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Recolonization of Burned Substrates by Lichens and Mosses in Yellowstone National Park

Abstract

We examined completely burned wood, soil and rock in 5 meadow and 27 forest sites in Yellowstone National Park to document early colonization by lichens and mosses 13 yr after the 1988 fires. Two mosses, *Bryum caespiticium* and *Ceratodon purpureus*, occurred in all 27 forest sites examined, recolonizing burned wood, soil, and cracks in rocks. *Polytrichum juniperinum* and *P. piliferum* were on soil in 11 sites. We identified 13 moss species on burned wood substrates and 3 from burned meadow soil. Sixteen lichen species, plus soredia and sterile *Cladonia* squamules, were identified from burned wood substrates. Species of *Cladonia* were the major recolonizing lichen on burned wood and soil. Nine lichen species were on burned rhyolite and granite. Douglas-fir sites had the largest number of lichen species (15), with 11 species in Engelmann spruce and lodgepole pine sites, and 6 species in whitebark pine sites. Spruce sites had significantly more moss recolonization on burned wood than Douglas-fir, lodgepole pine, and whitebark pine sites, and significantly more lichen recolonization than lodgepole pine sites. The recolonizing lichen species appeared within 13 yr after fires, and remain indefinitely in the sites, since they are also present in old forests. Numbers of lichen species increase with time since fire, but there is not apparent species replacement. A moss inventory has not been completed for the park; it is not known if more or different mosses will appear through time or succession.

Introduction

Yellowstone National Park is a large volcanic plateau with a continental climate and a well-documented history of forest fires. The fires of 1988 burned ~445,200 ha (4402 km²) within the park boundaries, about 44.5% of the park (Schullery 1989). Six per cent of the area burned was meadow-grassland and 94% was forests. Most of the burned forested areas were dominated by lodgepole pine (*Pinus contorta*), with smaller tracts of Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*). The burns were mosaic, leaving patches from a few m² to several km² of severely burned, moderately burned and unburned areas (Rothermel et al. 1994).

Many park projects have documented recovery of vascular plants, especially lodgepole pine and the understory perennials (Anderson and Romme 1991; Turner et al 1994, 1997; Baskin 1999; Reed et al. 1999; Tomback et al. 2001). They concluded that lodgepole pine has regenerated itself, as expected, from seed sources in adja-

cent unburned and lightly unburned and lightly burned patches. Herbaceous and shrubby understory regeneration has depended primarily on the plants that resprouted from surviving underground parts and from nearby seed sources. This study investigates the initial return of lichen and moss species, all of which were presumably incinerated when their substrates burned. None of the other Yellowstone studies included cryptogram observations.

Studies concentrating on recolonizing cryptogamic crusts, including mosses, algae, and lichens, on dryland soil after fires, have occurred in Utah (Johansen et al. 1984) and Australia (Eldridge and Bradstock 1994). Algae tended to return before lichens and mosses, especially during wet years, and after 5 yr the lichens and mosses were recovering but not yet to pre-burn cover. On peat surfaces in England, *Ceratodon purpureus* appeared to be insensitive to pH differences, and readily colonized ashed surfaces with 1 yr after fire; *Polytrichum piliferum* was dominant after 3 yr (Thomas et al. 1994). The lichens *Xanthoria parietina* and *Caloplaca aurantia* var. *aurantia* recolonized burned limestone within 4 yr after fire in Israel (Garty 1992). Most rock in Yellowstone National Park is igneous rhyolite or granite.

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In Canadian lodgepole pine forests (Brulisauer et al. 1996, Coxson and Marsh 2001) and spruce-lichen woodlands (Maikawa and Kershaw 1976, Morneau and Payette 1989), *Polytrichum piliferum* or *P. juniperinum* recolonized burned soil before other mosses, <20-50 yr after fire. Rowe and Scotter (1973) also identified the mosses *P. commune* and *Ceratodon purpureus* in an early post-fire spruce-lichen woodland. Early colonizing lichens varied, but usually included *Cladonia* spp., and, in spruce-lichen woodlands, *Trapeliopsis granulorum* and *T. uliginosa*. The moss *Pohlia nutans* was an important recolonizer in one study (Brulisauer et al. 1996) and in another location (Coxson and Marsh 2001), the lichens *Peltigera aphthosa*, *P. malacea* and *Sterocaulon alpinum* were significant early colonizers. After 50 yr, feather mosses (e.g., *Pleurozium schreberi*) and *Cladina* spp. increased. Stability in bryophyte communities was reached within 100 yr, but the organization among lichens, shrubs, forbs, and grasses was still changing after 100 yr (Brulisauer et al. 1996).

In studies focusing on wood and bark recolonization after fire, Longan et al. (1999) documented colonization in Spain of burned holly oak (*Quercus ilex*) stumps by *Cladonia* spp., *Agonimia allobata* and *Macetina dictyospora* within 11 yr after fire. Romagni and Gries (2000) followed initial recolonization of burned silverleaf oak (*Quercus hypoleucoides*) in southern Arizona where trees with rough-textured bark close to healthy lichens were recolonized within 3 yr by *Flavopunctelia praesignis* and *Punctelia hypoleucites*. Numbers of thalli increased more quickly on severely burned trees than on moderately burned trees.

The objective of this study was to document the initial return of lichens and mosses in 2001, 13 growing seasons after the 1988 fires were extinguished. We examined burned trees, soil, and rock. Eversman et al. (2002) identified 369 lichen species from Yellowstone National Park: 256 in Engelmann spruce stands, 206 in Douglas-fir, 133 in lodgepole pine/whitebark pine, and 152 in lodgepole pine stands. The presence of mature Douglas-fir and Engelmann spruce stands indicates that the sites were last completely burned >300 yr ago. Fire recurrence in lodgepole pine is generally at 100-300 yr intervals, and whitebark pine sites are usually >150 yr old (Romme and Despain 1989, Despain 1990). No moss inventory for the park has been completed, although the Yellowstone

National Park Herbarium has 120 species of mosses in 57 genera (Jennifer Whipple, Yellowstone National Park, personal communication).

Since Eversman et al. (2002) had identified so many more lichen species in the moister spruce and Douglas-fir forests, we hypothesized that in this study we would find more and different lichen species in these sites than in the drier lodgepole pine and whitebark pine sites. We also anticipated more moss species, and those more characteristic of moister habitats, in burned Douglas-fir and spruce than in the drier pine forests. Lodgepole pine and whitebark pine are generally on exposed ridges and plateau locations, while Engelmann spruce and Douglas-fir tend to be on more protected hillsides.

Methods

In June and July, 2001, we selected 5 sites in burned meadows and 27 sites in burned forest stands: 6 in Douglas-fir, 11 in lodgepole pine, 5 in Engelmann spruce, and 5 in whitebark pine forests. Elevations were 2090-2165 m for meadows, 1940-2202 m for Douglas-fir, 2033-2364 m for lodgepole pine, 2152-2383 m for Engelmann spruce, and 2527-2637 m for whitebark pine sites. Most of the sites were on hillsides with various exposures; three lodgepole pine sites were on level ground. Since most of the burned forests were lodgepole pine, those sites were easily found; burned stands from the other three forest types were more difficult to locate. We determined the types of burn sites according to adjacent tree types, incompletely burned trees, and type of tree reproducing. Each site was between 0.25-0.50 ha. We walked a loop through each site, recording lichen and moss species on completely blackened logs lying horizontally (downed logs) and standing burned stumps or snags, when present, and on soil. A snag is most of a burned, standing tree approximately its original height, and a stump is standing remains ~1.5 m or less. We examined 10 burned logs and 2-10 snags/stumps at each site. Samples of all species were taken for voucher specimens, and for laboratory identification when field identification was uncertain. We measured the length of fruticose and diameters of foliose lichen thalli. We estimated the distance from the center of each site to the nearest unburned trees, potential propagule sources, by pacing or driving.

We analyzed, according to forest type, the percentage of burned wood substrates in each site that were bare or recolonized by moss or lichens (ANOVA/MANOVA, STATISTICA, $P=0.05$). We correlated percentage of bare or recolonized wood substrates at each site with distance from the nearest unburned trees, potential propagule sources (Pearson Product-Moment Correlation, STATISTICA).

Nomenclature follows Dorn (1984) for vascular plants, Esslinger (1997) for lichens, and Anderson et al. (1990) for mosses. Voucher specimens were deposited in the Montana State University Herbarium (MONT).

Results

General Patterns

Burned logs and stumps/snags were recolonized by lichens or mosses alone or both together. Small polypore fungi and tiny ascomycetes were frequently on burned wood, and we saw occasional oyster mushrooms (*Pleurotus* sp.). Decorticated logs lying horizontally, and apparently unburned, were common in the lodgepole pine sites; they had no lichen or moss growth on them, merely occasional small ascomycetes. We observed no lichen or moss growth on any of the conifers that have grown since 1989. Nearly all of them were lodgepole pine, with small Engelmann spruce, Douglas-fir, and subalpine fir in moister sites, and none more than ~5m tall. A few whitebark pines repopulated the burned whitebark pine areas, but most of the young pines in those sites were also lodgepole pine. *Bryum caespitium* and *Ceratodon purpureus* were in all 27 forest sites, either on logs or soil, or both. All of the lichen and moss recolonizers, except the moss *Rhytidiopsis robusta*, were already parts of the collections in the Yellowstone National Park Herbarium.

Meadows

Available substrates for recolonization in meadows on hillsides between lodgepole pine stands were soil and rhyolite. Tall grasses were in these sites during the summer observations and inhibited visible growth of soil moss or lichen. Burned rhyolite boulders had no recolonization other than *Bryum caespitium* and *Ceratodon purpureus*, growing in cracks and around the bottom of boulders. In drier burned big sagebrush (*Artemisia*

tridentata) grassland, available substrates were soil, woody remains of big sagebrush shrubs, and granitic boulders. Cyanobacteria (*Nostoc*), lichens (*Cladonia chlorophaea* and *Peltigera rufescens*), and mosses (*Bryum caespitium*, *Ceratodon purpureus*, and *Tortula ruralis*) were on soil. The lichens *Buellia papillata*, *Caloplaca cerina*, *Rinodina turfacea*, and *Xanthoria fulva* covered woody plant debris, usually the remains of big sagebrush.

Mosses on Burned Wood

Engelmann spruce sites had significantly more moss colonization than the other three forest types (Figure 1). Of 27 forest stands, *Bryum caespitium* and *Ceratodon purpureus*, growing mixed together, were on burned wood in 24 sites (88.9%). The general pattern for moss growth was for *Bryum* and *Ceratodon* to start growing on the soil directly under the logs, and expand continuously upwards onto the logs, particularly in cracks in the wood and on the uphill or more shaded side of the logs. On most logs with mosses, the moss growth was a thin green film, in cracks, with small gametophytes and no sporophytes. On the bases of snags and stumps, again, moss growth was continuous with the same species growing on the adjacent soil. Qualitatively, the percentage for moss cover was greater than for lichen cover.

Ten moss species including *Bryum caespitium* and *Ceratodon purpureus* were on burned wood in spruce sites, and seven were in lodgepole pine (Table 1). They tended to be on shaded logs or the bases of burned stumps and snags, growing up onto the wood from the soil. We observed only *B. caespitium* and *C. purpureus* on burned wood in Douglas-fir and whitebark pine sites.

Mosses on Soil

The major mosses on burned soil were *Bryum* spp., especially *B. caespitium*, and *Ceratodon purpureus*, nearly always associated with downed logs or snags and stumps, and *Polytrichum juniperinum* and *P. piliferum* that formed mats on dry soil. The *Polytrichum* species were in 11 sites, evenly distributed among forest types, and their mats reached maximum diameters of 50-60 cm. *Polytrichum* never seemed to grow from soil upwards onto wood substrates. We found no *Funaria hygrometrica*, a common post-fire species. *Tortula ruralis* was in drier lodgepole pine

and meadow sites. *Marchantia polymorpha* was in two of the wettest spruce sites.

Mosses on Rock

Most rhyolite and granitic outcrops and boulders had no moss growth directly on the rock, but *Ceratodon* was usually around the bases. The mosses in cracks in the rock, again apparently growing together upward from the soil, were *B. caespiticium* and *C. purpureus*.

Lichens on Burned Wood

Engelmann spruce sites had significantly more lichen recolonization on burned wood than lodgepole pine sites (Figure 1). The largest number of species (15 plus soredia and *Cladonia* squamules) was in Douglas-fir types (Table 1).

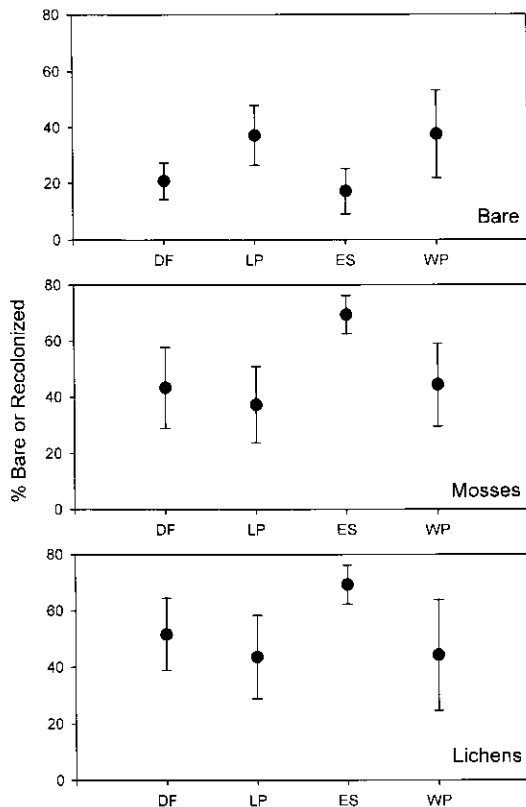


Figure 1. Percentage of burned wood bare or recolonized by mosses or lichens in each forest type (mean \pm 1.96 S.E.). DF = Douglas-fir, LP = lodgepole pine, ES = Engelmann spruce, WP = whitebark pine.

Sterile *Cladonia* squamules, *C. fimbriata*, and *C. coniocraea* accounted for the greatest amount of recolonization on burned wood (Table 1). Their usual location was in horizontal cracks towards the bottoms of the logs lying on the ground. Logs that were propped up from the ground by other logs or stumps, and the sides of standing snags and stumps, were recolonized least by either lichens or moss. The most favorable place for lichens on stumps was in concave depressions at the tops, on which *Xanthoria fulva* and generally unbranched threads of the fruticose species (*Bryoria fuscescens*, *Letharia vulpina*, *Usnea substerilis*) were attached. The longest thallus measured was 32 mm (*Bryoria fuscescens*) in an Engelmann spruce site, followed by maximum lengths of 30 mm for *L. vulpina* in a lodgepole pine site, and 16 mm for *U. substerilis* in a Douglas-fir site.

Lichens recolonized burned wood in all forest types, but only 5 lichens were in all forest types: *Cladonia* squamules, *Melanelia exasperatula*, *Parmeliopsis ambigua*, *Physcia* spp. (*P. dubia* or *P. dimidiata*), and *Xanthoria fulva*, plus yellow and white soredia (Table 1). *Bryoria fuscescens*, *Cladonia fimbriata*, *C. coniocraea*, *Letharia vulpina*, *Parmelia sulcata*, and *Usnea substerilis* were in all forest types except whitebark pine (Table 1).

Lichens on Burned Soil

Peltigera rufescens, and occasional *P. didactyla*, were on burned soil in 10 of the 27 sites; they were in 4 Douglas-fir sites and 2 of each of the other forest types. We saw patches of *Cladonia* squamules not associated with downed logs in only 5 lodgepole and whitebark pine sites. In one moist spruce site, *Cladonia macrophyllodes* formed patches 8-10 cm in diameter. We observed no other lichen species on soil. Where grasses had regenerated well, there were no visible mosses or lichens on soil.

Lichens on Burned Rock

Most of the burned rhyolite observed in lodgepole pine stands had no returning lichen growth. When the rock was being recolonized, however, the species of lichens were scattered areoles and occasional apothecia of *Candelariella aurella*, *Lecanora novomexicana*, *Lecanora polytropa*, and *Lecidea atrobrunnea*. *Aspicilia* spp. and *Rhizocarpon geographicum*, in patches of ~1 cm

TABLE 1. Percentages of bare burned wood and burned wood substrates with recolonizing lichens and mosses. Forest types are listed in approximate order from low to high elevations. The mosses *Bryum caespiticium* and *Ceratodon purpureus* usually grew mixed together.

Forest type	Douglas-fir		Lodgepole pine		Engelmann spruce		Whitebark pine	
Number of sites (s)	6		11		5		5	
Total number of burned wood substrates (w)	97		167		74		53	
	%s	%w	%s	%w	%s	%w	%s	%w
Bare logs, stumps, snags	100	21	91	37	80	17	100	38
Recolonized logs, stumps, snags	100	79	100	63	100	83	100	62
Mosses (total)	83	42	82	64	100	66	100	41
<i>Bryum caespiticium</i> ,								
<i>Ceratodon purpureus</i>	83	42	82	40	100	66	100	41
<i>Aulacomnium palustre</i>	—	—	9	1	—	—	—	—
<i>Brachythecium rutabulum</i>	—	—	9	1	20	1	—	—
<i>Brachythecium</i> spp.	—	—	—	—	60	4	—	—
<i>Bryum capillare</i>	—	—	—	—	20	1	—	—
<i>Dicranum</i> sp.	—	—	—	—	20	1	—	—
<i>Drepanocladus uncinatus</i>	—	—	—	—	20	1	—	—
<i>Leptobryum pyriforme</i>	—	—	9	1	20	4	—	—
<i>Plagiothecium denticulatum</i>	—	—	9	1	—	—	—	—
<i>Pohlia drummondii</i>	—	—	—	—	20	1	—	—
<i>Pohlia nutans</i>	—	—	9	1	—	—	—	—
<i>Rhytidiopsis robusta</i>	—	—	—	—	20	1	—	—
Lichens (total)	100	55	100	42	100	67	100	49
<i>Bryoria fuscescens</i>	33	4	46	5	40	3	—	—
<i>Candelariella aurella</i>	17	2	—	—	—	—	—	—
<i>Cladonia squamules</i>	67	11	73	16	100	43	80	21
<i>Cladonia coniocraea</i>	17	1	18	2	40	4	—	—
<i>Cladonia fimbriata</i>	67	6	36	5	80	24	—	—
<i>Lepraria cacuminum</i>	—	—	—	—	—	—	40	4
<i>Letharia vulpina</i>	67	13	36	2	40	7	—	—
<i>Melanelia exasperatula</i>	67	11	36	4	20	1	20	2
<i>Parmelia sulcata</i>	17	10	18	1	20	1	—	—
<i>Parmeliopsis ambigua</i>	67	6	18	1	20	3	20	2
<i>Physcia adscendens</i>	50	4	—	—	—	—	—	—
<i>Physcia dubia, dimidiata</i>	100	5	9	3	40	3	100	17
<i>Usnea substerilis</i>	100	24	73	13	80	1	—	—
<i>Xanthoparmelia</i> sp.	17	1	—	—	—	—	—	—
<i>Xanthoria fulva</i>	100	32	27	5	40	3	20	2
Soredia (white, yellow)	50	3	46	7	60	4	20	2

in diameter, were also on rock that appeared to have been burned.

Granite boulders were somewhat richer in recolonizing species. In addition to the six lichen species listed above, *Physcia dubia*, *Umbilicaria hyperborea*, and *Xanthoria elegans*, all with thalli of ~1 cm, were on granite in meadow sites.

Distances between the center of sites and the nearest unburned trees were 50-100 m in Douglas-fir, 30-1600 m in lodgepole pine, 20-50 m

in Engelmann spruce, and 100-1000 m in whitebark pine sites.

Discussion

We had hypothesized that more recolonization and more moss and lichen species would occur in Engelmann spruce and Douglas-fir sites than in whitebark and lodgepole pine sites, because the former two mature forest types have many more species of lichens than do the two mature pine

forest types (Eversman et al. 2002). The hypotheses were partially supported. Engelmann spruce sites had significantly higher moss recolonization than all other forest types, but more lichen colonization than only lodgepole pine sites (Figure 1). Douglas-fir sites were not significantly different from lodgepole and whitebark pine sites in percentage of recolonized burned wood (Figure 1). The number of lichen species on burned wood was greatest in Douglas-fir sites (15 identifiable species); however, Engelmann spruce and lodgepole pine sites each had 11 species, while whitebark pine had 7 species (Table 1). Two large leaning Douglas-fir trees that still retained some charred bark contributed to the unusually high presence of *Melanelia exasperatula*, *Parmeliopsis ambigua*, *Physcia adscendens*, *Letharia vulpina*, *Usnea substerilis* and *Xanthoria fulva*. Rough bark apparently provided an easy substrate to recolonize (Romagni and Gries 2000). Engelmann spruce sites had 10 moss species, and lodgepole pine sites had 7 mosses (Table 1). Only *Bryum caespitium* and *Ceratodon purpureus* were observed on burned wood in Douglas-fir and whitebark pine sites.

In comparison to post-fire observation of moss recolonization in the Canadian forests cited previously, the presence of *Polytrichum* spp. was similar to early post-fire colonization patterns there, but we recorded much more *Bryum* and *Ceratodon* than in those studies. We found no *Funaria hygrometrica*, a usual fire species; it may have been present immediately after the fires and replaced by *Ceratodon* and *Bryum* (Hoffman 1966, O'Toole and Synnott 1971). *Pohlia nutans*, a common colonizer in other burn studies (Thomas et al. 1994, Brulisauer et al. 1996), was present only in tiny amounts in Yellowstone sites. Moss growth on burned logs was significantly greater in Engelmann spruce sites, but a recolonization pattern similar to that of lichens is possible. That is, addition of species, not species replacement, may occur.

We assumed that sexual spores were the primary moss propagules. Twelve of the lichens recolonizing burned wood are sorediate, and *Melanelia exasperatula* is isidiate (Table 1), apparently indicating the dispersal efficiency of soredia and isidia, asexual reproduction structures containing both alga and fungus. The non-sorediate lichen species, *Candelariella aurella*, *Lepraria cacuminum*, and *Peltigera rufescens*, are abundant throughout the park. All of the species identified from the burned substrates were among the

most common and widespread lichen species in forests in Yellowstone National Park (Eversman et al. 2002), providing propagules for burned sites.

We presumed that sources of propagules for the mosses and lichens were the closest unburned substrates. The distance from the burn sites to unburned trees ranged from 20 m in small mosaic burns (adjacent unburned trees or across a road or creek) to ~1.6 km. Lichen propagules appeared to be somewhat more successful than moss propagules at traveling longer distances and recolonizing burned wood (Figures 2, 3). The r value for correlation between distance to unburned trees and moss colonization was -0.3181 , and that for lichens was -0.0476 . The sites 1000 m from nearest unburned trees were whitebark pine, ~2530 m in elevation, and the site 1600 m from unburned trees was a dry lodgepole pine site. If moss spores reached the sites, they may have had difficulty germinating or growing.

In Yellowstone National Park, apparently the most common and abundant species of lichens establish themselves early in post-fire succession and remain indefinitely since all of the colonizing species are also present in old forests. Greater diversity occurs with time since fire (Pharo and Beattie 1997), and in Yellowstone National Park is related to Douglas-fir and Engelmann spruce forests, more favorable habitats (Eversman et al. 2002). Succession sequences in the Yellowstone forests will be different from those in the conifer forests studied in Canada because *Cladina* species are not present (except in three thermal basins), Yellowstone National Park has fewer *Cladonia* species, and *Stereocaulon* is uncommon. In addition, early post-fire lichens in studies in Canadian lodgepole pine forests included *Peltigera aphthosa* and *P. malacea* (Brulisauer et al. 1996, Coxson and Marsh 2001), species more characteristic of mature Engelmann spruce forests in Yellowstone.

The moss flora of the park is basically undescribed, but mosses might follow the same pattern as lichens: the same common species of mosses appear first in all burned forest types. Later additions may vary, with different sequences or rates of colonization in the different forest types. If succession of mosses is similar to that of the Canadian lodgepole pine forests (Brulisauer et al. 1996, Coxson and Marsh 2001), feather mosses such as *Pleurozium schreberi* may appear 35-50 yr post-fire in moist forests.

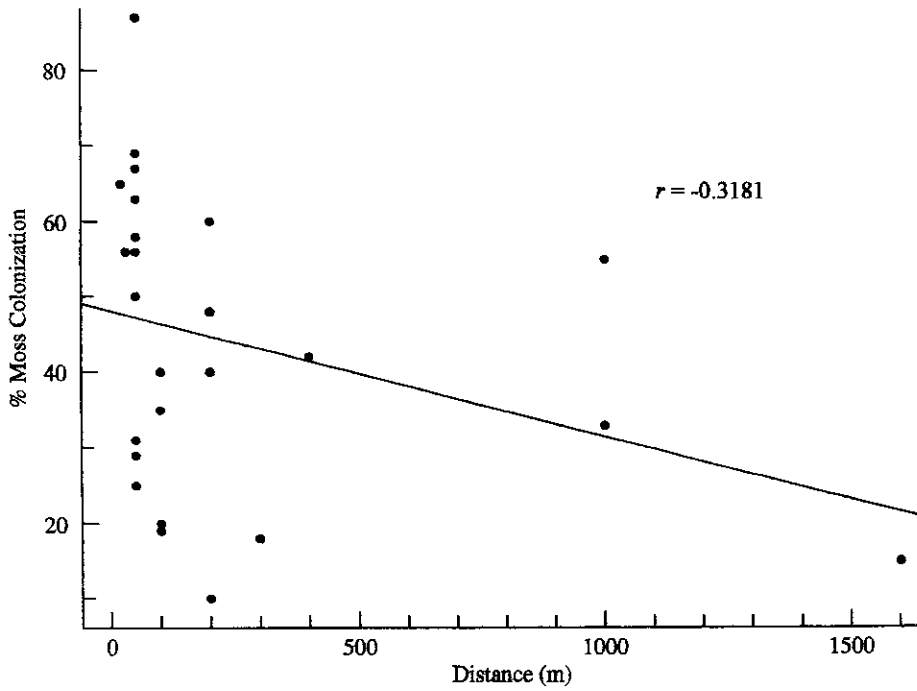


Figure 2. Significant correlation between percentage of burned wood recolonized by mosses with distance from center of each plot to nearest unburned trees.

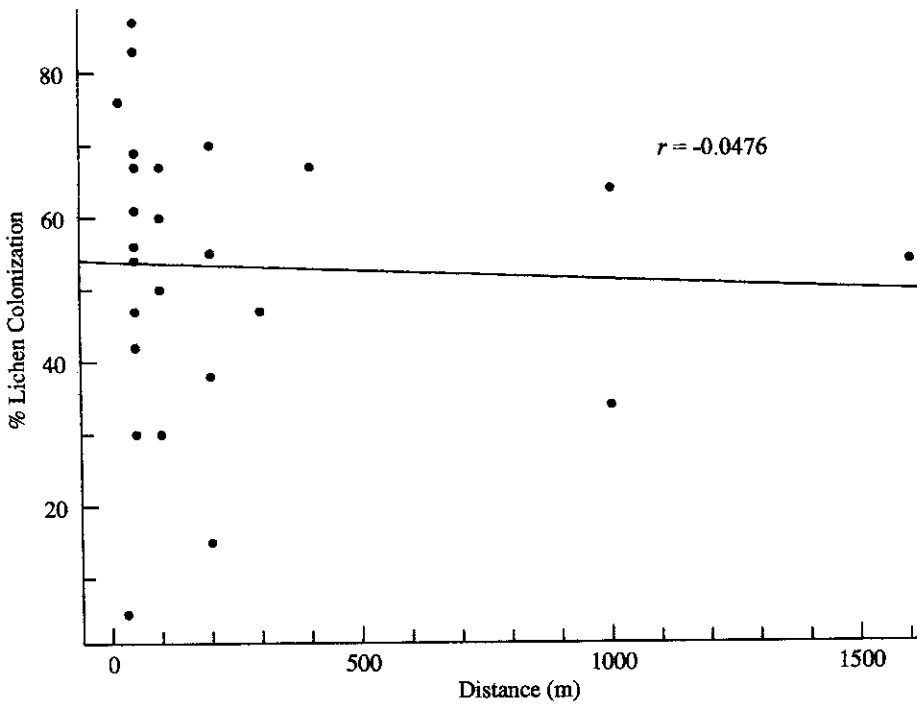


Figure 3. Significant correlation between percentage of burned wood recolonized by lichens with distance from center of each plot to nearest unburned trees.

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