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7 **Factors limiting the establishment of canopy-forming algae on artificial structures**

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18 **Abstract**

19 Macroalgal canopies are important ecosystem engineers, contributing to coastal
20 productivity and supporting a rich assemblage of associated flora and fauna. Yet, they are
21 often absent from infrastructures such as coastal defences and there has been a
22 worldwide decline in their distribution in urbanised coastal areas. The macroalga *Fucus*
23 *spiralis* is the only high-shore canopy forming species present in the Azores. It is widely
24 distributed in the archipelago but is never found on coastal infrastructures. Here we

25 evaluate factors that may potentially limit its establishment on artificial structures. A
26 number of observational and manipulative experiments were used to test the hypotheses
27 that: (i) limited-dispersal ability limits the colonisation of new plants onto artificial structures,
28 (ii) vertical substratum slope negatively influences the survivorship of recruits, and (iii)
29 vertical substratum slope also negatively influences the survivorship and fitness of adults.
30 Results showed that the limited dispersal from adult plants may be a more important factor
31 than slope in limiting the species ability to colonise coastal infrastructures, since the
32 vertical substratum slope does not affect its fitness or survivorship.

33 **Keywords:** coastal defences; intertidal; rocky shores; macroalgae; benthic communities;
34 coastal urbanization

35

36 **1. Introduction**

37 Canopy-forming algae are key species on intertidal rocky shores (Jonsson et al., 2006) as
38 they can provide shelter from environmental stressors (e.g. desiccation or ultraviolet
39 radiation) for a diverse range of flora and fauna. By doing this, they play an important role
40 in regulating community structure, nutrient cycling and primary production and therefore
41 their conservation should be considered a priority (Bertocci et al., 2011; Perkol-Finkel and
42 Airoldi, 2010; Perkol-Finkel et al., 2012). Despite their importance, marine canopy-forming
43 algae have declined over the past decades (Perkol-Finkel and Airoldi, 2010; Strain et al.,
44 2015), with major implications for the biodiversity and rocky reefs ecosystem goods and
45 services (Airoldi and Beck, 2007; Smale et al., 2013; Voerman et al., 2013). There is thus
46 a clear need to understand the drivers underlying their loss (Perkol-Finkel and Airoldi,
47 2010), the mechanisms that confer them stress tolerance (but see Martínez et al., 2012),
48 and how the relative balance of physical (e.g. wave action) and biological factors (e.g.

49 grazing) control their establishment and persistence (Davison and Pearson, 1996; Jonsson
50 et al., 2006). Evidence worldwide has demonstrated that stressors such as climate change,
51 eutrophication or urbanisation strongly affect marine canopies (e.g. Mangialajo et al.,
52 2008). However, both direct and indirect human-induced modifications on physical habitat,
53 acting as drivers for the decline of canopy-forming algae, have been usually overlooked
54 (Perkol-Finkel and Airoldi, 2010).

55 Many coasts are becoming increasingly urbanised worldwide. This coastal urbanisation
56 can result in extensive modification of natural shores, altering habitat heterogeneity,
57 complexity, slope and available area for benthic biota. This affects natural processes e.g.
58 recruitment, colonization, survival, population densities and connectivity, fecundity or/and
59 species interaction (Bulleri et al., 2004; Bulleri, 2005; Chapman and Bulleri, 2003; Moreira
60 et al., 2006; Perkol-Finkel and Airoldi, 2010). Several studies have investigated the
61 patterns of distribution of benthic communities supported by artificial coastal defence
62 structures and showed they are generally poor surrogates for the habitats they replace
63 (e.g. Moschella et al., 2005). Although a variety of factors differ between artificial
64 structures and the adjacent rocky shores, substratum slope is often fundamentally different.
65 This modified slope has been shown to be a major determinant influencing the structure of
66 intertidal assemblages (Bulleri and Chapman, 2004; Glasby and Connell, 2001). The
67 differences in assemblages generated and maintained by a combination of differential
68 recruitment and post-recruitment processes (Vaselli et al., 2008), result in considerable
69 changes to coastal ecology. Canopy-forming algae are strongly affected by urbanisation
70 (Airoldi and Beck, 2007; Benedetti-Cecchi et al., 2001), and little is known about the
71 consequences of changes in the habitat related characteristics of the shore for their
72 functional properties, like productivity and resilience (i.e. the ability of organisms to recover
73 after events of disturbance, Grimm and Wissel, 1997). Changes have already been

74 showed in demographic parameters such as growth or mortality of populations submitted
75 to disturbance (Araújo et al., 2011), or in morphological parameters such as thalli
76 thickness against desiccation stress or thalli size against wave exposure (Blanchette, 1997;
77 Jorve, 2008). The steep slope of artificial structures could alter the physical stress to which
78 plants are submitted, e.g. different desiccation regimes, and therefore change life-history
79 traits, namely differentiation of populations via phenotypic plasticity (Blanchette, 1997).
80 Moreover, although dispersal via drifting algal rafts has been cited as a mechanism to
81 increase its gene flow (Coleman and Brawley, 2005), gamete dispersal is limited in fucoids
82 (Coyer et al., 2011). This can limit its ability to colonise the “newer” habitats.
83 Understanding the processes that maintain differences in canopy-forming algae
84 recruitment, growth and survival among different substrata, and identifying the factors that
85 promote the loss of canopy-forming species, is thus of great importance in order to
86 evaluate the consequences of coastal urbanisation worldwide and effectively manage and
87 preserve marine coastlines (Coleman et al., 2008; Perkol-Finkel et al., 2012). But although
88 potential explanations have been suggested, experimental tests of causal effects are not
89 common and have usually focused on artificial substrata (Glasby, 2000).

90 In the Northeast Atlantic midshore there is generally a dynamic balance between fucoids,
91 barnacles and limpets on the shore (Hawkins and Hartnoll, 1983; Hawkins et al., 1992;
92 Thompson et al., 1996), although fucoids become less predominant at lower latitudes
93 (Ballantine, 1961). The upper eulittoral in the Azores oceanic archipelago (located
94 between 37-40°N and 25-31°W) is often dominated by two perennial macroalgae species,
95 the Ochrophyta *Fucus spiralis* Linnaeus and the Rodophyta *Gelidium microdon* Kützling,
96 1849. The desiccation-resistant *F. spiralis* is the unique species of the genus found in
97 Azores, where it forms scattered populations. It appears on exposed shores, in areas that
98 are partially sheltered and not directly exposed to the full force of the incoming waves

99 (Neto, 2000), and although it can appear on a variety of slopes, their abundance generally
100 increase with decreasing slope (pers. observ). In Azorean coasts, formed by steep cliffs
101 and volcanic rubbles, most artificial structures are used to protect nearby towns from high
102 sea levels during winter storms. Coastal defences are mostly built by deploying piles of
103 locally quarried rock or concrete boulders upon natural rocky shores, resulting in artificial
104 structures with steeper inclination than natural shores. Although epibenthic assemblage
105 composition differ (Cacabelos et al., in press), qualitative similarities were found on both
106 natural habitats and coastal defences. However, *F. spiralis* is conspicuously absent from
107 these coastal defences, even though it can occur in the adjacent rocky intertidal.

108 Here we investigate factors that could potentially limit the ability of *F. spiralis* from
109 establishing onto artificial structures. Specifically, we investigate the effects of substratum
110 slope (vertical vs horizontal) on the growth and the level of desiccation of adult *F. spiralis*,
111 and on the survival of recruits. In addition, we measured recruitment at several distances
112 from the nearest source of propagules (clumps of *F. spiralis*) to investigate the species
113 ability to disperse and colonise new areas.

114 **2. Material and Methods**

115 We tested the hypothesis that *F. spiralis* is absent from artificial structures because adult
116 plants do not survive on vertical or nearly vertical slopes. Adult individuals were collected
117 in the field from horizontal substrates and plants. They were weighed (fully hydrated wet
118 weight, WW) and the fronds length (L) and maximum circumference (perimeter, P)
119 measured. Dichotomies and receptacles were counted. Plants were then attached to nets
120 that were subsequently attached to the substratum using stainless screws. Experimental
121 plants were placed following the same procedure in interspersed areas with nearly
122 horizontal and nearly vertical surfaces in the natural shore. Plants transplanted to
123 horizontal surfaces were used to control the effects of manipulation (procedural control).

124 The entire procedure was accomplished *in situ* and as quickly as possible to minimize the
125 disturbance effect of the manipulation. Unmanipulated individuals (on horizontal surfaces)
126 were randomly selected and marked to be measured as above and used as controls (n =
127 6). For these, WW was estimated indirectly using WW-LC² regressions (Åberg, 1990).
128 The experiment was initiated at the end of July 2014 and replicated on two natural shores
129 of similar wave exposure (site 1, Farol; site 2, Vulcanológico). After 3 months plants were
130 re-measured and re-weighed, and linear growth, variations in biomass and number of
131 dichotomies and receptacles were calculated by subtracting the initial values to the final
132 ones.

133 The effect of slope on desiccation was investigated by comparing loss of water from plants
134 (n = 6) deployed on horizontal and vertical surfaces in mesocosm. Tissue weight (Wt) was
135 recorded for each plant every hour for a period of 5 hours, and finally, plants were dried at
136 60°C for 48h to estimate the dry weight (DW). The relative water content (RWC) of each
137 plant was calculated according to the formula $RWC = (Wt - DW) / (WW - DW)$ (DW, dry
138 weight; Shafer et al. 2007). RWC of each plant was plotted against elapsed time, and
139 exponential curves were fitted to each plot by using the formula $I_t = I_0 e^{-kt}$ (I_t , RWC at time t ;
140 I_0 , RWC at initial time; k , desiccation coefficient; Tanaka and Nakaoka, 2004).

141 To test the hypothesis that surface slope affects the early survivorship of recently recruited
142 plants, fertile receptacles of *F. spiralis* were collected from the field early April 2015 to be
143 used as source of zygotes. Receptacles were taken to the laboratory inside plastic bags in
144 an ice-chest and kept in darkness. Receptacles were then washed in cold seawater, wiped
145 with paper towels and placed on dry tissue paper at room temperature for zygotes release,
146 following the protocol of McLachlan et al. (1971). The partially dehydrated receptacles
147 were then placed inside dry grass covered Petri dishes and kept inside a culture chamber
148 at 8°C in the dark overnight. When zygotes started to release, receptacles were covered

149 with cold sterile seawater until zygotes complete release and sunk to the bottom of the
150 dish. Zygotes were then isolated from conspicuous mucilage, translated to aquaria with
151 sterile seawater where the bottom was covered with recruitment plates (6 x 6 cm), and
152 allowed to settle. Plates were incubated at room temperature, changing half of the water
153 every 3 days. After 10 days, the initial concentration of recruits in plates was counted in 6
154 fixed sub-quadrats 1.5 x 1.5 cm under binocular lens. Plates were then transported to the
155 field and randomly attached onto horizontal and vertical surfaces (n = 8) using stainless
156 screws. After a period of 24 h, plates were retrieved, carefully brought to the laboratory
157 where recruits density was estimated as described above. Percentage survivorship of
158 recruits was calculated as $N_f / N_0 * 100$, where N_f is the average number of surviving
159 settlers per plate at 24h, and N_0 is the number of settled recruits at the initial moment.

160 We further investigated if substratum slope influences local hydrodynamic conditions by
161 deploying pre-weighted plaster discs attached to the substratum in horizontal and vertical
162 areas of the shore (n = 5 per treatment). Discs were retrieved 48 h and one week later,
163 dried until constant weight was obtained and re-weighted to calculate weigh loss.

164 To test the hypothesis that the absence of *F. spiralis* on artificial structures is due to a
165 limitation of a source of propagules for colonisation we investigated recruitment rates at
166 increasing distances from clumps of mature plants. Recruitment plates (n = 5) 6 x 6 cm
167 were deployed in the field at three increasing distances from adults: 0 cm (i.e., under the
168 frond), 10 cm and > 0.5 m. After 75 days, plates were collected and carefully brought to
169 the laboratory where the number of recruits was counted on each plate under binocular
170 lens in four sub-quadrats (3.25 cm²) per plate.

171 *2.1. Data analysis*

172 A two-way mixed model analysis of variance (ANOVA) was used to compare linear growth,
173 variations in biomass, numbers of dichotomies and receptacles among sites (Si, random
174 factor, 2 levels) and treatments (Tr, fixed factor, 3 levels: Horizontal (procedural control),
175 Vertical, Control). Student-Newman-tests (SNK) were used to compare means within
176 significant terms. In order to examine initial differences among plants assigned to each
177 treatment, linear length, biomass, and numbers of dichotomies and receptacles measured
178 before manipulations were compared using ANOVA, with the same model described
179 above. A one-way ANOVA was used to compare the desiccation coefficients of adult
180 plants, recruit survivorship and weight loss of plaster discs between slopes (Or, fixed factor,
181 2 levels: Horizontal, Vertical). A two-way ANOVA was also used to compare the
182 recruitment rates among plates (Pl, random factor) at increasing distances (Dist, fixed
183 factor, 3 levels: 0 cm, 10 cm, > 0.5 m). Prior to analyses, Cochran's tests were used to
184 detect heterogeneity of variances and data were transformed where appropriate
185 (Underwood, 1997). When homogeneity of data was not achieved after transformation,
186 analyses were run on the untransformed data but using a more conservative significance
187 level ($\alpha < 0.01$) (Underwood, 1997).

188 **3. Results**

189 *Comparisons among plants before experimental manipulations*

190 ANOVA did not detect any significant differences among the measures of the plants
191 allocated to each treatment at the beginning of the study (Table 1).

192 *Effect of substratum slope.*

193 Significant variation was found in the length and number of dichotomies of *Fucus spiralis*
194 between treatments (Table 2). SNK tests showed that the length of *F. spiralis* transplanted
195 to vertical surfaces differed significantly from both plants transplanted to horizontal

196 surfaces and unmanipulated controls, while no significant difference was found between
197 the last two treatments (Table 2). *F. spiralis* transplanted to vertical surfaces suffered a
198 reduction in length (Fig. 1, mean \pm SE; site 1: -1.2 ± 1.1 cm, site 2: -3.7 ± 0.9 cm), whilst
199 plants transplanted to horizontal surfaces as well as controls grew similar lengths (site 1:
200 2.3 ± 0.3 , site 2: 0.0 ± 0.9 cm). Similarly, the number of dichotomies was also significantly
201 lower, and showed on average a 6.8 ± 3.3 reduction compared to original numbers) in
202 plants transplanted to vertical surfaces, whereas similar numbers of dichotomies were
203 found in plants transplanted to horizontal surfaces and controls and there were on average
204 11.0 ± 3.7 more dichotomies since the start of the experiment (Fig. 1, Table 2). Even
205 though *F. spiralis* wet weight and number of receptacles tended to increase in both
206 controls and plants transplanted to horizontal surfaces (especially on site 1), there was no
207 significant difference among treatments (Fig. 1, Table 2) as there was large variability
208 among individuals. There were also no differences on desiccation coefficients of adult
209 plants deployed on horizontal and vertical surfaces (Fig. 2, Table 3).

210 After 24 h, the survivorship of recruits deployed on horizontal and vertical surfaces was
211 similar, as was the mean weight loss of plaster discs across time (Fig. 3, Table 3).

212 *Ability of Fucus spiralis to disperse away from source plants.* Mean density of recruits on
213 plates deployed at different distances from source clumps of *F. spiralis* differed markedly.
214 While mean densities of up to 18 ind. cm² were observed under the canopy, fail
215 recruitments were observed at 10 cm and 0.5 m away from *F. spiralis* clumps (Fig. 4,
216 Table 4).

217 **4. Discussion**

218 There were negative effects of vertical slope on the development of adult *Fucus spiralis*.
219 Lower linear growth and increment in number of dichotomies on adults were observed on

220 vertical surfaces, suggesting that the different conditions were determinant for *F. spiralis*
221 populations. We expected differences would rely on hydrodynamic forces or desiccation
222 regimes to which plants are submitted. In fact, several studies concluded that wave force
223 was the dominant controlling factor affecting *Fucus* spp. and other canopy-forming algae
224 (Jonsson et al., 2006; Moschella et al., 2005; Perkol-Finkel et al., 2012), limiting their
225 survival through mechanical abrasion, dislodging or pruning. However, no differences were
226 found in the hydrodynamic regime among vertical and horizontal slopes (plaster discs), nor
227 on desiccation levels. This suggests that other physical and/or biological factors could be
228 involved in shaping *F. spiralis* populations, as mentioned by Thompson et al. (2004) for
229 algal biofilm. For example, grazers such as amphipods, limpets, periwinkle *T. striatus*, or
230 fishes such as *Salpa salpa*, usually present in the studied intertidal level, were not
231 excluded in our experimental study, and their effect on macroalgae may be among
232 possible relevant causes for obtained patterns. Previous studies showed grazing was
233 sufficient to prevent the establishment of macroalgae, being important determinants for
234 either adult or post-settler stages (Chapman, 1989; Creese, 1988; Jenkins et al., 2005 and
235 references therein). Besides variations in grazing and predation activity, changes in
236 geomorphology or whiplash by seaweed itself (see Chappuis et al. 2014), together with
237 wave exposure, barnacle presence or microtopography have been cited as other important
238 factors in determining the abundance of *Fucus* spp. at either juvenile or adult stages
239 (Chapman, 1989; Lamote and Johnson, 2008; Moschella et al., 2005). Findings for other
240 canopy-forming algae, *Cystoseira*, suggested that both the availability and the stability of
241 substrata, as well as biotic disturbances (both consumptive and non-consumptive
242 interactions), proved to be key determinants in limiting their abundance (Ferrario et al.,
243 2015; Perkol-Finkel and Airoldi, 2010). Therefore, these and other potential physical
244 and/or biological factors should be evaluated in further studies to determine their role in

245 shaping *F. spiralis* populations, e.g. when managing assemblages on newly built man-
246 made structures.

247 Our results on the recruitment patterns strongly contrast with those of Chapman (1989),
248 who found the intraspecific suppression of *F. spiralis* recruits by adult canopy. In our case,
249 the analysis of natural recruitment patterns on bedrocks showed that the most important
250 regulator of recruitment density was the presence of a canopy of conspecific adults,
251 whereas transplanted recruits did not show different survival patterns related to substratum
252 slope. Contrastingly, negative effect of increased slope (i.e. vertical) was evident from
253 transplantation experiments of adults. Reduced density of canopy-forming algae has been
254 already observed in urbanised coasts (e.g. in the Mediterranean, Benedetti-Cecchi et al.,
255 2001; in Sydney, Coleman et al., 2008). Responses obtained in this study, together with
256 the lack of surrounding adult fronds on Azorean artificial structures, and the fact that
257 distance from canopy greatly reduced juvenile recruitment, is sufficient to explain the
258 absence of canopies on these coastal defences. This knowledge could aid programmes of
259 restoration or rehabilitation of damaged habitats and contribute to the ecological criteria
260 that should be considered in the design and management of artificial structures.

261 Conservation, planning and policy targets for biodiversity enhancement could be
262 supported by establishment and recovery of canopy-forming species on rocks and
263 engineered structures (Coombes et al., 2013). Understanding how characteristics of
264 shores alter the structure and functioning of canopy-forming algae should be relevant
265 information to be used for conservation purposes, namely in definition of criteria to be
266 integrated into the design and construction of future urban structures (Coombes et al.,
267 2013; Perkol-Finkel et al., 2012). This information would minimise ecological impacts on
268 artificial structures, allowing targeted management of diversity and natural living resources.
269 Many habitat restoration efforts are concentrated on preservation of biodiversity, as well as

270 of the critical socioeconomic resources provided by many natural habitats, such as
271 canopies (Perkol-Finkel and Airoldi, 2010). Increase the supply of canopy-forming
272 propagules to artificial structures, turfs removal for extending the area over which canopies
273 can maintain free substratum for recruitment, or active canopy transplantation has been
274 proposed as means of aiding the restoration of forested landscapes and facilitating the
275 recovery of large gaps (Emmerson and Collings, 1998; Gorman and Connell, 2009; Irving
276 and Connell, 2006; Mangialajo et al., 2008). Although potential recovery measures have
277 been globally suggested in the literature, management requires approaches that focus on
278 local scales (Strain et al., 2015). Therefore understanding how local characteristics
279 modulate the structure and functioning of canopies should be information to be considered
280 for conservation purposes. Our study reinforces the notion that a greater proportion of
281 vertical surfaces compared to natural habitats, consequence of urbanisation, could
282 strongly affect Azorean canopy-forming algae. Assisted introductions for other canopy-
283 forming algae have been suggested as potential strategies for management of coastal
284 defences (Perkol-Finkel et al., 2012). Although we observed a high recruitment rate under
285 adult plants and successful survival rates for transplanted recruits, the negative effects
286 observed on adult growth do not insure assisted introductions as a promising measure to
287 facilitate the colonization of coastal defences. Climate-driven threats (e.g. increased
288 storminess, adding instability) could also play an important role in regulating the loss of
289 marine canopies, limiting their adaptive capacity to future scenarios (Perkol-Finkel and
290 Airoldi, 2010). These could have important effects on Azorean coasts, where *F. spiralis* is
291 the only leathery canopy-forming algae at upper intertidal level (Neto, 2000) ameliorating
292 the otherwise harsh conditions during low tides (Watt and Scrosati, 2014).

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448 **Tables**

449 Table 1. ANOVA testing for differences on *F. spiralis* linear length and numbers of
 450 dichotomies and receptacles and in wet weight at different sites and treatments (H
 451 Horizontal, V Vertical, C Control) (n = 6). * $P < 0.05$, ^{ns} no significant.

Source	df	Linear length		N dichotomies		N receptacles		WW	
		MS	F	MS	F	MS	F	MS	F
Site (=Si)	1	9.56	3.41 ^{ns}	11.11	0.14 ^{ns}	17.36	5.06*	0.29	0.93 ^{ns}
Treatment (=Tr)	2	3.92	1.40 ^{ns}	6.08	0.08 ^{ns}	1.36	0.40 ^{ns}	0.10	0.32 ^{ns}
Si x Tr	2	1.80	0.64 ^{ns}	37.53	0.49 ^{ns}	1.36	0.40 ^{ns}	0.04	0.12 ^{ns}
Res	30	2.81		76.99		3.42		0.31	
Total	35								
SNK									
Cochran's test		0.2411 ^{ns}		0.2812 ^{ns}		0.6110**		0.3636 ^{ns}	
Transformation		None		None		None		None	

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458 Table 2. ANOVA testing for the effects of site and treatment (H Horizontal, V Vertical, C
 459 Control) on *F. spiralis* linear growth and variation numbers of dichotomies and receptacles
 460 and in wet weight (n = 6). ** $P < 0.01$, * $P < 0.05$, ^{ns} no significant.

Source	df	Linear growth		N dichotomies		N receptacles		WW	
		MS	F	MS	F	MS	F	MS	F
Site (=Si)	1	41.11	6.90*	448.03	1.75 ^{ns}	462.25	6.45*	8.64	0.60 ^{ns}
Treatment (=Tr)	2	50.66	8.50**	1384.02	5.42**	103.86	1.45 ^{ns}	45.01	3.15 ^{ns}
Si x Tr	2	3.59	0.60 ^{ns}	105.86	0.41 ^{ns}	18.58	0.26 ^{ns}	12.36	0.87 ^{ns}
Res	30	5.96		255.33		71.68		14.29	
Total	35								
SNK		H diff V**		H diff V*					
		V diff C**		V diff C**					
		C = H		C = H					
Cochran's test		0.5071*		0.4543*		0.8070**		0.4718*	
Transformation		None		None		None		None	

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467 Table 3. ANOVA testing for the effects of slope on desiccation coefficient of *F. spiralis*
 468 adults (n = 6), and on survivorship of recruits (n = 8), and weight loss (WL) of plaster discs
 469 (n = 5) after different time periods. ** $P < 0.01$, * $P < 0.05$, ^{ns} no significant

	Desiccation coefficient			Survivorship (24h)			WL(48h)			WL(1week)		
Source	df	MS	F	df	MS	F	df	MS	F	MS	F	
Slope	1	0.0021	3.21 ^{ns}	1	507.38	1.05 ^{ns}	1	651.73	2.50 ^{ns}	627.74	3.23 ^{ns}	
Res	10	0.0007		14	482.97		8	260.34		194.59		
Total	11			15			9					
Cochran's test		0.8105 ^{ns}			0.5193 ^{ns}			0.9114*		0.9407*		
Transformation		X ³			None			None		None		

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480 Table 4. ANOVA testing for the effects of distance (0 cm, 10 cm, > 0.5m) and plate on *F.*
 481 *spiralis* recruitment (n = 4). ** $P < 0.01$.

Source	Recruitment		
	df	MS	F
Distance (D)	2	19910.8	9.21**
Plate (=PI)	4	2160.9	1.56 ^{ns}
Dist x PI	8	2160.9	1.56 ^{ns}
Res	45	1381.1	
Total	59		
Cochran's test		0.6764, $P < 0.01$	
Transformation		None	

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492 **Figure captions**

493 Fig. 1. Linear growth (A) and variation in wet weight (B) and number of dichotomies (C)
494 and receptacles (D) (mean number \pm SE, n = 6) associated with Horizontal (=procedural
495 controls), Vertical and Control treatments.

496 Fig. 2. Relative water content (RWC) of adult plants associated with horizontal and vertical
497 slope across time. Each line represents an individual.

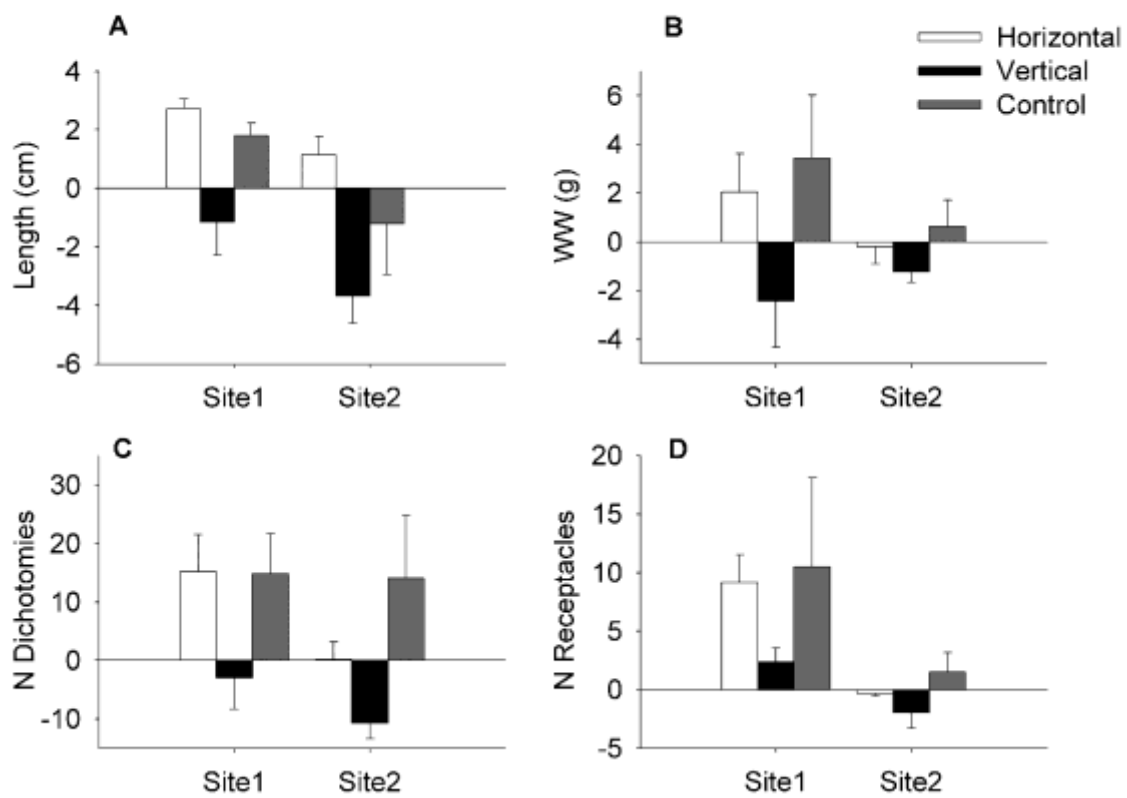
498 Fig. 3. (A) Survivorship (Mean \pm SE, n = 8) of *F. spiralis* germlings associated with
499 horizontal and vertical slopes; (B) Weight loss (Mean \pm SE, n = 5) of plaster discs with
500 horizontal and vertical slopes across time.

501 Fig. 4. Number of recruits (Mean + SE, n = 5) of *F. spiralis* found at increased distances
502 from adults.

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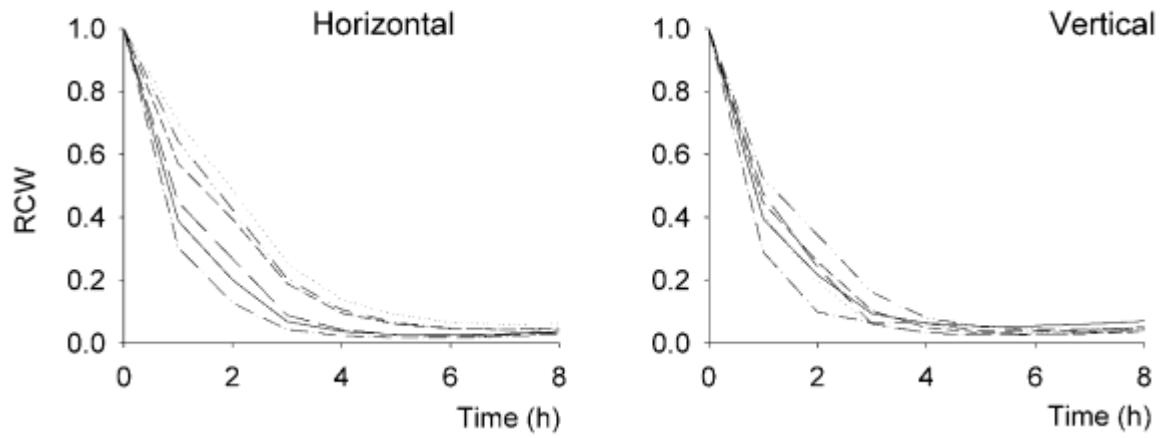
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Fig. 1. Cacabelos *et al.*

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Fig. 2. Cacabelos et al.

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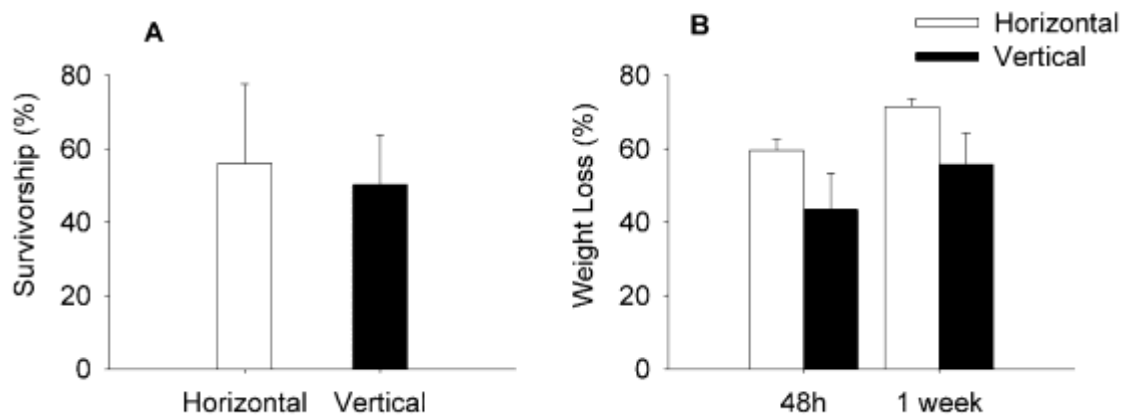
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Fig. 3. Cacabelos *et al.*

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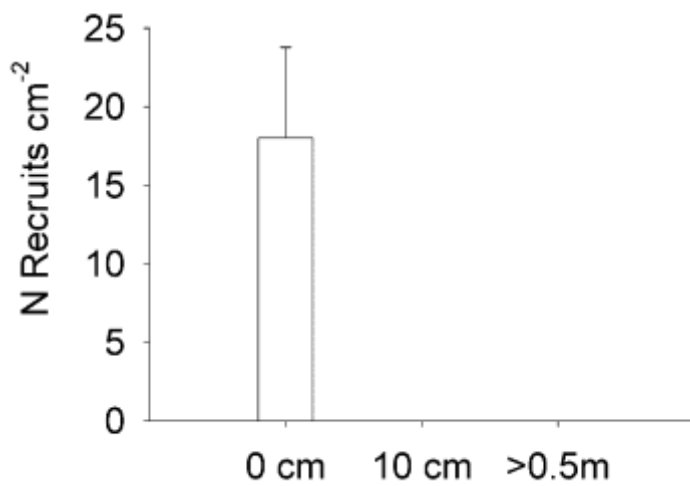
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Fig. 4. Cacabelos *et al.*

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