

# Invasion of *Agave* species (Agavaceae) in south-east Spain: invader demographic parameters and impacts on native species

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## ABSTRACT

Several mechanisms have been proposed to explain the success of invasive species in new environments. A species may become invasive when a new site provides the potential for positive rates of population growth. This may be the case of several *Agave* species introduced to Spain in the 1940s. In this paper we document factors that promote large increases of populations of these species, and their effects on native plant communities in two sites of SE Spain. Results showed higher rhizome and bulbil production, and higher establishment rates by agaves in sandy soils than in clay soils. In their native habitats, agaves have low establishment rates and sandy soils are rare. This suggests that sandy soils are an opportunity which releases the clonal reproduction of *Agave*. The effects of agaves on the physiological performance and reproduction of native species were negative, positive or neutral, depending on the size and rooting depth of neighbours. Assemblages of native species growing within *Agave* stands had lower diversity than non-invaded sites. Our data show that *Agave* stands have positive growth rates in SE Spain, and suggest that sandy soils are a niche dimension enhancing the invasion in these new habitats.

## Keywords

*Agave americana*, *Agave fourcroydes*, *Agave sisalana*, alien species, biological invasions, diversity, niche opportunity.

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## INTRODUCTION

Non-native ornamental and cultivated plants have become invasive in many ecosystems around the world (Williamson, 1996; Vitousek *et al.*, 1997). Some species have restricted distributions and low establishment rates in their native habitats but show explosive population growths once they arrive to new sites (Almasi, 2000; Lockwood *et al.*, 2001). Conditions and resources provided by the new habitat could mediate this invasive behaviour by improving the population growth rates of alien species (Tilman, 1982). In other words, the alien species finds a niche dimension in the new habitat that enhances its reproduction or establishment rate (Shea & Chesson, 2002). Most studies on plant invasions have been of C3 or C4 species, and few have evaluated the potential of succulent, CAM species to invade new areas (Dean & Milton, 2000; Gimeno & Vilà, 2002). CAM species are conspicuous elements in arid ecosystems of the New World and were introduced to many parts of the world outside their natural range for human consumption, livestock foraging and ornamental use (e.g. van Sitter, 2002). However, there are no studies on the factors that enhance population growth rates of CAM species to become invaders.

Once established, invasive species can affect the structure of the community by competing (Callaway & Aschehoug, 2000) or by facilitating other species (Alvarez & Cushman, 2002). The impact of CAM species on community structure is well known in their native habitats. For example, Valiente-Banuet *et al.* (1991a,b) and de Viana (1996) showed that columnar cacti from North and South American deserts depend on nurse plants for a successful establishment. Despite these positive interactions, cacti have strong negative effects on growth and survival of their nurses (McAuliffe, 1984).

*Agave* species (Agavaceae) are CAM species with characteristic nocturnal stomatal opening and tissue succulence. The family Agavaceae ranges from western North America to South America and Caribbean Islands; species in the genus *Agave* are found in deserts, grasslands, and oak-pine woodlands, growing on well-drained, rocky slopes (Nobel, 1988). Most *Agave* species are monocarpic (i.e. die after fruiting) and deplete their sugar reserves to produce a huge quantity of seeds (Nobel, 1988). Although produced seeds have high germination capacity, most seedlings die 8–9 days after germination (Jordan & Nobel, 1979; Arizaga & Ezcurra, 2002). Agaves also have clonal mechanisms of reproduction. Throughout their life span, agaves produce rhizomes, the apical meristems of which give rise to new individuals

(Arizaga & Ezcurra, 2002; Infante *et al.*, 2003). Another clonal mechanism of reproduction occurs in floral stems, where bulbils are developed from sterile meristems (Arizaga & Ezcurra, 1995; Arizaga & Ezcurra, 2002).

In Spain several species of *Agave* were introduced in the 1940s as ornamental and cultivated plants (Martín-Galindo, 1988), and recent field observations indicate that these species are spreading into new habitats, mainly on coastal sandy soils. In this paper we documented factors that promote large population increases of some species of *Agave* in the province of Almería, SE Spain. We hypothesized that invasion was mediated by soil quality, being sandy soils what enhances clonal reproduction of agaves in these new habitats. We also analysed the effects of agaves on native woody species and on community diversity in order to assess their effect on community functioning.

## METHODS

### Study sites and species

This work was carried out at two sites near the shoreline of the Mediterranean Sea in the Province of Almería, SE Spain (Fig. 1): Cabo de Gata Natural Park (36°50' N, 2°23' W) and Punta Entinas-Sabinar Nature Reserve (36°04' N, 2°42' W). Both sites are protected natural areas where agaves are invading native vegetation. Climate in both areas is Mediterranean semiarid, with average rainfall of 220 mm. Minimum temperatures are above 8 °C in winter and summers are warm, with temperatures exceeding 30 °C (Capel, 1990).

Dunes over clay soils and calcareous hardpans dominate the landscape in Cabo de Gata. The native community is a typical



Figure 1 Location of study sites in the Province of Almería, SE Spain. Cabo de Gata Natural Park and Punta Entinas-Sabinar Nature Reserve are shown with stars.

coastal matorral. The most common species are *Asparagus* spp. (Liliaceae) and *Thymus* spp. (Lamiaceae) along with *Helichrysum stoechas* (Asteraceae) and *Thymelaea hirsuta* (Thymelaeaceae). In 1940s and 1950s more than 600 ha of native matorral were replaced with mixed plantations of *Agave sisalana* and *A. fourcroydes* planted for fibre production. Plantations were abandoned 4 years later due to the low yield and the development of synthetic fibres (Martín-Galindo, 1988; Provansal & Molina, 1989) and were recolonized by native species. Plantations were located on clay soils and had initial densities of 4500 plants ha<sup>-1</sup> (Provansal & Molina, 1989). Agaves are currently growing on two main soil types that are easily identifiable: (1) sandy soil near coastal sand dunes; and (2) clay soil 4–5 km from the coast. Agaves on clay soil still show the plantation pattern whereas plant distribution on sandy soils is irregular, as agaves have escaped from the original geometrical design. The study area in Cabo de Gata was located approximately 4 km from the coast, where plantations on sandy and clay soils were adjacent to each other.

Punta Entinas-Sabinar is a dune field where *Agave americana* is spreading, interfering with the dominant native species, *Juniperus phoenicea* (Cupressaceae), and *H. stoechas*. Dunes are 7–8 m tall and the valleys in between are highly saline. At the valley bottoms clumps of *Pistacea lentiscus* (Plantaginaceae) and other halophytes like *Limonium* spp. (Plumbaginaceae) or *Inula crithmoides* (Asteraceae) are present, but no agaves are found. There are no records of the history of *A. americana* at this site, but it probably was introduced for sand dune stabilization.

### Reproduction and abundance of agaves

In both study sites no flowering agaves were found and clonal reproduction seems to be the main mechanism of propagation. Production of non-pollinated propagules (bulbils) predominates in floral stems and rhizome offshoots are easily identifiable in the soil. To assess the relationship between bulbil production and soil quality, 201 × 1 m quadrats were randomly placed on both sand and clay sites in Cabo de Gata. The number of non-established bulbils within each quadrat was recorded. All these bulbils were collected, dried and weighed. Additionally, six 5 × 5 m plots were randomly placed on each site to quantify the abundance of established bulbils, rhizome offshoots smaller than 20 cm, and larger individuals. Larger agaves were categorized in four size classes as (1) mature (dead or alive individuals with floral stem); (2) preadults (non-reproduced individuals taller than 100 cm); (3) juveniles (100–50 cm tall); and (4) recruits (50–20 cm tall). We used the number of living individuals per quadrat to estimate the current density of agaves on both soil types. Since *A. fourcroydes* and *A. sisalana* are mixed in plantations and species identification in the field was difficult, species identity was not included in the analyses.

Because in Punta Entinas-Sabinar *A. americana* grows exclusively on sand dunes, we only evaluated the most common propagation mechanism. One 1 × 1 m quadrat was randomly placed on the top of 20 invaded dunes and all established agaves were removed to identify their origin (rhizome or bulbils). We considered origin from rhizome when removed individuals were connected

with the same mother plant; otherwise, they were considered established bulbils.

### Impact on diversity and native species

To assess the impact of agaves on community diversity in Cabo de Gata, six 50 m-long transects were randomly laid out at both sand and clay sites. Cover of perennial, woody native species was recorded as the proportion covered by each species in the transect. Annual plants were not considered in these measurements because the species and their cover vary among seasons. Six additional transects were laid out on adjacent non-invaded dunes as control for the native community. All values of cover were standardized as percentages. Species cover data were used to calculate the Shannon-Weiner diversity ( $H'$ ) and the evenness ( $J'$ ) indices (Krebs, 1989).

In order to assess interaction strength between agaves and native species, we selected *H. stoechas* and *T. hirsuta*, the more common species within plantations at Cabo de Gata. We determined relative water content (RWC; Barrs & Weatherley, 1962), mean leaf area (LA; mm<sup>2</sup>) and specific leaf area (SLA; mm<sup>2</sup> mg<sup>-1</sup>) for both species. We hypothesized that values of RWC, LA and/or SLA within plantations must be lower than in non-invaded dunes. To determine RWC we collected one 10–15 cm long twig of 10 *H. stoechas* and *T. hirsuta* shrubs randomly selected at each site. Twigs were collected and the fresh mass (mg) was immediately measured. They were later stored in a dark humid chamber to allow rehydration until twig mass remained constant (saturated mass). Samples were then dried in a ventilated oven at 70 °C for 48 h and weighed again (dry mass). Ten undamaged leaves of *H. stoechas* and *T. hirsuta* were randomly collected from 10 shrubs to estimate LA and SLA. Leaf samples were digitized, placed in small paper bags and dried. Mean leaf area for each shrub was obtained from digitized images using the software Midebmp version 4.2 (Ordiales-Plaza, 2000). Due to their small leaf size *H. stoechas* and *T. hirsuta* dry leaves were weighed together for each shrub and the mass of a single leaf was estimated by dividing this total mass by the number of leaves. SLA for each plant was computed as the ratio between its average leaf area (mm<sup>2</sup>) and leaf mass (mg).

Because *H. stoechas* was a very common species in Cabo de Gata, 10 additional individuals were randomly selected on clay, sand, and non-invaded sites; 3–5 floral stems per individual were collected to determine stem length, stem dry mass, and number of inflorescences. In this species, the floral stem is a non-lignified structure that arises from a woody branch.

In Punta Entinas-Sabinar *H. stoechas* and *J. phoenicea*, the species sharing the top of dunes with *A. americana*, were chosen to evaluate the effects of agaves on native species. Seventeen *J. phoenicea* shrubs were selected and 10 mature fruits were randomly collected from different branches. Fresh mass, dry mass and water content were measured on each fruit. Fruit water content was computed as the difference between fresh and dry mass. These values were averaged for each shrub in order to perform statistical analyses. A further 12 *J. phoenicea* individuals were selected for RWC and SLA measurements as described above, but

to estimate SLA the leaf area was corrected by multiplying values by  $\pi/2$ , as leaves are nearly cylindrical (Cregg, 1992; Martínez-Ferri *et al.*, 2000). Alive agaves beneath selected *J. phoenicea* shrubs and 1 m around were counted, categorized in size classes and abundance of individuals in each size class was recorded. At this site, agaves were categorized as (1) mature (dead or alive individuals with floral stem); (2) preadults (non-reproduced individuals taller than 100 cm); (3) juveniles (100–50 cm tall); (4) recruits (50–20 cm tall); and (5) sprouts (smaller than 20 cm). Height and major and minor diameters of sampled *J. phoenicea* were also measured to include plant surface and volume as correction terms in the analyses of the effect of agaves.

Twenty *H. stoechas* shrubs growing with agaves (nearer than 30 cm) were selected in Punta Entinas-Sabinar and RWC, LA and SLA were estimated as described above. Twenty shrubs growing in isolation were used as control.

### Statistical analysis

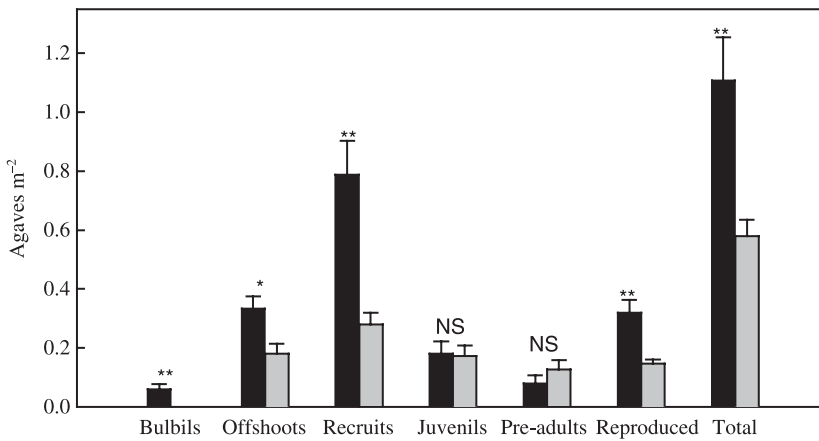
Variables related to abundance and reproduction of agaves on sand and clay in Cabo de Gata were compared using *t*-tests. Comparisons between  $H'$  indices were made using *t*-tests (Magurran, 1988), but the significance level ( $\alpha = 0.05$ ) was modified by Bonferroni's correction for simultaneous contrasts between the three sites (Neter *et al.*, 1996). Species cover within plantations on sand and clay, and the non-invaded dune community as well as RWC, LA and SLA and floral variables of *H. stoechas* and *T. hirsuta* were compared by one-way ANOVA. Where significances were found for species cover, these were further analysed using the posthoc Tukey test.

Reproductive (fruit dry mass and fruit water content) and functional variables (RWC, LA and SLA) measured on *J. phoenicea* in Punta Entinas-Sabinar were plotted against the abundance of agaves in each size class and dimensions of *J. phoenicea* shrubs (volume and surface, see above). Stepwise multiple linear regression methods were used in order to determine which variables affected *J. phoenicea* performance. RWC, LA, and SLA of *H. stoechas* with and without agaves in Punta Entinas-Sabinar were compared by *t*-tests. All data were log transformed prior to analysis.

## RESULTS

### Reproduction and abundance of agaves

Bulbil abundance on sand was nine times higher than on clay (120,000 ± 2210 vs. 14,000 ± 494 bulbils ha<sup>-1</sup>;  $t = 2.81$ , d.f. = 38,  $P < 0.01$ ). Bulbils were 30% heavier on average (1.54 ± 0.08 vs. 1.02 ± 0.09 g per bulbil;  $t = 2.45$ , d.f. = 102,  $P < 0.01$ ) on sandy soil. Total abundance of agaves, established bulbils, rhizome offshoots, recruits, and mature individuals were significantly greater on sand than on clay, but no differences were found for juvenile and preadult classes (Fig. 2). At both soil types, mortality was only recorded on mature reproduced individuals, and no dead individuals were detected in the smaller size classes. The estimated rate of successful bulbil establishment (abundance of released bulbils/number of established bulbils) was 1.3% on sand



**Figure 2** Abundances of established bulbils, rhizome offshoots, recruits, juvenile, preadults, reproducing, and total alive agaves at plantation on sand (black bars) and clay (grey bars) in Cabo de Gata. Data are means + 1 SE. Statistical differences between sites noted by \* $P < 0.05$  and \*\* $P < 0.01$ ; NS not significant.

|                               | Non-invaded               | Sand                      | Clay                      | F     | P      |
|-------------------------------|---------------------------|---------------------------|---------------------------|-------|--------|
| <i>Andryala ragusina</i>      | 1.62 ± 1.05               | 0.10 ± 0.07               | 0.00 ± 0.00               | 2.23  | 0.14   |
| <i>Artemisia barrelieri</i>   | NA                        | NA                        | 0.25 ± 0.17               | NA    | NA     |
| <i>Asparagus albus</i>        | 0.97 ± 0.93               | 0.73 ± 0.32               | 0.05 ± 0.05               | 0.70  | 0.51   |
| <i>Asparagus horridus</i>     | NA                        | 0.17 ± 0.17               | NA                        | NA    | NA     |
| <i>Fagonia cretica</i>        | NA                        | NA                        | 0.27 ± 0.23               | NA    | NA     |
| <i>Foeniculum vulgare</i>     | NA                        | 0.10 ± 0.10               | NA                        | NA    | NA     |
| <i>Helichrysum stoechas</i>   | 2.62 ± 1.37 <sup>a</sup>  | 12.50 ± 1.37 <sup>b</sup> | 4.60 ± 1.37 <sup>a</sup>  | 14.59 | < 0.01 |
| <i>Launaea arborescens</i>    | NA                        | NA                        | 0.03 ± 0.03               | NA    | NA     |
| <i>Lycium intricatum</i>      | 0.63 ± 0.63               | NA                        | NA                        | NA    | NA     |
| <i>Ononis natrix</i>          | 0.48 ± 0.25               | NA                        | NA                        | NA    | NA     |
| <i>Rubia peregrina</i>        | NA                        | 0.03 ± 0.03               | NA                        | NA    | NA     |
| <i>Thymelaea hirsuta</i>      | 7.38 ± 2.40               | 7.80 ± 0.99               | 4.95 ± 1.32               | 0.84  | 0.45   |
| <i>Thymus hyemalis</i>        | 0.67 ± 0.52               | 0.13 ± 0.13               | 0.28 ± 0.28               | 0.61  | 0.56   |
| <i>Ziziphus lotus</i>         | NA                        | NA                        | 0.07 ± 0.07               | NA    | NA     |
| Total cover by native species | 14.37 ± 2.25 <sup>a</sup> | 21.56 ± 0.95 <sup>b</sup> | 10.50 ± 1.20 <sup>a</sup> | 10.61 | < 0.01 |
| Total <i>Agave</i> spp. cover | 0.00 ± 0.00 <sup>a</sup>  | 34.37 ± 4.16 <sup>b</sup> | 10.87 ± 1.89 <sup>c</sup> | 5.15  | < 0.01 |

**Table 1** Percentage plant cover of species in the non-invaded dune community and *Agave* plantations on sand and clay in Cabo de Gata, Almería, Spain. Values are mean cover ± 1 SE. Table also shows results of ANOVA, and numbers in a row with different letters are significantly different (Tukey test;  $\alpha = 0.05$ ). Not applicable (NA) denotes that species was not encountered or analyses could not be done

and below 0.1% on clay. The current density of agaves on sand ( $11,600 \pm 1470$  individuals  $ha^{-1}$ ) differed significantly ( $t = 2.11$ , d.f. = 5,  $P = 0.04$ ) from the initial sowing density ( $4500$  individuals  $ha^{-1}$ ), but no differences between initial and current ( $5900 \pm 554$  individuals  $ha^{-1}$ ) densities were observed on clay ( $t = 0.96$ , d.f. = 5,  $P = 0.19$ ). These results indicate a positive population growth on sand and a stable population size on clay.

Rhizome offshoot abundance of *A. americana* was significantly greater than abundance of established bulbils ( $2.83 \pm 0.15$  vs.  $1.04 \pm 0.22$  individuals  $m^{-2}$ ) in Punta Entinas-Sabinar ( $t = 6.75$ , d.f. = 38,  $P < 0.01$ ), showing that rhizomes are the main propagation mechanisms of *A. americana* in this site, where mortality of established bulbils or rhizome sprouts were not detected within our samples.

### Impact on diversity and native species

#### Diversity

Eight native perennial woody species were recorded in the plantation on sand and clay, and seven in the non-invaded dune community. *Helichrysum stoechas* and *T. hirsuta* were the species

with highest percent cover at the three sites. Total cover by native woody species was higher in the plantation on sand than in the plantation on clay or the non-invaded dune community (Table 1). *H. stoechas* was the only species that showed significant differences in cover among sites, having higher cover in the plantation on sand (Table 1).

Native species assemblages growing within *Agave* plantations on sand ( $H'_{sand} = 0.40$ ) and clay ( $H'_{clay} = 0.47$ ) had lower diversity values than the non-invaded dune community ( $H'_{dune} = 0.65$ ). Diversity showed no differences between plantations on sand and clay ( $t = 0.71$ , d.f. = 48,  $P = 0.24$ ) nor between plantation on clay and non-invaded dune community ( $t = 1.52$ , d.f. = 74,  $P = 0.07$ ), but significant differences were detected between non-invaded dune community and plantation on sand ( $t = 2.55$ , d.f. = 64,  $P < 0.01$ ). The non-invaded dune community had also the highest value of evenness ( $J'_{dune} = 0.71$ ), while evenness within plantations was lower ( $J'_{sand} = 0.43$ ;  $J'_{clay} = 0.52$ ).

#### Functional and physiological plant data

Values of RWC for *H. stoechas* within plantations in Cabo de Gata were significantly higher than at the non-invaded community,

**Table 2** Relative water content (RWC), mean leaf area (LA), and specific leaf area (SLA) of *H. stoechas* and *Thymelaea hirsuta* as well as length (SL) and mass (SW) of floral stems, and the number of floral heads per inflorescence (NI) of *H. stoechas* in the non-invaded dune community and in plantations of agaves on sand and clay in Cabo de Gata, Almería, Spain. Values are means  $\pm$  1 SE. Table also shows results of ANOVA and numbers in a row with different letters are significantly different (Tukey test;  $\alpha = 0.05$ )

|                    |     | Non-invaded                   | Sand                          | Clay                          | F     | P      |
|--------------------|-----|-------------------------------|-------------------------------|-------------------------------|-------|--------|
| <i>H. stoechas</i> | RWC | 0.63 $\pm$ 0.01 <sup>a</sup>  | 0.71 $\pm$ 0.02 <sup>b</sup>  | 0.74 $\pm$ 0.01 <sup>b</sup>  | 13.14 | < 0.01 |
|                    | LA  | 14.5 $\pm$ 1.1 <sup>a</sup>   | 15.6 $\pm$ 1.3 <sup>a</sup>   | 9.6 $\pm$ 0.9 <sup>b</sup>    | 8.00  | < 0.01 |
|                    | SLA | 11.1 $\pm$ 0.6 <sup>a</sup>   | 9.3 $\pm$ 0.4 <sup>a</sup>    | 6.9 $\pm$ 0.3 <sup>b</sup>    | 14.70 | < 0.01 |
|                    | SL  | 16.3 $\pm$ 0.6 <sup>a</sup>   | 20.1 $\pm$ 1.3 <sup>b</sup>   | 14.5 $\pm$ 0.8 <sup>a</sup>   | 8.67  | < 0.01 |
|                    | SW  | 230.2 $\pm$ 23.9 <sup>a</sup> | 295.3 $\pm$ 12.6 <sup>b</sup> | 182.7 $\pm$ 15.5 <sup>a</sup> | 4.45  | 0.02   |
|                    | NI  | 17.5 $\pm$ 1.3 <sup>ab</sup>  | 21.2 $\pm$ 2.7 <sup>b</sup>   | 14.5 $\pm$ 1.4 <sup>a</sup>   | 4.42  | 0.02   |
| <i>T. hirsuta</i>  | RWC | 0.53 $\pm$ 0.03 <sup>a</sup>  | 0.62 $\pm$ 0.03 <sup>ab</sup> | 0.63 $\pm$ 0.01 <sup>b</sup>  | 4.52  | 0.02   |
|                    | LA  | 5.1 $\pm$ 0.5 <sup>a</sup>    | 3.2 $\pm$ 0.2 <sup>b</sup>    | 3.20 $\pm$ 0.15 <sup>b</sup>  | 11.32 | < 0.01 |
|                    | SLA | 4.3 $\pm$ 0.4                 | 4.1 $\pm$ 0.7                 | 3.45 $\pm$ 0.20               | 0.87  | 0.429  |

**Table 3** Relative water content (RWC), leaf area (LA), and specific leaf area (SLA) of *H. stoechas* growing with and without *Agave americana* in Punta Entinas, Almería, Spain. Values are means  $\pm$  1 SE

|     | With agaves     | Without agaves  | t    | P     |
|-----|-----------------|-----------------|------|-------|
| RWC | 0.72 $\pm$ 0.05 | 0.71 $\pm$ 0.09 | 0.13 | 0.89  |
| LA  | 20.5 $\pm$ 3.9  | 16.9 $\pm$ 2.6  | 2.02 | 0.05* |
| SLA | 12.7 $\pm$ 1.5  | 13.0 $\pm$ 1.4  | 0.46 | 0.65  |

Significant differences between groups (*t*-test) indicated by \* $\alpha = 0.05$ .

but no differences were found between plantations on sand and clay (Table 2). Significant differences in RWC for *T. hirsuta* were only observed between the plantation on clay and the non-invaded dune community, being higher in the latter (Table 2).

Mean LA and SLA of *H. stoechas* within the plantation on clay were significantly lower than at the plantation on sand or the non-invaded dune community (Table 2). Values of LA of *T. hirsuta* showed no differences between plantations, but shrubs in the non-invaded community showed significantly higher values of LA than shrubs in plantations. SLA of *T. hirsuta* showed no differences among the three sites (Table 2).

Floral stems of *H. stoechas* from the plantation on sand were significantly longer and heavier than those on the non-invaded dune community or the plantation on clay. The number of inflorescences was also higher in the plantation on sand than in the other two sites; however, a significant difference was only found between the plantations on sand and clay (Table 2).

In Punta Entinas-Sabinar, only the abundance of *A. americana* sprouts (smaller than 20 cm) was significantly associated with fruit dry mass, fruit water content, and SLA of *J. phoenicea*. No relationships were detected for the other size classes of *A. americana* nor for *J. phoenicea* surface and volume. Fruit dry mass (Fig. 3A) and fruit water content (Fig. 3B) showed strong negative relationships with abundance of *A. americana* sprouts; in contrast, RWC of *J. phoenicea* was not affected and SLA showed only a weak, marginal relationship with the abundance of sprouts (Fig. 3C).

In Punta Entinas-Sabinar, no differences were found for RWC or SLA of *H. stoechas* growing with and without agaves (Table 3). LA values showed only marginal differences, being higher for individuals growing with agaves (Table 3).

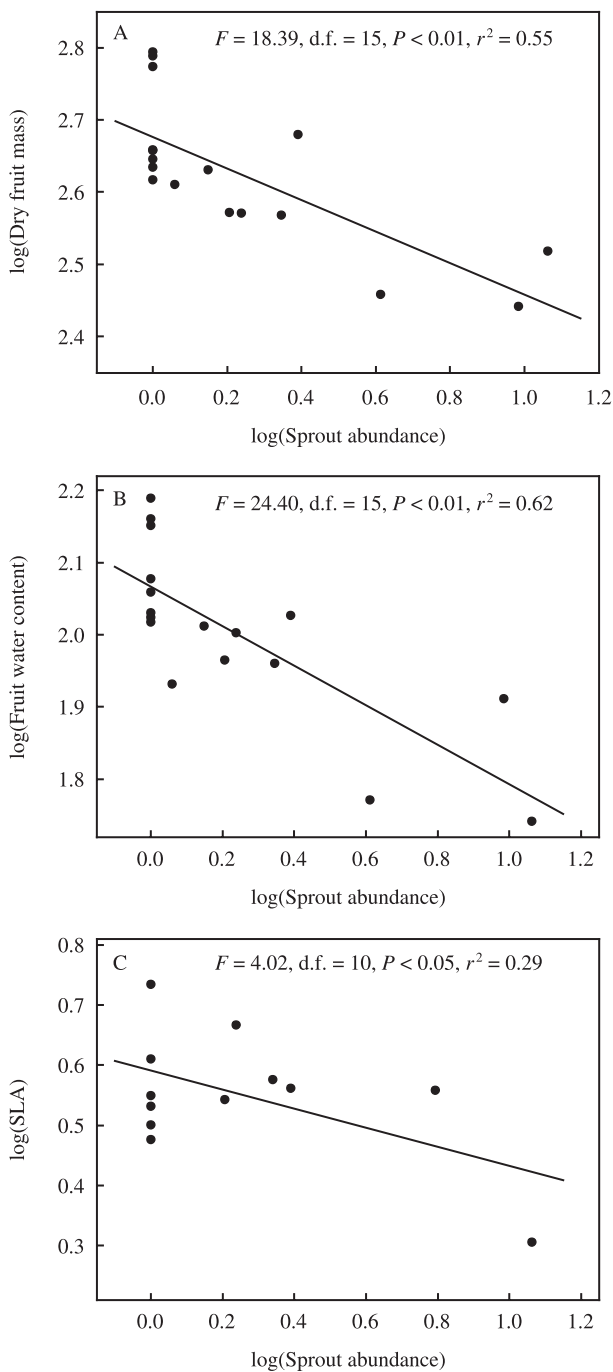
## DISCUSSION

### Agave invasion

The high abundance of established bulbils and the high production of rhizome offshoots at both study sites suggest that *Agave* populations in SE Spain are expanding by means of clonal reproduction, especially on sandy soils. On both sand and clay soil types, mortality seems to affect only mature individuals, and the absence of dead individuals in the smaller size classes suggests that agaves die only after bulbil production. Although this study was focused from a natural experiment perspective, and only one site colonized by each *Agave* species was considered, these results suggest that *Agave* spp. have a high potential to invade arid environments of SE Spain.

In Cabo de Gata, the high production of bulbils and rhizome offshoots in *Agave* plantations on sand, compared to the plantation on clay, indicates that sandy soils have important effects on the colonization success and population growth of agaves. The high number and quality (in terms of biomass) of bulbils, and the higher number of reproducing agaves suggest that sand enhances the potential of clonal reproduction in these species. Both the abundance of rhizome offshoots and the number of established bulbils indicate that sand is easier to colonize, and would explain the huge difference in density between the initial sowing and the current abundance of agaves on sand. In Punta Entinas-Sabinar, the more common reproductive mechanism was rhizome offshoot production. The high abundance of rhizome offshoots at the dune tops suggests a large deployment of *A. americana* roots, from which these sprouts are developed.

Although vegetative multiplication of agaves for agricultural practices in Mexico is made via bulbils or rhizomes (Infante *et al.*, 2003), the main reproductive mechanism in nature is seed production (Nobel, 1988; Arizaga & Ezcurra, 2002). However, in their native habitats the rates of successful establishment of *Agave* propagules are very low (Arizaga & Ezcurra, 2002; González-Iturbe *et al.*, 2002). In SE Spain, in contrast, agaves show vegetative reproduction as the main mechanism of population growth, and this reproductive trait may increase the potential of agaves as invaders of nearby communities. In their native habitats the species of *Agave* mainly establish on clay-rocky soils (Nobel, 1988). However, the stable size of the *Agave* plantation on clay in SE Spain suggests that this substrate does not affect its population



**Figure 3** Relationships between fruit dry mass (A), fruit water content (B), and SLA (C) of *Juniperus phoenicea* shrubs and the abundance of *Agave americana* sprouts in Punta Entinas-Sabinar Nature Reserve, Almería. Each figure includes the result of linear regression analysis.

growth rates. On the other hand, the high clonal reproduction of agaves on sandy soils suggests that this soil type provides a niche dimension that enhances their population growth rates. Therefore, we suggest that a niche opportunity release (Tilman, 1982) could be promoting the invasive behaviour of agaves in SE Spain.

### Impact of agaves on diversity and native species

Abandoned *Agave* plantations in Mexico are rapidly recolonized by other species and the new assemblages reach diversity values similar to undisturbed natural habitats (González-Iturbe *et al.*, 2002). Three factors determine this situation: the low population growth of agaves, their low negative interference with other species, and the facilitative processes mediated by agaves in the early succession (González-Iturbe *et al.*, 2002). In SE Spain, the analysed plant community attributes suggest that the woody species assemblage within the plantation on clay could evolve as abandoned plantations in Mexico. However, more data and experimental approaches are needed to make predictions about its recovery.

Because the  $H'$  index is sensitive to both species richness and evenness (Stirling & Wilsey, 2001), our results suggest that the occurrence of *Agave* on sand may modify the proportional cover of some species rather than the species richness. Within *Agave* stands on sand, relative cover by native species was larger than at the other sites, but a remarkable increase in the cover was observed in *H. stoechas* rather than in other species. Measurements of RWC, LA and SLA indicated no better physiological status in *H. stoechas* at the *Agave* plantation on sand compared to the plantation on clay and the non-invaded community. However, the length and dry mass of floral stems, and the number of floral heads per inflorescence indicated that growth and reproduction of *H. stoechas* would be better within this plantation, in contrast to the plantation on clay and the non-invaded dune community. This suggests positive effects of *Agave* spp. on *H. stoechas* performance, which would increase its abundance and obtain a dominant advantage over other native species at the plantation on sand.

In Cabo de Gata, the RWC of *T. hirsuta* indicated a better water status within the plantations than in the non-invaded dune community, while the SLA showed no differences among sites. However, the mean LA for this species decreased within the plantations, suggesting that perhaps nutrients were limiting growth. Since the efficiency of  $\text{CO}_2$  fixation depends on the photosynthetic surface (Mooney *et al.*, 1981), the reduction of leaf area within plantations suggests a negative effect of agaves on *T. hirsuta* growth. In general, competition for space is the main negative effect of invasive plants on native species (Almasi, 2000; Case & Crawley, 2000), but competition for water and nutrients is also important (Shea & Chesson, 2002). The cover of *T. hirsuta* at the plantation on sand and in the non-invaded dune community were similar, suggesting that space is not a limiting resource; but the reduction of leaf area suggests that competition for nutrients rather than for water could limit *T. hirsuta* growth, as the relative water content was higher at plantations than at the non-invaded dune community.

The negative relationships between fruit dry mass, fruit water content and SLA of *J. phoenicea* and the abundance of *A. americana* sprouts in Punta Entinas suggests a strong competition for resources at the top of dunes. These results suggest density- or biomass-dependent competitive effects of agaves on this native plant, as *A. americana* tends to occupy the space with a dense

network of rhizome offshoots that could draw resources and hence affect the status of this native species. On the other hand, the RWC and the SLA of *H. stoechas* with and without agaves indicate that *A. americana* does not affect its water status. As in the Cabo de Gata site, the effects of *A. americana* on *H. stoechas* are neutral or positive if variables such as LA are considered, suggesting that rooting depth may determine the intensity of competition between agaves and their neighbours.

## CONCLUSIONS

Our results suggest that sand may improve the population growth rates of *Agave* in SE Spain by increasing their clonal reproduction. This population growth suggests that these species are potential invaders of nearby communities, implying a risk for community functioning of study sites, which are protected areas.

In opposition to our expectations, the effects of *Agave* spp. on native species were negative, positive or neutral. These results suggest that competitive or facilitative effects of agaves could 'switch' depending on the habitat type, the concerned species, and/or the parameter used to measure the effect.

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## REFERENCES

- Almasi, K.N. (2000) A non-native perennial invades a native forest. *Biological Invasions*, **2**, 219–230.
- Alvarez, M.A. & Cushman, J.H. (2002) Community-level consequences of a plant invasion: effects on three habitats in coastal California. *Ecological Applications*, **12**, 1434–1444.
- Arizaga, S. & Ezcurra, E. (1995) Insurance against reproductive failure in a semelparous plant: bulbil formation in *Agave macroacantha* flowering stalks. *Oecologia*, **101**, 329–334.
- Arizaga, S. & Ezcurra, E. (2002) Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette. *American Journal of Botany*, **89**, 632–641.
- Barrs, H.D. & Weatherley, P.E. (1962) A re-examination of the relative turgidity technique for estimating water deficits in leaves. *Australian Journal of Biological Sciences*, **15**, 413–428.
- Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, **290**, 521–523.
- Capel, J.J. (1990) *Climatología de Almería. Cuadernos Monográficos 7*. Instituto de Estudios Almerienses, Almería, Spain.
- Case, C.M. & Crawley, M.J. (2000) Effect of interspecific competition and herbivory on the recruitment of an invasive alien plant: *Conyza sumatrensis*. *Biological Invasions*, **2**, 103–110.
- Cregg, B.M. (1992) Leaf area estimation of mature foliage of *Juniperus*. *Forest Science*, **38**, 61–67.
- Dean, W.R.J. & Milton, S.J. (2000) Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents? *Journal of Arid Environments*, **45**, 305–314.
- Gimeno, I. & Vilà, M. (2002) Recruitment of two *Opuntia* species invading abandoned olive groves. *Acta Oecologica*, **23**, 239–246.
- González-Iturbe, J.A., Olmsted, I. & Tun-Dzul, F. (2002) Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. *Forest Ecology and Management*, **167**, 67–82.
- Infante, D., González, G., Peraza-Echeverría, L. & Keb-Llanes, M. (2003) Asexual genetic variability in *Agave fourcroydes*. *Plant Science*, **164**, 223–230.
- Jordan, P.W. & Nobel, P.S. (1979) Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the northwestern Sonora desert. *American Journal of Botany*, **66**, 1079–1084.
- Krebs, C.J. (1989) *Ecological methodology*. Harper & Row, New York.
- Lockwood, J.L., Simberloff, D., McKinney, M.L. & von Holle, B. (2001) How many, and which, plants will invade natural areas? *Biological Invasions*, **3**, 1–8.
- Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton.
- Martínez-Ferri, E., Balaguer, L., Vallardes, F., Chico, J.M. & Manrique, E. (2000) Energy dissipation in drought-avoiding and drought-tolerant tree species at midday during the Mediterranean summer. *Tree Physiology*, **20**, 131–138.
- Martín-Galindo, J.L. (1988) *Almería, paisajes agrarios, espacio y sociedad*. Universidad de Valladolid, Valladolid, Spain.
- McAuliffe, J.R. (1984) Sahuaro–nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia*, **64**, 319–321.
- Mooney, H.A., Field, C., Gulmon, S.L. & Bazzaz, F.A. (1981) Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. *Oecologia*, **50**, 109–112.
- Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. (1996) *Applied linear statistical models*. McGraw-Hill, Boston.
- Nobel, P.S. (1988) *Environmental biology of agaves and cacti*. Cambridge University Press, New York.
- Ordiales-Plaza, R. (2000) *Midebmp, Version 4.2*. Estación Experimental de Zonas Áridas, Almería, Spain.
- Provansal, D. & Molina, P. (1989) *Campo de nîjar: cortijeros y areneros*. Instituto de Estudios Almerienses, Almería, Spain.
- Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.
- van Sittert, L. (2002) 'Our irrepressible fellow-colonist': the biological invasion of prickly pear (*Opuntia ficus-indica*) in the Eastern Cape c. 1890–c. 1910. *Journal of Historical Geography*, **28**, 397–419.
- Stirling, G. & Wilsey, B. (2001) Empirical Relationships between species richness, evenness, and proportional diversity. *American Naturalist*, **158**, 286–299.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton.

- Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G. & Vazquez, E. (1991b) Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science*, **2**, 15–20.
- Valiente-Banuet, A., Vite, F. & Zavala-Hurtado, J.A. (1991a) Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. *Journal of Vegetation Science*, **2**, 11–14.
- de Viana, M.L. (1996) Spatial distribution of *Trichocereus pasacana* (Cactaceae) in relation with available space and the seed bank. *Journal of Tropical Biology*, **44**, 95–103.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. & Westbrooks, R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, **21**, 1–16.
- Williamson, M. (1996) *Biological invasions*. Chapman & Hall, London.