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Original article

Ecophysiology of the invader *Pennisetum setaceum* and three native grasses in the Canary Islands

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ABSTRACT

Pennisetum setaceum (fountain grass) is an aggressive invader in the arid and semi-arid habitats of the tropics and subtropics. In the last twenty years the spread of fountain grass in the Canary Islands has been very rapid. We compared its ecophysiological, architectural and reproductive traits with those of three native grasses (*Hyparrhenia hirta*, *Cenchrus ciliaris* and *Aristida adscensionis*) in two habitats of Tenerife Island which differ in rainfall. The detection of traits that differ between native and invader grasses may provide information for the improved control and eradication of the latter contributing to protect the native plant diversity. *P. setaceum* and the native grasses differed in all measured traits and in their response to water availability which is more restricted in the southern site. Specific leaf area was lower in *P. setaceum* than in the native grasses. Although this reduces carbon assimilation per unit area, it also reduces transpiration, increasing water use efficiency and contributes to the maintenance of high relative water content. Leaf N in *P. setaceum* was lower than in the native grasses indicating higher nitrogen use efficiency. The activity of photosystem II was higher and lasted longer in *P. setaceum* than in the native grasses. The ecophysiological traits of *P. setaceum* support its large size, extensive canopy and shorter leaf senescence period. They confer considerable competitive advantage to the invader and partially explain its success in the Canary Islands. The differences between the invader and the native grasses were maintained in both sites revealing a good adaptation of *P. setaceum* to the low resource local habitats in the Canary Islands and confirms its large plasticity. The large invasive potential of *P. setaceum*, in concert with the projected global changes, forecast eventual risks for the conservation of the endemic flora and remaining native communities in the Canary Islands.

1. Introduction

Fountain grass (*Pennisetum setaceum* (Forsk.) Chiov.) is one of the most invasive plants in the dry tropics and subtropics (GISD, 2008). Islands are particularly sensitive to invasive species due to their impoverished biotas and open access (Vitousek et al., 1987; Millennium Ecosystem Assessment, 2005). *P. setaceum* was introduced as an ornamental in the Canary Islands during the last century and its invasive spread has been remarkable in the last twenty years (Garcia Gallo et al., 1997). Here, *P. setaceum* and 80 more vascular plants are considered invasive and represent serious threats to native ecosystems in this biodiversity "hot spot" (Myers et al., 2000; Martín Esquivel et al., 1995). In the Canary Islands, *P. setaceum* ranges from sea level up to 1000 m a.s.l, prevailing below 500 m a.s.l. In this altitudinal range *P. setaceum* has invaded the protected areas of the coastal xerophytic scrub and the endemic comunities dominated by *Euphorbia canariensis* (native cardoon) and *Euphorbia balsamifera* (sweet tabaiba). Here, *P. setaceum* first coexists with, and eventually replaces, the native grasses *Hyparrhenia hirta*, *Cenchrus ciliaris*, and *Aristida adscensionis* ssp. *coerulescens* as urban areas enlarge (Martín Esquivel et al., 1995). In addition, *P. setaceum* has expanded along the roads from the urbanized towards natural areas and it is found in 30% of all protected areas in the Islands. This invasion is expected to increase with further human occupation. Local administrations carry out control and eradication programs with variable success (Pérez de Paz et al., 1999; Gobierno de Canarias, 2008).

In addition to escape from enemies and habitat disturbance, the success of invasive plants has been attributed to several ecophysiological traits that make them more efficient in resource use than native plants (Lockwood et al., 2007). Among these traits are high

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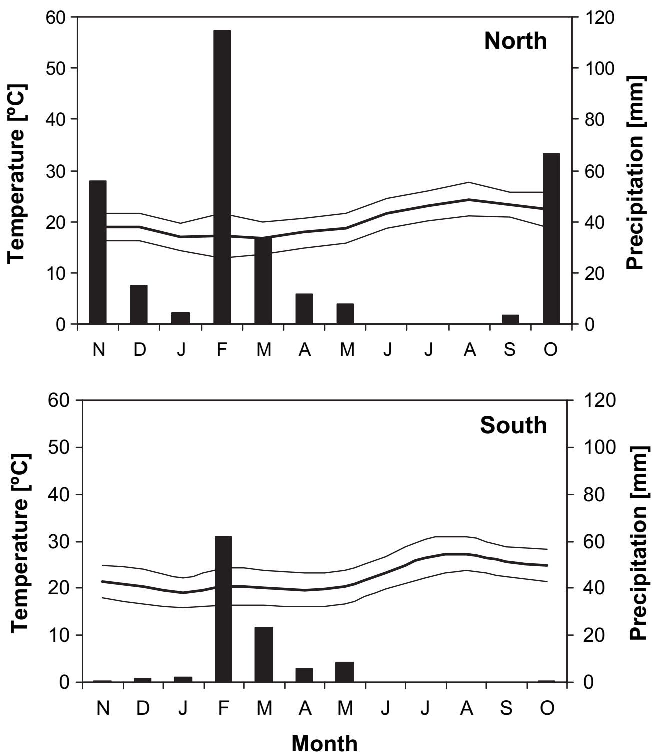

Fig. 1. Monthly precipitation (bars). Total precipitation during study year: southern site = 104 mm; northern site = 312 mm. Air temperature during the study (lines: mean, minima and maxima). Mean annual temperature: southern site = 22.3 °C; northern site = 20.2 °C.

specific leaf area (SLA, leaf area per unit leaf mass) and leaf N content which are correlated to high assimilation and growth rates (Poorter and Bergkotte, 1992; Pattison et al., 1998; Baruch and Goldstein, 1999; Smith and Knapp, 2001). These and other traits, such as the efficiency of water use and the allocation of reserve assimilates are responsible for plant growth. All of them influence plant size, biomass accumulation and reproductive output which are related to competitive ability and are expected to be more developed in invader than in native plants.

The performance of co-occurring native and invasive plants depends on available resources (light, water and/or nutrients) in their habitat. Native species tend to outperform invaders under stressed conditions or in low resource habitats (Daehler, 2003). Therefore, it is important to compare natives and invaders under similar conditions, in order to provide time and site-specific management strategies for the control of the latter (Parker et al., 1999). Here, we compare several ecophysiological, architectural and reproductive traits between three native grasses and *P. setaceum* from two sites in order to test the invasive potential of *P. setaceum* under contrasting conditions in Tenerife Island. The identification of the traits that differ among the native and the invader grasses may provide information for improved eradication or control of the latter and assist in the conservation of biodiversity of the Canary Islands.

2. Materials and methods

2.1. Study sites and species

Two study sites were established below 100 m a.s.l. in Tenerife Island. The first is close to Buenavista town in the windward north (28°22′39″N; 16°50′57″W) and the other is near Güimar town in the leeward south of the island (28°14′35″N; 16°24′19″W). In both sites the climate is arid and warm with rainfall during the winter months (Del Arco et al., 2006a). Buenavista soils are clayey Aridisols with low organic matter and permeability whereas those of Güimar are shallow, sandy and rocky Entisols (Fernández Caldas et al., 1982).

P. setaceum is a perennial, C_4 caespitose or bunch grass native of arid regions in the Middle East (Williams et al., 1995; Lovich, 2000). It is also a wind dispersed, facultative apomictic (Williams and Black, 1993; Poulin et al., 2005). The native grasses are also C_4 caespitose perennials. *H. hirta* (L.) Stapf, *C. ciliaris* L. and *A. adscensionis* L. ssp. *coerulescens* (Desf.) Bourreil, Trouin, Auquier & J. Duvign are considered natives that have arrived from Africa and colonized the islands without human assistance (Clayton and Renvoize, 1986; Valdés et al., 1987; Martín and Izquierdo, 2004). The three native species are typical of the associations of pastures from the Order *Hyparrhenietalia* found in the coastal xerophytic scrub. They form dense groups over relatively large areas but are of minor value as forages (Del Arco et al., 2006b). Henceforth, the grasses will be named by genus alone.

2.2. Methods

In November 2005, five individuals per species were randomly selected and marked at both sites. For one year, the sites were surveyed monthly when, for each individual, we: (i) measured plant height at the uppermost leaf, (ii) labelled the existing inflorescence stalks and counted the newly emerged ones, (iii) determined plant canopy (projected) area by measuring its length and width and calculating the area as an ellipse, and (iv) visually scored the vegetative status on a scale from 0 to 5 corresponding to 0, 20, 40, 60, 80 and 100% of remaining live leaf surface which we named "greenness". During the same monthly surveys we measured maximum photochemical capacity of photosystem II (PSII) as the ratio of variable fluorescence to maximum fluorescence (F_v/F_m) on dark adapted leaves (3 measurements on 3 plants per species/site) with a time-resolving portable fluorometer (Handy PEA, Hansatech, U.K.) with 2 min exposure to actinic light with a flux of 3000 μmol m^{-2} s^{-1} at 690 nm. For the following determinations, leaf samples were sealed in plastic bags, brought to the laboratory and kept in cold storage until analysis: (i) SLA and relative water content (RWC, Turner, 1981) were measured monthly on 3 recently expanded leaves per species/site and (ii) leaf N concentration (Kjeldahl method), chlorophyll *a*, *b* and total carotenoids (Lichtenthaler, 1987), and total non-structural carbohydrates [soluble sugars (Irigoyen et al., 1992) and starch (Rose et al., 1991)], were analyzed four times per year also on 3 recently expanded leaves per species/site. Daily precipitation and temperature data were recorded from two nearby (5–15 km) stations within the same bioclimatic regions of the study sites

Table 1
Soils characteristics in both experimental sites. Means ($n = 3$) and standard error of: cation exchange capacity (CEC), pH, organic matter (OM), exchangeable cations (Ca, Mg, Na and K) and electrical conductivity (EC). Significance levels: ns, $p > 0.05$; $^{***}p < 0.001$.

Site		CEC, Meq/100 g	pH	OM, %	Ca, Meq/100 g	Mg, Meq/100 g	Na, Meq/100 g	K, Meq/100 g	EC, mS/cm
North	Mean	10.33 ns	8.07 ns	0.53 ns	7.34 ns	1.68 ns	0.79 ***	0.53 ***	1.02 ns
	Std. error	4.93	0.22	0.18	3.53	0.79	0.36	0.26	0.17
South	Mean	17.00	8.16	0.63	6.74	2.42	4.31	3.53	1.57
	Std. error	2.00	0.10	0.33	1.96	0.88	0.34	0.32	0.34