

Population size and fire intensity determine post-fire abundance in grassland lichens

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Abstract

Questions: What is the variability in abundance of lichens on grassland soil between and within fields after prescribed fire? Is post-fire lichen abundance an effect of pre-fire population size?

Location: Cedar Creek Natural History Area, Minnesota, USA.

Methods: Lichen abundance, estimated as ground cover and dominated by *Cladonia* spp., was mapped in plots in two fields before prescribed burning on 06.10.2003 and 15.10.2003 for the first time since abandonment in the 1950s. The plots were resurveyed one year post-fire.

Results: Post-fire cover of *Cladonia* spp. varied strongly between the fields, most likely due to different weather conditions between the burn events, which resulted in different fire intensities, one of low and one of high intensity. In the field that experienced the low intensity fire, post-fire cover of *Cladonia* spp. was still relatively high, and showed a positive relationship with pre-fire cover, while no such relationship was found after the high intensity fire. In that field *Cladonia* spp. experienced high mortality rates irrespective of pre-fire cover.

Conclusions: This study provides an example of how species response to disturbance can be a function of population size, but that this relationship can be non-linear; lichens in grassland can survive a low intensity fire proportionally to pre-fire population size, but experience high mortality rates above a fire intensity threshold. The applications of these results are that fire intensity matters to species response to prescribed fire, and that the persistence of climax lichen communities and biodiversity in the study system needs a broad range of fire intervals.

Keywords: *Diploschistes*; Disturbance threshold; Extinction risk; Life history; Old field; *Peltigera*; Prescribed fire.

Nomenclature: Esslinger (1997).

Abbreviation: CCNHA = Cedar Creek Natural History Area.

Introduction

Fire is an important component in grassland ecosystems. In absence of natural fires, prescribed burning is a common practice to manage remnant grasslands and prevent them from succession into dense woody shrublands. Decisions governing the applied burning regimes are then often based on conservation goals and knowledge of plant species response to fire. For vascular plants, there is an extensive literature on the effects of fire, showing, for example how species' life histories determine their response and can predict post-fire community patterns (e.g. Menges & Kohfeldt 1995; Ghermandi et al. 2004). For lichens in grasslands there is, however, a very limited literature on the role of fire (cf. Holt & Severns 2005); studies that include pre- and post-fire data especially are lacking.

In general, lichens are drastically reduced at burned sites (Bliss & Wien 1972; Antos et al. 1983; Schulten 1985, Johansen 2001; Reinhart & Menges 2004; Holt & Severns 2005). Their vulnerability to fire is often explained by their slow growth- and colonization rates, and by their lack of apparent means of surviving fire through underground parts (Antos et al. 1983; Schulten 1985; Johansen 2001; Holt & Severns 2005). However, Bowker et al. (2004), in a recent study of fire impacts on biological soil crusts in the Snake River grasslands in eastern Oregon, did not find reduced lichen cover at burned compared with unburned sites. They suggested that fire intensity was not high enough to cause significant reductions in lichen cover, and contrasted their results with the pervasive findings in the literature of fire as the cause of drastic reduction or eradication of lichens. They suggested that these contrasting results could be explained by overall differences in fire behaviour among different grassland types. However, fire intensity also can vary strongly within similar grassland types (Gibson et al. 1990). Understanding the nature and consequences of such variability is important when examining post-fire community patterns.

In October 2003 we conducted an opportunistic study, on short notice before prescribed burning, of fire effects on lichens in two old, abandoned, agricultural fields at Cedar Creek Natural History Area in eastern Minnesota, USA. Lichens are common in old fields at Cedar Creek, and together with mosses they can comprise ca. 20% of the ground cover 20–40 years after abandonment (Inouye et al. 1987). Dominant lichen species include *Cladonia* spp. Collecting pre- and post-fire data on these lichens provided the opportunity to examine variability in fire induced mortality and the effect of pre-fire population size on lichen persistence and post-fire abundance. In general, population size is a good predictor of species extinction risk, and during a disturbance event, rare species/small populations face higher risk of extinction than common species/large populations (Pimm et al. 1998; O'Grady et al. 2004).

The aims with this study were to examine (1) variability, assumed to be a function of fire intensity, in post-fire abundance of lichens on grassland soil within similar grasslands, and (2) the relationship between pre- and post-fire lichen abundance. Specifically, we asked if: (1) variability in post-fire lichen abundance occurs between fields, among sites within fields or within sites; (2) lichen abundance after prescribed fire is an effect of pre-fire population size. We predicted overall high mortality rates, but also expected that post-fire lichen abundance could be positively related to pre-fire abundance. There were no large variations in terms of fuel load between or within the fields, but we expected that spatial variation in fire intensity could result from small-scale variation in bare soil- and litter cover as well as random variation due to wind behaviour during the burns. Greater bare soil- and moss cover could slow down the rate of fire spread and hence fire intensity; in contrast, heavier plant- and litter cover, which provide fuel, possibly could increase fire intensity and lichen mortality. Therefore we also examined the effect of these variables on the post-fire lichen abundance.

Methods

Study area

The study was carried out in two old, abandoned agricultural fields at CCNHA in eastern Minnesota, USA. The soils at CCNHA are outwash sediments of fine and medium sands, which are poor in nitrogen (Inouye et al. 1987). Abandoned, agricultural fields in the area are colonized by non-native as well as native prairie forbs and grasses, and eventually by woody plants (Dovčiak et al. 2005), but succession is slow due to the nitrogen limitation (Inouye et al. 1987; www.lter.umn.edu). The

slow succession rates create good opportunities for terricolous lichens to establish, and *Cladonia* spp. are common. Besides *Cladonia* spp., common lichens are *Diploschistes muscorum* and *Peltigera didactyla*, which are widespread but most often occur as scattered, small thalli. Biological soil crusts, as described from more arid environments (Belnap et al. 2001), are rare but may occur at burned sites, and are formed by cyanobacteria, algae, and the lichen *Thrombium epigaeum* (pers. obs.). Within the fields, lichen distribution depends on field microtopography. At drier sites ('high' elevation), where herbs and grasses are sparse, *Cladonia* spp. may form continuous patches while at more productive 'low' elevation sites, dense grass swards outcompete the lichens (pers. obs.). At intermediate sites, *Cladonia* spp. often grow beneath the grass- and forb layers.

Study design and field methods

On short notice in October 2003, we set up an opportunistic study before prescribed burning of two fields, nos. 49 and 62. These fields were abandoned in the mid-1950s and have open, fairly homogeneous grass- and forb layers without shrubs or tree saplings. The fields had not previously been burned as part of the prescribed burning management program at Cedar Creek. This program has run since 1964, to maintain oak-sand savanna, as well as to provide a large-scale fire treatment experiment (www.lter.umn.edu).

To examine small- and large-scale variation in fire effects on the lichens, we set up sample-plot grids at three sites in each field. The sites were chosen visually at high to intermediate elevation sites; i.e. where lichens could be expected. The sites were located at least 50 m apart. At each site we established 12 sample plots, 0.5 m × 0.5 m, 1 m apart in a squared grid. The sample plot size was designed to be large enough to effectively sample any present lichen vegetation, but small enough for a time-efficient survey. In October 2003, for each plot we estimated lichen abundance as ground cover (in cm²) of each lichen species. We also recorded the cover of mosses (without identification to species level), bare soil, litter, and vascular plants as well as the average plant height. The ground cover of lichens and the other variables was estimated visually by using a 1-dm² sample plot. The plots were surveyed again in October 2004, one year post-fire. We then only estimated the cover of living lichens, i.e. lichens that turned green when sprayed with water, indicating living algae and hence photosynthetic capacity (cf. Holt & Severns 2005). The lichen vegetation was dominated by *Cladonia* spp., and due to difficulties in identifying phyllocladia (the basal vegetative parts) to species level, especially in the post-fire survey, we

treated *Cladonia* spp. together in the following statistical analyses.

Fire descriptions

Field 49 was burned on 06.10.2003. The weather was sunny with 11 hours of sun that day and max. temperature of 22-25 °C. The wind was S at 2-4 m/s, and the humidity 32% and decreasing. Field 62 was burned on 15.10.2003. The weather was partly cloudy with 6 hours of sun and a max. temperature of 11-13 °C. The humidity was 40% and increasing, and the wind NW of 5-7 m/s. The fire that burned field 49 was fast, burned most of the litter layer, and the fire intensity was estimated as similar or slightly above a mean savanna prescribed fire at CCNHA (Steve Bauer pers. comm.). The fire at field 62 on the other hand, burned slowly, left about 2/3 of the litter layer, and was estimated to be of lower fire intensity than a mean savanna fire (Bauer pers. comm.). To keep this fire going the head-fire had to be maintained with drip torches. The fuel load was comparable between the fields and the difference in fire behaviour was most likely explained by the different weather conditions (Bauer pers. comm.).

Statistical analysis

Due to the limited occurrences of lichens other than *Cladonia* spp., we examined only this taxon in a formal statistical model. The analysis aimed at examining the variability in *Cladonia* spp. post-fire cover at sample plot level as a function of moss-, bare soil-, litter- and plant cover, average plant height, pre-fire *Cladonia* cover and site location. Moss cover was excluded due to uneven distribution among sites and plots, and a large number of zero-values (Table 1). Plant cover was excluded due to a high correlation with pre-fire *Cladonia* cover at sites 49A and 49B, resulting in a variance inflation factor >10 in site-specific regressions. The remaining independent variables showed no, or weak, correlations. To adjust for skewed distributions, bare

soil and litter cover were ln-transformed, and pre-fire *Cladonia* cover was square-root transformed. The effects of site, bare soil- and litter cover, average plant height, and pre-fire *Cladonia* cover for the *Cladonia* post-fire cover were then examined in a general linear model with general and site-specific slope coefficients for the independent variables to account for site-dependent relationships ($y = \text{site} + \text{var. } a + \text{var. } a(\text{site}) + \text{var. } b + \text{var. } b(\text{site}) + \text{etc.}$). Backward elimination was used to select the final model, removing at each step the variable with the highest *P*-value. We kept variables in the final model at *P* < 0.10. The analyses were performed in Proc corr, Proc reg and Proc glm in SAS (Anon. 2000).

Results

In the pre-fire survey in 2003 we identified nine species of *Cladonia*. The dominant species were *Cladonia cariosa*, *C. cervicornis*, and *C. rei*, while *Cladonia cristatella*, *C. fimbriata*, *C. mitis*, *C. peziziformis*, *C. pyxidata* and *C. rangiferina* were less common or rare. *Diploschistes muscorum* and *Peltigera didactyla* were found in 16 and 18 sample plots, respectively, and when present they were sparse, often with no more than a few cm² (Table 2). One year post-fire *D. muscorum* was almost totally extinct from the sample plots, and occurred in only one plot in field 62 (Table 2). *Peltigera didactyla* was still present in six sample plots at four of the sites, even after the high intensity fire (Table 2).

In field 62, after the low intensity fire, post-fire cover of *Cladonia* spp. was still relatively high (typically ca. 50% as high as pre-fire) and showed a strong dependence on pre-fire cover (Table 2, Fig. 1). In field 49 no such relationships were seen (Fig. 1). Instead, in that field *Cladonia* spp. experienced high mortality rates irrespective of pre-fire cover (Table 2, Fig. 1). This result was also confirmed in the general linear model, where pre-fire *Cladonia* cover was the only significant

Table 1. Plant height and pre-fire cover of vascular plants, bare soil, litter and mosses, averaged per site and given as proportions of sample-plot area.

Field	Site	Plant height (cm)	Plant cover	Bare soil cover	Litter cover	Moss cover
49	A	66.2	73.1	5.8	8.2	0.2
49	B	59.4	68.9	3.5	6.5	1.3
49	C	53.3	53.8	2.5	3.3	27.8
62	D	35.1	66.9	5.9	4.6	11.6
62	E	51.3	59.8	18.3	5.7	8.1
62	F	41.1	88.9	7.8	1.7	0.4

Table 2. Pre- and one-year post-fire lichen cover, averaged per site and given as proportions of the sample-plot area.

Field	Site	<i>Cladonia</i> spp.		<i>Diploschistes muscorum</i>		<i>Peltigera didactyla</i>	
		Pre-fire	Post-fire	Pre-fire	Post-fire	Pre-fire	Post-fire
49	A	12.7	<0.1	<0.1	0	<0.1	0
49	B	19.7	<0.1	<0.1	0	<0.1	<0.1
49	C	12.5	0.5	<0.1	0	<0.1	<0.1
62	D	11.0	4.6	<0.1	0	<0.1	<0.1
62	E	8.0	5.4	<0.1	<0.1	0	0
62	F	1.2	0.7	0	0	<0.1	0.1

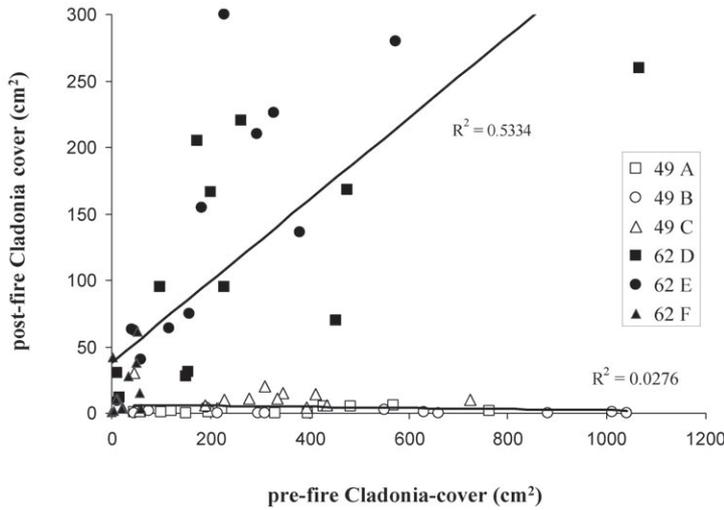


Fig. 1. Relationships between pre- and one year post-fire cover of *Cladonia* spp. in 0.5 m × 0.5 m sample plots grouped by site (A-F), in two fields (49 and 62) subjected to prescribed fire. Field 49 experienced high fire intensity, while field 62 experienced low fire intensity. The linear relationships for the observed pre- and post-fire *Cladonia* cover and their r^2 -values are shown for the sites grouped by field.

predictor variable of post-fire cover (Table 3). The effect of pre-fire cover was site-specific with strong positive slope estimates for site D and E, in contrast to non-existing relationships for all sites after the high intensity fire in field 49 (Table 3). Average plant height, bare soil- and litter cover had no effects on post-fire lichen cover.

Even if *Cladonia* cover was drastically reduced in the high fire intensity field, there were still some phyllocladia present, especially at site C (Table 2, Fig. 1). These occurrences, as well as at the other sites, originated from both post-fire colonization and surviving lichen thalli (pers. obs.). Site C differed from the other sites by having a high pre-fire moss cover (Table 1). This could suggest that mosses can protect lichen thalli either by reducing the rate of fire spread or by sheltering lichens growing within moss patches.

Table 3. Final model for post-fire *Cladonia* spp. cover, including only the site-specific estimate for pre-fire *Cladonia* spp. cover (model $r^2 = 0.80$). The site-specific coefficient estimates show strong positive relationships between pre- and post-fire lichen cover at site D and E (the low fire intensity field), but no such relationship at sites A, B and C (the high fire intensity field).

Effect	SS	df	F
Pre-fire <i>Cladonia</i> cover (site)	333475.9	6	43.97***
Error	82164.2	65	
Parameter	Estimate	t-value	p
Intercept	-2.0879	-0.20	0.84
Pre-fire <i>Cladonia</i> cover site A	0.2401	0.30	0.76
Pre-fire <i>Cladonia</i> cover site B	0.1190	0.19	0.85
Pre-fire <i>Cladonia</i> cover site C	0.7049	0.87	0.38
Pre-fire <i>Cladonia</i> cover site D	7.8708	9.41	<0.001
Pre-fire <i>Cladonia</i> cover site E	11.0845	11.24	<0.001
Pre-fire <i>Cladonia</i> cover site F	3.9779	1.50	0.13

Discussion

We examined variability in post-fire lichen abundance, and its causes, within and between two old, abandoned fields burned by prescribed fire. There was a strong difference between the fields in post-fire abundance of *Cladonia* spp., and we conclude that this variability was totally a function of the different fire intensities observed between these fields. These different fire intensities were, in turn, most likely a result of the different weather conditions between the burn events.

We also examined if post-fire lichen abundance was a function of the pre-fire population size. The first visual impression, immediately after the fires in both fields, was a complete consumption of plants. However, one year after the low intensity fire in field 62, cover of *Cladonia* spp. was relatively high and showed a strong positive relationship with pre-fire cover. After the high intensity fire in field 49, on the other hand, no such relationship was found. Thus, this study provides an example of how species persistence during a disturbance event can be a function of population size, but that this relationship; i.e. species response to disturbance, can be non-linear. During a disturbance event, species persistence can be expected to be proportional to population size, given everything else being equal. But species persistence will also depend on disturbance intensity, with critical threshold levels above which population size does not matter – all individuals are killed (cf. Romme et al. 1998; Spiller et al. 1998). For lichens in the grassland at Cedar Creek, this threshold seems to be below or close to an average prescribed savanna fire. In natural grassland systems it is unlikely that individual low intensity fires like the one that burned field 62 ever would have a large spatial extent because these fires simply die out. In prescribed burning programs, how-

ever, such fires are more likely to occur because they are maintained by drip torches.

Other variables examined, e.g. bare soil- and litter cover, had no effects on post-fire lichen cover in the statistical model. Compared with the effect of weather, on fire behaviour and fire intensity, small-scale variation in e.g. bare soil- and litter cover, as at the sample plot level, was likely not enough to significantly affect fire intensity. At site E, however, a high number of gopher mounds resulted in a fairly high proportion of bare soil, which possibly could have further reduced the low fire intensity at that site.

There were nine identified *Cladonia* spp. within the sampled plots and a range of life history strategies among these species could affect their response to disturbance. For example, Schulten (1985) found early recovery of mainly *Cladonia cariosa* after fire at a prairie site in Iowa. Besides *Cladonia* spp., we also recorded *Diploschistes muscorum* and *Peltigera didactyla*. Both species are widespread but sparse in fields at Cedar Creek (pers. obs.), and both had small population sizes in the pre-fire plots. One year post-fire *D. muscorum* was locally eradicated from all but one plot, while *P. didactyla* was found in several plots, in both fields. This may illustrate that species with small population sizes are prone to local extinction, as in the case of *D. muscorum*, but that life history strategy determines their post-disturbance recovery, as in the case of *P. didactyla*. *P. didactyla* is a cyanobacterial lichen known as a pioneer on disturbed soils (Jahns & Ott 1997; Brodo et al. 2001).

We had expected high lichen mortality rates from the fire, and this was seen after the fire in field 49, which was an average to slightly above average intensity fire at CCNHA. Lichens such as *Cladonia* spp. show a time lag up to several decades before post-fire recovery (Maikawa & Kershaw 1976; Menges & Kohfeldt 1995), and at Cedar Creek, 20-40 year old fields have the highest cover of non-vascular plants (Inouye et al. 1987). Thus, the average response for lichens in the Cedar Creek grasslands to prescribed fire intervals less than at least 5-10 years is likely an extensive reduction in overall abundance, especially for the dominant species such as *Cladonia cariosa*, *C. cervicornis* and *C. rei*.

Besides fire intensity, the long-term effects of prescribed burning will also depend on fire frequency (e.g. Collins et al. 1995). For lichens, with slow growth rates, increasing fire frequency could drastically reduce the recovery rates (e.g. Shay et al. 2001; Holt & Severns 2005). Visual inspection of fields that are burned every second or third year at Cedar Creek revealed only scattered and small occurrences of *Cladonia* spp., *Peltigera didactyla* and *Thrombium epigaeum* (pers. obs.). Even if fuel load in these fields is lower than in unburned

fields due to repeated burning, it seems to allow fires intense enough to drastically reduce the lichen populations over time. The overall lichen diversity in the burned grasslands may not be much affected in this generally species-poor system. Rather, the most important effect of reduced lichen cover is likely that possible interactions with mosses and vascular plants are altered.

The main conclusion from this study is that grassland lichens can survive a low intensity fire proportionally to their pre-fire population size, but experience high mortality rates above a certain fire intensity threshold. There are still few explicit examples in the literature of non-linear relationships between pre- and post-disturbance population size as a function of disturbance intensity, and to our knowledge, none for lichens. The applications of these results in the management of this specific study system are that weather conditions and the resulting fire intensity matters to species response to prescribed fire, and that the persistence of climax lichen communities and current biodiversity needs a broad range of fire intervals (cf. Menges & Reinhart 2004; Holt & Severns 2005).

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