

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

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Abstract Disturbances such as fire have the potential to remove genetic variation, but seed banks may counter this loss by restoring alleles through a reservoir effect. We used allozyme analysis to characterize genetic change in two populations of the perennial *Hypericum cumulicola*, an endemic of the fire-prone Florida scrub. We assessed genetic variation before and 1, 2, and 3 years after fire that killed nearly all aboveground plants. Populations increased in size following fire, with most seedlings likely recruited from a persistent seed bank. Four of five loci were variable. Most alleles were present in low frequencies, but our large sample sizes allowed detection of significant trends. Expected heterozygosity increased, and allele presence and allele frequencies showed marked shifts following fire. The post-fire seedling cohort contained new alleles to the study and one new allele to the species. Population differentiation between the two study sites did not change. Our study is the first to directly document genetic changes following fire, a dominant ecological disturbance worldwide, and is also one of the few to consider shifts in a naturally recruiting post-disturbance seedling cohort. We demonstrate the potential

of seed banks to restore genetic variation lost between disturbances. Our study demonstrates that rapid genetic change can occur with disturbance and that fire can have positive effects on the genetics of rare species.

Keywords Allozymes · Fire · Florida scrub · Genetic variation · *Hypericum cumulicola*

Introduction

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

Fire is probably the predominant ecological disturbance worldwide, controlling much variation in vegetation, carbon, and nutrient dynamics (Bond and Keeley 2005). However, no studies have investigated the effects of fire as a driver of genetic change. For plant species that are generally killed by fire and recover via a persistent seed bank, there is great potential for such change. Seed banks can be genetically distinct from aboveground plants, and can serve as genetic reservoirs, harboring and replenishing variation that has been lost aboveground (Del Castillo 1994). They have the potential to affect the evolutionary potential of plant populations (McCue and Holtsford 1998; Mahy et al. 1999) by dispersing genes through time (Tonsor et al. 1993). If built up over many years, seed banks can store genetic memory of variation lost in aboveground plants

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(Templeton and Levin 1979; Cabin 1996) due to inbreeding and drift. Yet, field studies of seed bank genetics (Baskin and Baskin 1978; Tonsor et al. 1993; Peroni and Armstrong 2001; Mandák et al. 2006) and the genetics of naturally occurring seedling cohorts (Epperson and Alvarez-Buylla 1997) are rare.

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

Although the effects of fire on the demography of several Florida scrub endemics have been documented (e.g., Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio 2004; Menges et al. 2006), no previous study has examined the effects of fire on genetic change in a Florida scrub plant. We used allozyme markers to study genetic changes following fire in the federally endangered *Hypericum cumulicola* (Small) P. Adams (Clusiaceae) at two sites on the Lake Wales Ridge in central Florida. Complete censuses were conducted pre-fire at both sites. Fires the following year killed almost all aboveground plants. We then sampled all seedlings emerging each of the next 3 years. These seedlings were assumed to have derived from the seed bank based on the extremely limited seed dispersal documented for this species (Quintana-Ascencio et al. 1998). Congruent spatial patterns within populations pre-fire versus post-fire (Quintana-Ascencio et al. in preparation) also suggest limited dispersal. Thus, we were able to track genetic changes occurring post-fire by comparing genetic variation in pre-burn aboveground populations with that in cohorts of emerging post-fire seedlings.

Seed banks are notoriously difficult to study, but can be very important life stages when considering metapopulation dynamics and genetic structure. This is especially true in rare plants with few populations, where the seed bank may represent a significant proportion of the gene pool. Prior genetic studies of seed banks relied on meticulously recovering seeds from soil cores and germinating them in greenhouses under artificial conditions (e.g., McGraw 1993; Cabin 1996; McCue and Holtsford 1998; Mandák et al. 2006). Our study system overcomes several shortcomings of this approach: (1) seed banks can be large and aggregated, making it hard to know where to collect samples at a site (Cabin 1998); (2) recovery of seeds from seed cores often results in few available seeds to grow into seedlings, so previous studies looked at few seed genotypes and therefore lacked statistical power to detect low frequency

alleles (e.g., Mahy et al. 1999). Our in situ system and large sample sizes make our study one of the most comprehensive studies of genetic change in a wild plant species yet conducted.

Materials and methods

Study species

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

Florida rosemary scrub probably burns infrequently, about every 15–30 (Menges 2007) or 20–80 years (Menges and Hawkes 1998). Fire kills aboveground *H. cumulicola* plants (Menges and Kohfeldt 1995) as well as the dominant Florida rosemary (Johnson 1982). Reestablishment of both species occurs primarily from a persistent seed bank (Quintana-Ascencio et al. 1998), with *H. cumulicola* establishment enhanced during wet winters (Quintana-Ascencio et al. 2007). Survival and growth are greatest in recently burned patches (Quintana-Ascencio et al. 2003), where there is less competition due to the temporary removal of aboveground shrub biomass and ground lichens (Quintana-Ascencio and Morales-Hernández 1997).

Study sites

We studied genetic shifts in *H. cumulicola* with fire at two sites: Archbold Biological Station (ABS) and Lake Placid Scrub (LPS). At each site, *H. cumulicola* occurs primarily

in rosemary scrub, and periodic fires have been part of the recent history of each site. The patch at Archbold extends for ca. 400 m from north to south and is 80 m at its widest. The patch at Lake Placid Scrub extends for ca. 90 m from northwest to southeast and is 35 m at its widest. Sites are 6 km apart and suitable habitat is discontinuous between the sites due to wetlands and human-caused habitat fragmentation. For both sites, complete pre-fire censuses for *H. cumulicola* were conducted in preparation for planned prescribed fires.

At ABS, an accidental fire ignited by a passing train burned over the study site in February, 2001. This was a high intensity fire burning during an extreme drought (Weekley et al. 2007). Unlike most landscape fires over the years, this fire burned completely through seasonal ponds (that were bone dry) In addition, it produced unusually little variation in fire intensity in xeric uplands such as rosemary scrub (ABS fire data and Menges, personal observations). In particular, this fire burned > 99% of the area in the patch, killing most standing *H. cumulicola*. Fewer than 1% (8 of 842) of all plants survived through 2002; only three of them survived to 2003. The surviving plants were unburned and located in a single gap at the south end of the patch. Because of the large scale and homogeneity of this fire, along with the poor dispersal of *H. cumulicola* fruits, we believe the vast majority of post-fire seedlings derived from on-site seeds in the persistent seed bank.

At LPS, the prescribed fire occurred as planned in July, 2001, just after the 2001 drought (Weekley et al. 2007).

Because of higher humidity, this prescribed fire resulted in a patchy burn. Nevertheless, most standing *H. cumulicola* plants in this patch were also killed. Fourteen plants (7.5% of 186 total plants in the patch) in 6 gaps that did not burn on the eastern part of the Lake Placid patch survived through 2002; four of them survived through 2004.

Recruitment of new seedlings began during the winter of 2001–2002. We located, marked and mapped with a laser (Impulse, Laser Technology Inc., Englewood, Colorado, USA, 1 cm accuracy) every new recruit between July and September of 2002, 2003 and 2004 within all gaps at Archbold and Lake Placid scrub patches (a total of over 1,700 seedlings) Sites were visited 2–3 times every other week during peak germination time to increase chances of finding seedlings.

Allozyme analysis

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

Material was sent to Butler University via overnight mail, where standard procedures for starch gel electrophoresis for allozymes were conducted with recipes following Dolan et al. (1999). Gels were stained for the five variable

Table 1 Allele frequencies for the four polymorphic loci, for entire above-ground populations by site and year

		ABS					LPS				
		Pre-fire	2002	χ^2	2003	2004	Pre-fire	2002	χ^2	2003	2004
<i>N</i>		816	699		1,430	1,454	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	–	–		–	–

Pre-fire 2000. The fires occurred in 2001, but no plants emerged that year. *N* number of plants sampled. Percentage (%) percent of total population. Contingency analysis Chi-square (χ^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. χ^2 results are not included for *IDH* at ABS and *MNR* at LPS due to the presence of sparse cells

*** $P < 0.001$

loci identified in our previous, extensive, species-wide survey of *H. cumulicola* (Dolan et al. 1999): isocitrate dehydrogenase (*IDH*), malate dehydrogenase 1 (*MDH1*), malate dehydrogenase 3 (*MDH3*), menadione reductase (*MNR*), and 6-phosphoglucomutase (*6PGD*). We used the GDA software of Lewis and Zaykin (1999) for genetic analysis. Because sample sizes were large (at least 699 at ABS and 172 at LPS for each year) and nearly complete we applied no cut-off criterion for considering a locus polymorphic, including all alleles detected in our analyses. The few plants that survived the fire at either site were included in pre-fire genetic analyses but not the post-fire analyses.

Statistical analyses

Expected heterozygosity was calculated for each study site pre-fire (2000) and post-fire (2002, 2003, 2004). We used contingency chi-square tests (recommended by Ryman and Jorde 2001 over other tests) generated by Systat software (Academic Distributing, Inc., Dewey, AZ, USA) to compare allele frequencies between pre-fire plants and 2002 post-fire plants derived from the seed bank. Alpha levels are adjusted via Bonferroni correction to reduce the likelihood of type I errors. Genetic structure between the two sites was analyzed using θ_p , a measure of the extent to which populations are differentiated (Weir 1996).

Results

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

Quantitative shifts in allele frequencies following fire were often marked, were present in seedlings recruited the first year post-fire, and persisted throughout our study. At ABS, three of the four variable loci had significant allele frequency shifts in 2002, the first year seedlings were present following the burn (Table 1). *MDH3*-a increased almost five-fold while *6PGD*-b decreased by about one-third. *6PGD*-d, present at 0.4% frequency pre-fire, was not detected in the first survey year post-fire, but was found the next 2 years. At LPS, one of the two variable loci had

significant allele frequency differences following the burn compared to pre-fire. There was a 42% reduction in frequency of *MDH3*-b in the first sample year post-burn. All significant allele frequency shifts were robust enough that they continued to be significant ($P < 0.05$) even when alpha levels are adjusted via Bonferroni correction to reduce the likelihood of type I errors.

Population size at ABS increased 75% after the fire, increasing for at least 3 years, through 2004 (Fig. 1). Similarly, population size at LPS increased 95% after the fire, peaking 2 years post-fire in 2003 (Fig. 1). Both sites experienced increases in expected heterozygosity (that mostly paralleled population size increases) by the end of the study period (50% at ABS, 62.5% at LPS), following slight drops in the first post-fire census year, 2002 (Fig. 1).

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

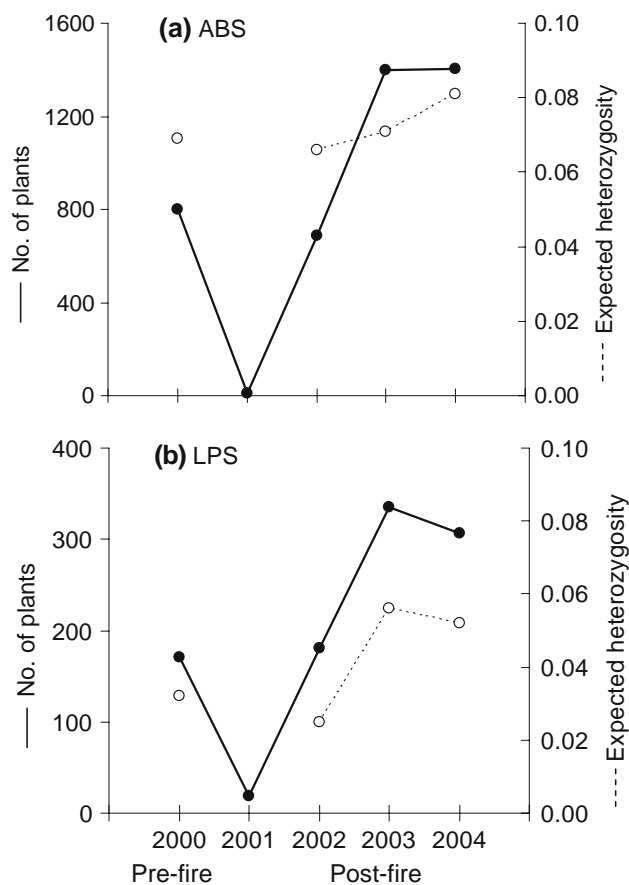


Fig. 1 Population size (closed circles and solid lines) and expected heterozygosity (open circles and dashed lines) for study populations, **a** ABS and **b** LPS. Data are shown for pre-fire (2000), the year of the fire (2001) and 3 years post-fire (2002–2004). Expected heterozygosity was not calculated in the fire year (2001)

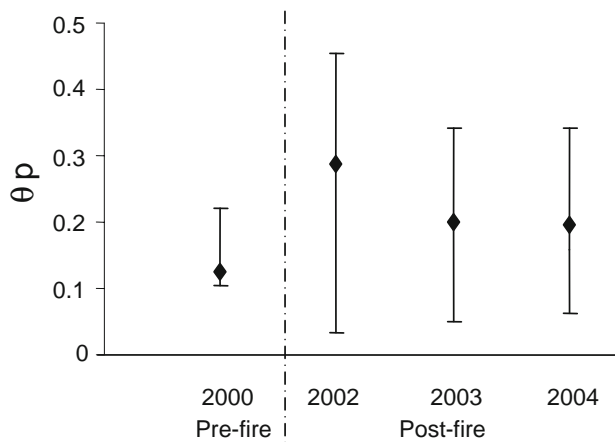


Fig 2 Degree of population differentiation (θ_p), with 95% confidence intervals indicated, between study populations ABS and LPS, pre-fire (2000) and 3 years post-fire. θ_p values greater than zero indicate significant differentiation

Discussion

The seed bank of *H. cumulicola* has the potential to serve as a genetic reservoir, storing and accumulating genes of the fittest plants over many years and under a range of environmental conditions. The formation of a persistent seed bank allows *H. cumulicola* to reverse population declines that occur between fires in Florida scrub (Quintana-Ascencio et al. 2003, 2007). The moderate (15–30 years) fire return frequency proposed for rosemary scrub (Menges 2007) allows sufficient time for a fecund species such as *H. cumulicola* to build up a very large seed bank. Although the longevity of its seed bank is not known (it is at least 2 years; Quintana-Ascencio et al. 1998), other species found in rosemary scrub may have seeds that can persist for at least 7 years (Menges and Quintana-Ascencio 2004).

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

Qualitative and quantitative differences in alleles between aboveground plants and their associated seed banks have been found in several other studies. Cases of both alleles present aboveground and missing belowground and vice-versa have been reported (Cabin et al. 1998; McCue and Holtsford 1998; Tonsor et al. 1993; Mahy et al. 1999; Mandák et al. 2006). Alleles involved were rare and usually

found in very low frequency, as were the one lost aboveground and three gained in our study (mean frequency 0.4%). Alleles with frequencies this low would likely have been missed in studies with smaller sample sizes.

Long-term seed banks play an important role in *H. cumulicola* demography, being critical to reduce risks of decline or extinction during unfavorable years in fire-suppressed habitats (Quintana-Ascencio et al. 2003) and increasing effective population size, as has been shown in other species (e.g., Nunney 2002). For *H. cumulicola*, environmental conditions decline between fires as growing shrubs become more competitive neighbors (Quintana-Ascencio and Morales-Hernández 1997; Quintana-Ascencio et al. 1998). Seedling recruitment declines greatly with time since fire (Quintana-Ascencio et al. in preparation). Emigration from unfavorable patches is unlikely because dispersal distances are small and suitable patches usually too far away.

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

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

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