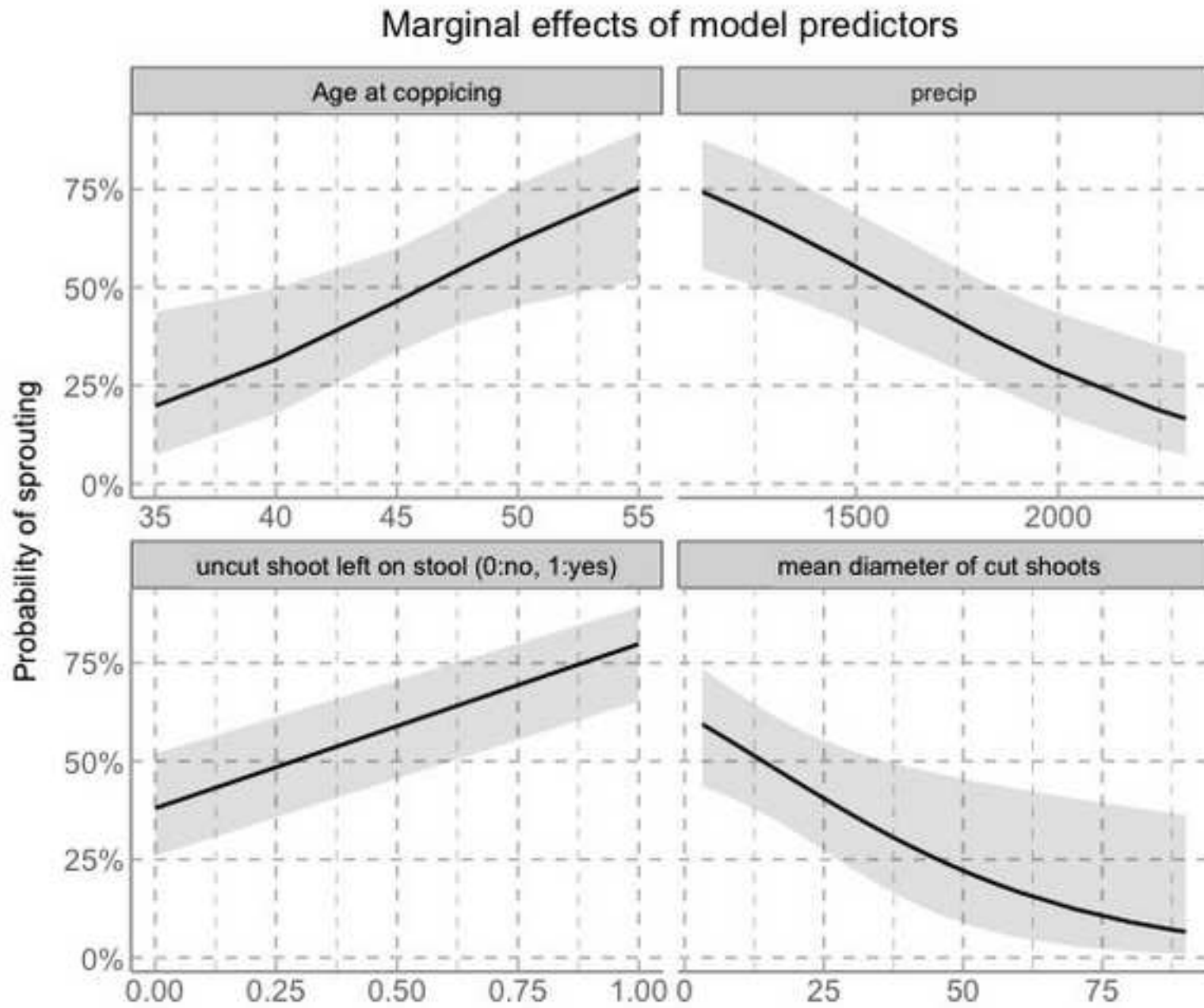


Figure 6
[Click here to download high resolution image](#)

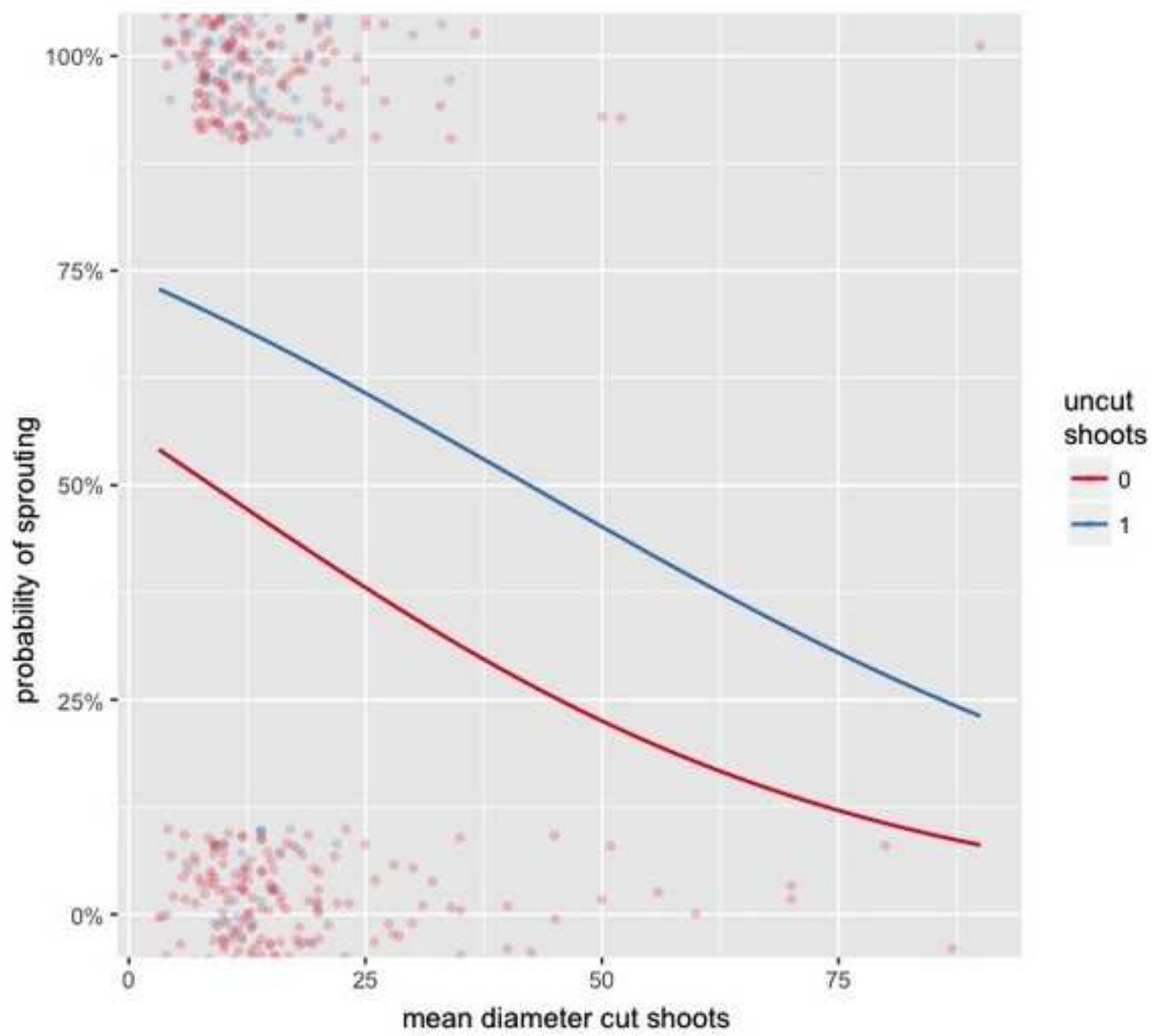


Figure 7
[Click here to download high resolution image](#)

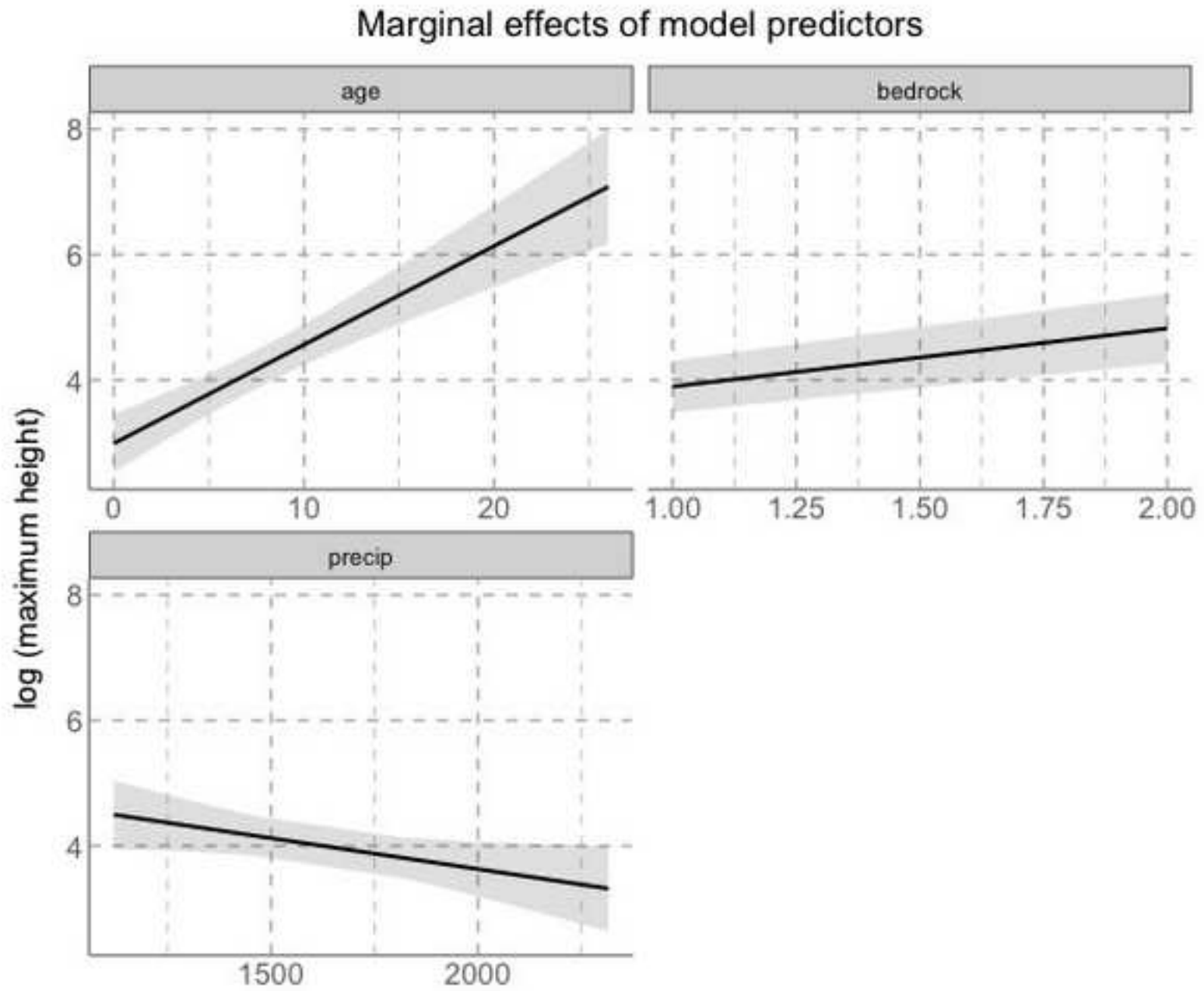


Figure 8
[Click here to download high resolution image](#)

