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**Genetic change following fire in populations of a
seed-banking perennial plant**

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41 **Abstract**

42 Disturbances such as fire have the potential to remove genetic variation, but seed banks
43 may counter this loss by restoring alleles through a reservoir effect. We used allozyme
44 analysis to characterize genetic change in two populations of the perennial *Hypericum*
45 *cumulicola*, an endemic of the fire-prone Florida scrub. We assessed genetic variation
46 before and one, two, and three years after fire that killed nearly all aboveground plants.
47 Populations increased in size following fire, with most seedlings likely recruited from a
48 persistent seed bank. Four of five loci were variable. Most alleles were present in low
49 frequencies, but our large sample sizes allowed detection of significant trends. Expected
50 heterozygosity increased, and allele presence and allele frequencies showed marked shifts
51 following fire. The post-fire seedling cohort contained new alleles to the study and one
52 new allele to the species. Population differentiation between the two study sites did not
53 change. Our study is the first to directly documents genetic changes following fire, a
54 dominant ecological disturbance worldwide, and is also one of the few to consider shifts
55 in a naturally recruiting post-disturbance seedling cohort. We demonstrate the potential
56 of seed banks to restore genetic variation lost between disturbances. Our study
57 demonstrates that rapid genetic change can occur with disturbance and that fire can have
58 positive effects on the genetics of rare species.

59

60

61

62 **Keywords**

63 allozymes, fire, Florida scrub, genetic variation, *Hypericum cumulicola*

64 **Introduction**

65 Rapid shifts in the genetic structure of populations are increasingly recognized as
66 important responses of wild plants and animals to environmental changes such as global
67 warming (Bradshaw and Holzapfel 2001), alterations in soil chemistry (Snaydon and
68 Davies 1982), or invasion of exotic species (Groman and Pellmyr 2000). Ecological
69 disturbances, by causing mass mortality and allowing prodigious recruitment, should also
70 be capable of causing rapid genetic changes. However, this process remains virtually
71 unstudied.

72

73 Fire is probably the predominant ecological disturbance worldwide, controlling much
74 variation in vegetation, carbon, and nutrient dynamics (Bond and Keeley 2005).

75 However, no studies have investigated the effects of fire as a driver of genetic change.

76 For plant species that are generally killed by fire and recover via a persistent seed bank,

77 there is great potential for such change. Seed banks can be genetically distinct from

78 aboveground plants, and can serve as genetic reservoirs, harboring and replenishing

79 variation that has been lost aboveground (Del Castillo 1994). They have the potential to

80 affect the evolutionary potential of plant populations (McCue and Holtsford 1998; Mahy

81 et al. 1999) by dispersing genes through time (Tonsor et al. 1993). If built up over many

82 years, seed banks can store genetic memory of variation lost in aboveground plants

83 (Templeton and Levin 1979; Cabin 1996) due to inbreeding and drift. Yet, field studies of

84 seed bank genetics (Baskin and Baskin 1978; Tonsor 1993; Peroni and Armstrong 2001;

85 Mandák et al. 2006) and the genetics of naturally occurring seedling cohorts (Epperson

86 and Alvarez-Buylla 1997) are rare.

87

88 Florida scrub is a fire-prone, disturbance mediated habitat (Menges 2007). Fire reduces
89 aboveground biomass and releases herbaceous species from competition (Quintana-
90 Ascencio and Morales-Hernández 1997). Many of these herbaceous plants are killed by
91 fire, but populations are rapidly restored by recruitment from seeds in a persistent seed
92 bank (Menges and Kohfeldt 1995). Post-fire seeders are particularly well-represented
93 among rare plants of Florida scrub, which is itself a hotspot for endemism (Christman
94 and Judd 1990; Estill and Cruzan 2001).

95

96 Although the effects of fire on the demography of several Florida scrub endemics have
97 been documented (e.g., Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio
98 2004; Menges et al. 2006), no previous study has examined the effects of fire on genetic
99 change in a Florida scrub plant. We used allozyme markers to study genetic changes
100 following fire in the federally-endangered *Hypericum cumulicola* (Small) P. Adams
101 (Clusiaceae) at two sites on the Lake Wales Ridge in central Florida. Complete censuses
102 were conducted pre-fire at both sites. Fires the following year killed almost all
103 aboveground plants. We then sampled all seedlings emerging each of the next three
104 years. These seedlings were assumed to have derived from the seed bank based on the
105 extremely limited seed dispersal documented for this species (Quintana-Ascencio et al.
106 1998). Congruent spatial patterns within populations pre-fire vs. post-fire (Quintana-
107 Ascencio et al. in preparation) also suggest limited dispersal. Thus, we were able to track
108 genetic changes occurring post-fire by comparing genetic variation in pre-burn
109 aboveground populations with that in cohorts of emerging post-fire seedlings.

110

111 Seed banks are notoriously difficult to study, but can be very important life stages when
112 considering metapopulation dynamics and genetic structure. This is especially true in
113 rare plants with few populations, where the seed bank may represent a significant
114 proportion of the gene pool. Prior genetic studies of seed banks relied on meticulously
115 recovering seeds from soil cores and germinating them in greenhouses under artificial
116 conditions (e.g., McGraw 1993; Cabin 1996; McCue and Holtsford 1998; Mandák et al.
117 2006). Our study system overcomes several shortcomings of this approach: 1) seed
118 banks can be large and aggregated, making it hard to know where to collect samples at a
119 site (Cabin 1998); 2) recovery of seeds from seed cores often results in few available
120 seeds to grow into seedlings, so previous studies looked at few seed genotypes and
121 therefore lacked statistical power to detect low frequency alleles (e.g., Mahy et al. 1999).
122 Our *in situ* system and large sample sizes make our study one of the most comprehensive
123 studies of genetic change in a wild plant species yet conducted.

124 **Materials and Methods**

125 **Study species**

126 *Hypericum cumulicola*, the Highlands scrub hypericum, is a short-lived perennial herb. It
127 is a federally listed endangered plant endemic to the Lake Wales Ridge in central Florida
128 (Christman and Judd 1990). It grows in xeric, open areas of well-drained white sand in
129 Florida scrub dominated by Florida rosemary (*Ceratiola ericoides*) and scrub oaks
130 (*Quercus* spp.) (Menges 1999). Populations tend to occur in discrete patches that are
131 separated by large patches of unsuitable habitat (Quintana-Ascencio and Menges 1996).
132 Plants are self-compatible and have high rates of inbreeding (Dolan et al. 1999)
133 Pollinators of *H. cumulicola* are bees that forage locally in a trap-line fashion and are
134 unlikely to travel between patches of occupied habitat (Boyle and Menges 2001). Seeds
135 and fruits disperse on average less than a meter (Menges et al. 1998). Consequently, most
136 seedlings are found in the vicinity of fruiting plants (Quintana-Ascencio et al. 1998,
137 Quintana-Ascencio et al. in preparation). Interpopulation gene flow, via either pollen or
138 seeds, is therefore quite unlikely. As a consequence, F_{ST} , the proportion of genetic
139 variation found among populations, at patch level, is extremely large (0.72; Dolan et al..
140 1999; this study included 34 populations including the two populations included in this
141 study). No populations were in Hardy-Weinberg equilibrium.

142

143 Florida rosemary scrub probably burns infrequently, about every 15-30 (Menges 2007) or
144 20-80 years (Menges and Hawkes 1998). Fire kills aboveground *H. cumulicola* plants
145 (Menges and Kohfeldt 1995) as well as the dominant Florida rosemary (Johnson 1982).
146 Reestablishment of both species occurs primarily from a persistent seed bank (Quintana-

147 Ascencio et al. 1998), with *Hypericum cumulicola* establishment enhanced during wet
148 winters (Quintana-Ascencio et al. 2007). Survival and growth are greatest in recently
149 burned patches (Quintana-Ascencio 1997), where there is less competition due to the
150 temporary removal of aboveground shrub biomass and ground lichens (Quintana-
151 Ascencio and Morales-Hernández (1997).

152

153 **Study sites**

154 We studied genetic shifts in *H. cumulicola* with fire at two sites: Archbold Biological
155 Station (ABS) and Lake Placid Scrub (LPS). At each site, *H. cumulicola* occurs
156 primarily in rosemary scrub, and periodic fires have been part of the recent history of
157 each site. The patch at Archbold extends for *ca.* 400 m from north to south and is 80 m at
158 its widest. The patch at Lake Placid Scrub extends for *ca.* 90 m from northwest to
159 southeast and is 35 m at its widest. Sites are 6 km apart and suitable habitat is
160 discontinuous between the sites due to wetlands and human-caused habitat fragmentation.
161 For both sites, complete pre-fire censuses for *H. cumulicola* were conducted in
162 preparation for planned prescribed fires.

163

164 At ABS, an accidental fire ignited by a passing train burned over the study site in
165 February, 2001. This was a high intensity fire burning during an extreme drought
166 (Weekley et al. 2007). Unlike most landscape fires over the years, this fire burned
167 completely through seasonal ponds (that were bone dry) In addition, it produced
168 unusually little variation in fire intensity in xeric uplands such as rosemary scrub (ABS
169 fire data and Menges, personal observations). In particular, this fire burned >99% of the

170 area in the patch, killing most standing *H. cumulicola*. Fewer than 1 % (8 of 842) of all
171 plants survived through 2002; only three of them survived to 2003. The surviving plants
172 were unburned and located in a single gap at the south end of the patch. Because of the
173 large scale and homogeneity of this fire, along with the poor dispersal of *H. cumulicola*
174 fruits, we believe the vast majority of post-fire seedlings derived from on-site seeds in the
175 persistent seed bank.

176

177 At LPS, the prescribed fire occurred as planned in July, 2001, just after the 2001 drought
178 (Weekley et al. 2007). Because of higher humidity, this prescribed fire resulted in a
179 patchy burn. Nevertheless, most standing *H. cumulicola* plants in this patch were also
180 killed. Fourteen plants (7.5 % of 186 total plants in the patch) in 6 gaps that did not burn
181 on the eastern part of the Lake Placid patch survived through 2002; 4 of them survived
182 through 2004.

183

184 Recruitment of new seedlings began during the winter of 2001-2002. We located, marked
185 and mapped with a laser (Impulse, Laser Technology Inc., Englewood, Colorado, USA, 1
186 cm accuracy) every new recruit between July and September of 2002, 2003 and 2004
187 within all gaps at Archbold and Lake Placid scrub patches (a total of over 1700 seedlings)
188 Sites were visited 2-3 times every other week during peak germination time to increase
189 chances of finding seedlings.

190

191 **Allozyme analysis**

192 Small samples of leaf and stem or flower buds were collected from each plant larger than
193 2 cm at both study sites (ABS and LPS) during the summer of 2000 (pre-fire) and 2002
194 (post-fire). Additionally, during 2003 and 2004, samples from newly established
195 seedlings were collected. Almost all plants were large enough to be sampled (Table 1).

196

197 Material was sent to Butler University via overnight mail, where standard procedures for
198 starch gel electrophoresis for allozymes were conducted with recipes following Dolan et
199 al. (1999). Gels were stained for the five variable loci identified in our previous,
200 extensive, species-wide survey of *H. cumulicola* (Dolan et al. 1999): isocitrate
201 dehydrogenase (*IDH*), malate dehydrogenase 1 (*MDH1*), malate dehydrogenase 3
202 (*MDH3*), menadione reductase (*MNR*), and 6-phosphoglucomutase (*6PGD*). We used
203 the GDA software of Lewis and Zaykin (1999) for genetic analysis. Because sample
204 sizes were large (at least 699 at ABS and 172 at LPS for each year) and nearly complete
205 we applied no cut-off criterion for considering a locus polymorphic, including all alleles
206 detected in our analyses. The few plants that survived the fire at either site were included
207 in pre-fire genetic analyses but not the post-fire analyses.

208

209 **Statistical Analyses**

210 Expected heterozygosity was calculated for each study site pre-fire (2000) and post-fire
211 (2002, 2003, 2004). We used contingency chi-square tests (recommended by Ryman and
212 Jorde 2001 over other tests) generated by Systat software (Academic Distributing, Inc.,
213 Dewey, AZ, USA) to compare allele frequencies between pre-fire plants and 2002 post-
214 fire plants derived from the seed bank. Alpha levels are adjusted via Bonferroni

215 correction to reduce the likelihood of type I errors. Genetic structure between the two
216 sites was analyzed using θ_p , a measure of the extent to which populations are
217 differentiated (Weir 1996).

218

219

220

221

222 **Results**

223 We found several changes in allele presence during our study. A total of 12 alleles were
224 detected for the 5 loci assayed (Table 1). *MDH1*, surveyed because it was variable at
225 some sites in our previous work (Dolan et al. 1999) was not variable in either site in any
226 year. The population at ABS had greater allelic richness, with alleles for *IDH* and *6PGD*
227 that were not present during any sample years at LPS. The very low frequency *IDH-b*
228 allele was lost from ABS following the fire. Three alleles were detected in our study sites
229 only after the fire: *MDH3-c* and *6PGD-a* at ABS and *MNR-c* at LPS. *6PGD-a* is a
230 globally new allele; not being found in our previous species-wide survey (Dolan et al
231 1999).

232

233 Quantitative shifts in allele frequencies following fire were often marked, were present in
234 seedlings recruited the first year post-fire, and persisted throughout our study. At ABS,
235 three of the four variable loci had significant allele frequency shifts in 2002, the first year
236 seedlings were present following the burn (Table 1). *MDH3-a* increased almost five-fold
237 while *6PGD-b* decreased by about one-third. *6PGD-d*, present at 0.4% frequency pre-
238 fire, was not detected in the first survey year post-fire, but was found the next two years.
239 At LPS, one of the two variable loci had significant allele frequency differences
240 following the burn compared to pre-fire. There was a 42% reduction in frequency of
241 *MDH3-b* in the first sample year post-burn. All significant allele frequency shifts were
242 robust enough that they continued to be significant ($p < 0.05$) even when alpha levels are
243 adjusted via Bonferroni correction to reduce the likelihood of type I errors.

244

245 Population size at ABS increased 75% after the fire, increasing for at least three years,
246 through 2004 (Fig. 1). Similarly, population size at LPS increased 95% after the fire,
247 peaking two years post-fire in 2003 (Fig. 1). Both sites experienced increases in expected
248 heterozygosity (that mostly paralleled population size increases) by the end of the study
249 period (50% at ASB, 62.5% at LPS), following slight drops in the first post-fire census
250 year, 2002 (Fig. 1).

251

252 Populations at ABS and LPS were significantly differentiated genetically in all sample
253 years (95% confidence intervals of θ_p did not overlap zero; Fig. 2). The magnitude of
254 the differentiation was similar in all sample years(95% confidence intervals overlap).

255

256 **Discussion**

257 The seed bank of *Hypericum cumulicola* has the potential to serve as a genetic reservoir,
258 storing and accumulating genes of the fittest plants over many years and under a range of
259 environmental conditions. The formation of a persistent seed bank allows *H. cumulicola*
260 to reverse population declines that occur between fires in Florida scrub (Quintana-
261 Ascencio et al. 2003, 2007). The moderate (15-30 years) fire return frequency proposed
262 for rosemary scrub (Menges 2007) allows sufficient time for a fecund species such as *H.*
263 *cumulicola* to build up a very large seed bank. Although the longevity of its seed bank is
264 not known (it is at least two years; Quintana-Ascencio et al. 1998), other species found in
265 rosemary scrub may have seeds that can persist for at least 7 years (Menges and
266 Quintana-Ascencio 2004).

267

268 Recruitment in *H. cumulicola* is highest just after fire, although some germination occurs
269 every year (Quintana-Ascencio et al. 2003). Although the initial flush of plants must have
270 come from the persistent seed bank, some seedlings may have subsequently been
271 produced from early-flowering post-fire plants. Therefore, we do not know how many of
272 seedlings we analyzed arose from the seed bank. Therefore, continued seedling
273 recruitment may dilute the seed bank reservoir effect. Nonetheless, even these additional
274 seedlings may harbor alleles that owe their post-fire existence to prior storage in the soil
275 seed bank.

276

277 Qualitative and quantitative differences in alleles between aboveground plants and their
278 associated seed banks have been found in several other studies. Cases of both alleles

279 present aboveground and missing belowground and vice-versa have been reported (Cabin
280 et al. 1998; McCue and Holtsford 1998; Tonsor 1993; Mahy et al. 1999; Mandák et al.
281 2006). Alleles involved were rare and usually found in very low frequency, as were the
282 one lost aboveground and three gained in our study (mean frequency = 0.4%). Alleles
283 with frequencies this low would likely have been missed in studies with smaller sample
284 sizes.

285

286 Long-term seed banks play an important role in *H. cumulicola* demography, being critical
287 to reduce risks of decline or extinction during unfavorable years in fire-suppressed
288 habitats (Quintana-Ascencio et al. 2003) For *H. cumulicola*, environmental conditions
289 decline between fires as growing shrubs become more competitive neighbors (Quintana-
290 Ascencio and Morales-Hernandez 1997; Quintana-Ascencio et al. 1998). Seedling
291 recruitment declines greatly with time since fire (Quintana-Ascencio et al. in
292 preparation,). Emigration from unfavorable patches is unlikely because dispersal
293 distances are small and suitable patches usually too far away.

294

295 Matrix models of *H. cumulicola* indicate that seeds constitute 90-99 % of population
296 stable stage distributions in most habitats (particularly long unburned habitats; Picó et al.
297 2003), and that seed transitions have large influences on population growth (Quintana-
298 Ascencio et al. 2003). Since seeds are the dominant stage both in terms of numbers and
299 in terms of their impact on population growth, small evolutionary changes in seed
300 survival and seed dormancy can have profound consequences for *H. cumulicola*
301 persistence.

302

303 Our study demonstrates that rapid and significant genetic change can occur with
304 disturbance. Fire, the principal disturbance responsible for shaping community structure
305 in rosemary scrub vegetation, can also significantly influence genetic patterns in
306 individual species. Fire both kills all (aboveground) *H. cumulicola* plants and triggers a
307 flush of germination from a persistent seed bank. In so doing, it also triggers rapid
308 genetic change and allows genetic material stored in the soil seed bank to once again be
309 expressed in growing plants.

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315 interns (for complete list see [http://www.archbold-station.org/abs/staff/emenges/
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319

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Table 1. Allele frequencies for the four polymorphic loci, for entire aboveground populations by site and year. Pre-fire = 2000. The fires occurred in 2001, but no plants emerged that year. N = number of plants sampled. % = percent of total population. Contingency analysis Chi-square (X^2) values are given for loci that differed significantly in allele frequencies between pre-fire and 2002. Allele frequencies in subsequent years were not significantly different from those present in 2002. X^2 results are not included for *IDH* at ASB and *MNR* at LPS due to the presence of sparse cells.

		ABS					LPS				
		Pre-fire	2002	X^2	2003	2004	Pre-fire	2002	X^2	2003	2004
N		816	699		1430	1454	172	182		337	309
%		100	86.6		88.9	99.7	100	95.7		92.3	99.7
Locus	Allele										
<i>IDH</i>	a	0.995	1.000		1.000	1.000	1.000	1.000		1.000	1.000
	b	0.005	-		-	-	-	-		-	-
<i>MDH3</i>	a	0.016	0.076	66.6***	0.084	0.084	0.018	0.092	97.3***	0.071	0.074
	b	0.984	0.924		0.910	0.910	0.836	0.483		0.564	0.570
	c	-	-		0.006	0.006	0.146	0.424		0.365	0.356
<i>MNR</i>	b	0.807	0.862	15.9***	0.815	0.816	1.000	0.995		0.977	0.977

	c	0.193	0.138		0.185	0.184	-	0.005		0.023	0.023
<i>6PGD</i>	a	-	-		0.001	0.001	-	-		-	-
	b	0.169	0.055	107.0***	0.076	0.098	-	-		-	-
	c	0.823	0.945		0.908	0.886	1.000	1.000		1.000	1.000
	d	0.009	-		0.015	0.015	-	-		-	-

*** = $p < 0.001$

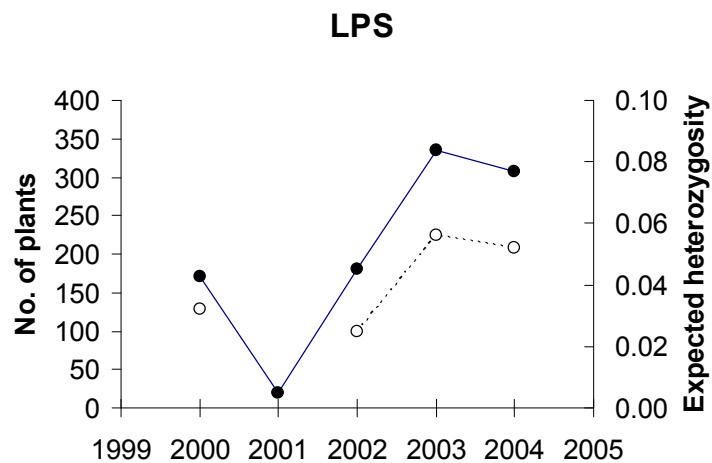
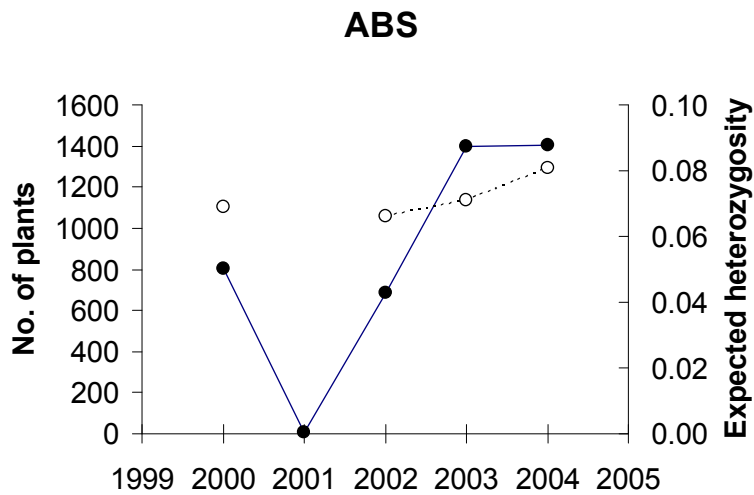


Figure 1 Population size (closed circles and solid lines) and expected heterozygosity (open circles and dashed lines) for study populations ABS and LPS pre-fire (2000), the year of the fire (2001) and the three sample years post-fire. Expected heterozygosity was not calculated in the fire year.

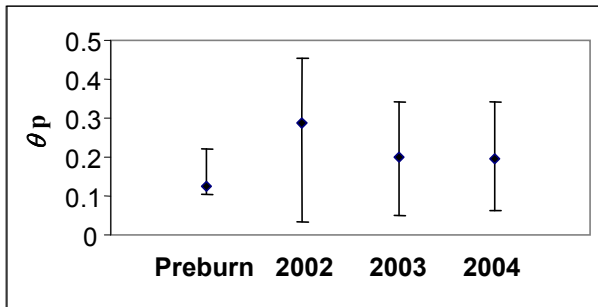


Figure 2 Degree of population differentiation (θ_p), with 95% confidence intervals indicated, between study populations ABS and LPS, pre-fire (2000) and the three sample years post-fire. θ_p values greater than zero indicate significant differentiation.