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EFFECTS OF FIRE ON POPULATION DYNAMICS OF AN ENDEMIC HIGH ALTITUDE RUPICOLOUS GEOPHYTE

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ABSTRACT
Stevia camporum (Asteraceae) is a threatened and endemic geophyte of the rocky outcrop vegetation in the high altitude grasslands on the top of the Itatiaia massif. This is a locally abundant plant, which establishes itself preferentially on vegetation mats dominated by pioneer species such as mosses (*Campylopus pilifer*) and by the vascular endemic plants *Fernseea itatiaiae* and *Barbacenia gounelleana*. With a very distinctive morphology, these nurse plants may differently influence the dynamics of *S. camporum*. These relations were previously studied for two years when a 3-day unnatural fire burned the grassy vegetation around the rocky outcrops, thereby affecting indirectly the vegetation mats (islands) growing at the exposed rocky surfaces, through ash emissions and changes on the availability of nutrients. We described pre-fire (1999-2001) and post-fire (2002-2003) population demography and growth of *S. camporum* under the hypothesis that *Stevia* demography would change due to effects of fire, such as nutrient income and, further, that responses would vary according to the dominant pioneer species of each vegetation mat. Forty-three islands containing *S. camporum* (total area of 30.08m^2) were monitored. Despite considerable variation in rainfall between years, population structure and dynamics of *S. camporum* were very similar in the two pre-fire growing seasons. A massive increase in the frequency of branches in the first size class followed fire, but with nearly no changes in the other classes with a thinning process being observed. The height, number of nodes and number of fruits of *Stevia camporum*'s ramets showed significant differences when comparing the values for periods before and after the fire. *Stevia*'s demography on *Fernseea* (Bromeliaceae) mats was significantly different in relation to the other mat species, after fire. In Itatiaia, indirect effects of smoke produced by fire episodes seem to trigger rapid responses on rupicolous communities followed by rapid return to previous conditions, particularly in secondary species. Prolonged effects on more often disturbed communities remain to be seen, and might be relevant to community structure of high altitude outcrop vegetation.
Keywords: demography; Itatiaia National Park; nurse plant; rocky outcrop; *Stevia camporum*.

INTRODUCTION

The rocky outcrop vegetation in the Itatiaia massif (ca. 2000-2800 m a.s.l.) has a high number of endemic and rare species (Ribeiro *et al*. 2007, Aximoff & Ribeiro 2012), which are highly specialized to local conditions and therefore sensitive to physical or climatic changes (Behling 1998, Laurance *et al.* 2011). Studies have indicated the ecophysiological specialization of some plants of this flora (Scarano *et al.* 2001) and also the importance of a few nurse plants in creating safe sites for the germination and growth of many secondary species (Medina *et al.* 2006, Scarano 2009). The geophyte *Stevia camporum* Baker (Asteraceae) is endemic to high altitude rock outcrops of south-east Brazil, and is locally highly abundant (Ribeiro *et al.* 2007). It often grows in association to pioneer species that occupy bare rocky surfaces, forming vegetation mats (or islands). This geophyte grows preferentially on vegetation islands dominated by mosses such as *Campylopus pilifer* Brid. (Dicranaceae) (Medina *et al.* 2006). There are also vascular mat-forming species that represent important establishment sites, such as the endemics *Fernseea itatiaiae* Wawra

(Bromeliaceae) and *Barbacenia gounelleana* (Beauv.) Menezes (Velloziaceae), whereupon *S. camporum* also grows in great abundance. Each one of these species has very unique characteristics (see Scarano 2002, Medina *et al.* 2006, Ribeiro *et al.* 2007), which may influence the dynamics of a secondary species like *Stevia*.

For instance, population dynamics of endemic plants in response to disturbance has only very rarely been examined in such tropical elevated areas (*e.g.* Safford 2001, Aximoff 2011). In Brazil, high altitude vegetation has been examined mostly from floristic viewpoints, phytogeography and climate, as in the case of the Itatiaia massif (*e.g.* Segadas-Vianna & Dau 1965, Martinelli 1996, Safford 1999a, b, Ribeiro et al. 2007). In the tropics, despite some significant efforts, there are still major gaps in the understanding of high altitude vegetation dynamics (see reviews in Spehn *et al.* 2006, Scarano *et al.* 2007), and further knowledge is needed to support conservation and management decisions. In this paper, we examine the potential effects of fire as a disturbance regime on *Stevia*. It is unlikely that fire has been historically a selective force in these altitudinal grasslands inserted in the Atlantic forest domain, due to high humidity and protection by the forest belt, but fire events probably increased along the XIX and XX centuries due to establishment of agricultural practices in the region (Aximoff 2011). Three of the largest fires in high altitude grasslands in Itatiaia massif occurred in the last 15 years (2001, 2007 and 2010; Aximoff 2011). It is also probable that the grassland matrix surrounding the rocks has been more regularly subjected to fire in the drier past (Safford 2001, Behling 2002), thousands of years ago. Rupicolous vegetation is usually protected from fire due to its inaccessibility to flames and can play an important role in biodiversity maintenance in a condition of fire incidence, although it is not completely immune to it.

In this context, we describe population demography and growth of the geophyte *S. camporum* during pre-fire (1999-2001) and post-fire (2002-2003) periods. Considering that a) fire smoke reaches the nutrient-poor vegetation-mats on rock surface, probably changing the nutrient balance; b) these habitats are not subjected naturally to the fire events, and c) the specific characteristics of the pioneer mat species can affect *S. camporum* dynamics, our expectation was that *Stevia* demography should be affected by the indirect effects of fire, with intensity depending on the identity of pioneer mat species where the geophyte is established.

MATERIAL AND METHODS

Study site

The Itatiaia massif (22°21'S, 44°40'W), protected by Itatiaia National Park since 1937, is part of a large mountain chain, named Serra da Mantiqueira, that runs parallel to the Atlantic Ocean, in south-eastern Brazil. It has a high altitude plateau with a mean altitude of ca. 2,400 m a.s.l., and its highest peak at 2,791 m a.s.l. (Aximoff & Ribeiro 2012). It is dominated by a high altitudinal grassland vegetation (*campos de altitude*), with the massive presence of rock outcrops and boulders (Brade 1956, Segadas-Vianna 1965), which in turn harbor a high proportion of grassland species, associated to the more specialized ones (Ribeiro *et al.* 2007). The high diversity is often assigned to the proximity to the Atlantic rain forest and complex climatic/ vegetation dynamics history (Behling 2002). Mean annual rainfall (ca. 2,400 mm) is highly concentrated in the summer (September to March). Rainfall data was provided by a meteorological station located in the same plateau (ICMBio 2013). The winter (April to August) is dry, with reduced cloudiness and high solar radiation; ca. 55 nights per year have below 0°C temperatures, and minimal temperatures may reach -10°C, subjecting plants to freezing (Segadas-Vianna & Dau 1965, Scarano *et al.* 2001, Scarano 2002). Freezing temperatures, drought and high solar radiation are reportedly exacerbated on rocky surfaces (Larson *et al.* 2000).

The study site was located at 2,450 m a.s.l. on a rocky outcrop named *Prateleiras*. In this site, the small crystals and high dissolution rates of the nepheline-sienite rocks (of rare occurrence in Brazil) allow the formation of concavities with smooth borders, like canals and pools, rather than fissures and cracks (Leinz & Amaral 1989, Aximoff *et al.* 2014), which has a relationship with the dominance of herbaceous plants (Ribeiro et al.

2007). Due to the severity of the environment, pioneer plant species are usually confined within these concavities, forming vegetation islands (Medina *et al.* 2006). The largest fires in the plateau occurred in years with less rainfall than the historical average (Tomzhinski *et al.* 2012) and these were of anthropogenic origin (Aximoff 2011, Aximoff *et al.* 2016; in this issue).

Studied species

The endemic geophyte *Stevia camporum* Baker (Asteraceae) has underground storage organs called hibernacles (see Verburg & During 1998). The many branches produced aboveground may reach ca. 30 cm of height before flowering and dry out in the winter, when *Stevia* remains in the environment as hibernacles and seeds. New individuals emerge from seeds and new branches from hibernacles usually in the beginning of the wet season (September-October). Branches are emitted every year and from April on, all branches started to dry out (personal observation of the authors).

The main pioneer mat species are *Fernseea itatiaiae* Wawra (Bromeliaceae), *Barbacenia gounelleana* Beauverd (Velloziaceae) and the moss *Campylopus pilifer* Brid. (Dicranaceae) sometimes associated with other moss species. They form isolated vegetation islands in the rock surface. *Fernseea itatiaiae* has more densely packed rosettes with scarce retention of debris, while *B. gounelleana* grows towards the border of the mat, which allows more retention of debris in its center (Figure 1). The conservation status of both species is "endangered", according to the Brazilian legislation (Portaria 443, from 17/12/2014, from the Brazilian Environmental Ministry). The mosses' islands are more cushion shaped and lower in height (for more details see Scarano *et al.* 2001 and Medina *et al.* 2006).

Sampling schedule and statistical analyses

We monitored 43 islands containing *S. camporum* (total area of 30.08 m^2), and each one was individually labelled during the study for quantification of dynamics before and after the fire event in July 2001. We recorded pre-fire monthly variation of population parameters of *S. camporum* in a rainier year (1999-2000) and a drier year (2000-2001). Population parameters were abundance, height (cm) variation, leaf emission, number of nodes (leaf emission), and proportion and number of fertile branches (reproductive stage). The same variables were measured after fire (2002-2003) but not monthly. Fruit production by branch was estimated by multiplying the number of capitula by five, since we had previously observed that each capitulum has exactly five flowers and each flower produces one achene. Fruit number was counted by a different method in 2000 so comparisons were not possible in this case. We also assessed annual differences in size inequality of the population by comparing coefficient of variation for branch height. Mortality was calculated between December, the most populated month in both years, and March, when most part of the population was reproductively mature**.**

We analysed the population parameters between years (2000 - 2003; data from March) and between pioneer mat species (*F. itatiaiae*, mosses and *B. gounelleana*). The vegetation islands were mostly formed by a single pioneer species (87%). When two species occur together on the same island, then one of them became dominant. The amount studied was partitioned between the mosses' islands (n = 21), the *B. gounelleana*'s islands (n = 12) and *F. itatiaiae*'s islands (n = 10).

We used different statistical tests for variables with different characteristics: (i) factorial ANOVAs for height, number of nodes and fruit number, (ii) factorial ANCOVAs for abundance, number and proportion of fertile branches, and fruit number per fertile branch, with vegetation island area as covariate and islands as units, and (iii) Z tests for the coefficient of variation (CV) of height. For each year, we verified if there were differences between the abundances in size classes according to branch height (in cm: 0.5 – 5, 5.5 – 10, 10.5 – 20, 20.5 – 30, > 30) using ANOVA. When necessary, data were log transformed to reach normality and variance homogeneity. Proportions were transformed by arc sine. Contrasts between population parameters using *S. camporum* branches as units were based in Tukey *a posteriori* tests. We used simple linear regression analysis to test for pairwise associations between *S. camporum* branches abundance and vegetation island area, in each year.

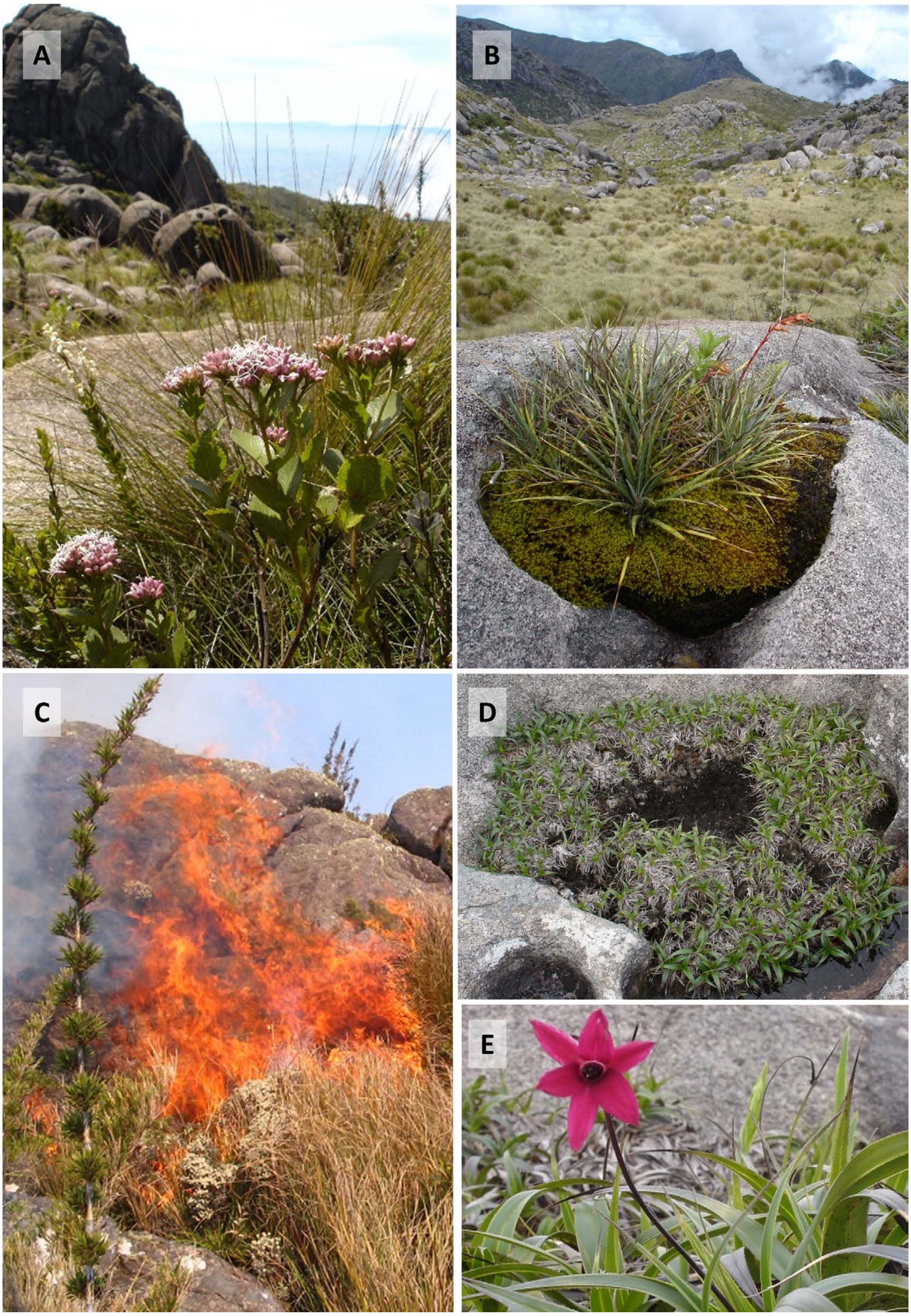

Figure 1. The main pioneer mat species are usually confined within rocky concavities. forming vegetation islands on a rocky outcrop named *Prateleiras.* (A) The endemic geophyte *Stevia camporum* Baker (Asteraceae). The endangered pioneer mat-forming species, (B) The hemicriptophyte *Fernseea itatiaiae* (Bromeliaceae) in a well-drained shallow depression and within a flooded rock pool associated to the moss *Campylopus pilifer* forming horseshoe shaped islands, (C) Fire in the high altitude, and (D e E) An island formed basically by the geophyte *Barbacenia gounelleana* Beauverd (Velloziaceae) that was in a clear splitting process, with plant parts surviving better in the shallow depressions.

RESULTS

Population parameters in: (1) a rainier year (1999-2000), (2) a drier year (2000-2001) in the two pre-fire growing seasons and (3) after fire (2002-2003).

Despite the variation in rainfall between years (Figure 2), population structure and dynamics of *S. camporum* were overall very similar in the two pre-fire growing seasons (Figure 3A-F), except by a difference in the coefficient of variation (CV) of height. Height variation was nearly constant during the year with more rain, whereas a peak in the CV was observed at the onset of the drier year (Figure 3C). There was also a slightly higher mortality in the drier (15.8%) than in the rainier year (10.9%). However, toward the end of the summer, CV values were again very similar between years (Figure 3C). The frequency of distribution of branches per size class before the fire event was stable (2000: $F_{(4, 80)} = 1.43$, p = 0.23; 2001: $F_{(4,78)} = 4.56$, p = 0.77), different from recorded after this event (2002: $F_{(4, 99)} = 5.43$, p = 0.001 2003: $F_{(4, 109)} = 5.79$, p = 0.003; Figure 4). An increase in the frequency of branches in the first size class in the first year after fire was identified, but no changes in other classes (Figure 4). Higher CV values were detected in both years after the fire (Z test, Table 1), with a thinning process being observed.

Influence of pioneer species

The identity of the pioneer mat species played a role in the difference observed between years, for parameters that describe growth, such as differences in height and number of nodes (Table 2; Figure 5) and reproduction, such as fruit production and number of fertile branches (Table 3; Figure 6). There was a general tendency of higher values in growth and fruit production before the fire event (Table 3; Figure 6). *Fernseea itatiaiae* was the main factor for the differences between years, notably in height (Figure 5). In the mosses' islands, fruit quantity and height did not vary

Table 1. Pairwise comparison of coefficients of variation (CV) for stem height (cm) of *Stevia camporum* between years, before (2000-2001) and after fire (2002-2003) in the high altitude grasslands of Itatiaia massif, Rio de Janeiro State. Asterisks indicate significant differences between z-values at a *p*-level of 0.05.

		Pre-fire		Post-fire	
		2000	2001	2002	2003
Pre-fire	2000	-	-0.71	-6.71*	-6.14*
	2001		-	11.13*	11.89*
Post-fire	2002			-	1.79
	2003				-

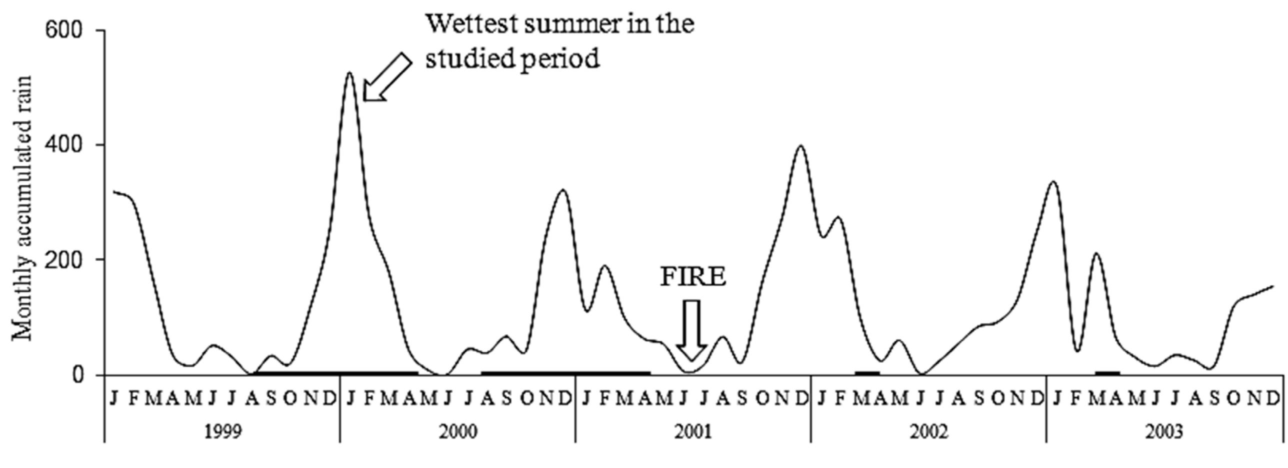

Figure 2. Monthly accumulated rainfall (mm) of the study period (1999-2003) in the high altitude grasslands of the Itatiaia massif, Rio de Janeiro State (data obtained by Furnas Centrais Elétricas S.A.). The dark lines in the *x* axis indicate the periods of *Stevia camporum* population study.

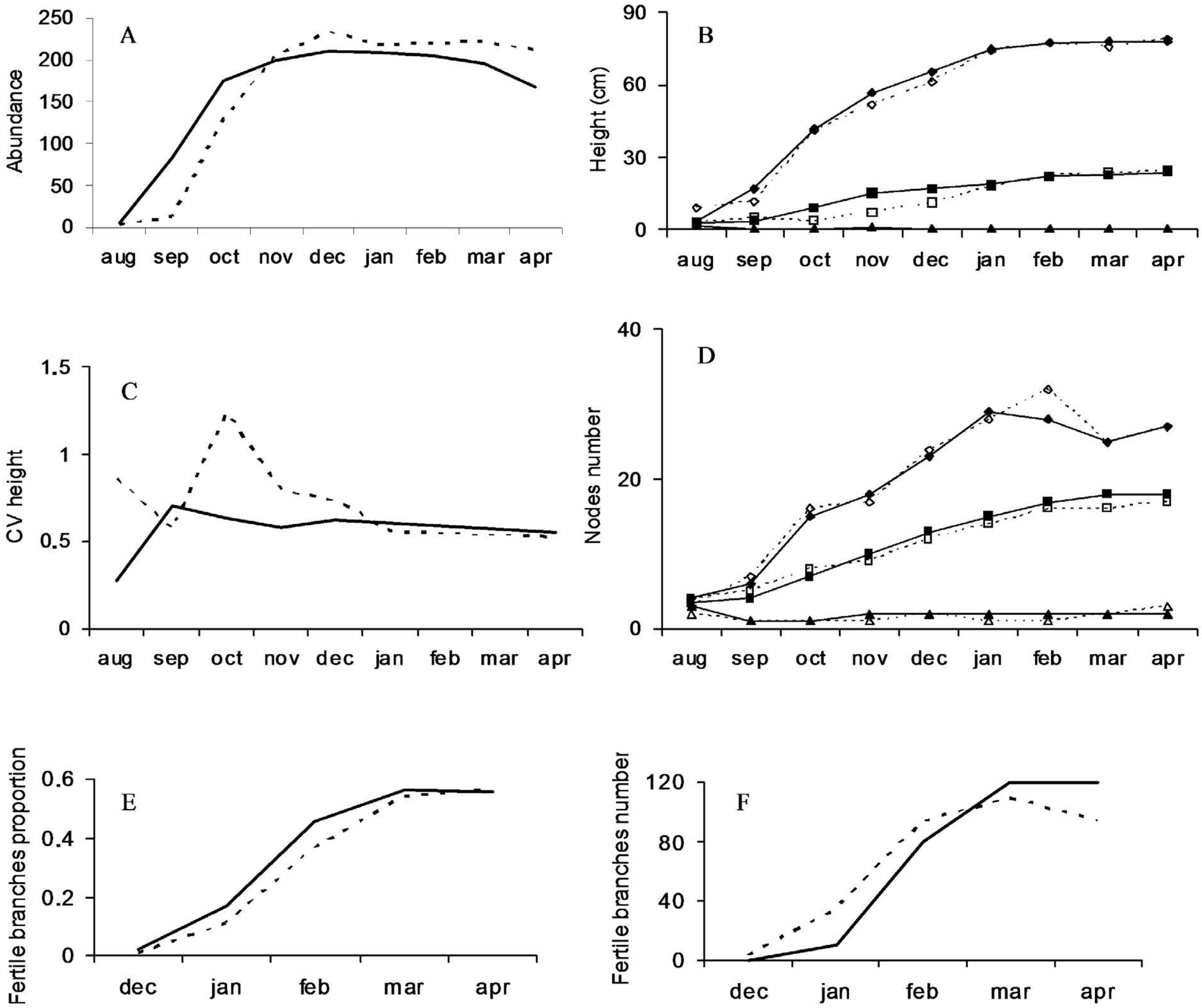

Figure 3. Pre-fire monthly variation of population parameters of *Stevia camporum* in a rainier year (1999-2000, dashed line, open symbols) and a drier year (2000-2001, full line, dark symbols) in the Itatiaia massif, Rio de Janeiro State. Parameters were: A) Abundance, B) Maximum (diamond), median (square) and minimum (triangle) height, C) Height variation (CV), D) Leaf emission, as assessed by maximum (diamond), median (square) and minimum (triangle) number of nodes, E) Proportion of fertile branches, F) number of fertile branches.

between years, and in the *B. gounelleana*'s islands, the recovery to the pre-fire stage was less evident than in the *F. itatiaiae*'s islands (Figure 5).

Analysing pre- and post-fire parameters

Height, number of nodes and number of fruits of *S. camporum*'s ramets differed between periods pre- and after-fire, and an additional effect of the nurse plant identity on *S. camporum* demography was detected (Figure 5). For the number of fertile branches and number of fruits by fertile branches the interaction between year and pioneer mat species identity was not significant (ANCOVA results in Table 3). The proportion of fertile branches was only influenced by the period analysed: before the fire, the proportion was larger than after the event, and two years after the fire, the values were intermediate between just before and after, indicating population recovery. Abundance of *S. camporum* was more related to area than to the pioneer species identity or year (Table 3), but the strength of this relationship varied between years, showing the strongest relation in the year just after the fire (2002; R^2 = 0.315) (Figure 7).

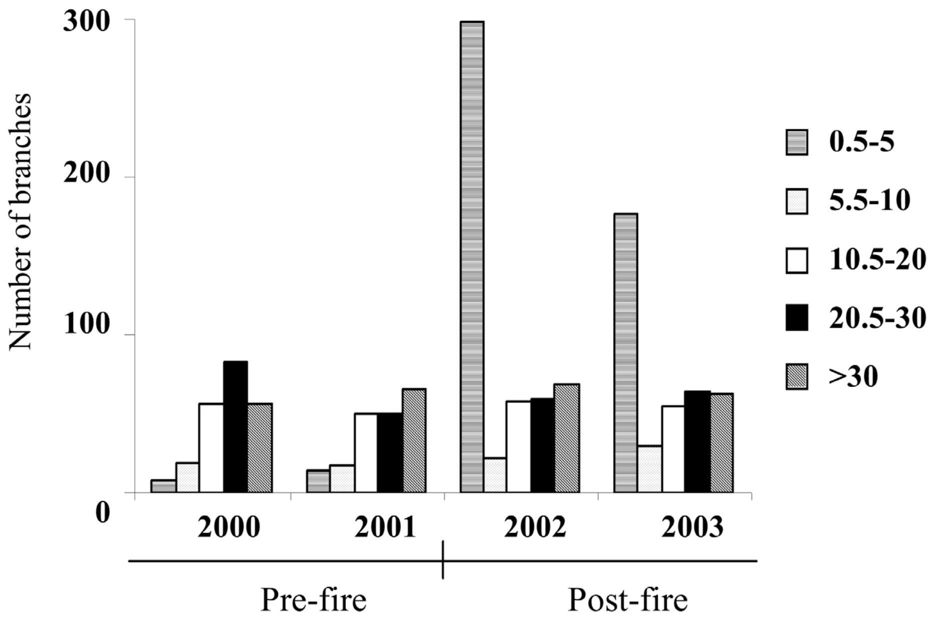

Figure 4. Frequency distribution of branches or individuals of *Stevia camporum* per five classes of height. Asterisks indicate significant differences at a *p*-level of 0.05. ANOVA results comparing the frequency in each height class per year.

Table 2. Factorial ANOVAs results for population parameters using *Stevia camporum* branches as units (n = 1,311), data from March 1999-2003, in the high altitude grasslands of Itatiaia massif, Rio de Janeiro State. Asterisks indicate significant differences.

Population parameter	SS	df	MS	F	*p*
Height					
Year*	92.375	3	30.792	107.504	0.000
Pioneer mat species*	1.803	2	0.902	3.148	0.043
Year ×Pioneer mat species*	25.413	6	4.236	14.788	0.000
Nodes number					
Year*	22.207	3	7.402	92.630	0.000
Pioneer mat species	0.057	2	0.028	0.350	0.701
Year × Pioneer mat species*	3.887	6	0.648	8.110	0.000
Fruit number (n = 1090)					
Year*	103.350	2	51.674	52.586	0.000
Pioneer mat species*	7.002	2	3.501	3.562	0.028
Year × Pioneer mat species*	28.696	4	7.174	7.300	0.000

DISCUSSION

Stevia camporum was both resistant and resilient to the indirect effects of fire. Being a geophyte that lives in a deeply seasonal environment with a clear unfavourable period, with pronounced dry and cold conditions, *S. camporum* dynamics of branches show dramatic evolution along each year. Nevertheless, the similarity in the *S. camporum* population parameters between years before the fire event, despite the great variation in precipitation, may be related to the

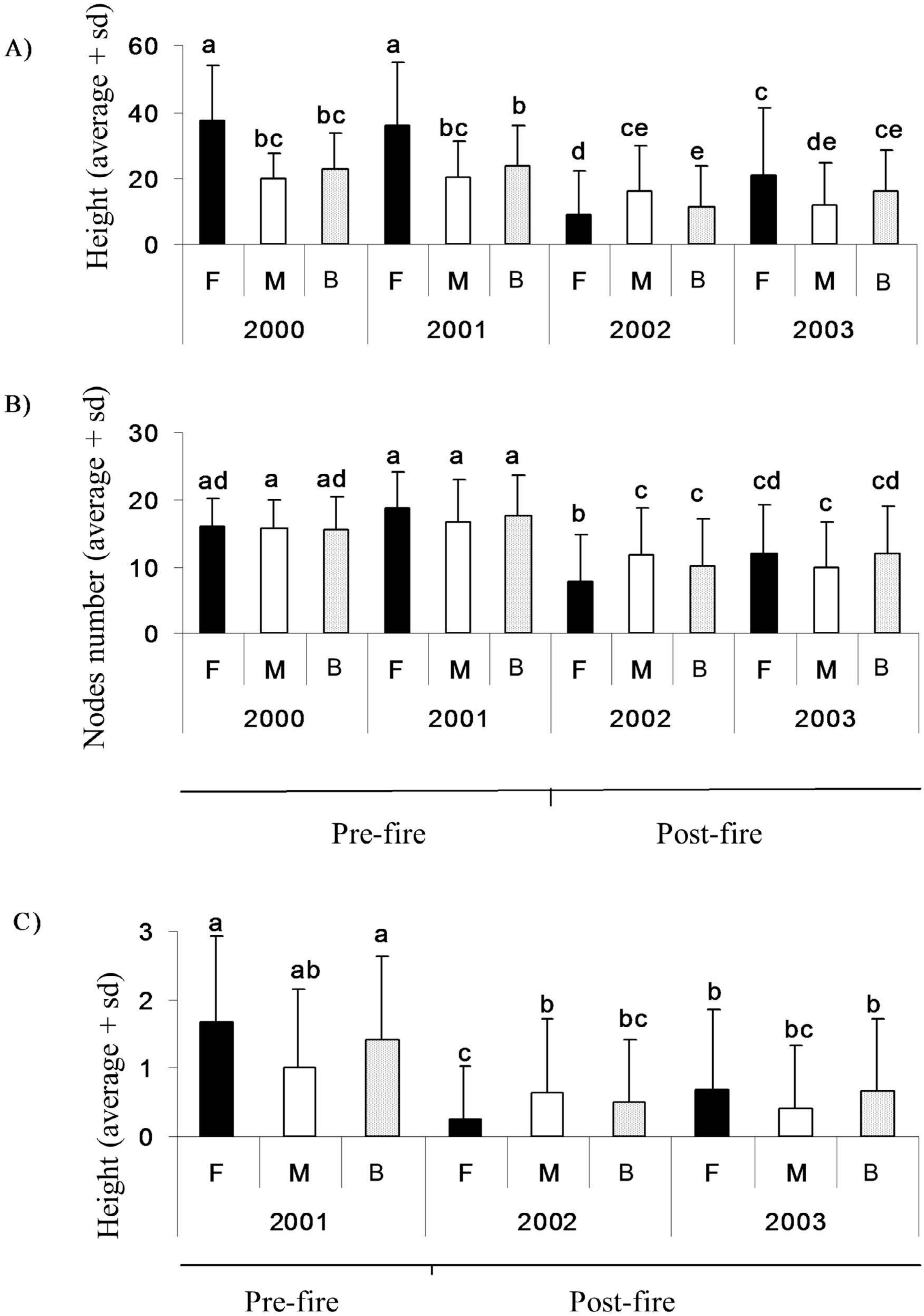

Figure 5. Contrasts between population parameters using *Stevia camporum* branches as units. Different letters indicate significant difference at a *p*-level of 0.05. Data shown are averages + standard deviation (sd) in each pioneer mat species (F- *Fernseea itatiaiae*, M - mosses, B - *Barbacenia gounelleana*) per year: A) Height, B) Nodes number (leaf emission), C) Fruit number. For fruit number the 2000 data was obtained by a different method so comparisons were not possible.

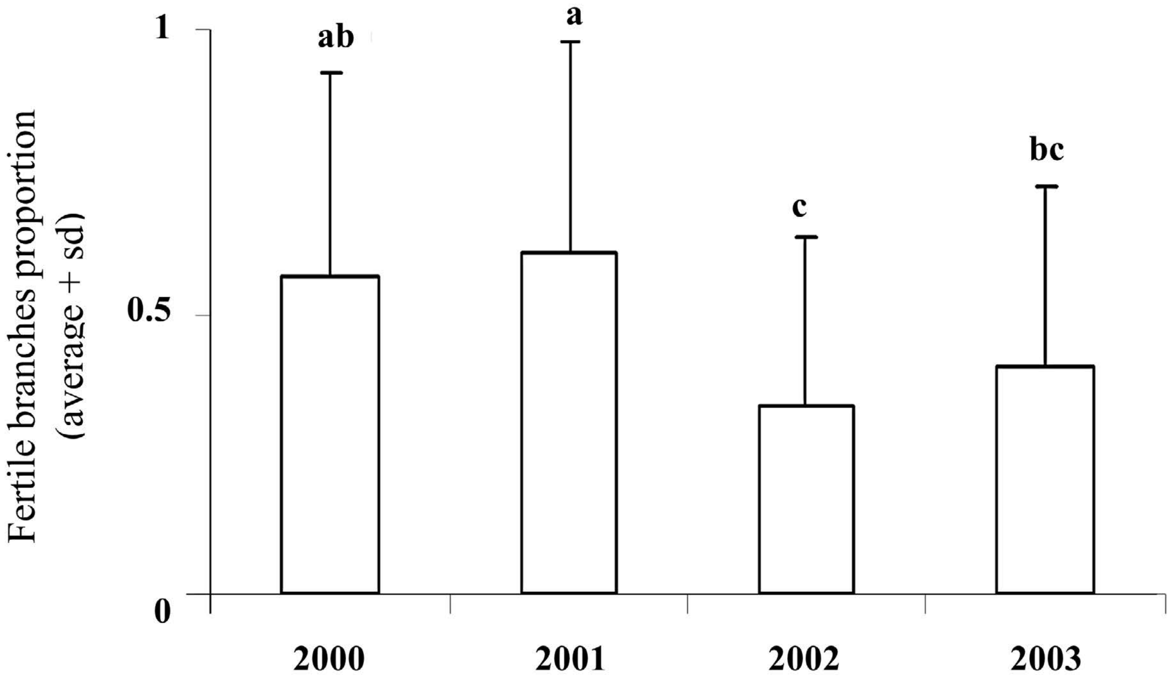

Figure 6.Contrasts between *Stevia camporum* fertile branches proportion in each year in the high altitude grasslands of Itatiaia massif, Rio de Janeiro State. Different letters indicate significant difference at a *p*-level of 0.05. Data shown are averages + standard deviation (sd) in each year (there is no influence of pioneer mat species).

low nutritional budgets in the places where these plants grow (Benites *et al.* 2003), which derives mainly from retained debris. Moreover, in the case of *S. camporum*, the availability of large storage of reserves in hibernacles, which are claimed to buffer possible effects of annual variation in rainfall and/or nutrients in clonal geophytes, may permit a more stable population dynamics over the years (Hara *et al.* 1993, Verburg & During 1998, Ekstam 1995, Suzuki & Hutchings 1997, Tyler & Borchart, 2002). The difference between height variability (CV) in the two pre-fire years is similar to the pattern of clonal plants, which suggests that some competition may have taken place between branches in the early summer of the drier year (Suzuki & Hutchings 1997, Cirne & Scarano 2001), possibly in response to lower water supplies at the moment of germination or resprouting.

Nevertheless, the stable condition observed before the fire that occurred in the winter of 2001, during *S. camporum* hibernation, changed just after the fire. The most drastic change was the massive regeneration following fire, with an increase in the frequency of branches in the smaller size classes. The number of regenerant branches, however, decreased considerably in the second year after fire. This may suggest that the geophytic life form and the formation of hibernacles in *S. camporum*, in addition to favoring persistence in seasonal environments (Pavón *et al* 2000, Ribeiro *et al*. 2007) such as the Itatiaia plateau, may have allowed fire survival and resilience (see also Bowen & Pate, 1993, Tyler & Borchert, 2002). Nevertheless that, the response of *S. camporum* individuals, or branches in the same individual, varies slightly according to the pioneer mat species where they are established, as we expected. At the *F. itatiaiae* islands, the differences in responses to the indirect effects of fire were more intense. In a previous paper (Medina *et al.*, 2006), we described a greater density of *S. camporum* branches in mosses' islands, considering abundance in islands of different sizes along four years, but with the occurrence of fire, this apparent "preference" disappeared. Yet, *S. camporum* population dynamics was more stable in these pioneer moss species, and did not seem to suffer an important

Table 3. Repeated measures factorial ANCOVAs for population parameters using *Stevia camporum*, data from March 1999-2003, in the high altitude grasslands of Itatiaia massif, Rio de Janeiro State. Island area as a covariate, n=43. Asterisks indicate significant differences.

	SS	df	MS	F	p
Abundance					
Area*	2,546.208	1	2,546.208	20.607	5.3×10^{-6}
Pioneer mat species	218.312	2	109.156	0.883	0.421
Year	335.906	3	111.969	1.980	0.121
Year × area*	1,169.676	3	389.892	6.894	0.000
Year × pioneer mat species	270.523	6	45.087	0.797	0.574
Fertile branches proportion					
Area	0.007	1	0.007	0.030	0.863
Pioneer mat species	0.085	2	0.042	0.188	0.830
Year*	123.674	3	0.412	4.550	0.005
Year × area	0.007	3	0.002	0.027	0.994
Year × pioneer mat species	0.246	6	0.041	0.452	0.843
Fertile branches number					
Area*	1,929.859	1	1,929.859	11.427	0.002
Pioneer mat species	56.863	2	28.432	0.168	0.846
Year	76.772	3	25.591	1.623	0.188
Year × area	97.853	3	32.618	2.069	0.108
Year × pioneer mat species*	212.059	6	35.343	2.242	0.044
Fruit number / fertile branches					
Area	15.393	1	15.393	0.161	0.691
Pioneer mat species	37.221	2	186.106	1.941	0.157
Year	71.344	3	35.672	0.820	0.444
Year × area	26.439	3	13.219	0.304	0.739
Year × pioneer mat species*	541.796	6	13.545	3.115	0.020

influence of indirect effects of fire, although leaf emission decreased until two years after fire.

In the case of *S. camporum*, the identity of the pioneer species whereupon it grows influences its response to the indirect effects of fire on growth and resprouting (or germination), leaf emission and fruit production. *Fernseea itatiaiae* plants are more densely packed, which results in etiolation of *S. camporum* branches, as suggested by a higher difference in height than in the number of nodes. We conjecture that *F. itatiaiae*'s morphology may also lead to ash retention for a longer time, which could favor seedling recruitment just after the fire, resulting in lower average height and number of nodes in the cycle just after the fire event. The islands mainly formed by *B. gounelleana* and by mosses are shallower and have a more open shape, being less protected from lixiviation than *F. itatiaiae* islands. Despite the differences in the structure between *B. gounelleana* and mosses' islands (Medina *et al.* 2006), the dynamics of *S. camporum* were similar in these two pioneers.

The positive effects of direct burning or from indirect effects of the smoke in seedling and sprout emergence of specific species have been thoroughly described (*e.g.*, Enright *et al.* 1997, Pugnaire & Lozano 1997, Rees 1997, Kenny 1999, Read *et al.* 2000, Cirne *et al.* 2003), although the benign effects of fire depends heavily on its frequency and intensity (Whelan 1995, Tyler & Borchert 2002).

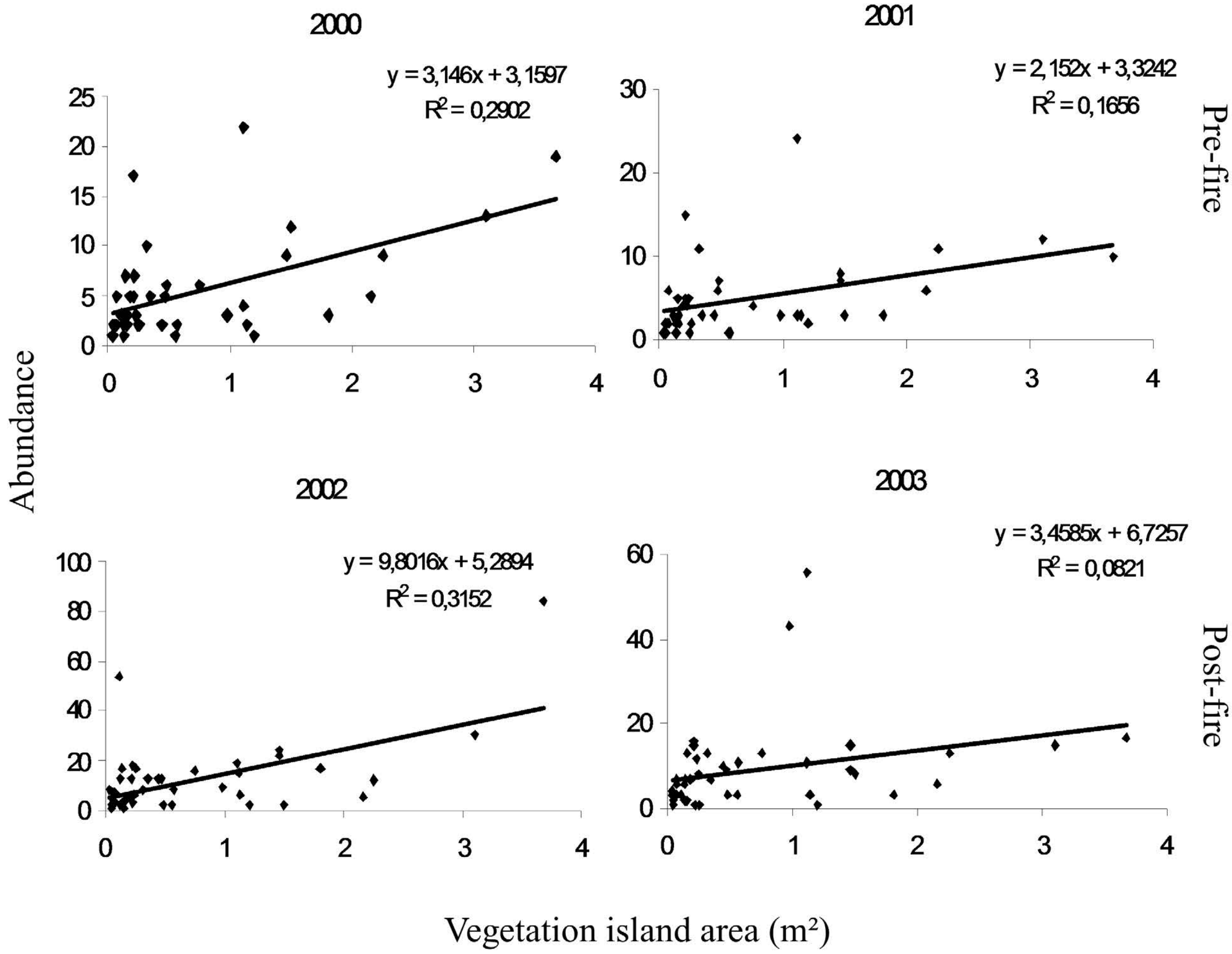

Figure 7. Simple linear regression analyses between *Stevia camporum* branches abundance and vegetation island area, in each year, in the high altitude grasslands of Itatiaia massif, Rio de Janeiro State.

We speculate that the sudden change in population structure and dynamics towards a condition typical of post-disturbance response is probably related to the extensive deposition of ash during and after the fire event, including washing of rock surfaces. In the peak of the dry and cold season characterized by strong winds and very low air humidity, ash dispersal and maintenance on the soil were probably favoured, contributing to a change in nutrient composition. Despite some of the positive effects already observed, related to ash and nutrient deposition during fire on rocky outcrop vegetation (*e.g.* Formenti *et al.* 2003), these effects should not last too long given the high degree of exposition of such environments and the reduced amount and depth of soil (Verboom *et al.* 2002, Formenti *et al.* 2003), which would lead to a return to the previous conditions of nutrition and population structure. In the case of *S. camporum,* a thinning process was observed when comparing the two years after fire, with no difference in the number of branches of the higher classes and a reduction in the number of branches in the smallest size class from 2002 to 2003. Therefore, our initial expectation was confirmed, and the pioneer mat species identity had an influence in the population dynamics of *S. camporum* and response to indirect effects of fire.

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