



Original article

Seedling growth of a native (*Ampelodesmos mauritanicus*) and an exotic (*Pennisetum setaceum*) grass

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ABSTRACT

Scarce information is available on the biological reasons why a small subset of introduced species can effectively establish within novel ecosystems. A comparison of early growth traits can help to explain the better performance of alien invasive species versus native co-occurring species. In one year-long experiment, we compared the early life stages of *Ampelodesmos mauritanicus* (Poir.) Dur. & Schinz (*Amp*), a native perennial Mediterranean grass, and *Pennisetum setaceum* (Forssk.) Chiov (*Penn*), an emerging invader grass in sub-arid and Mediterranean-climate areas. The *Penn* seedlings grew significantly faster and were approximately 2.5 times taller than the *Amp* seedlings, reaching a final average height of 90 cm. The shoot and root dry masses of the *Penn* seedlings were, respectively, more than 14 times and 4 times higher than those of the *Amp* seedlings. As a consequence, the shoot:root ratio was significantly higher in *Penn*, which resulted in a greater allocation of resources to the photosynthetic organs. *Penn* showed a more rapid life cycle compared with *Amp*. *Penn* produced seeds 9 months after sowing while no spikelet was produced by *Amp* until the end of the experiment. As a consequence, *Penn* may gain a reproductive advantage due to rapid seed dissemination. Ultimately, a suite of peculiar early growth traits makes *Penn* an aggressive competitor against *Amp*, which is an important floristic element of native Mediterranean grasslands. *Penn* seems better suited than *Amp* in colonizing frequently disturbed sites with fluctuating resource availability or irregular rainfall distribution and *Penn* is gradually replacing *Amp*.

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1. Introduction

Alien invasive plants represent one of the main threats to biodiversity on a global scale, and huge costs are required annually to prevent, control and eradicate them (Williamson, 1996). Many hypotheses have been proposed in an attempt to explain why some plant species behave differently in the exotic range, where they attain high density, may displace native species and in some cases deeply change the characteristics of whole ecosystems (Richardson et al., 2000). However, there is limited knowledge on the biological mechanisms through which some non-native plants may successfully outcompete native species. Generally, a single cause is not sufficient to explain invasive success, which rather depends upon a number of interrelated ecological and anthropic factors (Lake and Leishman, 2004; Blumenthal, 2005). Although man is the main responsible for the spread of invasive plants, these plants should have the capability to effectively take advantage of the opportunities and resources that become available in their new ranges. Many studies have attempted to identify a set of biological traits, which being most commonly found in invasive alien species can help to

provide an identikit of current invaders, which may also serve as a tool for forecasting future invaders (Goodwin et al., 1999; Lloret et al., 2005).

However, the importance of biological traits is recognized to vary both in time and space because it is strongly stage- and habitat-dependent (Sakai et al., 2001). For instance, fast initial growth rates may ensure a competitive advantage in disturbed habitats and early successional communities, as well as nutrient-rich sites and herbaceous communities (Grime, 1973; Davis et al., 2000). Indeed, there is growing evidence that invasive herbaceous species grow faster, under the same environmental conditions, than native co-occurring species (Daehler, 2003; James and Drenovsky, 2007). In 105 commonly occurring herbs in the U.K., the maximum relative growth rate was found to be positively correlated with the invasiveness of these plants at a global level (Dawson et al., 2011), suggesting this could be a key trait to gain a competitive advantage over native species. *Pennisetum setaceum* (Forssk.) Chiov. (Fountain Grass; hereafter *Penn*) is a C₄ perennial bunchgrass native to Africa and the Middle East. It has been widely introduced into many regions worldwide, such as Arizona, California, Florida, Hawaii, Fiji, South Africa and Australia (Williams et al., 1995), Spain and the Canary Islands (González-Rodríguez et al., 2010), as well as Sicily, the largest island in the Mediterranean Sea (Pasta et al., 2010). *Penn* is a very aggressive in-

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vader of many arid and semi-arid habitats, such as thermo-xerophilous and dry grasslands and shrublands, where it establishes almost monospecific stands and causes long-lasting ecological consequences (Cordell and Sandquist, 2008; González-Rodríguez et al., 2010). Due to its broad ecological tolerance and high phenotypic plasticity *Penn* is capable to thrive under sub-optimal ecological conditions and then, as soon as favorable conditions occur, the rapid exploitation of available resources such as water and nutrients may enable it to overcome native coexisting species (Williams and Black, 1993; Poulin et al., 2007; Rahlao et al., 2010). Furthermore, under drought or limited resources conditions, the alteration of biomass allocation patterns in favor of roots suggests a conservative strategy (Williams and Black, 1994; Rahlao et al., 2010). This explains why *Penn* is an excellent invader of habitats characterized by fluctuating resources, frequently disturbed or with an irregular rainfall pattern (Davis et al., 2000), which are common in many Mediterranean-climate areas. However, until now, little information is available about the competitive ability of *Penn* when competing with native species in Mediterranean areas, where it is rapidly spreading (Sanz-Elorza et al., 2004; Pasta et al., 2010).

Penn was introduced into Sicily as an ornamental plant during the 1940's and just twenty years later it began to regenerate naturally, spreading into surrounding areas (Pasta et al., 2010). Currently, it has successfully invaded many coastal and hilly areas up to 500 m a.s.l., mainly on south-facing slopes within the thermo-Mediterranean bioclimatic belt (Brullo et al., 2010). *Penn* is found preferentially along roadsides and disturbed sites but it also successfully establishes within semi-natural grasslands, as well as in low-altitude cliff vegetation, where it represents a growing threat for native flora. Due to its high ecological plasticity, it has invaded not only xerophilous but also mesophylous native grasslands, mainly those dominated by *Ampelodesmos mauritanicus* (Poir.) Dur. et Schinz.

Ampelodesmos mauritanicus (Mauritanian Grass; hereafter *Amp*) is a C₃ perennial native bunchgrass typical of coastal and hilly areas throughout the Mediterranean Basin, from southern Portugal to western Greece (Vilá and Lloret, 2000). In Sicily, *Amp* grasslands are commonly found from 0 to 1200 m a.s.l., chiefly within the meso-mediterranean and thermo-mediterranean bioclimatic belts (Brullo et al., 2010). These grasslands are seminatural formations that, apart from playing an essential role in the stabilization of steep slopes, host an important heritage for animal and plant biodiversity, so that they have been included among the priority habitats protected under the EU Natura 2000 Network, according to Habitat Directive (92/43/CEE). *Penn* and *Amp* differ in the photosynthetic pathway (C₄ vs. C₃) and tend to establish in more xeric or more mesic habitat, respectively, being the alien species typically more drought tolerant than the native species (Williams and Black, 1994; Mingo and Mazzoleni, 1997). A number of traits may be taken into account to assess the competitive interactions between *Amp* and *Penn*, such as seed (size, weight, number per plant) or seedling characteristics, the seed dispersal and establishment strategies or the response to specific disturbance event (fire or grazing). However, these two grasses actually coexist in different sites where they compete for the same resources. Although they share some biological traits (e.g. life form) and anthropogenic disturbance adaptation (e.g. Incerti et al., 2013), the successful establishment of *Penn* within *Amp* grasslands has been increasingly observed. Some authors state that interspecific competition, during the first phases of the invasion process, is likely to be one of the main determinants for invasive establishment (Vilá and Weiner, 2004; Mangla et al., 2011).

Hence, this research was focused on test whether differences during the early life stages may help to explain the competitive ability shown by *Penn* vs. *Amp* in Mediterranean basin. In particular, our

research was focused on a one-year seedlings pot experiment in order to compare the growth performance and biomass allocation pattern.

2. Materials and methods

2.1. Study site

Mature seeds of *Ampelodesmos mauritanicus* (*Amp*) and *Pennisetum setaceum* (*Penn*) were collected during the winter season (December) from natural populations occurring in the "Monte Gallo" Natural Reserve (38°12'52" N, 13°19'16" E; 54 m a.s.l.). The collection site is characterized by limestone soils and a typical Mediterranean climate with a mean annual precipitation of approximately 600 mm, occurring mainly during the coldest months of the year (from December to March), and a mean annual temperature of 19 °C (Drago et al., 2002).

2.2. Seed and germination traits

Seed weights were obtained by taking the mean weights of batches of 100 seeds (25 × 4 replicates). Seed weight was expressed in g*1000 seeds. The experiment was performed at CREA-SFM (38°05'02" N, 13°31'18" E; 23 m a.s.l.). A preliminary laboratory germination test was performed to evaluate the seed germination percentage, based on 150 seeds per species. Fifty seeds per species were placed on 15-cm sterilized Petri dishes containing double layered Whatman No. 1 filter paper moistened with 10 ml of double sterilized water and incubated at 20 ± 2 °C. Germination was recorded every day until a constant number of germinated seeds were reached. Each germination test was replicated 10 times per species.

2.3. Growth experiment

For the *in vivo* experiment, sowing was performed at the end of December in polystyrene pots (135 holes per pot) filled with limestone soil. Three polystyrene pots per species were placed inside an east-west-oriented greenhouse (540 m²) with a steel structure and a polymethacrylate methyl cover maintained under controlled conditions (T = 20 ± 2 °C; RH = 65 ± 5%). One hundred individuals per species were transplanted, at the second true leaf status, into 7-l pots (22 cm diameter x 22 cm of depth) filled with 70:20:10 (v/v/v) limestone soil, sand and perlite (Agrilit3[®] purchased from Perlite Italiana s.r.l., Milano, Italy). The pots were maintained under open-air conditions (Fig. 1) and irrigated to field capacity once a week (if rainfall did not occur) during the winter season and twice a week during the summer season.

The pots were rotated once a week to avoid the effect of position. After two weeks of acclimatization and every 3 months, 5 plants per species were randomly selected and destructively sampled. Biometrical parameters (height, root length, number of culms, root and shoot dry weight) were recorded. Plant height was measured at the uppermost leaf. The root and shoot dry weight (RDW and SDW) were determined after oven-drying at 70 °C for 48 h. The relative growth rate (RGR) was calculated on a dry mass basis as the difference between the final plant dry weight and the seed dry weight divided by the elapsed time, as suggested by Graebner et al. (2012).

2.4. Experimental design and statistical analysis

A completely randomized design was adopted. The data were statistically analyzed using the SAS 9.2 statistical package (SAS Institute, 2008). In accordance with the chosen experimental design,

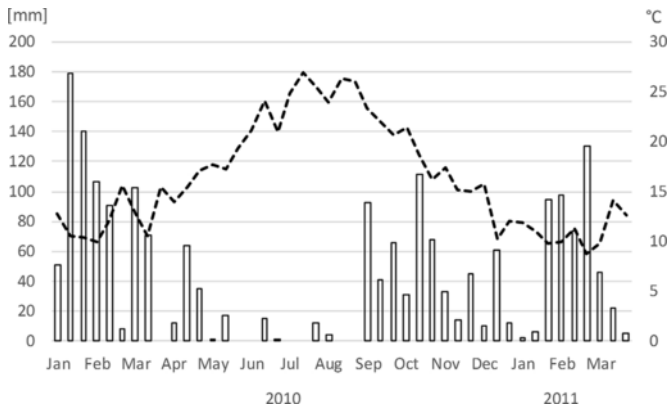


Fig. 1. Temperature and rainfall patterns during the experiment. Each column represents rainfall accumulation per ten days. Dotted line represents the average daily temperature.

the data were analyzed using ANOVA (GLM procedure), and means were compared using the Tukey HSD test at the 0.05 level of significance.

3. Results

3.1. Seed and germination traits

Significant statistical differences between *Amp* and *Penn* were recorded in terms of seed weight (3.864 ± 0.064 g*1000 seeds vs. 1.532 ± 0.015 g*1000 seeds, respectively) and *in vitro* germination percentage ($59 \pm 4.99\%$ vs. $70 \pm 1.99\%$, respectively). Similar germination data were recorded for the *in vivo* experiment. Seedling emergence was registered 6 days after sowing (DAS) in *Penn* versus 13 DAS in *Amp*.

3.2. Growth experiment

The *Penn* seedlings were significantly taller than the *Amp* seedlings. At 336 DAS, the *Penn* plants were approximately three times taller (93.20 ± 2.40 cm) than the *Amp* ones (35.00 ± 3.70 cm) (Fig. 2). A considerable difference in the life cycle was found in terms of the RGR. *Penn* exhibited maximum growth from 245 to 336 DAS, but appeared to stop growing at 410 DAS. Conversely, *Amp* grew much slower but grew until the end of the experiment. Signifi-

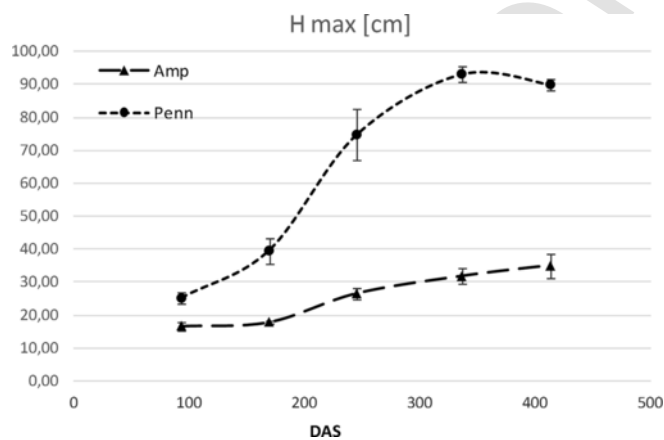


Fig. 2. Performance of height over time of *Ampelodesmos* (*Amp*) and *Pennisetum* (*Penn*) seedlings. DAS: Days after sowing. Vertical bars at each point indicate the standard error.

cant differences in the RGR pattern were recorded as early as 90 DAS (Fig. 3). *Penn* exhibited a near-exponential RGR and reached its maximum growth in December (around 336 DAS), with a value of 10.69 g g⁻¹ d⁻¹. In *Amp*, the RGR slowly increased and reached a maximum value at the end of the experiment, equal to 1.41 g g⁻¹ d⁻¹. It is noteworthy that just prior to the end of the experiment, we observed that approximately half of the *Penn* individuals had started to flower, whereas flowering was not observed in the *Amp* individuals (data not shown).

Significant differences were recorded between the species in terms of the root dry weight (RDW), shoot dry weight (SDW), shoot/root ratio (S/R ratio) and numbers of culms (Table 1), whereas there was no significant difference in root elongation (Table 1). Both the RDW and SDW were significantly higher in *Penn* compared with *Amp*. The RDW and SDW were, respectively, 182.6% and 402.9% higher in *Penn* compared with *Amp* at 413 DAS. In both species, the shoot/root ratio increased until reaching a maximum value on 169 DAS (*Penn*) and 245 DAS (*Amp*), after which this ratio progressively decreased (Table 1).

4. Discussion and conclusion

In order to get a deeper understanding of the biological reasons underlying the invasive success of an alien species, it might be useful to compare growth performance between the alien and native co-occurring competitors (Daehler, 2003; Vilá and Weiner, 2004; Blank, 2010; Vehra and Khan, 2011). For instance, within early successional plant communities, knowledge of how fast plants grow and accumulate biomass during the early stages of life provides crucial information on the likelihood of effective establishment and potential competitive ability of alien species (Davis et al., 2000; Funk, 2008). Through the comparison of seedling performance in a pot experiment we found large differences between a native C₃ (*Amp*) and an exotic C₄ grass species (*Penn*) in seed characteristics, as well as in early growth traits and resources allocation pattern. *Penn* seeds were significantly smaller than *Amp* ones; this may allow a more effective wind dispersal and, moreover, herbaceous plants with small seeds tend to grow fast (Seibert and Pearce, 1993). However, also a lower resistance to environmental stress may be expected, due to a smaller starting capital (Bazzaz et al., 1989). The higher germination percentage of *Penn* is an important evaluation parameter, but used alone, it does not necessarily translate into a higher number of seedlings in the field or provide an indication of superior competitive ability. During the trial, the *Penn* seedlings grew significantly faster and reached a significantly greater final height compared with the *Amp* seedlings.

Our results do provide further evidence of the general trend exhibited by invasive species, especially herbaceous ones, displaying higher growth rates compared with native or non-invasive alien species (James and Drenovsky, 2007; Young and Mangold, 2008; van Kleunen et al., 2010; Graebner et al., 2012). The different photosynthetic pathway, together with the environmental growth conditions, presumably played an important role in determining a higher growth rate in the invasive C₄ rather than in the native C₃ grass species. During summer, diurnal temperature regime, associated with sufficient water availability, represent the most suitable growth condition for a typical warm-season grass like *Penn* (Collatz et al., 1998; Sweet and Holt, 2015). In winter, despite temperature regime may favor the native C₃, the availability of adequate light and water could greatly reduce the potential gap between the two grass species (Lara and Andreo, 2011). Furthermore, recent investigations about the interspecific competition of *Penn* have pointed out the crucial role

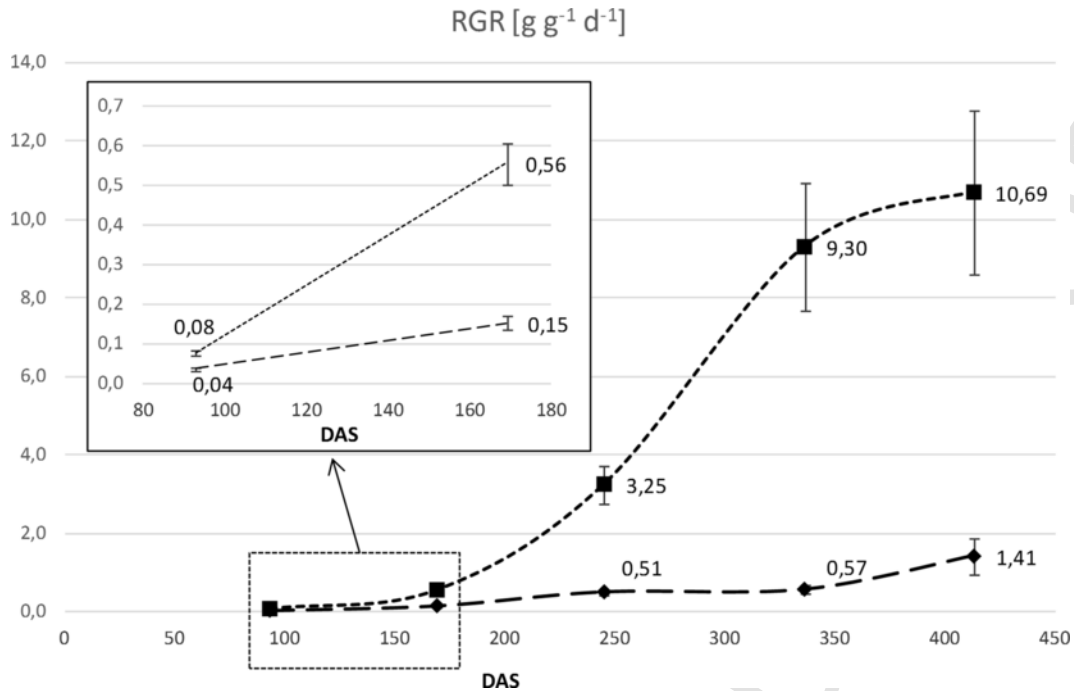


Fig. 3. Relative growth rate ($\text{g g}^{-1} \text{d}^{-1}$), expressed on a biomass basis, of *Ampelodesmos* (*Amp*) and *Pennisetum* (*Penn*) seedlings. DAS: Days after sowing. Significant differences are based on Tukey's test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Table 1

Biomass and growth parameters of *Ampelodesmos* (*Amp*) and *Pennisetum* (*Penn*) seedlings. Values presented are the mean (\pm SE). Significant differences are reported based on Tukey's test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). RDW: root dry weight; SDW: shoot dry weight; S/R: shoot/root.

Species	DAS	RDW [g]	SDW [g]	S/R ratio (dry)	N° Culms
<i>Amp</i>	93	0.01 \pm 0.002	0.02 \pm 0.002	1.70 \pm 0.356	1 \pm 0.0
	169	0.09 \pm 0.010	0.17 \pm 0.022	1.94 \pm 0.128	4 \pm 0.2
	245	0.44 \pm 0.079	0.80 \pm 0.078	2.01 \pm 0.245	5 \pm 1.4
	336	1.00 \pm 0.237	0.92 \pm 0.174	1.10 \pm 0.232	4 \pm 0.2
	413	3.88 \pm 1.536	1.96 \pm 0.426	0.64 \pm 0.100	5 \pm 1.5
<i>Penn</i>	93	0.03 \pm 0.004	0.04 \pm 0.003	1.30 \pm 0.117	1 \pm 0.0
	169	0.23 \pm 0.025	0.71 \pm 0.077	3.08 \pm 0.341	8 \pm 1.1
	245	2.34 \pm 0.116	5.62 \pm 1.139	2.38 \pm 0.458	12 \pm 1.6
	336	10.28 \pm 2.058	20.96 \pm 3.498	2.09 \pm 0.129	29 \pm 2.6
	413	15.80 \pm 2.463	28.36 \pm 6.563	1.75 \pm 0.289	21 \pm 4.4
Species	***	***	***	***	***
DAS	***	***	**	***	***
Species \times DAS	***	***	n.s	**	**

played by climatic conditions in driving competitive dynamics in the field. Although cool winter season favored the native species, *Penn* was able to resist to competition and in the following warmer summer it displayed an increased growth and a higher competitive ability, even in the absence of rainfall (Sweet and Holt, 2015).

Despite this background, the magnitude of this difference in growth rate was not expected and it is to some extent rather surprising, considering that *Amp* is considered an excellent pioneer species capable of successfully and quickly colonizing open areas (e.g. after fire, Vilà et al., 2001). This finding is particularly interesting because at the same study site from where the seeds were collected, adult *Amp* individuals are much taller and larger than *Penn* (Corona et al., 2016; Pasta et al., 2010). Because large-size individuals are known to be strongly competitive against neighboring plants in herbaceous communities (Grime, 1973), the ability of *Penn* to enter mature and close *Amp* grassland is likely to be quite low. Our personal observa-

tions, and phytosociological surveys (Pasta et al., 2010), seem to corroborate this hypothesis. However, the alien species may be able to suppress or hinder the regeneration of the native species through competitive mechanisms acting at a previous stage, i.e., the seedling stage.

Biomass production (both above and belowground) was significantly higher in the alien species, but the considerably higher difference in the shoot dry mass resulted in a significantly higher shoot:root ratio in *Penn*. This species showed a much greater ability to allocate its resources to the photosynthetic organs in the presence of sufficient soil water availability compared with *Amp*. A comparison of native and introduced grass species conducted by Wilsey and Polley (2006) indicated a similar pattern, with introduced species generally allocating relatively fewer resources to roots. This behavior appears to be confirmed by González-Rodríguez et al. (2010), who reported the capability of *Penn* to sustain high growth rates and produce well-developed leaves when water resources are not limiting. Such an unbalanced resources allocation in favor of the epigeous organs may appear surprising considering that *Penn* is a well-recognized drought-tolerant species (Williams and Black, 1994) and the root/shoot ratio tends to be higher in plants originating from dry areas with low annual rainfall (Mokany et al., 2006). However, phenotypic plasticity has been recognized as one of the key features of its invasive success worldwide, which has allowed this species to invade a wide range of ecosystem types (Williams and Black, 1993; Williams et al., 1995; González-Rodríguez et al., 2010). Indeed, as soon as water availability is reduced, *Penn* is particularly able to selectively increase its root investment, and this capability is recognized to be very effective in facing the drought period under Mediterranean conditions (Williams and Black, 1994; Grotkopp and Rejmanek, 2007; Rahlao et al., 2010). A comparative study ascertained that the magnitude of this shift in biomass partitioning was much higher in *Penn* than in *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult., a native Hawaiian grass species with which *Penn* competes (Williams and Black, 1994). On the contrary, *Amp* does not

seem to be able to enhance root growth during periods of water shortage, and this could be related to its relatively moderate resistance to drought (Mingo and Mazzoleni, 1997). However, this comparison needs to be carried out in our environments; in particular, the response of *Penn* and *Amp* under the same soil water conditions, including stressful conditions, is worthy to be investigated in the next future.

Another factor that may contribute greatly to the high competitive ability of *Penn* is the rapidity with which it reached sexual maturity in our study, which was 9 months after sowing, whereas no spikelet had been produced by *Amp* individuals until the end of the experiment. As a consequence, *Penn* may gain a reproductive advantage due to rapid seed dissemination. Hence, the seedling and early growth traits appeared to play an important role in the invasive success of *Penn*, as has been ascertained for other invasive herbaceous species (Blank, 2010; Mangla et al., 2011; Han et al., 2012). Seabloom et al. (2003) identified three main mechanisms by which an introduced species may reach dominance within grassland communities: superiority of the alien species, reliance on anthropogenic disturbance (the alien species is not competitively superior) or simply the first species that reaches a suitable microsite may successfully establish and be resistant to competitive suppression. Based on our pot experiment, although the performance of seedlings subjected to competition was not effectively assessed, our results suggest the idea that *Penn* may be a superior competitor than *Amp*, at least at seedling stage. *Penn* seedlings, being faster growing, taller and larger than *Amp* ones, and with a higher number of culms, are expected to be more competitive in the areas where the two grass species coexist (Mangla et al., 2011). Indeed, such seedlings may be able to occupy first the suitable microsites and to exploit more efficiently the available resources (light, water and nutrients), thus reducing the chance of survival for *Amp* seedlings. However, we recognize the limitations of our research, which has investigated only some aspects of the complex dynamics of the interspecific competition between *Penn* and *Amp*. More focused research will be needed to confirm the reasonable suspicion that the alien *Penn* is a better competitor than the native *Amp*.

A suite of peculiar early growth traits makes *Penn* an aggressive competitor against native Mediterranean flora, including *Amp*. In particular, because of its high growth rate, *Penn* seems much better suited than *Amp* in colonizing frequently disturbed sites with fluctuating resource availability or an irregular rainfall regime (Grime, 1973; Davis et al., 2000). All of these characteristics are common to Mediterranean coastal grasslands. In the absence of appropriate management actions, such as eradication interventions, at least within areas of conservation value, the further spread of this invasive will likely to replace native *Amp* grasslands in a long-term perspective, bringing devastating ecological consequences, not yet sufficiently known.

Author contribution statement

EB; collected and analyzed data, wrote manuscript, made figures, MM; field support, analyzed data, wrote manuscript, made figures, TLM; field support, analyzed data, wrote manuscript, experimental design; GG; logistical support, collected and analyzed data, wrote manuscript, made figures.

All authors have approved the final article before submission.

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