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A comparative study of resource allocation in *Pteridium* in different Brazilian ecosystems and its relationship with European studies

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Abstract

Pteridium is a cosmopolitan genus that acts as an invasive species in many parts of the world. Most research on this genus has occurred in Europe, and there is a lack of data on it from South America, in spite of causing considerable conservation problems. We compared the biomass allocation of *P. esculentum* subsp. *arachnoideum* in two ecosystems in Brazil - Atlantic forest and Brazilian savanna. We measured the biomass of fronds, rhizomes and above-ground litter. We also compared the density, length and biomass of fronds from this Brazilian study with similar data of *P. esculentum* subsp. *arachnoideum* derived from Venezuela and *P. aquilinum* from Europe. *P. esculentum* subsp. *arachnoideum* showed a wide response range. We found a negative relationship between frond and necromass , indicating a negative feedback effect, while a positive relationship was observed between frond and rhizome biomass. The continental comparison of relationships showed that *Pteridium* responds in a different way in both Brazil and Europe, and that in Brazil fronds tend to be longer and heavier, presumably as a result of the continuous growing season in South America while is shortened in Europe by frost. The paper shows the ability of *Pteridium* to adapt to different ecosystems.

Keywords: bracken, resource partitioning, Atlantic Forest, Cerrado, biomass.

Estudo comparativo da alocação de recurso em *Pteridium* em diferentes ecossistemas brasileiros e sua relação com estudos na europa

Resumo

Pteridium é um gênero cosmopolita que inclui espécies invasoras em várias partes do mundo. Os estudos sobre o gênero têm ocorrido principalmente na Europa, e existem poucas informações para as espécies que ocorrem na América do Sul. Nesse estudo comparamos a alocação de biomassa de *P. esculentum* subsp. *arachnoideum* em dois ecossistemas brasileiros – Mata Atlântica e Cerrado - em cada um dos quais medimos a biomassa nos rametas, nos rizomas e na serapilheira. Comparamos, também, a densidade, comprimento e biomassa dos rametas com informações obtidas sobre *P. esculentum* subsp. *arachnoideum* na Venezuela e *P. aquilinum* na Europa. *P. esculentum* subsp. *arachnoideum* apresentou respostas distintas. Encontramos uma relação negativa entre a biomassa de rametas e da serapilheira, indicando uma retro-alimentação negativa, enquanto houve uma relação positiva entre a biomassa dos rametas e dos rizomas. A comparação das relações entre os continentes indicou que *Pteridium* responde diferentemente no Brazil e na Europa, e também que no Brasil os rametas são maiores e contêm mais biomassa, possivelmente devido à estação de crescimento contínua, enquanto na Europa o crescimento é limitado pelas baixas temperaturas. Esse estudo demonstra o sucesso adaptativo de *Pteridium* em diferentes ecossistemas.

Palavras-chave: samambaião, alocação de recursos, Mata Atlântica, Cerrado, biomassa.

1. Introduction

Considering the impact that invasive species has been put on biological diversity all over the world, understanding how these species colonize successfully different ecosystems is a central goal in ecology. Invasive plant species, for example, are able to maintain or even increase its fitness across a range of environmental conditions through phenotypic plasticity (Richards et al, 2006; Rejmanek, 2011). Phenotypic plasticity refers to the ability of plants to modify its phenotype in response to environmental changes, with physiological and/or morphological adjustments at the individual level. Most classical examples of phenotypic plasticity are based on morphological traits: variations of leaves in response to variation of sun exposure (Bradshaw, 1963); changes on root growth in response to different concentrations of nutrients in heterogeneous soils (Miner et al., 2005; Jiménez-Ambriz et al., 2007); and differences in resource allocation, through changes in the allometric trajectories in response to environmental conditions (Carnier, 1991; Fan et al., 2009; Weiner, 2004).

Despite the controversial about resource allocation strategies (McConnaughay and Coleman, 1999; Fan et al., 2009), two main hypothesis have been proposed to describe biomass allocation (Muller et al., 2000; Shipley and Meziane, 2002; Niklas, 2005; McCarthy and Enquist, 2007; Yang et al., 2009): 1) the optimal partitioning hypothesis considers that plants allocate proportionally more biomass to a given organ to maximize their growth in response to environmental changes (Yang et al., 2009), while according to 2) the isometric allocation hypothesis the allocation does not change in response to environmental variations (Niklas, 2005; Yang et al., 2009). Thus, considering the relationship between the above and belowground biomass, the slope of the regression is 1.0 in case of isometric partitioning and variable for the optimal partitioning pattern.

Variations on biomass allocation can affect survival, growth and reproduction of individual plants and consequently shape the establishment and invasiveness in different habitats. *Pteridium* is a cosmopolitan genus occurring in a wide range of habitats worldwide, except in the polar regions (Marrs and Watt, 2006). Over much of its range it is a serious weed problem. Although a great deal is known about *Pteridium* ecology, its form and function, and control measures, most of this has been derived from studies in Europe about *Pteridium aquilinum* (*L.*) *Kuhn* (Marrs and Watt, 2006), and until recently there has been much less data from South America (Alonso-Amelot and Rodulfo-Baechler, 1996; Thomson and Alonso-Amelot, 2002; Hartig and Beck, 2003; Alonso-Amelot and Oliveros-Bastidas, 2005; Silva and Silva Matos, 2006; Silva Matos and Belinato, 2010; Miatto et al., 2011). This lack of data from South America is surprising because *Pteridium esculentum arachnoideum* abundance is causing concern for animal health across the continent (França et al., 2002; Marçal et al., 2002; Marçal, 2003). Thus, from both ecological and economic viewpoints there is a need to collect data on *P. esculentum subsp. arachnoideum* from South America and to relate this to the existing data available from Europe. This comparison would clearly facilitate the exchange of management practices for controlling this aggressive weed. The ideal way to study species performance across regions in the first instance is to compare biomass allocation data. Accordingly, here the allocation strategies of *Pteridium* were measured in Brazil, and compared to available literature data derived from elsewhere in South America, but mainly from the Europe. We looked for patterns of correlations in biomass allocation between two major plant pools that could reflect functional linkages between some species attributes. Such allocation differences would result because resource allocation to one organ or function would not be available for use by other organs or functions (Stuefer et al., 2002; Weiner, 2004).

In temperate climates *Pteridium* produces large stands with a dense canopy of green fronds, recruitment is rare in nature; patch expansion is achieved by vegetative growth through the rhizomes, the rate of frond decomposition is low and the litter layer can be very deep (Marrs and Watt, 2006). Whilst litter would normally be considered as part of the necromass, it provides a major ecological function for the species in terms of modification of the microclimate through frost protection (Marrs and Watt, 2006) and in suppressing the ingress of other species (Ghorbani et al., 2006; Marrs and Watt, 2006). We hypothesized that as *Pteridium* is considered an aggressive and invasive plant, changes in biomass allocation would be expected due to climatic differences representing the adaptation of this genus to occupy different ecosystems. In this case the optimal partitioning hypothesis (Yang et al., 2009) would be accepted. Therefore, we aimed to answer the two following questions: (1) is the biomass allocation similar in two contrasting Brazilian ecosystems? (2) Are the European and South American *Pteridium* comparable, so that management control strategies derived in one region might be applicable elsewhere?

2. Material and Methods

2.1 Measurement of biomass allocation in Pteridium esculentum subsp. arachnoideum

Pteridium esculentum (G.Forst.) Cockayne subsp. *arachnoideum* (Kaulf.) J.A.Thomson, Dennstaedtiaceae, is a neotropical species within the *Pteridium* genus found in Brazil, according to Thomson (2012). The biomass of this species was sampled from july to september in two different Brazilian ecosystems, Atlantic Forest and Cerrado (hereafter named as Savanna) located in eight biological reserves (see Table 1). The Atlantic Forest is one of world most luxurious and important ecosystems for conservation because of its high biodiversity and high proportion of endemic species (Myers et al. 2000). Nowadays, it is reduced to 8% of its original area (Fundação SOS Mata Atlântica; INPE, 2009). Brazilian Savanna is the world's most biologically-rich savanna ecosystems (The Nature Conservancy, 2010); originally it occupied 21% of the Brazilian territory (about 2 million km^2), however at least 48% percent of it has already been severely degraded (Pereira and Gama, 2010). In both ecosystems, *P. esculentum subsp. arachnoideum* has been described as invasive affecting the structure of their plant community Silva Matos et al. 2002, 2005; Silva and Silva Matos 2006; Silva Matos and Belinato, 2010; Miatto et al., 2011).

Within eight biological reserves covering the two ecosystems (Atlantic rain forest, n=4; Savanna, n=6, see Table 1), ten sites covered by *P. esculentum subsp. arachnoideum* were identified. Within each site, five replicate sampling positions were located randomly. At each of these positions a 0.5 × 0.5 × 0.5 m quadrat was positioned and all living fronds and litter biomass (hereafter named as necromass) was harvested, and the length of all fronds were measured. In this paper, we will hereafter use the term frond to represent collectively all fronds from each individual position. A soil pit was then dug and all rhizomes were removed by hand from the excavated soil

Table 1. Description of the ten study sites across the two Brazilian ecosystems.

Ecosystem	Study site location	Longitude, latitude	Altitude (m)	Climate Mean temperature (ºC) Mean-rainfall (mm/year)	Soil description
Atlantic Forest	Parque Estadual Carlos Botelho (PECB)	S 24°04' 23" W 47°59'52"	710	18-20 1,500-2,200	Hydromorphic, yellow-red latosols and podzol
	Parque Estadual Campina do Encantado (PECE)	S24°39'029" W47°49' 835"	12	17.5-27 1,600-2,200	Quartzarenic Neosol
	Parque Estadual de Jacupiranga (PEJ)	S 24°30' 146" W 47°50' 303"	548	17-35 1,600-2,200	Hydromorphic, yellow-red latosols and podzol
	Parque Estadual Ilha do Cardoso (PEIC)	S 25°12' 45" W 47°59'48"	5	21.2 3,000	Sandy soils
Savanna	Reserva de Cerrado da UFSCar, adjacent to the riparian forest (UFSCar1)	S 21°57' 971" W 47°52' 150"	860	22.1 1,339	Alic red-yellow and distrophic red-yellow latosols
	Reserva de Cerrado da UFSCar 800m from the riparian forest (UFSCar 2)	S 21° 58'125" W 47°51' 882"	866	22.1 1,339	Alic red-yellow and distrophic red-yellow latosols
	Estação Ecológica de Itirapina (EEI)	S 22°12'382" W 47°55'840"	737	22.0 1,339	Quartzarenic Neosol
	Parque Estadual de Porto Ferreira (PEPF)	S 21°50' W 47°28'	540	17.2-22.8 1,300	Distrophic red-yellow latosols
	Reserva Biologica do IBGE (Brasilia) (RECOR 1)	S 15°56'394" W 47°51'960"	1120	23 1,527	Dark-red latosols
	Reserva Biologica do IBGE (Brasilia) (RECOR 2)	S 15°56'313" Wo 47°52'026"	1135	23 1,527	Dark-red latosols

and washed free of surface soil; the quality assurance procedure for rhizome sampling of Le Duc et al. (2003) was followed. Both frond and rhizome samples were then dried at 80ºC for 48 h and weighed.

2.2 Assessment of literature data on biomass allocation in Pteridium

In order to compare the Brazilian data with data obtained from other regions of the world, a Systematic Review using two literature databases was performed (Web of Science, Google Scholar), using "bracken" and "*Pteridium*" as key search terms. All papers identified were inspected, and a subset of papers that included data on biomass allocation was selected and the biomass data abstracted (see Table 2). Most papers contained data on the above-ground components; there was much less information about rhizomes so that comparisons were not viable.

2.3 Data analysis

Differences in *P. esculentum subsp. arachnoideum* performance between Brazilian ecosystems (Atlantic Forest and Savanna) were assessed between ecosystems using two-sample t-test with pooled variances of the Systat statistic package. In order to cope with errors on both axes and doesn't assume which is the dependent variable, reduced major axis regressions (RMA) were estimated to data derived from the two ecosystems using PAST (Hammer et al., 2001) and Spearman's correlation coefficients were calculated to assess the significance of these relationships. The comparisons of the slopes were performed through the analysis of covariance for RMA, using the significance of the Bartlett-corrected likelihood ratio statistic testing for common slope (LR), within the R statistical environment (R v.2.10.1, R Development Core Team, 2004).

In order to assess differences in resource partitioning, RMA regressions were fitted to the South American and European data (data abstracted from references in Table 2). The linear regressions obtained were compared through analysis of covariance as described above. The relationships were derived from the mean values for each variable at each site; where only a range was reported the average of the minimum and maximum value was used.

Table 2. Comparative dataset on *Pteridium* biomass allocation derived from the literature from Europe, South America and this study.

Region	Site/ecosystem	Leaf density (m^{-2})	leaf length (cm)	Frond biomass (g m^{-2})	Source
Europe	Bealieu heath	-	-	892	Pearsall and Gorham (1956)
	Stony Cross	-	-	1408	Pearsall and Gorham (1956)
	North Bentley	-	-	1072	Pearsall and Gorham (1956)
	South Bentley	-	-	848	Pearsall and Gorham (1956)
	Bowland Forest	-	-	1104	Pearsall and Gorham (1956)
	Lakenheath grassland A	1.5	31.5	5.9	Watt (1964)
	Lakenheath grassland B	2.95	35.5	15.5	Watt (1964)
	Lakenheath grassland C	22.85	64	183.5	Watt (1964)
	Lakenheath grassland D	50.25	125	923.5	Watt (1964)
	Lakenheath grassland E	31.05	47.5	167.5	Watt (1964)
	Weeting	23	142.5	520	Lowday and Marrs (1992)
	Cavenham	24	100	385	Marrs et al. (1998)
	Stanford PTA. Norfolk	35		590	Pakeman and Marrs (1994)
	Mull	32	132.1	533	Paterson et al. (1997)
	Sourhope	31.5	87	382.5	Paterson et al. (1997)
	Lake District	32.5	71.5	346	Paterson et al. (1997)
	Clywd	28.5	111	546	Paterson et al. (1997)
	Breckland	31	76.5	371	Paterson et al. (1997)
	Devon	15.5	113	322	Paterson et al. (1997)
	Lindale	-	-	985	Lawson et al. (1986)
	Sourhope 1	58.8	56.5	391.3	Le Duc et al. (2000)
	Souhope 2	26.5	69.9	297.5	Le Duc et al. (2000)
	Peak	42.6	91.1	521.9	Le Duc et al. (2000)
	Carneddau	44	74.1	537.6	Le Duc et al. (2000)
	Cannock 1	36.8	105.9	676.4	Le Duc et al. (2000)
	Cannock 2	29.7	73.7	294.2	Le Duc et al. (2000)
	Open	15.4	245	731.1	den Ouden (2000)
	Larix woodland	8.1	241	313.5	den Ouden (2000)
	Larix woodland	8.5	216	316.5	den Ouden (2000)
	Larix woodland	6.1	203	207.7	den Ouden (2000)
	Larix woodland	6.2	193	136.8	den Ouden (2000)
	Larix woodland	6.4	165	175.9	den Ouden (2000)
	Pinus woodland	7	210	234.2	den Ouden (2000)
	Pinus woodland	3.1	213	101.9	den Ouden (2000)
	Pinus woodland	12.9	129	177.8	den Ouden (2000)
	Quercus woodland	3.4	174	79.4	den Ouden (2000)
	Quercus woodland	3.7	216	135.4	den Ouden (2000)
	Quercus woodland	3.9	176	104.4	den Ouden (2000)
	Quercus woodland	4.4	136	79.7	den Ouden (2000)
S. America	Venezuelan montane savanna	5.1	89	287.4	Alonso-Amelot and Rodulfo-Baechler (1996)
	Venezuelan montane savanna	1.6	76.59	53.2	Alonso-Amelot and Rodulfo-Baechler (1996)
	EEI	20.4	146	1,236.0	This study
	PEPF	17.6	231	1,448.8	This study
	RECOR1	9.6	243	481.2	This study
	RECOR2	4.6	147	522.0	This study
	UFSCar1	13.6	321	1,178.9	This study
	UFSCar2	10.4	180	933.9	This study
	PEJ	19.2	190	1,610.0	This study
	PECE	10.4	288	817.3	This study
	PEIC	20.0	184	1,179.4	This study
	PECB	10.4	209	951.9	This study

3. Results

3.1 Biomass allocation in Brazilian P. esculentum subsp. arachnoideum

There were no significant differences between the ecosystems for all variables: frond biomass, rhizome biomass, necromass, frond density, and frond length (see Table 3). Frond biomass was very variable in the Savanna and in the Atlantic Rain Forest, ranging from 114-2353 g m^{-2} and from 284-1912g m^{-2}, respectively. A similar pattern was found for necromass (Savanna = 0-2970 g m^{-2}; Atlantic Rain Forest = 213-2264 g m^{-2}). Leaf density and rhizome biomass, however, did not show as extreme a pattern as these other two variables. Savanna still had the greatest variability (1-28 leaves m^{-2}) overlapping the ranges of the Atlantic Rain Forest (4-20 leaves m^{-2}), and rhizome biomass ranging from 23.5 to 2757 g m^{-2} in the Savanna and from 219 to 1477 g m^{-2} in the Atlantic Rain Forest. Length of expanded leaf ranged from 0.5 to 4.2 m in the Savanna, and from 1 to 4.1 m in the Atlantic Rain Forest.

When all data were combined, significant positive relationships were found between: (1) frond and rhizome biomass and (2) frond biomass and necromass, while no relationship was observed between the rhizome/frond biomass ratio and necromass (see Table 4). Additionally, considering the ecosystem types, positive relationships were significant only for the Savanna (see Figure 1, Table 4).

There were no significant ecosystems differences in the slopes of the relationship between (1) rhizome and frond biomass (LR=3.050, p=0.080), (2) rhizome biomass and necromass (LR=1.056, p=0.304), and (3) leaf density and frond biomass (LR=0.749, p=0.387). On the other hand, there were significant differences in the slopes of the relationships between (1) frond biomass and necromass (LR=6.651, p=0.010), albeit weakly, (2) rhizome/frond biomass and necromass (LR=7.900, p=0.005) and (3) frond biomass and total biomass (LR=4.186, p=0.041).

3.2 Comparison of biomass allocation in Pteridium between South-America and Europe

A comparison of absolute values (see Table 2) showed that frond density is, in general, greater in Europe than in South America (t-test, t= 2.55, p= 0.015). However, leaf length (t= 2.82, p= 0.007), frond biomass (t= 4.0, p= 0.002), and leaf biomass (t= 8.04, p< 0.001), calculated by dividing the total frond biomass (g m^{-2}) by leaf density (leaves m^{-2}), were significantly greater in the South American samples. The range of frond lengths from both regions showed substantial overlap, but the European fronds were in the lower part of the range and the South American fronds in the upper part.

The relationship between European variables indicated a negative significant relationship between (1) leaf density and leaf length and (2) leaf length and leaf biomass, whereas a positive relationship was detected between leaf density and leaf biomass (see Figure 2 and Table 4). We observed significant relationship for data from South America only between density and leaf biomass (LR=11.903, p=0.0006). There was no significant difference in the slope for the relationship between (1) leaf length and leaf biomass (LR= 2.318, p= 0.128) and (2), leaf density and leaf length (LR=0.256, p=0.613) (see Figure 2).

4. Discussion

4.1. Biomass allocation

In Brazil *Pteridium esculentum subsp. arachnoideum*is is found in both Atlantic Forest and Savanna, suggesting that this species is able to colonize contrasting ecosystems habitat. There were no significant differences in frond biomass, frond length, frond density and litter biomass, but the significant differences found on the variances, in general greater in the Savanna, indicated differences between study sites rather than ecosystems. Because of its large area, Savanna includes a high diversity of soil types, climate and vegetation types (Silva et al., 2006). We could expect such variation as a function of these environmental heterogeneity.

Table 3. Biomass allocation in *P. esculentum subsp. arachnoideum* stands of different Brazilian ecosystems. Mean ± SE, t-values and significance (p) values are presented;

Variable	Savanna	Atlantic Forest	t	p
Frond biomass	966.8 ± 104.9	1139.6 ± 116.8	1.08	0.286
Rhizome biomass*	696.3 ± 121.7	795.2 ± 85.4	0.60	0.964
Total biomass	1663.1 ± 183.8	1934.8 ±171.1	1.02	0.311
Leaf biomass*	88.5 ± 11.7	93.4 ± 7.5	0.33	0.742
Density of leaves	12.7 ± 1.2	12.8 ± 1.3	0.04	0.964
Rhizome/frond biomass*	0.8 ± 0.15	0.9± 0.15	0.31	0.760
Leaf length*	2.1±0.11	2.1±0.08	0.21	0.831
Necromass*	1073.1 ± 161.6	964.2 ± 128.1	0.53	0.600

*indicates unequal variances according to Levene's test ($p<0.05$). Biomass and necromass are given in g/m^2, density as the number of individual fronds/ m^2 and mean frond length in m. Fronds were considered as the whole group of leaves sampled at each plot. Number of samples was 30 for Savanna and 20 for the Atlantic Forest; 75 leaves were measured in the Atlantic Forest and 82 in Savanna.

It has been suggested that the development of a complex rhizome system requires a substantial investment and with this comes a considerable measurable risk (de Kroon and van Groenendael, 1997). Our results suggest that a common rhizome mass is able to support a large variation in frond biomass, which can be expressed through differences in both frond density and frond length. In tropical areas we could expect more investment in above-ground biomass, as frond longevity is greater as a consequence of the less harsh climate and hence productivity should also be greater.

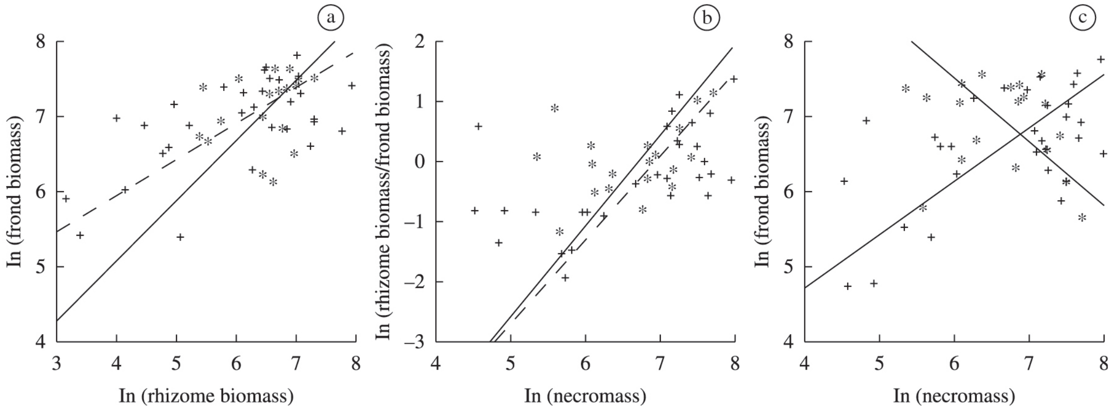

Figure 1. Relationships between production-related variables from *Pteridium esculentum subsp. arachnoideum* in all the points of sampling in Atlantic forest and Savanna ecosystems in Brazil: (a) Frond biomass vs Rhizome biomass, (b) Rhizome/frond biomass ratio vs Necromass, and (c) Frond biomass vs Necromass. All data were ln transformed. Key: Savanna = + and continuous line; Atlantic Forest= *and dashed line. Regression equations are shown in Table 4a. Frond biomass, rhizome biomass and necromass are given in g per m^2.

Table 4. Parameters of the reduced major axis regression estimated for data illustrated in (a) Figure 1 and (b) Figure 2. Spearman's correlation coeficients (r_s) and significance (p) are presented.

(a) Number of samples was 30 for Savanna and 20 for the Atlantic Forest, all analyses were performed using ln transformed data.

Variables	Ecosystem	a	b	$R^2_{adjusted}$	r_s	p
Frond biomass vs Rhizome biomass	Combined	0.65	1.18	0.32	0.437	0.002
	Savanna	0.60	3.05	0.38	0.614	<0.001
	Atlantic Forest	1.00	0.38	0.09	0.308	0.186
Rhizome biomass/Frond biomass vs Necromass	Combined	0.77	0.95	0.17	0.227	0.121
	Savanna	0.93	–6.89	0.334	0.578	0.021
	Atlantic Forest	1.01	–7.15	0.137	0.370	0.108
Frond biomass vs Necromass	Combined	0.97	–3.05	0.27	0.548	<0.001
	Savanna	0.72	1.80	0.33	0.618	<0.001
	Atlantic Forest	–0.85	12.61	0.04	–0.20	0.389

(b) Number of samples was 32 for Europe and 12 for the South America, all analyses were performed using ln transformed data.

Variables	Continent	a	b	$R^2_{adjusted}$	r_s	P
Leaf density vs Leaf length	Europe	–0.54	6.16	0.08	–0.2758	0.12653
	S. America	0.57	3.88	0.459	0.677	0.0155
Leaf density vs Leaf biomass	Europe	1.04	2.70	0.661	0.813	0.0001
	S. America	1.26	3.65	0.898	0.974	0.0001
Leaf length vs Leaf biomass	Europe	1.89	–3.51	0.10	0.321	0.073
	S. America	2.21	–4.93	0.54	0.735	0.006

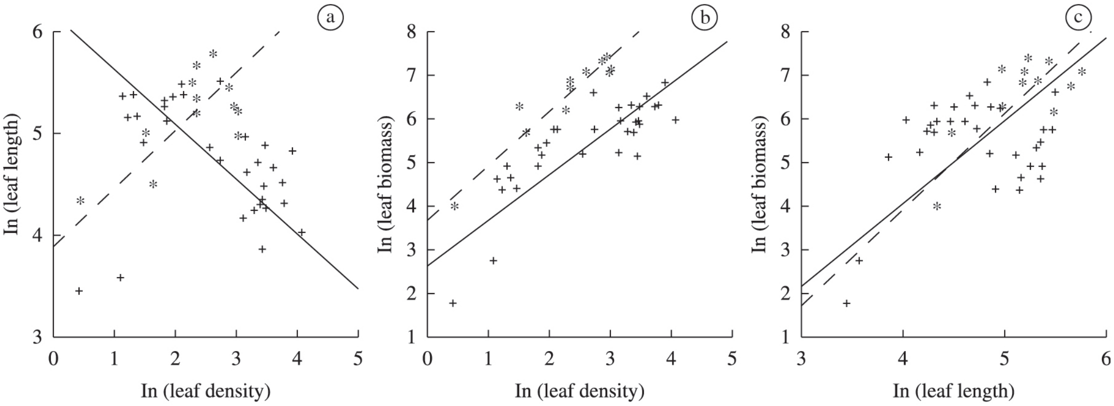

Figure 2. Relationships between production-related variables from *Pteridium* of South America and Europe: (a) leaf density vs leaf length, (b) leaf density vs leaf biomass and (c) leaf length vs leaf biomass. Brazilian data (*Pteridium esculentum subsp. arachnoideum*) = *and continuous line; + and dashed line = European data (*Pteridium aquilinum*). All data were ln transformed. Regression equations are shown in Table 4b. Leaf density is given by the number of leaves per m^2, leaf length in cm and leaf biomass is the weight of individual leaf in g.

Environmental heterogeneity in tropical ecosystems, in terms of canopy coverage, may be a factor determining the above-ground biomass variation, considering that individual ramets have to struggle for light, to maintain the productivity of the overall clone (Huber and Hutchings, 1997).

In terms of vegetation dynamics two important results were obtained. The first was the negative relationship between frond and litter biomass found to Atlantic Forest data, indicating that the dense litter layer developing under the *P. esculentum subsp. arachnoideum* may be harmful for its own regeneration, as first suggested by Watt (1945, 1947, 1976) as well as for other species (Marrs, 1988; Marrs et al., 2007). The second was the dense canopy of *P. esculentum subsp. arachnoideum* fronds which is also an important factor contributing to its ability to become a dominant species and being able to prevent the colonization by other species (Marrs, 1988; Marrs and Pakeman, 1995; Ghorbani et al., 2006). Both dense canopy cover and depth litter layer can also get one further problem with *Pteridium* colonization: the impoverishment of the soil seed bank (Ghorbani et al, 2006). A reduction in species present in the seed bank of Atlantic Forest was found in a previous study (Silva and Silva Matos, 2006).

Another direct consequence of such a deep litter layer (necromass) is that the risk and intensity of fire is increased in both ecosystems. Normally, natural fires occur in the Savanna every two to three years (Hoffmann, 1996), but non-natural, human-induced fires are increasingly common albeit unpredictable including in the moist Atlantic Forest (Silva Matos et al., 2002, 2005). Unfortunately, the relationship of *P. esculentum subsp. arachnoideum* and fire in the Savanna is still unclear, but we might hypothesize that a positive feedback of fire on *P. esculentum subsp. arachnoideum* will develop: fire keeps the woody vegetation under control which allows *P. esculentum subsp. arachnoideum* to spread increasing its biomass, which in turn increases the risk, intensity and frequency of fire events, leading to the decrease in the biological diversity changing the structure of the community (Hoffmann and Moreira, 2002; Pivello, 2006).

These results are worrying because these are both ecosystem types of considerable international conservation importance (Myers et al., 2000) and the *P. esculentum subsp. arachnoideum* here exhibits a very large range of allocation responses, implying considerable plasticity, and hence must be viewed as a major potential future invasive threat.

4.2. Comparison of biomass allocation between European and South American Pteridium

Different biomass allocation strategies were detected between European and South American *Pteridium*. In Europe, the frond life-cycle is expected to last at most seven months in any given annual season because all fronds are killed by winter frost (Pakeman, et al., 1994; Pakeman and Marrs, 1996; Pottier, et al., 2005; Marrs and Watt, 2006), and there should therefore be less investment in fronds, in terms of biomass/length and biomass/density. In tropical South America, by the other hand, we could expect an increase of leaf biomass after the maximum length is attained as leaves live longer than in Europe. However, the higher slope observed in the leaf density x leaf biomass relationship for the South America data, indicates that the increase of fronds causes a negative effect on the biomass allocation of *P. arachnoideum*. According to Weiner (2004) environmental selection pressures drive changes on plant resource allocation. So, in a large-scale comparison, between Brazil and Europe, we can assume that differences on the biomass allocation patterns resulted from different climate pressures and speciation, while in the comparison of Brazilian ecosystems such pattern resulted from small-scale environmental heterogeneity, as discussed earlier. This broad plasticity might have allowed *Pteridium* to develop as an invasive genus in diverse bio-climatic regions.

For the conservation of endangered ecosystems *Pteridium* poses substantive actual and potential threats (Pakeman and Marrs, 1992). Its wide geographic range coupled with the environmental plasticity demonstrated here allows it to succeed in a wide range of habitats, and also makes it difficult to predict its invasiveness (Goodwin et al., 1999). As the *Pteridium* patch increases mainly through rhizome expansion (Marrs and Watt, 2006), it should be possible to control it by manipulating resource allocation between the rhizomes and fronds. In Europe, frond removal by cutting and other mechanical treatments is used routinely to control *Pteridium*. A similar approach should be even more effective in South America where there is a greater proportion of the resource allocated to the production of a large frond biomass. However, this strategy needs to be tested experimentally.

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