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Authors: Roos, Kristin, Rollenbeck, Rütger, Peters, Thorsten, Bendix, Jörg, and Beck, Erwin

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Growth of Tropical Bracken (*Pteridium arachnoideum*): Response to Weather Variations and Burning

Kristin Roos, Rütger Rollenbeck, Thorsten Peters, Jörg Bendix, and Erwin Beck*

The ecology of tropical bracken, which occurs in tropical regions, is not well known. We studied its response to weather variations and burning in the south Ecuadorian Andes, where this weed had already overgrown 40% of the pastureland. In field observations, a constant 1 : 1 ratio of emerging and dying leaves suggested limitation of frond density by nutrient shortage. Short-term deviations from that ratio could be related to weather variations. Spells of dry weather temporarily increased mortality but stimulated emergence of new fronds. Lifespan of the fronds produced immediately after a fire was longer than of those produced during unaffected bracken growth. A burst of frond development during the initial 2 to 3 mo was observed after a fire followed by self-thinning to a stable level. To analyze the effect of fire on bracken, rhizomes were treated with heat pulses. Rhizomes were heat tolerant up to 70 C, and frond production from short shoots was enhanced by elevated temperature. Burning apparently releases apical dominance of developed fronds, as does cutting, and stimulates bud break. The local practice of pasture maintenance in Ecuador of repeated burning favors growth of the fern.

Nomenclature: Bracken, *Pteridium aquilinum* agg. (L.) Kuhn; tropical bracken (bracken of the southern hemisphere), e.g., neotropical *Pteridium arachnoideum* (Kaulf.) Maxon and *Pteridium caudatum* (L.) Maxon.

Key words: Tropical bracken, invasive ferns, vegetation dynamics, fire ecology, heat effects on rhizome.

Bracken (*Pteridium* spp.) is one of the most aggressive weeds worldwide, infesting pastures, forested areas, and bushland and causing severe problems for farmers, foresters, and conservationists (Pakeman et al. 1994). Because of its variable and robust rhizome system, it resists any kind of mechanical, herbicidal (Le Duc et al. 2003; Marrs et al. 1998), or biological control (Burge and Kirkwood 1992; Burge et al. 1986). It propagates readily by spores and also by long-living rhizomes, is highly resistant against pathogenic microorganisms, and is poorly palatable for grazing animals. Its allelopathic effects on other plant species, its tolerance of weather extremes and bush fires, and its remarkable genetic plasticity strengthen its competitiveness as a weed (Page 1986). Bracken [*Pteridium aquilinum* (L.) Kuhn] as a cosmopolitan plant is genetically not uniform and appears as an aggregate that by morphological and molecular characters can be differentiated into a northern and a southern group (Der et al. 2009; Page 1976). The northern group, whose leaves are not frost resistant (the "*aquilinum*" complex), is ecophysiologically characterized by a life cycle that is synchronized by the winter break. The southern group [including the diploid *Pteridium arachnoideum* (Kaulf.) Maxon and the allotetraploid *Pteridium caudatum* (L.) Maxon (nomenclature based on Der et al. 2009)] comprises mainly tropical representatives with year-round growing (Thomson 2000). Uninterrupted growth of rhizomes and leaves results in tall plants, whose fronds can grow as high as 4 m at the edge of a forest (K. Roos, unpublished data). In contrast to the well-defined ecological requirements of the northern bracken (Ader 1990; Evans et al. 1990; Page 1986; Pakeman et al. 2000), ecophysiology of the tropical bracken is less well known (Alonso-Amelot and Rodulfo-Baechler 1996; Bray 1991; Hollinger 1987; Quitete Portela et al. 2009). Previous observations suggest that higher rainfall has a positive effect on growth, whereas low temperature has a negative effect (Quitete Portela et al. 2009).

In the Andes of southern Ecuador, vast areas of primary mountain forest have been cleared by slash and burn to produce pasture (Beck et al. 2008a; Hartig and Beck 2003).

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* First and fifth authors: Ph.D Student and Professor, Department of Plant Physiology, University of Bayreuth, Universitaetsstr. 30, 95440 Bayreuth, Germany; second and fourth authors: Research Assistant and Professor, Laboratory for Remote Sensing and Climatology, Department of Geography, University of Marburg, Deutschhausstr. 10, 35032 Marburg, Germany; third author: Research Assistant, Institute for Geography, University of Erlangen, Kochstr. 4, 91054 Erlangen, Germany. Corresponding author's E-mail: kristin.roos@uni-bayreuth.de

Interpretive Summary

Tropical bracken is the most aggressive invader of pastures in southern Ecuador where it competes with the equally fast growing introduced pasture grass *Setaria sphacelata* (Schumach.) Stapf & C.H. Hubb.. The customary weed control by periodical burning, however, results in shifting the competitive strength of both species in favor of the fern. The heat pulse boosts both growth of the frond producing lateral rhizomes but also bud break and frond emergence. Thus, bracken gets a head start after the fire and finally forms a stable weed vegetation whose density mirrors the nutrient availability in the soil. These causal interrelations are demonstrated in the paper with results from field studies and laboratory experiments.

After burning all fallen trunks and branches, pasture grasses such as *Setaria sphacelata* (Schumach.) Stapf and C.E. Hubb. ex Chipp. and *Melinis minutiflora* P. Beauv. are planted or sown. For the first years, the grasses develop well, but gradually bracken takes over, prompting farmers to set fire to the pastures, which damages the fern less than the grasses. Eventually, the pastures are abandoned and farmers clear another piece of the pristine forest. In the study region in the southern Ecuadorian Andes, about 40% of the area where forest has been cleared consists of such bracken-dominated sites (Göttlicher et al. 2009).

There are numerous reports that fire kills the standing fronds but stimulates growth of bracken (Agee and Huff 1987; Ingram 1931; Sharik et al. 1989). However, in an experiment by Flinn and Pringle (1983), rhizomes of northern bracken were not heat resistant. Bracken rhizomes consist of a fast-growing main axis, termed long shoot, which usually does not produce fronds, and the frond-producing lateral (short) shoots (Watt 1940). Long shoots are found deeper in the soil than the laterals, which usually concentrate in the top soil and thus should be particularly endangered by fires. Intermediates of both rhizome types have also been found (Watt 1940; Webster and Steeves 1958).

In this study, we report on growth dynamics of the neotropical bracken, *P. arachnoideum*, as affected by weather variations and burning. Different weather variables were used to identify possible triggers of frond emergence and dying at an undisturbed bracken site in southern Ecuador. After burning, regrowth of bracken populations of varying density were studied and compared with the growth dynamics of the undisturbed bracken vegetation. The field studies were supplemented by laboratory experiments to investigate the effects of heat pulses on the bracken rhizome. We investigated heat tolerance of long and short shoots separately and examined survival, growth, and frond production. In a field experiment, frond emergence after burning was compared with that after cutting to examine whether frond emergence after fire results only from release of apical dominance of resting frond buds (Burge and Kirkwood 1992) or is stimulated by burning.

Material and Methods

The Study Site. The study area, located in the upper Rio San Francisco valley in the Andes of southern Ecuador, extends over a horizontal distance of 1.2 km and vertically from 1,800 to 2,200 m above sea level. It borders the "Reserva Biológica San Francisco" (3°58′30″S, 79°4′25″W) which is part of the Podocarpus National Park. A comprehensive geographical description of the area has been presented by Beck et al. (2008b). The steep slopes harboring the research area are covered by open vegetation consisting of sporadic tussocks of pasture grass *S. sphacelata* under a more or less closed canopy of bracken fronds, up to 2 m high, which is interspersed with scattered bushes. Suppression and displacement of the pasture grasses by bracken has been attributed to the common practice of pasture maintenance by burning (Beck et al. 2008a; Hartig and Beck 2003). The study area was abandoned and had not been used as pasture for at least 11 yr.

Long-Term Field Observations. *Growth of Bracken.* Within an area of 3.5 ha, six circular plots with a diameter of 2 m each (3.14 m^2) were randomly established. These are referred to as control plots. Each bracken frond in the plots was individually tagged and followed from emergence until death. From November 2005 until May 2008, the total numbers of fronds, new leaves, and dead leaves were recorded every 4 wk. Additionally, the developmental states of the individual bracken fronds (unfolding, mature, senescent = browning of ≥50% of the frond area, and dead) were monitored on two of these plots. Thus, the total lifespan and the length of the developmental phases of bracken fronds could be determined.

To assess the effect of weather variations on the growth of bracken, weather conditions were continuously recorded with an automated climate station[1] (Rollenbeck et al. 2007), which was installed about 1 km away from the study site (03°58′21″S, 79°04′35″W, altitude: 1,960 m above sea level).

Frond Regeneration after Fire. In October 2004 and December 2005, big bushfires devastated major parts of the study area. However, the area with control plots was not affected. Immediately after the fires, sites for monitoring regrowth of bracken were selected. After the fire in 2004, an area of 7.4 ha was selected for that purpose, and after the fire in 2005, another area of 3.7 ha was designated. Within the first site, 13 plots and, in the second, 10 plots were established. Plot size and mode of monitoring were identical to the control plots. The first series of plots were investigated for 18 mo and the second for 12 mo.

Heat Penetration Study. To examine heat penetration into soil, a bracken-covered area (50 by 20 m) was burned 2 d after the last rain, and soil temperatures were measured every 5 min at 2 and 5 cm depth with PT1000 thermocouples[2] connected with an automated climate station.[1]

Frond Regeneration after Cutting vs. Heating. To analyze whether frond emergence after fire results only from release of apical dominance of resting frond buds or is additionally stimulated by burning, nine plots of 1 m^2 each with similar bracken frond densities (on average, 12 fronds m^{-2}) were installed randomly in the field (in an area of 50 by 100 m). Simultaneously, one set of three plots was burned, whereas in another set (three plots), bracken fronds were cut near the ground, and the remaining three plots were left untreated (controls). On all plots, the emerging fronds were tagged, and regeneration was observed.

Heat Pulse Treatment of Bracken Rhizomes. To examine reactions of rhizomes with respect to temperature in more detail, a heat pulse experiment was conducted in which survival, extension growth, and frond production were determined. Rhizomes (in total 469) were collected in the field and separated into long and short shoots (Watt 1940). Rhizomes with a minimum length of 12 cm, [mean length 26.6 ± 0.4 cm (SE)] were used, and the numbers of buds on the individual rhizomes were determined before heat treatment. Most of the rhizomes had at least one bud, but rhizomes without buds also were tested to assess the importance of buds for survival. Applied temperatures were 40, 45, 50, 55, 60, 70, and 80 C. Heat treatments were administered in two ways: (1) by dipping the rhizomes for 2 min in a preheated water bath or (2) heating them together with original moist soil in a temperature-controlled oven to the desired temperatures, at which they remained for 10 min. Warming up the soil (with rhizomes) took between 20 and 60 min, depending on the final temperature. Heating in soil is closer to the situation in the field because it allows for slow penetration of the heat wave in moist soil. After exposure to the elevated temperatures, the samples were cooled to ambient room temperature. Thereafter, all rhizomes were planted in original soil and cultivated at near-natural temperature conditions under a plastic roof (to avoid soaking of the rhizome bed by daily rains). The rhizomes were excavated after 2 mo of cultivation, and their condition, change in length, and frond production were determined. Survival of rhizomes was assessed by their consistency and color. Healthy rhizomes have a durable coat and their interior is white, whereas dead rhizomes are soft and brown. Control rhizomes were handled in the same manner, but without the heat treatment.

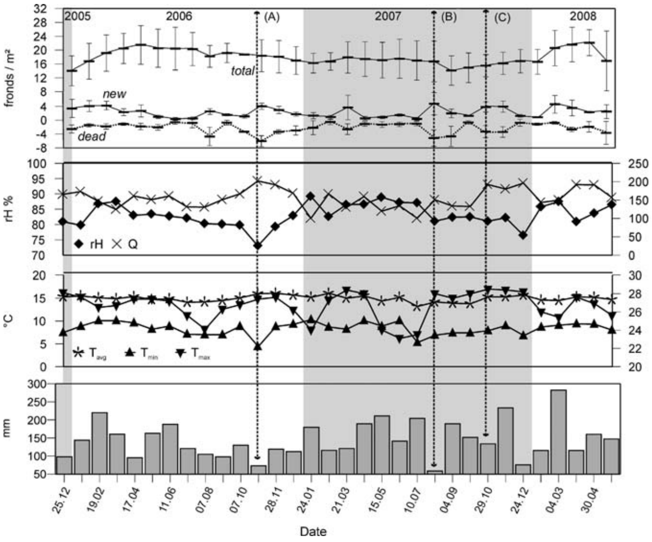

Figure 1. Monthly bracken frond density (mean ± SE m^{-2} of six plots, observed in 4-wk intervals) and the 4-wk averages of relative humidity (rH), solar irradiance (*Q*), temperature (*T* average, minimum, and maximum), and rainfall sums at the Estación Científica San Francisco meteorological station in the course of 2.5 yr. Note that the dates along the abscissa represent the last day of each 4-wk period. (A–C) Arrows mark extreme weather situations.

Data Analysis. The program SPSS 13.0 (SPSS 2004) was used for statistical analyses. Normality of data distribution was evaluated with the Shapiro–Wilk test. In the case of newly emerging and dying fronds (at the control plots), length increment and frond production after heat pulse, data were not normally distributed (even after different trials of data transformation); therefore, direct relations were analyzed with Mann–Whitney *U* tests. A Spearman correlation was used to prove the coincidence of emerging and dying fronds at the untreated plots. A binary logistic regression was used to determine the effects of different variables on survival of rhizomes after the heat shock experiment.

With regard to the relation between weather and frond dynamics, the data for precipitation, air temperature, relative air humidity, and solar irradiance (original temporal resolution is 10 min) were aggregated to four-weekly sums of rainfall and four-weekly averages of solar radiation, air humidity, and air temperature (encompassing average minimum and maximum air temperature) to match the 4-wk period of bracken monitoring (Figure 1). The Pearson correlation coefficient was used to analyze the relation between emergence and dying of bracken fronds and weather parameters (Table 1). Because 4-wk sums and average values will not show shorter periods of extreme climate stress that might affect bracken frond dynamics, additional analyses were carried out to detect such events. Three variables were selected:

Table 1. Correlations (*r* values) between weather elements and frond dynamics for the 4-wk periods. T = air temperature, rH = relative air humidity, Q = solar irradiance, R = Rainfall. For other acronyms refer to equations 1–3. Significant *P*-values are given in bold.

	Emerging fronds	Dying fronds
T_{avg}	+0.24 (P = 0.18)	+0.07 (P = 0.70)
T_{max}	**+0.36 (P = 0.04)**	+0.17 (P = 0.35)
T_{min}	−0.02 (P = 0.91)	**−0.37 (P = 0.04)**
rH	−0.22 (P = 0.22)	**−0.43 (P = 0.01)**
$f\mathrm{rH}_{<70}$	**+0.42 (P = 0.02)**	**+0.42 (P = 0.02)**
Q	**+0.37 (P = 0.04)**	+0.26 (P = 0.15)
$fQ_{>190}$	**+0.52 (P = 0.002)**	+0.31 (*P* = 0.08)
R	−0.04 (P = 0.82)	−0.31 (P = 0.08)
$fR_{<0.1}$	+0.20 (P = 0.27)	+0.21 (P = 0.24)

(1) The relative fraction of days per monitoring period with rainfall < 0.1 mm ($fR_{<0.1}$)

$$fR_{<0.1} = \sum_{1}^{d} D_{<0.1} \Big/ d \qquad [1]$$

where $fR_{<0.1}$ is the relative frequency of days with rainfall < 0.1 mm, d is the total number of days of the respective bracken frond monitoring period, and $D_{<0.1}$ is the number of days with rainfall < 0.1 mm.

(2) The relative frequency of days with low average relative air humidity (<70%) per monitoring period ($f\mathrm{rH}_{<70}$)

$$f\mathrm{rH}_{<70} = \sum_{1}^{d} D_{<70} \Big/ d \qquad [2]$$

where $f\mathrm{rH}_{<70}$ is the relative frequency of days with average relative air humidity $< 70\%$, d is the total number of days of the monitoring period, and $D_{<70}$ is the number of days with average relative air humidity $< 70\%$.

(3) The relative frequency of days with high average daily irradiance (>190 W m^{-2}) per monitoring period ($fQ_{>190}$)

$$fQ_{>190} = \sum_{1}^{d} D_{>190} \Big/ d \qquad [3]$$

where $fQ_{>190}$ is the relative frequency of days with average solar irradiance > 190 W m^{-2}, d the total number of days of the bracken monitoring period, and $D_{>190}$ the number of days with average solar irradiance > 190 W m^{-2}.

The three resulting frequency time series were correlated (Pearson correlation analysis) with the time series of new and dead frond abundance to investigate the effect of extreme weather situations on bracken frond dynamics.

Results and Discussion

Undisturbed Growth of Bracken. In contrast to the annual growth pattern of the northern bracken, which is interrupted and thus synchronized by the winter break, the tropical bracken shows continuous growth. The lifetime of the individual fronds showed a median of 8 mo (upper quartile [75th percentile] = 10; lower quartile [25th percentile] = 5, maximum 18 mo, minimum < 1 mo), which is longer than the frost-limited lifespan of leaves of the northern bracken (~6 mo). Unfolding took less than 1 mo, the length of the mature state was between 3 and 7 mo, and the phase of senescence lasted up to 2 mo. In the course of years 2005 to 2008 in the control plots, on average, 16% of the fronds were unfolding, 22% senescent, and 62% considered mature. Frond density showed moderate fluctuations (Figure 1) around an average value of 17.2 ± 0.7 (SE) fronds m^{-2} during the observation period of 2.5 years. Frequently, dying of old leaves coincided temporally with the emergence of new ones (r_s = 0.51, P < 0.001), and the average rates of both processes were not significantly different [2.0 ± 0.3 (SE) dying fronds m^{-2} mo^{-1} and 2.3 ± 0.2 developing fronds m^{-2} mo^{-1}, P > 0.40]. This almost perfect 1 : 1 ratio suggests a physiological interrelation of both processes, given that both take place on the same set of rhizomes. A similar observation has been reported from pastures in New Zealand, which were infested by another species of tropical bracken, *Pteridium esculentum* (Bray 1991). The studies reported here were performed in open bracken vegetation and the balance between dying and emerging leaves did not exhibit a noticeable seasonal variation. This close interrelation could be explained as resulting from inorganic nutrient shortage when the development of a new leaf requires nutrients remobilized from senescing leaves. Bracken generally prefers soils with a medium to high nutrient content (Ader 1990; Waring and Major 1964), but the topsoils of the study site are poor in macronutrients (Hamer et al. 2009; Potthast et al. 2010). Limitation of bracken growth by edaphic factors is also indicated by the long-lasting differences in the density of the bracken canopy on the investigated plots. An average and stable density between 15 and 20 fronds m^{-2} (Figure 1) constitutes a moderate level of bracken infestation, whereas frond densities of 3 to 4 fronds m^{-2} indicate less favorable conditions, such as compact or waterlogged or extremely nutrient-poor soils (Brown 1986; Watt 1976).

Weather Effects on Growth Dynamics. In all plots, bracken frond dynamics showed only short-term deviations from the mentioned 1 : 1 ratio that can be related to spells of weather extremes (Table 1). The emergence of new fronds correlates with periods of higher maximum air temperature, enhanced irradiance (daily average > 190 W m^{-2}), and periods of reduced air humidity. High irradiance and air temperatures also led to increased soil temperatures, which confirms previous findings with northern bracken that frond emergence is triggered by higher soil temperatures (Pitman and Pitman 1990) and that bracken growth is promoted by direct radiation (Bendix et al. 2009).

The dieback of old fronds shows slightly different relations to the observed weather patterns (Table 1). We found significant negative correlations between the average air humidity and the number of dying fronds. The positive correlation to the spells of low air humidity extremes ($r = +0.42$ for days with humidity $< 70\%$) indicates that exceptionally dry periods led to enhanced frond mortality, which is in line with the findings by Roberts et al. (1980). The significant negative correlation between frond mortality and minimum temperatures can be interpreted as a side effect of extreme low humidity concomitant with low cloudiness and, thus, nocturnal radiative cooling of the air. This is confirmed by the highest correlation of meteorological parameters between relative air humidity and minimum temperature ($r = +0.57$, $P < 0.001$).

One reason for the relatively low correlations in Table 1 might be the relative low temporal resolution of the time series. Extraordinary weather events of shorter duration (few days) most likely affect frond emergence and mortality but might be hidden in the 4-wk averaging of the meteorological data. However, the following detailed analysis of short time periods demonstrates the modulation of bracken dynamics by short weather extremes. The best example is the dry period in October/November 2006 (Figure 1, line A). This period was characterized by the lowest average humidity and the highest average irradiance, resulting in elevated air temperature during the day, but low nocturnal temperatures because of unhampered radiation emission. During this spell, relative humidity was below 60% for five consecutive days (and even below 50% for 2 d). Highest monthly frond mortality was observed during that period, concomitant with an increased emergence of new fronds. Other periods of enhanced frond development were in August 2007 and in October/November 2007 (Figure 1, lines B and C). August 2007 was characterized by a slightly reduced average humidity on single days, whereas solar irradiance was on the level of the long-term average, except on three consecutive clear days with an averaged radiation > 200 W m^{-2}. The strikingly low precipitation combined with that spell of high radiation was paralleled by an enhanced frond mortality, which in that case slightly exceeded frond emergence. The situation in October/November 2007 (Figure 1, line C) was somewhat different from the above-mentioned October 2006 (Figure 1, line A). Precipitation and relative humidity were higher than 1 yr before, whereas solar radiation was similarly high. Under these conditions frond production slightly exceeded frond mortality.

In summary, days with solar radiation averaging >190 W m^{-2} correlated best with frond emergence, whereas spells of dry days (humidity $< 70\%$) matched frond mortality. This implies that high solar irradiance fostered leaf development and low air humidity enhanced frond mortality.

Regrowth of Bracken after a Fire. In the pilot heat penetration study, heat pulses up to 40 C at 2 cm, and up to 30 C at 5 cm soil depth were recorded. At both soil depths, the maximum temperatures were measured about 12 min after the arrival of the fire at the particular area, but cooling was much slower. At 2 cm depth, the initial temperature of 16 C was approached after 3 hr, whereas at 5 cm depth, it took 5 hr. Leaf emergence from the burnt soil was apparently not stopped by that low intensity of heat; however, young fronds emerging from the burnt soil during the first days after the fire did not survive the first month. A burst of frond production was recorded 2 mo after the fire, and depending on the original density of the bracken rhizomes, a more or less closed bracken canopy formed (Figures 2B, 2C, and 3). Maximum bracken frond density occurred between 5 and 7 mo of regeneration.

Dynamics of regrowth was plotted separately for plots exhibiting different levels of infestation by bracken. On slightly infested areas, a patchy bracken canopy formed at an average density of 3 fronds m^{-2} and a maximum density up to 8 fronds m^{-2}. On such areas, resprouting was observed from bunches of the former pasture grass that had survived the fire. On moderately infested areas, the bracken canopy leveled off at an average density of 13 fronds m^{-2} (Figure 3A), passing through a maximum value of 24 fronds m^{-2} at some plots (not shown in the figure, which presents average values and standard errors). A few small grass tufts were observed beneath fronds, and young shoots of fire-resistant bushes like *Ageratina dendroides* (Spreng.) R.M.King & H.Rob. and *Baccharis latifolia* (Ruiz & Pav.) Pers. sprouted from the scattered rootstocks. Such accompanying flora were not observed on heavily infested plots in which an average of 28 (Figure 3B) and a maximum of 41 fronds m^{-2} were recorded (not shown in the figure).

Obviously, burning of the vegetation had a synchronizing effect on the development of bracken fronds. Mass dying of fronds was observed when their maximum lifetime was reached (Figure 2D). However, this effect did not result in a pronounced wave-like characteristic of the frond density because new fronds immediately replaced the dead ones. Only a slight reduction of the leaf density was observed 10 to 11 mo after the maximum rate of frond emergence (12 to 13 mo after fire; Figure 3), reflecting synchronous dying of the initially produced leaves. In the less and moderately infested plots, a slightly elevated rate of leaf production followed that decrease. In the heavily

Figure 2. Dynamics of bracken after a fire. (A) The day after the fire; (B) 1 mo later with some new emerging fronds (red arrows); (C) closed canopy 3 mo after the fire; (D) large-scale dying of the first generation of fronds 1 yr after the fire.

infested plots, a substantial dieback of leaves (around 17%; Figure 3B) was recorded 12 to 13 mo after the fire. On average, on the burnt plots, bracken frond cover declined by 23% during the following 14 mo. Infraspecific competition resulting in self-thinning appears to be the cause for this reduction to a stable level. Northern bracken is known as a light-demanding, shade-intolerant pioneer species (Ingram 1931; Stewart 1988), and the tropical bracken apparently is no exception. Overlapping of the fronds, resulting in a steep gradient of light intensity in the canopy layer, might cause premature senescence of the shaded fronds.

Records of individually tagged fronds showed a significantly increased average lifetime of those fronds produced immediately after the fire (9 mo) compared with the fronds in the undisturbed plots (8 mo) ($n = 1{,}174$, $Z = -6.18$, $P < 0.001$). The increased lifespan by 1 mo supports the idea that low nutrient availability restricts the lifetime of fronds in the undisturbed plots. In a perhumid climate (>10 humid months per year; Lauer and Bendix 2004), nutrients are quickly allocated after a fire from the ash to the topsoil, thus alleviating the nutrient shortage of the plant for a while. Beneficial effects of burning on northern bracken have also been reported (Page 1982).

Most short rhizomes grow in the soil layer at between 2 and 9 cm depth (Beck et al. 2008a) and were not damaged by the heat pulse from the fire, which in the moist soil is very moderate. Stimulation of leaf bud sprouting by the transient heat (30 to 40 C), as measured in the pilot burning experiment, is conceivable.

Examination of Heat Tolerance of Bracken Rhizomes. To investigate the physiological effects of the moderate heat pulses on the tropical bracken, rhizomes were separated

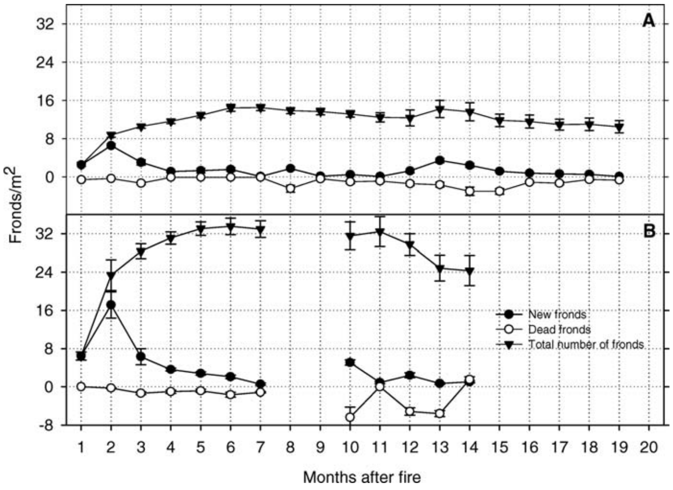

Figure 3. Regrowth of bracken after the fires in October 2004 (A) and December 2005 (B), respectively, resulting in a moderate (A) and high-density (B) canopy. Means ± SE m^{-2} of five plots each are shown in each graph.

into long and short shoots and subjected to heat treatments at various elevated temperatures. In the work of Flinn and Pringle (1983), rhizomes were immersed in a preheated water bath. In nature, rhizomes of the tropical bracken are commonly embedded in moist soil and therefore in the work presented here heat pulses were applied to the rhizomes in original soil (in an oven) and for comparison without soil in a preheated water bath.

Survival. Overall, dipping the rhizomes for 2 min in preheated water was less harmful than heating them in wet soil, for which, however, more time was required to attain the maximum test temperature. Some damage might have already occurred during this warm-up phase. Statistical analysis of the results (Table 2) revealed that the temperature and the mode of heating, in addition to the type, diameter, and length of rhizome, were the important variables for the susceptibility and reactions of bracken rhizomes to a heat pulse. In contrast, the initial number of buds had no influence on the survival of heated rhizomes. Fewer than 25% of all rhizomes died in the course of the posttreatment cultivation period (Figure 4). Rotting of the cut ends was observed frequently also on control rhizomes. Therefore, rhizomes that were only slightly rotted were counted as survivors. With respect to survival, long shoots were less resistant than short shoots, especially when they had been subjected to the heat pulse in soil. Under these conditions, few samples survived temperatures above 50 C, whereas most survived heat treatment in the water bath even at 80 C (Figure 4). However, the short shoots survived 80 C irrespective of the mode of heat pulse and thus were significantly more heat resistant than the long shoots ($P < 0.001$). This was not unexpected because the long shoots are commonly found deeper in the soil where heat waves from bushfires do not penetrate. A similar explanation was presented by Flinn and Pringle (1983) for an "(imprecise) correlation between depth of location of rhizomes and their resistance to heat damage." Because heat tolerance of the short rhizomes was remarkably high, they have a good chance of surviving the common bushfires that generate soil temperatures well below 100 C, as measured in the pilot burning experiment.

Table 2. Influence of different variables on survival of rhizomes after heat pulse. Analyses were done with binary logistic regression with method of heat treatment and rhizome type as categorical variables, *B* gives the slope and *W* is the *Wald* value corresponding to P; significant P values are given in bold.

Variable	*B*	*W*	*P*
Temperature	**−0.23**	**7.47**	**0.006**
Method of heat treatment: (1) water/(0) oven	**1.95**	**37.17**	**<0.001**
Rhizome type: (1) short/(0) long shoot	**1.36**	**13.72**	**<0.001**
Length of the rhizome	**0.06**	**6.41**	**0.011**
Diameter of the rhizome	**2.22**	**5.76**	**0.016**
N. of buds on the rhizome (inclusive, without buds)	0.24	2.69	0.101

Effect of a Heat Pulse on Elongation Growth. With long shoots, heat pulses did not stimulate elongation growth. On the contrary, growth of the long shoots was significantly inhibited at most experimental temperatures, irrespective of how the heat pulse was applied (Figure 5). Inhibition was mainly due to rotting, partly of the tissue damaged by the heat and partly by natural rotting of the cut rhizomes. Short shoots, however, showed a significant increment after the heat pulses in soil at 40 and 55 C, and at 50 C in the water bath (Figure 5). Apparently the heat treatment in soil was more effective in stimulating growth.

Effect of Heat Pulse on Frond Production. A significant stimulation of frond production from short rhizomes was observed by heat pulse temperatures between 40/45 and 55 C (Figure 6). The positive effect of the heat treatment was more pronounced when the rhizomes were heated in soil compared with the wet heat pulse. Above 55 C (wet heat pulse) and 60 C (in soil), fronds were not produced, although the rhizomes survived heating up to 80 C. In the study of Flinn and Pringle (1983), survival and resprouting after the heat treatment was investigated, and although some of the rhizomes survived 55 C, resprouting was consistently less than in the control. This behavior was different from a burning experiment, in which bracken was the first of six rhizomatous species to resprout after the fire (Flinn and Wein 1988). In the experiment reported here, short shoots of southern tropical bracken did survive not

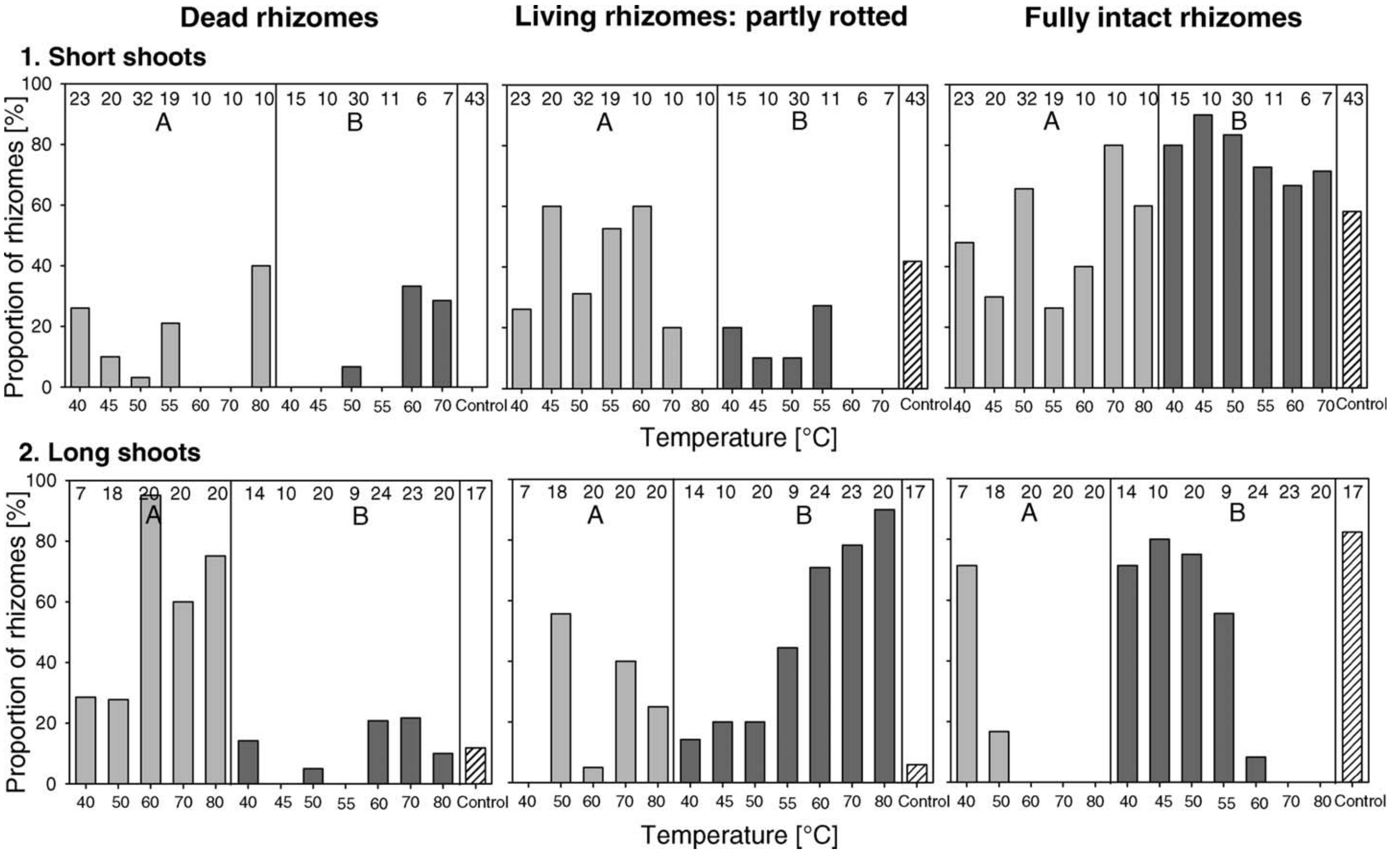

Figure 4. Survival of bracken long and short shoots after heat treatments (A) in soil and (B) in a water bath at various temperatures and subsequent cultivation for 2 mo in soil under seminatural environmental conditions. Rhizomes (short and long shoots) were differentiated into dead and living, and living rhizomes were further differentiated into partly rotted (if length after 2 mo was shorter than before) and fully intact. The numbers in the top of the panels indicate the size of the samples subjected to the respective treatment.

only temperatures above 55 C but could react to a transitory heat pulse up to 60 C (in soil) by activating dormant buds and producing new fronds.

Comparison of the Effects of Cutting and Burning on Frond Production. Fronds develop from buds on the short shoots. Production of a leaf could therefore inhibit sprouting of neighboring buds by apical dominance (Burge and Kirkwood 1992). To examine whether the initial burst of leaf emergence after a fire (as observed under field and laboratory conditions) could be explained only by an alleviation of apical dominance after killing of the fronds or resulted from an additional stimulation by the heat pulse, regrowth of bracken on moderately infested plots after controlled burning and cutting, as well as frond production on untreated plots, was compared. High rates of frond emergence were observed on the burned plots (Figure 7). In the first 4 mo of regeneration, regrowth after burning was twice as much as after cutting or on the control plots. Until the end of the observation time, this difference between the controls and the burned plots leveled off. But after 7 mo, regrowth after cutting was half as much as after burning. Therefore, the additional stimulation of buds by the heat pulse of a fire has to be appreciated when discussing bracken control measures. In addition to an enhanced spore formation after a fire (Conway 1957), the invasive power of bracken as a postfire colonizer (Gliessman 1978; Lyon and Stickney 1976) appears to rest primarily with the rhizomes and, more precisely, with the heat-resistant and frond-developing short shoots. Thus, the local practice of pasture maintenance by repeated burning favors the fern while concomitantly weakening the pasture grasses.

Sources of Materials

[1] Automated climate station from Thies, Göttingen, Germany.

[2] High-resolution Platinum Resistance Thermometer with a resistance of 1,000 Ω at 0 C, from HERAEUS, Hanau, Germany, self-configured.

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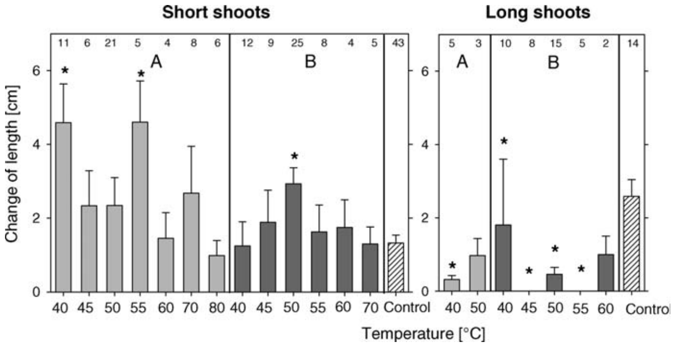

Figure 5. Change of length of short and long shoots 8 wk after heat treatment (A) in soil and (B) in a water bath (means ± SE, significant differences between heat-treated rhizomes and controls were calculated by Mann–Whitney *U* tests with all P < 0.003 and are marked with an asterisk). The numbers in the top of the panels indicate the actual numbers in the respective category. Only fully intact rhizomes were counted.

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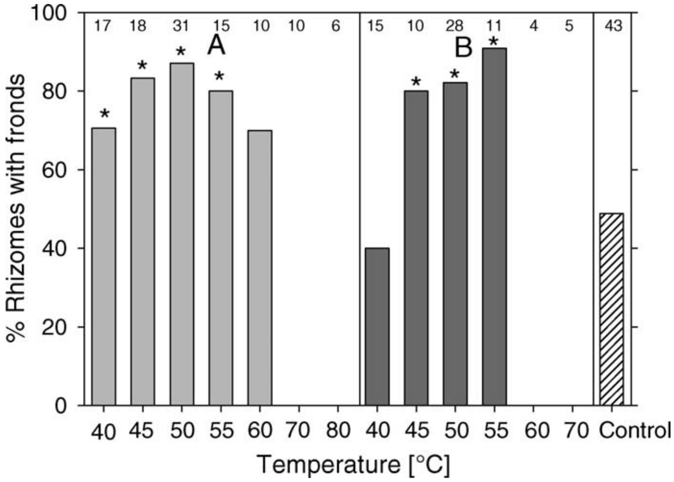

Figure 6. Frond production from short shoots after heat treatment (A) in soil and (B) in water bath measured 8 wk after treatment (significant differences between heat-treated rhizomes and controls were calculated by Mann–Whitney *U* tests with P < 0.05 and are marked with an asterisk). The numbers in the top of the panels indicate the actual numbers in the respective category. Only the surviving rhizomes were counted.

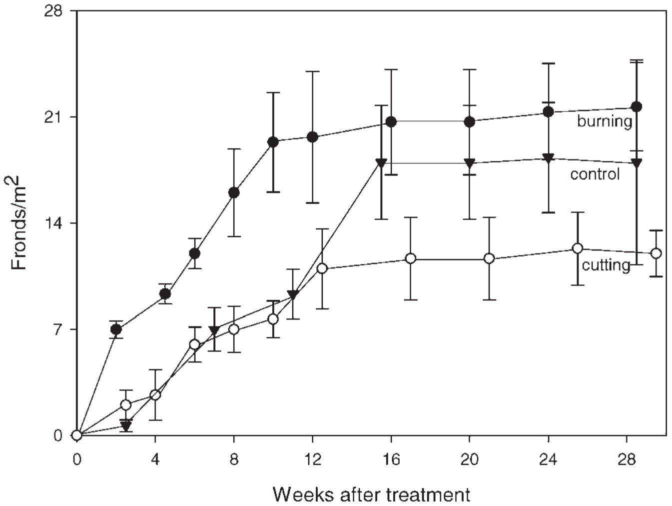

Figure 7. Regrowth of tropical bracken (number of newly emerged fronds, means ± SE) after cutting of the fronds, or burning of the areas, and without treatment (controls) on three 1-m^2 plots each.

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