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Effects of heat on the germination of sclerophyllous forest species in the highlands of Madagascar

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24 **Abstract**

25 The effects of fire on germination have been extensively studied in many ecosystems.
26 Several studies have shown that plant species in ecosystems frequently exposed to fire can
27 survive through two main mechanisms: vegetative regeneration (re-sprouts) and recruitment of
28 new individuals from a fire-resistant seed bank. In Africa, an increase in temperature can break
29 seed dormancy and stimulate germination of some herbaceous and woody species. In
30 Madagascar, the once widespread highland ecosystems dominated by woody species are now
31 highly fragmented and dominated by anthropic grasslands and fields, with a significantly
32 reduced area occupied by sclerophyllous forests referred to as "tapia woodlands". Six species
33 of this endemic vegetation type were studied: *Abrahamia ibityensis* (Anacardiaceae), *Aphloia*
34 *theiformis* (Aphloiaceae), *Carissa edulis* (Apocynaceae), *Pentachlaena latifolia*
35 (Sarcolaenaceae), *Uapaca bojeri* (Phyllanthaceae) and *Vaccinium secundiflorum* (Ericaceae).
36 Germination tests were conducted 1) by soaking seeds in water for 24 hours (imbibition) or 2)
37 by exposing the seeds to dry heat. Four different temperatures (40°C, 60°C, 80°C and 120°C),
38 where seeds were exposed for 10, 30, 60 and 90 minutes. To simulate hotter-faster fires, two
39 higher temperatures (100°C and 120°C) were also evaluated by exposing seeds to dry heat for
40 5 minutes. The results did not reveal any significant effect of water 24-hour imbibition on
41 germination. For most species germination decreased with increasing temperature of treatment
42 using dry heat. *Uapaca bojeri* did not germinate under any treatment. Further studies on the
43 biological and ecological characteristics of tapia woodland species in response to fire are
44 needed to help guide conservation, management and restoration activities focusing on this
45 vegetation type.

46 **Key words:** Tapia woodland, Ibity mountain, conservation, *Abrahamia ibityensis*, *Aphloia*
47 *theiformis*, *Carissa edulis*, *Pentachlaena latifolia*, *Uapaca bojeri*, *Vaccinium secundiflorum*.

48

50 1. Introduction

51 Fire is a natural disturbance element in many ecosystems, such as savannas and sclerophyllous
52 woodlands in Africa (Kikula 1986; Campbell 1996; Kull 2000) and South America (Cerrado:
53 Simon *et al.* 2009), and several Mediterranean-like ecosystems (Pausas *et al.* 1999, 2004;
54 McCoy *et al.* 2002; Syphard *et al.* 2006; Schaffhauser *et al.* 2012). Fire determines the
55 physiognomy and structure of vegetation and often influences species diversity (Bond and
56 Keeley 2005). In fire-prone ecosystems, plant species can survive by using two main strategies:
57 1) resprouting, in which plants regenerate their above-ground biomass by growing from
58 dormant buds on branches, trunks and underground; and 2) seedlings, which enable plants to
59 recruit new individuals from a fire-resistant seed bank (Keeley and Zedler 1978; Pausas *et al.*
60 2004; Paula and Pausas 2008). Species are thus classified as 'resprouters' or 'seeders',
61 according to the main mechanism involved in regeneration after fire, although both may be
62 used. Other characteristics related to recruitment in fire-prone environments include post-fire
63 seed dispersal and fire-induced flowering (Keeley and Fotheringham 1998).

64
65 The effects of fire on germination have been extensively studied in many ecosystems associated
66 with this form of disturbance (Keeley 1987; Brown 1993; Mucunguzi and Oryem-Origa 1996;
67 Gashaw and Michelsen 2002; Syphard *et al.* 2006; Chou *et al.* 2012). A large number of studies
68 have concluded that temperature increase and smoke from burning, or their interaction, can
69 break seed dormancy (Brown 1993; Keeley and Fotheringham 1998; Dayamba *et al.* 2010) and
70 can stimulate germination of herbaceous and woody species (Keeley 1987; Mucunguzi and
71 Oryem-Origa 1996; Keeley and Fotheringham 1998; Chou *et al.* 2012). These phenomena have
72 been described for several families (e.g. Fabaceae, Rhamnaceae, Convolvulaceae, Malvaceae,
73 Cistaceae, and Sterculiaceae) that have physically dormant fire-tolerant seeds (Baskin and
74 Baskin 2000). In some species, germination is favored only when soil heating is low and time
75 of heat exposure is short (Mucunguzi and Oryem-Origa 1996; Gashaw and Michelsen 2002).
76 Other studies have shown that although fire increases the germination of some species, it may
77 also inhibit germination, increase seed mortality and reduce seedling establishment (Moreno
78 and Oechel 1991; Dayamba *et al.* 2008).

79
80 In the highlands of Madagascar, spatial and temporal mosaics of forests, savannas, woodlands
81 and shrublands are the result of fire regimes that existed long before the arrival of humans ca.
82 2,000 years ago (Burney 1987; Dewar and Burney 1994). Currently, the highland ecosystems
83 dominated by woody species are highly fragmented and dominated by anthropic grasslands and
84 fields, with a significantly reduced area occupied by sclerophyllous forests referred to as "tapia
85 woodlands" (Koechlin *et al.* 1974; Cornet and Guillaumet 1976), which have some
86 similarities to the African "miombo" (Kull 2002). Tapia woodlands are dominated by the tapia
87 tree *Uapaca bojeri* (Phyllanthaceae) associated with other woody species belonging to families
88 endemic to Madagascar, such as Sarcocaulaceae and Asteropeiaceae (Lowry II *et al.* 1997). The
89 woody species present in tapia woodlands are fire tolerant: adult individuals typically have
90 thick, spongy bark and weakly flammable leaves, and can re-sprout after fire (Campbell 1996).
91 Previous studies have, however, shown that fire can be a significant threat to this distinctive
92 vegetation type (Kull 2002; Birkinshaw *et al.* 2006) because it causes changes in structure and
93 composition (Alvarado *et al.* 2014a) and reduces natural regeneration by killing seedlings
94 (Perrier de la Bâthie 1921; Gade 1996).

95
96 The biological characteristics (e.g. seed dispersal, germination, phenology, etc.) of the species
97 present in tapia woodlands, most of which are endemic to Madagascar, are still poorly known.
98 Fruit production and dispersal of tapia woodland species occur mainly during the rainy season,

99 between November and May (Alvarado *et al.* 2014b), a pattern that is also observed in some
100 other tropical ecosystems, such as the Cerrado (Batalha and Mantovani 2000; Weiser and
101 Godoy 2001) and the Atlantic forests (Morellato *et al.* 2000) of Brazil. Germination thus also
102 potentially occurs in the rainy season, when soil moisture is higher, which increases seed
103 hydration.

104
105 Understanding the biological and ecological characteristics of tapia woodland species in
106 response to fire is important for the conservation, management and restoration of this vegetation
107 type, which is currently only partly protected within the Ibity and Itremo New Protected Areas
108 and Isalo National Park. Restoration of degraded areas and the reinforcement of wild
109 populations of threatened and/or ecologically important plant species requires the use of seeds
110 and/or seedlings, and this must be based on sound knowledge of the processes involved and
111 how best to manage storage and germination. The study of environmental drivers like fire is
112 important to get an understanding of how this disturbance affects seed germination and in
113 consequence how fire has the potential to affect reproduction rates/success. This information is
114 important to better manage vegetation. In order to help address this need, an *ex-situ* study was
115 thus performed on the main woody species of tapia woodlands to determine the effects of
116 imbibition and fire on seed germination. Our goals were to determine whether 1) precipitation
117 and thus imbibition alone stimulate their germination; and 2) if the seeds of these species can
118 survive after being affected by different scenarios of fire, and thus whether fire could represent
119 a barrier to natural regeneration in this vegetation type.

120

121 **2. Methods**

122 **2.1. Seed material**

123 Six species were studied: *Abrahamia ibityensis* (H. Perrier) Randrian. & Lowry, ined.
124 (Anacardiaceae), *Aphloia theiformis* (Vahl) Benn. (Aphloiaceae), *Carissa edulis* (Forssk.) Vahl
125 (Apocynaceae), *Pentachlaena latifolia* H. Perrier (Sarcolaenaceae), *Uapaca bojeri* Baill.
126 (Phyllanthaceae) and *Vaccinium secundiflorum* Hook. (Ericaceae). The choice of species was
127 based on two considerations: 1) the selected species were the dominant woody elements in the
128 canopy and mid-storey (trees and shrubs with a DBH > 1cm): *U. bojeri*, represents 82% of the
129 trees counted on Ibity (Alvarado *et al.* 2014a) and the other species are common in the lower
130 canopy and mid-storey; and 2) these species are endemics to Madagascar and are potentially
131 threatened by changes in fire regimes (Alvarado *et al.* 2014b). It is thus important to study their
132 biology to increase knowledge within the framework of future conservation, restoration or
133 reinforcement programs. Seeds used in this study were collected on the Ibity Massif, a New
134 Protected Area, located in the Antananarivo province, in Madagascar's Central Highlands,
135 200km south of the capital city, Antananarivo, and 25km south of the town Antsirabe (47°07'S
136 20°01'E). The area's climate, classified as Cwb according to the Köppen system (Peel *et al.*
137 2007), is characterized by a well-defined dry season (June-October) and wet season (November
138 to May). Average annual rainfall reaches 1583mm and average temperature is 17.5°C, with a
139 mean maximum temperature of 27.0 °C and a mean minimum temperature of 9.1 °C in the wet
140 season and a mean maximum temperature of 27.3 °C and a mean minimum temperature of
141 5.5°C in the dry season (based on data from 1961 to 1990; Meteorology Service of
142 Ampandrianomby). Seeds were harvested randomly from 5-10 mother-plants of each species
143 during the wet season (November-December) in 2010 and 2011, according to their availability;
144 seeds were stored in a dry place at the laboratory; germination trials were run during the
145 following 1-2 months.

146

147 **2.2. Germination trials**

148 Germination experiments, conducted using a series of treatments (Table 1), were performed at
 149 the Laboratory of Plant Physiology at the University of Antananarivo. One set of trials was
 150 done without pre-germination treatment on a set of “control” seeds, and a second set was
 151 performed to determine water requirements for germination (imbibitions) by soaking seeds in
 152 water for 24 hours prior to the germination tests. Using a third set of seeds, the effect of pre-
 153 germination dry heat was tested on four of the six species studied (*Aphloia theiformis*, *Carissa*
 154 *edulis*, *Uapaca bojeri* and *Vaccinium secundiflorum*) to simulate increased temperature
 155 produced by fires. Four different temperatures (40°C, 60°C, 80°C and 120°C) were used,
 156 following the protocol of Munyanziza and Msanga (1996). For the other two species
 157 (*Abrahamia ibityensis* and *Pentachlaena latifolia*), we did not have enough seeds to run the dry
 158 heat tests. Almost 50% of seeds of these two species germinated in the paper bags before to
 159 start the trial. Seeds were heated in a mufla oven with an external thermometer to verify the
 160 required temperatures; another thermometer was placed inside the oven to double-check the
 161 temperature. Seeds were introduced into the mufla after five minutes of constant temperature.
 162 For each temperature, seeds were separated in paper bags and exposed in Petri dish for 10, 30,
 163 60 and 90 minutes in an oven. To simulate hotter-faster fires, the effects of two higher
 164 temperatures (100°C and 120°C) were also evaluated by exposing seeds to dry heat for 5
 165 minutes. Seeds of all species were heated together for a same treatment, but replicates were
 166 heated separately in order to avoid pseudoreplication in the experimental design (Morrison and
 167 Morris 2000). Treatments were designed to cover the range of conditions that seeds could
 168 potentially encounter on the ground or in open sites during wild fires (Keeley 1987).

169
 170 After treatment, seeds were sown on 90 × 15mm Petri dishes covered with Whatman 90mm
 171 diameter filter paper, and placed in a growth chamber at a constant temperature of 25°C and a
 172 12 hour light regime, following the protocol of Baskin & Baskin (2000). The numbers of
 173 replicates (=petri dishes) and of seeds used for each species depended on their availability and
 174 on seed size (15, 25, 30 or 100 seeds per dish, Table 2).

175
 176 The seeds were monitored every 2 days for 8 weeks. Germination was recorded when a 2 mm
 177 seed radicle had emerged. The effect of each treatment on seed germination was measured as
 178 the percentage of germination (PG) and mean germination time (MGT) (Munyanziza and
 179 Msanga 1996; Chou *et al.* 2012), calculated using the following formulas:

180
 181
$$PG(\%) = \frac{\sum n_i}{N} \times 100 \quad \text{and} \quad MGT = \frac{\sum(t_i \times n_i)}{\sum n_i}$$

182
 183 where n_i is the number of germinated seeds, N is the total number of seeds, and t_i is the day
 184 when n_i seeds had germinated.

185
 186 **2.3. Statistical analyses**

187 The effects of treatments on germination were examined using generalized linear models with
 188 a binomial error structure (Zuur *et al.* 2009). Separate analyses were performed for each species.
 189 The response variable was the percent of germinated seeds after 8 weeks. First, the imbibition
 190 treatment and the control were used as factors and compared with one another. Then dry heat
 191 treatments were compared with the control. We used Akaike’s Information Criterion to select
 192 the best model(s) (Akaike 1973; Burnham and Anderson 2002).

193
 194 To assess the difference in MGT between the pre-germination imbibition treatment and the
 195 control, t-tests were performed for each species. Two-way ANOVAs were conducted to
 196 determine the effects of temperature (40°C, 60°C, 80°C, 100°C and 120°C) and exposure time
 197 (5, 10, 30, 60 and 90 minutes) on MGT. For all ANOVA, MGT values were treated as variables

198 and temperature and exposure time as factors. The normal distribution of data values was
199 verified with the Shapiro-Wilk test (<40 data) or the Lilliefors test (>40 data) and square root
200 transformations were performed as necessary. The homogeneity of variances was confirmed
201 with Bartlett's tests. When two-way ANOVA were significant ($P < 0.05$), post-hoc Tukey tests
202 were performed. When the normal distribution of data was not confirmed, Kruskal-Wallis tests,
203 followed by Wilcoxon tests, adjusted with the Bonferroni correction, were performed. All tests
204 were performed using R software (The R Foundation for Statistical Computing, version 2.15.1,
205 (R Development Core Team 2012).

206

207 **3. Results**

208 **3.1. Germination**

209 The germination treatment by imbibition had no significant effect on any of the five species
210 studied (Table 3). Germination percentages were similar between the control and the imbibition
211 treatment: they are relatively high for *Abrahamia ibityensis* ($77.9 \pm 7.5\%$) and *Carissa edulis*
212 ($97.6 \pm 1.1\%$), intermediate for *Aphloia theiformis* ($42.0 \pm 1.8\%$) and *Pentachlaena latifolia*
213 ($43.9 \pm 3.74\%$), and comparatively low for *Vaccinium secundiflorum* ($26.2 \pm 3.47\%$). No
214 germination was observed for *Uapaca bojeri*.

215

216 Only one species, *Carissa edulis*, had a significant difference in MGT between the two
217 treatments: the imbibition treatment lowered MGT by one day (Table 3). *Pentachlaena latifolia*
218 germinated in 3.98 ± 0.26 days (Table 3), whereas *Vaccinium secundiflorum* germinated in
219 19.7 ± 0.63 days (Table 3). MGT is intermediate for the other three species: *Abrahamia ibityensis*
220 (5.9 ± 0.71 days), *Aphloia theiformis* (11.3 ± 0.37 days) and *Carissa edulis* (6.9 ± 0.20 days).

221

222 **3.2. Effect of dry heat on seed germination**

223 Temperature had a significant effect on PG and MGT for all tested species except *Uapaca*
224 *bojeri* which did not germinate under any conditions. PG for *Aphloia theiformis* was
225 significantly different between treatments ($P(>Chi) < 0.001$; Figure 1a). For this species,
226 maximum PG was obtained from control seeds ($43.3 \pm 2.8\%$) which was not significantly
227 different from seeds heated at 40°C or 80°C ; the PG was lower for seeds heated at 120°C for
228 10 minutes ($6.7 \pm 1.1\%$) and significantly the lowest for seeds heated at 120°C for 30, 60, 90
229 minutes ($0 \pm 0\%$, Table 4, Figure 1a). Heating increased MGT, which was maximum when seeds
230 were treated at 120°C (27.7 ± 1.6 days; $F_{\text{Temperature}} = 49.9$, $P < 0.001$, Table 4). *Carissa edulis* PG
231 were significantly different between treatments ($P(>Chi) < 0.001$, Figure 1b). For this species,
232 maximum PG was obtained from control seeds and those heated at 40°C for 30 minutes
233 ($96 \pm 1.95\%$ and $97.54 \pm 1.6\%$, respectively, Table 4, Figure 1b) and was not significantly
234 different from seeds heated at 40°C for 10, 60 and 90 minutes or 60°C for 10, 30, 60 minutes ;
235 PG was intermediate for seeds heated at 60°C for 90 minutes ($73.6 \pm 4.1\%$) or 100 and 120°C
236 for 5 minutes (81.6 ± 3.9 and 75.2 ± 4.08 respectively) and significantly the lowest for seeds
237 heated at 80 and 120°C for more than 10 minutes ($4.8 \pm 1.96\%$, Table 4, Figure 1b); the MGT
238 varied from 5.7 days to 7.9 days, depending on temperature (Kruskal-Wallis
239 $\chi^2_{\text{Temperature}} = 38.23$, $P < 0.001$, Table 4). Finally, for *Vaccinium secundiflorum*, PG was
240 significantly different between treatments ($P(>Chi) < 0.001$, Figure 1c). The maximum PG for
241 *V. secundiflorum* was obtained from control seeds ($26.2 \pm 3.5\%$, Table 4, Figure 1c) and was not
242 significantly different from seeds heated at 40°C for 10 or 90 minutes, at 80°C and at 120°C
243 for 10 and 30 minutes; the PG was significantly the lowest for seeds heated at 60°C for 60 and
244 90 minutes, at 100°C for 5 minutes and at 120°C for 60 and 90 minutes (Table 4, Figure 1c).
245 At 80°C , PG was higher (between 17.2 ± 0.23 and $20.2 \pm 0.79\%$) than at 60°C but did not reach
246 the level obtained in the control. The MGT for this species varied depending on the temperature
247 at which the seeds were heated and the time of exposure to heat ($F_{\text{Temperature} \times \text{Time}} = 5.52$, $P <$

248 0.001, Table 4). The highest value of MGT was observed when seeds were heated at 120°C for
249 5 minutes and at 60°C for 60 minutes (34.5±1.2 and 32.93±1.6 days, respectively), and the
250 lowest when they were preheated at 120°C for 120 minutes (2.7±2.7 days respectively).

251

252 **4. Discussion**

253 **4.1. Germination**

254 Two of the six species studied (*Carissa edulis* and *Abrahamia ibityensis*) exhibited percentages
255 of germination (PG) over 84% under the control treatment, indicating that their seeds are mainly
256 not dormant. The other four species examined had PG values under 45.5%. The water
257 imbibition treatment did not significantly improve germination success in the species tested,
258 but only resulted in a slight decrease in the mean germination time (MGT) of one species, *C.*
259 *edulis*. The results show that none of the tapia woodland species considered in our study
260 increase the percent of germination by imbibition alone. However, more germination tests
261 including other combinations of factors (e.g. different incubation temperatures, ripening or
262 stratification prior to germination, etc.) are needed to increase knowledge on seed physiology
263 and ecology, and to confirm whether there is any kind of dormancy. In tropical dry woodlands
264 and savannas, establishment from seeds has been reported as a rare event (Sarmiento and
265 Monasterio 1983) and the seed ecology of germination for woody species is variable: some
266 species exhibit seed dormancy (Brown 1993; Mucunguzi and Oryem-Origa 1996; Dayamba *et*
267 *al.* 2008), some have non-dormant seeds, and others are recalcitrant (Oliveira and Valio 1992).

268

269 A phenology study performed on selected woody tapia woodland species (Alvarado *et al.*
270 2014b) shows that seed dispersal takes place during the rainy season for five of the species
271 studied: *Abrahamia ibityensis*, *Aphloia theiformis*, *C. edulis*, *Uapaca bojeri* and *Vaccinium*
272 *secundiflorum*. Seed germination of these and other woody species is potentially linked to
273 rainfall because precipitation brings an increase in soil moisture, which promotes germination
274 (Oliveira and Silva 1993; Baskin and Baskin 2000). This finding makes it difficult to interpret
275 the results of the imbibition tests; we expected germination to be improved by water imbibition,
276 as shown by Choinski and Tuohy (1991) for two African trees, *Acacia tortilis* (Forssk.) Hayne
277 and *Acacia karroo* Hayne.

278

279 Concerning the dominant species of tapia woodlands, *Uapaca bojeri*, we did not observe any
280 germination in our laboratory tests, regardless of the treatment. Kull *et al.* (2005) reported that
281 *U. bojeri* seeds are recalcitrant, losing their viability within a few months after dispersal, a
282 finding that was confirmed by Randrianavosoa *et al.* (2011). They also found that the percent
283 of germination of *U. bojeri* in laboratory experiments was between 45% and 95%, when seed
284 water content was 20-30%, regardless of whether lowered water content was obtained after 10-
285 15 days of drying in the shade or 26 days storage at a relative humidity of 60-84%. On-site
286 experiments in local soil, at the Ibity nursery, showed 17.8% germination after three months,
287 with germination beginning six weeks after seeds were sowed (Alvarado *et al.* 2010). This could
288 explain the absence of germination *U. bojeri* after eight weeks of observation in laboratory
289 conditions. Moreover, since the viability of the seeds was not tested, it is not possible to
290 conclude whether this result is due to the fact that the seeds were dormant or dead.

291

292 With the exception of *Abrahamia ibityensis* and *Carissa edulis*, we found that germination of
293 the studied species was less than 50%. In *A. ibityensis* and *C. edulis*, PG values in the field
294 nursery were lower (*A. ibityensis* 35.7% and *C. edulis* 22.4%, Alvarado *et al.* 2010) than in the
295 laboratory (*A. ibityensis* 84.3% and *C. edulis* 96%). In *Aphloia theiformis*, PG in the nursery
296 (26.9%; Alvarado *et al.* 2010) was just over half that in the laboratory (42.0%).

297

298 **4.2. Effect of dry heat on seed germination**

299 High temperatures failed to induce germination in the three species studied, suggesting that they
300 have a germination strategy different from that of typical species found in most fire-adapted
301 ecosystems, where fire at low intensities stimulates germination and at high intensities increases
302 seed mortality (Keeley 1987; Moreno and Oechel 1991; Mucunguzi and Oryem-Origa 1996).
303 Although the seeds of *Aphloia theiformis*, *Carissa edulis* and *Vaccinium secundiflorum* can
304 tolerate moderate temperatures (60°C – 80°C depending of the species), they are not resistant
305 to fire, as a reduction of PG was observed after both short or long exposure to high temperatures.
306 Stimulation of germination by fire is common among species of Fabaceae (Portlock *et al.* 1990;
307 Tarrega *et al.* 1992; Bradstock and Auld 1995; Mucunguzi and Oryem-Origa 1996; Auld and
308 Denham 2006), Combretaceae (Dayamba *et al.* 2010) and Ericaceae, which do not have the
309 ability to re-sprout after fire, and are thus totally dependent on the seed bank for reestablishment
310 after burning (Keeley 1987). These species exhibit physical or physiological dormancy and
311 germination is frequently stimulated by smoke or a combination of heat and smoke (Auld and
312 Ooi 2008). However, we found that germination of the ericaceous species *V. secundiflorum* was
313 not stimulated by increased temperature, a result contrary to the findings reported by Gonzalez-
314 Rabanal & Casal (1995) for Mediterranean species, who noted that germination in the Ericaceae
315 they studied was stimulated by heat shock, however, a wide range of responses can be detected
316 in members of this family. Even if *V. secundiflorum* germination does not increase with high
317 temperatures as expected, it is relevant to note that this species is at least fire tolerant. For the
318 other two species examined in our study, exposure to moderate heat (<60°C for *A. theiformis*
319 and <80°C for *C. edulis*), even for long periods, did not affect germination, whereas at
320 temperatures >100°C, their seeds were sensitive to the time of exposure, which is similar to the
321 response of certain woody species in Australia and Burkina Faso (Auld and O'Connell 1991;
322 Zida *et al.* 2005). Fire temperature has been measured in several tropical ecosystems, ranging
323 from 47°C (50 cm above the ground surface) to 537.5°C (at the surface) in Brazilian savannas
324 (Fidelis *et al.* 2010), from 98-458°C in Australian savannas (Morgan 1999), and up to 150°C
325 in Australian woodlands (Bradstock and Auld 1995). While some studies suggest that
326 temperatures above 60°C as being fatal to plant tissues (Whelan 1995), but exposure to dry heat
327 at 60°C and 100°C renders seeds of some species more permeable, thus promoting germination
328 (Baskin and Baskin 2000).

329
330 Although tapia woodlands are a vegetation formation in which fire is a natural disturbance (Kull
331 2000, 2002), germination was not stimulated by dry heat in any of the species we studied. They
332 showed varying levels of tolerance to different temperatures and duration of exposure to heat.
333 *Carissa edulis* was the most sensitive, surviving in temperatures up to 60°C, regardless of the
334 time of exposure to dry heat without reducing seed viability, but suffering significant reduction
335 in PG (to less than 20%) at 80°C, although exposure for 5 minutes to 120°C did not kill seeds
336 and only slightly reduced PG. *Aphloia theiformis* was less sensitive to dry heat. At 40°C, PG
337 remained close to that observed in the control, but exposure to 40°C for 90 minutes and to 80°C,
338 regardless of exposure time, PG decreased from 10-30%, and at 120°C all seeds died. In this
339 species, higher temperatures reduced germination and increased MGT. *Vaccinium*
340 *secundiflorum* had the most variable behavior faced with dry heat of the three species studied:
341 high temperatures (80°C and 120°C) had a less negative impact on germination than low
342 temperatures (40°C and 60°C).

343 344 **5. Conclusion**

345 Seed germination varied among the woody species we studied, but germination was low in
346 untreated samples for 4 species out of 6 (exceptions: *Abrahamia ibityensis* and *Carissa edulis*)
347 and decreased with increasingly hot shock treatment using dry heat for most species. Contrary

348 to our expectation, water imbibition did not stimulate seed germination. The reduced percentage
349 of germination with increasing temperature suggests that high temperatures reduced viability.
350 According with the literature and as suggested by our results, at least one of the species (*Uapaca*
351 *bojeri*) has recalcitrant seeds and it is quite possible that some of the other species have similar
352 (or at least intermediate) seeds. However, in order to conclude if seeds are dormant or
353 recalcitrant, viability tests should be carry out to confirm if the lack of germination in the
354 controls is due to seeds being dormant or dead. On Ibity Mountain, where the current fire regime
355 has been modified by human activities, fires had a variable impact on seed germination in these
356 species. Our results provide some useful insights, but further studies of the seed ecology (e.g.
357 the role of smoke, the possible role of seed scarifications, etc.) of these and other species
358 occurring in tapia woodlands are required in order to develop a better understanding of the
359 relationship between fire and germination, and of the impacts of the current human-caused fire
360 regime found on Ibity Mountain. Insights from additional studies would also be valuable for
361 developing improved conservation and management strategies for the native species of tapia
362 woodlands, especially with regard to efforts aimed at reintroducing species to areas where they
363 have been extirpated and reinforcing populations that have been impacted in this localized and
364 threatened ecosystem.

365

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375

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519 Table 1: Summary of treatments applied to the seeds of six tapia woodland species (*Abrahamia*
 520 *ibityensis*, *Aphloia theiformis*, *Carissa edulis*, *Pentachlaena latifolia* *Uapaca bojeri* and
 521 *Vaccinium secundiflorum*. For additional information on the seeds, see some photos on
 522 *Electronic appendix 1*).

Treatment	Treatment details		Species tested
Control	No pre-germination treatment		All species
Imbibition	Seeds soaked in water for 24 hours prior to germination		All species except <i>V. secundiflorum</i>
Dry heat	40°C	10, 30, 60 or 90 minutes	All species except <i>A. ibityensis</i> and <i>P. latifolia</i>
	60°C	10, 30, 60 or 90 minutes	All species except <i>A. ibityensis</i> , <i>A. theiformis</i> and <i>P. latifolia</i>
	80°C	10, 30, 60 or 90 minutes	All species except <i>A. ibityensis</i> and <i>P. latifolia</i>
	120°C	10, 30, 60 or 90 minutes	All species except <i>A. ibityensis</i> and <i>P. latifolia</i>
Fast burnt	100°C	5 minutes	<i>C. edulis</i> , and <i>V. secundiflorum</i>
	120°C	5 minutes	<i>C. edulis</i> , and <i>V. secundiflorum</i>

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526 **Table 2:** Studied species and details of the experimental setup. Number of replicates, seeds/dish, total number of treatments and total number of
527 seeds are indicated for each species.

Species	Family	Life-form/habit	Geographic distribution	Replicates (Petri dishes)	Seeds / dish	Total treatments	Total seeds
<i>Abrahamia ibityensis</i>	Anacardiaceae	Shrub	Endemic to Madagascar (Ibity and Itremo massifs only)	7	10	2	140
<i>Aphloia theiformis</i>	Aphloiaceae	Shrub or tree	Madagascar, Comoros, Mascarenes, Seychelles, Africa	5	30	14	2100
<i>Carissa edulis</i>	Apocynaceae	Shrub	Madagascar, Africa, Indian Ocean islands. Asia (India)	5	25	20	2500
<i>Pentachlaena latifolia</i>	Sarcolaenaceae	Shrub or tree	Endemic to Madagascar (Ibity only)	4	15	2	120
<i>Uapaca bojeri</i>	Phyllanthaceae	Tree	Endemic to Madagascar (widespread)	6	10	20	1200
<i>Vaccinium secundiflorum</i>	Ericaceae	Shrub	Endemic to Madagascar (widespread)	3	100	19	5700

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Table 3: Average percent of germination (PG) and mean germination time (MGT) of six woody species from tapia woodland (Madagascar) tested under laboratory conditions for water imbibition before the start of germination tests. Germination was monitored for 8 weeks in a culture chamber at a constant temperature of 25°C and a 12 hours light regime. No water imbibition tests were carried out for *Vaccinium secundiflorum* (NT = not tested).

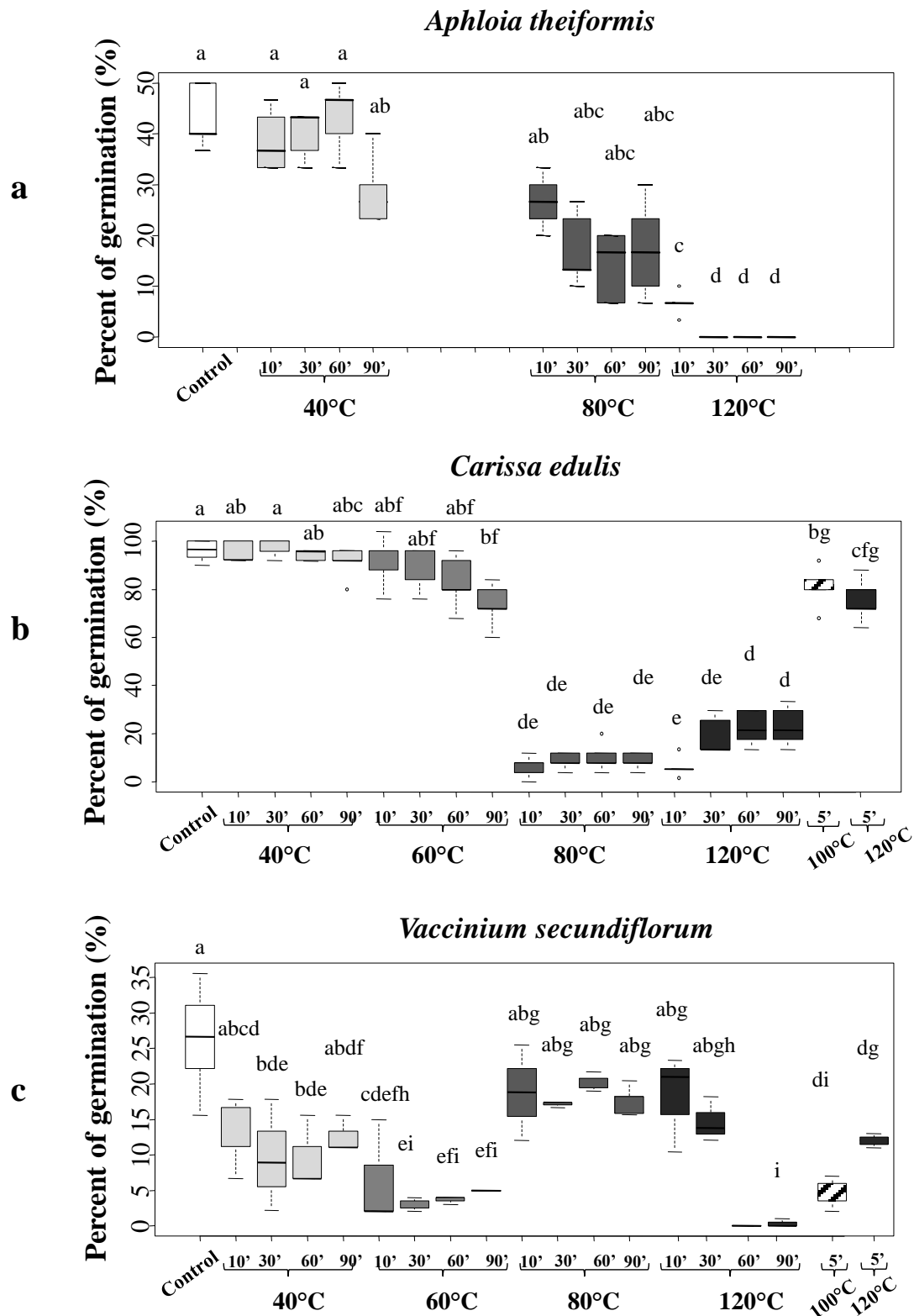
Species	PG (%)		Significance (PG)	MGT (days)		Significance (MGT)	
	Mean ± se			Mean ± se		t	P
	Imbibition	Control	P(>Chi)	Imbibition	Control		
<i>Abrahamia ibityensis</i>	71.4±14.4	84.3±4.8	0.07	7.0±1.21	4.7±0.48	t _{Treatment} =1.77,	0.12
<i>Pentachlaena latifolia</i>	42.3±4.7	45.5±6.8	0.71	3.8±0.52	4.2±0.13	t _{Treatment} =-0.84	0.46
<i>Aphloia theiformis</i>	40.7±2.4	43.3±2.8	0.64	10.8±0.56	11.8±0.41	t _{Treatment} =-1.48	0.18
<i>Carissa edulis</i>	99.2±0.8	96±1.95	0.08	6.3±0.13	7.4±0.12	t _{Treatment} =-6.09	<0.001 ***
<i>Uapaca bojeri</i>	0	0	-	0	0	-	-
<i>Vaccinium secundiflorum</i>	NT	26.2±3.5	-	NT	19.7±0.63	-	-

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538 **Table 4:** Average percent of germination (PG) and mean germination time (MGT) of three woody species from tapia woodland (Madagascar)
 539 tested under laboratory conditions for control and dry heat treatments. Germination was monitored for 8 weeks in a culture chamber at a constant
 540 temperature of 25°C and a 12 hours light regime. No germination was observed in *Uapaca bojeri* (NT = not tested). NC = not calculated. GLM
 541 results for PG were significant for the interaction Temperature × Time for all species.

Temperature	Time	<i>Aphloia theiformis</i>		<i>Carissa edulis</i>		<i>Vaccinium secundiflorum</i>	
		PG Mean ± SE	MGT Mean ± SE	PG Mean ± SE	MGT Mean ± SE	PG Mean ± SE	MGT Mean ± SE
Control		43.3 ± 2.8	11.8 ± 0.4	96 ± 1.95	7.4 ± 0.1	26.2 ± 3.5	19.7 ± 0.6
40	10	38.7 ± 2.7	11.6 ± 0.9	95.3 ± 1.9	7.7 ± 0.1	13.4 ± 3.4	19.1 ± 0.3
40	30	39.9 ± 2.1	13.9 ± 1.0	97.5 ± 1.6	7.8 ± 0.3	9.6 ± 4.5	22.1 ± 2.2
40	60	43.3 ± 3.0	13.3 ± 0.9	94.3 ± 1.0	8.0 ± 0.3	9.7 ± 3.0	21.4 ± 1.1
40	90	28.7 ± 3.1	13.7 ± 0.7	91.2 ± 3.0	8.2 ± 0.4	12.6 ± 1.5	20.3 ± 1.2
60	10	NT	NT	91.2 ± 4.6	6.6 ± 0.1	6.3 ± 4.3	31.4 ± 2.5
60	30	NT	NT	88.8 ± 3.9	6.8 ± 0.2	3.0 ± 0.6	27.0 ± 3.8
60	60	NT	NT	83.2 ± 5.0	7.1 ± 0.2	3.7 ± 0.3	33.3 ± 1.8
60	90	NT	NT	73.6 ± 4.1	9.0 ± 0.7	5 ± 0.0	32.9 ± 1.6
80	10	26.7 ± 2.4	14.8 ± 0.8	6.4 ± 2.0	5.1 ± 1.3	18.8 ± 3.9	18.5 ± 0.7
80	30	17.3 ± 3.2	15.3 ± 0.9	8.8 ± 1.5	6.6 ± 0.9	17.8 ± 0.2	19.1 ± 0.6
80	60	14.0 ± 3.1	16.6 ± 0.6	10.4 ± 2.7	6.9 ± 0.5	20.2 ± 0.8	20.7 ± 0.04
80	90	17.3 ± 4.3	17.6 ± 2.2	8.8 ± 1.5	5.0 ± 0.6	17.4 ± 1.6	20.8 ± 0.2
120	10	6.7 ± 1.1	27.7 ± 1.6	4.8 ± 2.0	4.8 ± 1.7	18.2 ± 4.0	23.4 ± 0.4
120	30	0 ± 0	NC	17.6 ± 3.5	6.4 ± 0.5	14.7 ± 1.8	23.4 ± 0.6
120	60	0 ± 0	NC	20.8 ± 3.2	6.0 ± 0.4	---	NC
120	90	0 ± 0	NC	21.6 ± 3.7	5.6 ± 0.23	0.3 ± 0.3	2.7 ± 2.7
100	5	NT	NT	81.6 ± 3.9	7.4 ± 0.8	4.7 ± 1.5	21.9 ± 0.9
120	5	NT	NT	75.2 ± 4.08	7.4 ± 0.3	12 ± 0.6	34.5 ± 1.2
Statistic result		P(>Chi) Temperature x Time < 0.001	F _{Temperature} =49.9, P<0.001	P(>Chi) Temperature x Time < 0.001	Kruskal-Wallis chi ² Temperature = 38.23, p- value<0.001	P(>Chi) Temperature x Time < 0.001	F _{Temperature x Time} = 5.52, p-value<0.001

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 544 **Figure 1: Percent of germination of the three (out of five) species studied using various**
 545 **treatments to test the effect of dry heat pre-germination. Four temperatures (40°C, 60°C,**
 546 **80°C and 120°C) were evaluated; for each temperature, seeds were exposed to heat for**
 547 **10, 30, 60 and 90 minutes. To simulate a hot, fast-burning fire, seeds were exposed to dry**
 548 **heat at two temperatures (100°C and 120°C) for 5 minutes. a) *Aphloia theiformis*, b)**
 549 ***Carissa edulis*, c) *Vaccinium secundiflorum*. White bars (control), light grey bars (seeds**
 550 **heated at 40°C), grey bars (seeds heated at 60°C), dark grey bars (seeds heated at 80°C),**

- 551 **black bars (seeds heated at 120°C), barred bars (seeds heated at 100°C for 5 minutes).**
- 552 **Post-hoc results are showed by letters on the bar (a, b, c, etc.).**

