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Effect of fire on the germination of spores of *Pteridium caudatum*, an invasive fern

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Abstract: *Pteridium caudatum* is a fern that frequently invades burnt areas in the Yucatán Peninsula and other neotropical sites. While post-fire regeneration of this fern apparently occurs mainly by vegetative means, little is known about the role of its spores in post-fire regeneration and in colonization of newly invaded fields. Central to these questions is whether bracken fern spores maintain their viability after fires. Here we experimentally evaluate the effect of fire-induced temperatures on *Pteridium caudatum* spore germination. We used 1200-cm^3 blocks containing a constant fuel load of 47.4 g of litter, in which we placed spores at three different depths. The blocks were then ignited, and temperatures at each depth were monitored at 1-min intervals for 2 h. One day after the experimental fires, spores were dug out and cultured at 25 °C and 12-h light/dark cycles. Soil temperatures decreased significantly in relation to depth during fires. Spores on the surface were severely affected by fire, while those buried at 1 and 3 cm showed 77% germination. Germination in unburned controls was 86%. Our results suggest that during fires, *Pteridium caudatum* spores buried a few centimetres below the surface have a high percentage of viability, which could explain the rapid establishment of this species in burnt fields.

Key Words: bracken spread, burial depth, Mexico, post-fire regeneration strategies, soil heating, soil temperatures, Yucatán Peninsula

INTRODUCTION

The widespread occurrence of fire in the tropics has favoured the expansion of invasive species such as *Pteridium caudatum* (L.) Maxon. This fern is a post-fire colonizer and is widely distributed across the Yucatán Peninsula, where it forms monospecific patches in recently cleared and burnt areas (Gliessman 1978). In this region, *P. caudatum* invasion is a complex process, which involves environmental degradation, land-use strategies and fire (Schneider & Fernando 2010). Schneider (2006, 2008) described the development of monodominant *P. caudatum* patches as starting with a few plants shaded by secondary vegetation, which expand drastically once secondary vegetation is cleared through fires or agricultural activities.

It is widely accepted that the spread of bracken stands depends on vegetative growth, but the expansion of existing populations, re-establishment after fires in already invaded fields, and colonization of new sites, could occur by spores arising from spore banks (Dyer 1989). Additionally, some evidence suggests that the occurrence of fire is required for *P. caudatum* spore germination (Gliessman 1978) and that conditions encountered following fire, such as elimination of competitors and creation of sterile, alkaline and nutrient-rich substrate, are very close to the optimal conditions for sporeling establishment (Page 1976, 1982, 1986).

Post-fire regeneration from propagule banks in the soil largely depends on the temperatures occurring in the topsoil during fires (Auld 1986, Bond *et al.* 1990, Bradstock & Auld 1995, Hodgkinson 1991, Moreno & Oechel 1991a, 1991b; Schimmel & Granström 1996). Excessive heat can be lethal for seeds or spores near the soil surface (Baskin & Baskin 1998, Keeley 1977,

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Keeley & Zedler 1978, Zammit & Zedler 1988), but a brief exposure to the high temperatures caused by fire might be sufficient to stimulate the germination of buried, dormant propagules (Baeza & Vallejo 2006, Gashaw & Michelsen 2002, Thanos & Goerghiou 1988, Williams *et al*. 2004).

Because soil is an effective insulator against high fire-induced temperatures (Agee 1993, Whelan 1995), the depth at which the seeds and spores are buried in the soil modifies the conditions that these propagules undergo during a fire (Auld 1986, Bradstock & Auld 1995, Odion & Davis 2000, Pickup *et al*. 2003), hence influencing their post-fire survival and germination (Bradstock & Auld 1995, Bradstock *et al.* 1992, Gill 1981). The relationships between fire-induced temperatures, seed burial depth and seed germination have been studied in several species of angiosperms (Auld 1986, Auld & O'Connell 1991, Gill 1981), but their effects on fern spores have not been evaluated. This paper evaluates the effect of temperatures generated during experimental fires on the germination of *P. caudatum* spores buried at three soil depths. Concretely, we hypothesized that the spores of bracken fern remain viable after fires, due to the insulating effect of soil. We also documented the temperatures reached and the duration of maximum temperatures during fires, and evaluated the impacts of these two factors upon spore germination. Finally, we quantified the proportion of spores of this species that remain viable in the soil after 2 y, to evaluate whether an effective spore bank exists.

METHODS

Study species

Pteridium caudatum, like all species of bracken, is one of the most successful invasive species in the world (Taylor 1990). It is present in Bermuda, southern Florida, the West Indies, Central America and northern South America, mainly in deforested, agricultural and fire-prone areas (Page 1986). Some of the characteristics that make this species a successful competitor, capable of creating monospecific patches, include high resistance to diseases and pests (Cooper-Driver 1990), allelopathic effects (Gliessman & Muller 1976), abundant vegetative propagation (Page 1986), tolerance of a broad range of climatic and edaphic conditions (Gliessman & Muller 1976), elevated spore production (Conway 1957), high dispersal rate (Gregory & Hirst 1957) and resistance to fire (Gliessman 1978). Perhaps its most prominent fire adaptation is its buried rhizome, which sprouts vigorously following fires (Fletcher & Kirkwood 1979). Additionally, bracken fern spores invade recently burned areas, allowing it to establish in the basic conditions created by fire. Other tropical ferns (e.g. some members of Gleicheniaceae) have a similar ecological behaviour in the Asia–Pacific region (Cohen *et al*. 1995, Russell *et al*. 1998) and other locations of the neotropics (Slocum *et al*. 2004, Walker 1994, Walker & Boneta 1995, Zimmerman *et al.* 2000).

Study site

In July 2005 we collected soil, litter and *P. caudatum* spores from seasonally dry secondary forest at El Edén Ecological Reserve, located 38 km north-west of the city of Cancun, in the state of Quintana Roo, Mexico. The weather in this site is warm and humid, with a seasonal period of rainfall from June to December, a mean annual temperature of 24.7 °C and a mean annual precipitation of 1511 mm. Soils at this site are very young and shallow (0–4 cm), covering limestone rock. Vegetation in the area includes semi-deciduous seasonal forest, tropical savanna and secondary vegetation in different stages of succession. The study area has experienced a long history of both natural (e.g. hurricanes) and anthropogenic (e.g. fires, harvesting of timber and non-timber forest products) disturbances. There are also sites affected by recurring fires during the dry season, which are currently covered with *P. caudatum.*

Experimental fires

The effect of fires on germination of bracken spores was tested in 12 experimental fires conducted in the Pteridology Laboratory of the Universidad Autónoma Metropolitana. Spores used in these treatments were obtained from 15 adult sporophytes at the study site. Fertile pinnae with mature sporangia were stored inside paper bags and left to dry at environmental temperature to facilitate spore release. The contents of the bags were sifted with a metallic mesh, and the spores obtained were stored under dry conditions in glass bottles until used in experimental fires, 1 mo after collection. Each fire was achieved in a block containing 1200 cm^3 of dry soil and a constant fuel load of 47.4 ± 5.3 g ($\pm$ SE) of dry litter of *P. caudatum*. Litter and soil samples used in this experiment were dry when collected, but to ensure homogeneity of treatments, were further dried for 48 h at 70 °C before being weighed and used for the experimental blocks. The fuel load used in the above described blocks is similar to that found in *P. caudatum*-invaded fields at the study site, and was obtained by collecting the litter present in 30 randomly located 20 × 20-cm quadrats in the field. To test for the presence of viable spores in soils of the study area (i.e. spore bank), additional soil samples without previous treatment were used in germination trials.

Before ignition, three containers of iron mesh with 1 mg of *P. caudatum* spores (without previous treatment) were placed in each of the 12 blocks of soil, one on the soil surface, and the other two buried at 1 and 3 cm, respectively. To bury the containers we made a *c.* 2-cm diameter hole, inserted the iron mesh containers and covered the hole. In each soil block, three K-type thermocouples (Onset Computer Corporation, Pocasset, MA, USA) connected to data loggers (model U12–014, HOBO, Onset Computer Corporation, Pocasset, MA, USA) were inserted in the blocks at the same depth as the spores and adjacent to the spore containers. All sensors were activated approximately 1 min before fires were lit. Litter was subsequently ignited, and the temperatures at each depth were recorded each minute for 2 h. The maximum temperature and duration of the maximum temperature were obtained from the data loggers.

Spore germination

The spore containers were dug out 1 d after the fires, and spores were sown within the next 48 h on 5-cm diameter Petri dishes containing previously sterilized agar with Thompson's nutrients (Klekowski 1969). Spores were spread on the surface of the solidified medium with a fine brush. Three replicates for each depth per block were incubated at 25 °C and illuminated with fluorescent light under a photoperiod of 12 h light/12 h darkness for 2 mo. Untreated spores were used as controls and were incubated under the same laboratory conditions.

Spore germination in Petri dishes after experimental fires was recorded weekly for 2 mo with the help of a stereoscopic microscope (American Optical, Stereo Star ZOOM, AO Company, USA). The number of germinated spores (gametophytes) was counted in each replicate in five 0.5 × 0.5-cm fields, and the results were expressed as the mean number of gametophytes developed in 0.25 cm^2. We calculated the germination percentages of spores that were exposed to fire at the soil surface and of those that were buried at 1 and 3 cm in the 12 experimental fires.

To verify the presence of reservoirs of viable spores of *P. caudatum* in the soil at the study site, we evaluated germination of spores according to the method described by Ramírez-Trejo *et al.* (2004) at two different times: 13 d after the collection in the field and after 2 y. Soil samples were taken from 45 points randomly chosen within the study site. Having removed the litter layer in each point, soil samples were collected by inserting a steel cylinder (8 cm length, 5 cm diameter) vertically in the soil to a depth of 3 cm. Each soil sample was completely removed from the steel cylinder and placed in polyethylene bags for transport to the laboratory. Three days after the collection in the field a total of 45 samples of approximately 50 g of soil were placed in transparent plastic containers (5 cm diameter), covered with a transparent plastic, kept damp, and placed under solar lamps (75 W F96T12/D day light, photon flux density = 437 μmol m^{-2} s^{-1}) for a photoperiod of 12 h of light, at 18 °C to induce spore germination. After 10 d, spore germination was recorded with a stereoscopic microscope (American Optical, Stereo Star ZOOM, AO Company, USA), by counting the total number of spores that germinated in each container. Results were expressed as the mean number of germinating spores cm^{-2} in the germination vessel. For 2 y, soil samples were kept dry at room temperature in polyethylene bags. After that time, soil samples were again cultured following the same procedure.

Statistical analyses

Maximum temperature, duration of the maximum temperature and germination percentages recorded at the different depths were compared using a blocked design analysis of variance. Post hoc comparisons were done with a Tukey's test. The effects of depth, maximum temperatures and duration of the maximum temperatures on the germination percentage of *P. caudatum* were determined with a stepwise regression analysis. Angular transformation of the percentage data was conducted to homogenize the variance between groups and to comply with the conditions of normality (Sokal & Rohlf 1995). Similarly, the data for maximum temperature and duration of maximum temperature were log- and square root-transformed, respectively. All error terms are standard errors. Analyses were conducted using the SYSTAT 11 statistical package (SYSTAT Software, Inc).

RESULTS

Behaviour of the soil temperature

Mean maximum temperatures and mean duration of maximum temperatures recorded during the fires were significantly influenced by depth ($F = 25.2$, $F = 34.1$; respectively, in both cases $P < 0.001$) with a negative relationship of depth and maximum temperature and a positive relationship between depth and duration of maximum temperatures. In neither case was there an effect of blocks. The heat pulse generated by the passage of the flames produced a significant increase in the surface soil temperature, where a mean maximum temperature of 172 °C ± 25.8 °C was recorded. With increasing depth, the maximum temperature was significantly reduced. At 1 and 3 cm in depth, soil heating was moderate and the mean maximum temperature was 42.0 °C ± 3.5 °C and 32.7 °C ± 2.0 °C, respectively, with no significant differences between these levels. On the soil surface, there was substantially more variation in the maximum temperatures (range of 290 °C) than beneath surface. The range of maximum temperatures was 30.4 °C at 1 cm and 16.2 °C at 3 cm. Maximum temperatures were of relatively short duration at the three soil depths. On the surface, and at 1 cm, the durations were 1.2 and 1.4 min, respectively, whereas at 3 cm the average duration of the maximum temperature was significantly increased to 3.2 min.

As the flames progressed, temperatures on the surface suddenly rose, and the maximum temperatures were recorded at a mean time of 6.1 min after ignition. This brief initial heat pulse was followed by a rapid decrease in temperature (Figure 1a). At a depth of 1 cm, the maximum temperature was reached 2.7 min later than at the surface, but the cooling was comparatively slower than at the surface, and, in some cases, several minutes passed before the initial temperature was reached (Figure 1b). At 3 cm, the heat penetrated slowly and produced a minimal and gradual increase of the soil's temperature, so the maximum temperature occurred, on average, 22.3 min after the fires started (Figure 1c).

Effect of the temperature and burial depth on spore germination

Germination of *P. caudatum* spores was recorded when soil temperatures ranged between 26.5 °C to 60 °C. The highest germination percentage (89%) occurred in spores that, during fires, remained at 3 cm in depth, where a maximum soil temperature of 33 °C was reached (Figure 2). The mean germination percentage was significantly influenced by the depth at which the spores remained buried during fires ($F = 44.7$, $P < 0.001$), with no block effect. The increase in depth produced a drastic decrease in the soil's temperature; thus spores unexposed to fire had higher mean germination percentages (86%) than those exposed to fire at any of the three soil depths (Figure 3). Spores placed on the surface were severely affected by the direct exposure to flames, which resulted in a high mortality and, therefore, a low germination response (2.1% ± 1.4%), while spores buried at 1 and 3 cm showed significantly higher germination percentages (~77%), without significant difference between depths (ANOVA, Tukey's test HSD, $P > 0.05$; Figure 3).

The stepwise regression analysis revealed that depth and maximum temperatures had significant effects on the germination percentage of *P. caudatum* spores. When these variables are accounted for, the duration of the maximum temperatures does not account for any additional variance in the model. The equation in the stepwise regression that best explained the post-fire germination of *P. caudatum* spores was: $y = 1.55 + (0.331 \times \text{depth}) - (0.745 \times \text{maximum temperature})$, where y is the arcsine-transformed proportion of germinated *P. caudatum* spores ($R^2 = 0.85$, $P < 0.001$).

In terms of viable bracken fern spores, a total density of 1.8 germinating spores cm^{-2} germinated in soil samples evaluated 13 d after collection. After 2 y, spore germination was reduced to 0.02 germinating spores cm^{-2}.

DISCUSSION

Our results demonstrate that superficial fires affected the germination of spores of *P. caudatum* located in the topsoil, as a function of the temperature reached at each depth at which spores were buried. Experimental fires produced a considerable increase in the temperature of the soil surface, lethal for most spores of *P. caudatum* exposed to the flames. Nevertheless, at 1 and 3 cm in depth, the soil acted as an effective insulator to moderate the temperature increase, and the buried spores retained their viability, as expressed by a germination percentage ~ 77%. The insulating properties of soil during a fire are widely documented (Agee 1993, Baskin & Baskin 1998, Bradstock & Auld 1995, Bradstock *et al.* 1992, Gill 1981, Williams *et al.* 2004). In the context of the Yucatán Peninsula, the insulating properties of the soil become more relevant because the propagule banks (spores, seeds, buds, etc.) and the rhizome system are immersed in a very thin layer of mineral soil or survive between fissures in the limestone rock (Allen *et al.* 2003), giving them unique protection against the lethal effects of high fire-induced temperatures.

To our knowledge, this is the first study that analyses the relationship between the temperature reached during a fire and the subsequent germination of fern spores, although a few studies have evaluated the effect of temperature per se on spore germination (Dyer 1979, Miller 1968, Pérez-García & Riba 1982, Raghavan 1980, Ranal 1999). Spores of *Pteridium* spp. are able to germinate under a wide temperature range, from 1 °C (Conway 1949) to 35 °C (Dyer 1979). Our results show that, during the experimental fires, dry (not imbibed) spores of *P. caudatum* tolerated higher temperatures (e.g. at 1 cm the mean temperature was 42.0 °C), retaining their viability and producing a high germination percentage. Our results also show that fire is not a necessary requirement for spore germination (Gliessman 1978), as untreated spores had higher germination than fire-exposed spores at any soil depth.

Vegetative growth is unquestionably an important mechanism explaining the re-establishment of *P. caudatum* after fires (Dyer 1989). However, our results suggest that spores buried at 1–3 cm from the soil surface, could eventually germinate and become established. In this case, re-establishment would also be the result

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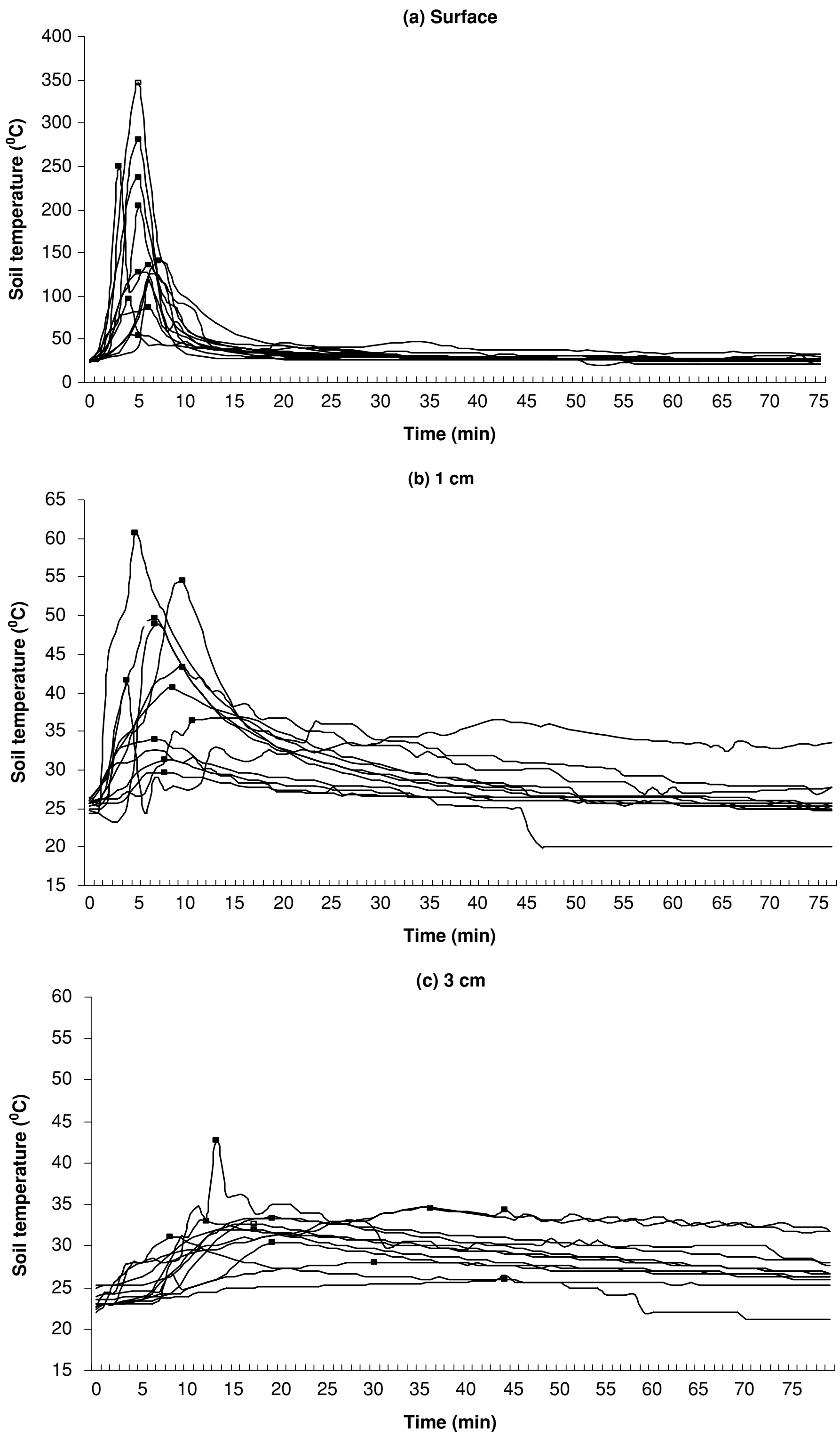

Figure 1. Temperatures recorded at the soil surface (a) and at depths of 1 cm (b) and 3 cm (c) during 12 experimental fires. Squares indicate maximum temperatures.

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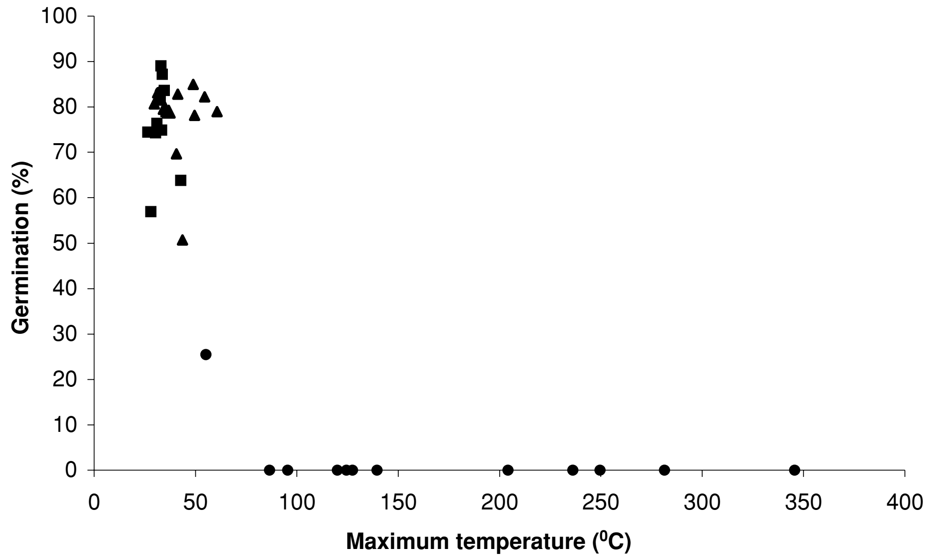

Figure 2. Post-fire germination of *Pteridium caudatum* spores in relation to the soil maximum temperature recorded during 12 fires at different depths: soil surface (●), 1 cm (▲) and 3 cm (■). n = 36.

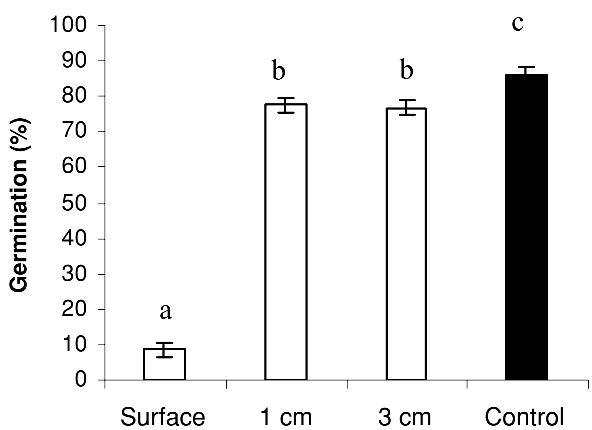

Figure 3. Germination percentages of *Pteridium caudatum* spores exposed to fire, at three depths (white bars) and unexposed controls (black bar). Different letters denote values that are significantly different at $P < 0.05$.

of sexual reproduction. This would imply that patches dominated by bracken fern constitute true populations, and not just one large individual ramet.

Spores of bracken can remain viable in the soil for approximately 1 y (Dyer 1989). Although spore viability was greatly reduced in soil samples after 2 y, our results confirm the presence of viable spores in the topsoil of the study site. Spores that maintain their viability after fires at 1–3 cm deep could be brought to the surface through any sort of soil disturbance. These spores may be sufficient in a long-lived perennial species to allow new populations to colonize and enlarge (Dyer 1989).

In seasonally dry tropical forests, seeds buried in dry soil might be more tolerant of heat because they are dehydrated and metabolically inactive for most of the year (Garwood 1983). This is a highly relevant point because, in the tropics, fires set for agricultural purposes take place during the dry season (Otterstrom *et al.* 2006), the period when fires might reach their highest temperatures (Williams *et al.* 2004).

Research on a wide variety of ecosystems shows that there is great variation in soil temperatures during a fire (Cautinho 1978, Gimeno-García *et al.* 2004, Miranda *et al.* 1993), which largely depends on the fuel loads, fuel moisture, and fuel size distribution, which in combination with meteorological conditions and topography affect the intensity of fires (Agee 1993, Busse *et al.* 2005, Massman *et al.* 2003). In our study site, fuel loads of the litter layer were 1.2 kg m^{-2}, and the mean temperatures produced with the same loads in laboratory conditions were 172 °C, 42 °C and 32.7 °C on the surface and at 1 and 3 cm, respectively. In a seasonally dry tropical forest in Bolivia, fuel loads of 2.2 kg m^{-2} resulted in superficial temperatures of 225 °C, with no temperature increase at 3 cm deep, while fuel loads of 48 kg m^{-2} increased temperatures to 704 °C and 227 °C at the surface and 3 cm deep, respectively (Kennard & Gholz 2001). Fuel loads in secondary forests with 2–5 y of fallow in the Yucatán Peninsula had fuel loads of 2.1 kg m^{-2} (Read & Lawrence 2003). If *P. caudatum* spores are present in the soil of secondary forests 2–5 y in the Yucatán, it might be possible that they will remain viable after these forests are slashed and burned for agricultural use as long as they remain 1–3 cm deep in the soil. In that case, viable buried spores of *P. caudatum* could explain the new colonization of sites burned repetitively for agricultural purposes in the Yucatán Peninsula.

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Temperatures recorded at each soil depth in this study are consistent with the results of other investigations reporting higher temperatures for shorter periods of time at the surface and lower temperatures for longer periods of time deeper in the soil (Bradstock & Auld 1995, Bradstock *et al*. 1992, Portlock *et al*. 1990). The time interval during which the propagules are exposed to heat produced by a fire can influence germination and mortality (Lonsdale & Miller 1993, Zabkiewicz & Gaskin 1978). In this study, the duration of maximum temperatures did not have a significant effect on the germination percentage of *P. caudatum* spores, thus corroborating results by Keeley *et al*. (1985) and Odion & Davis (2000), who found that seeds in the soil are more sensitive to maximum temperatures than to heating duration. It is nonetheless important to consider that longer exposure times may have detrimental effects on spores and that both variables can affect different species in a variety of ways (Lonsdale & Miller 1993).

From our experiments, we can conclude that *P. caudatum* spore germination does not depend on fire, but spores buried 1–3 cm in the soil maintain high germination percentage after fires. This, in addition to the fact that spores might remain viable in the soil for up to 2 y, suggests that re-establishment of *P. caudatum* after fires can be achieved not only by vegetative growth, but also by germination of spores and the subsequent establishment of new individuals, which implies that bracken fields consist of true populations of *P. caudatum*.

Some studies conducted in tropical deciduous forests of western Mexico (Miller 1999) and of the Yucatán Peninsula (Rico-Gray & García-Franco 1992) document a drastic reduction of seed density from the soil seed banks after fire. In the Yucatán Peninsula, a significant decrease of seeds of tree species after disturbance was found. Both could create new niches that could be occupied by spores of *P. caudatum*, which, once established, can be capable of promoting the colonization of new sites and eventually create spore banks (Dyer 1989). Additionally, after fires, bracken spores maintained their viability at 1–3 cm from the soil surface, suggesting that *P. caudatum* spore viability in the soil might also explain partially how this species is able to colonize new sites affected by fires repeatedly in the Yucatán Peninsula.

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