

Site-specific reproductive performance of an invasive fleshy-fruited tree in remnant grasslands of the Argentinean Pampas

S M ZALBA & M R AMODEO

GEKKO (Grupo de Estudios en Conservación y Manejo), Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, Bahía Blanca, Argentina

Received 10 October 2014

Revised version accepted 13 May 2015

Subject Editor: Stephen Novak, Boise, USA

Summary

Prunus mahaleb (Saint Lucie's cherry) is a fleshy-fruited small rosaceous tree, native to the Mediterranean region that has been extensively used as a rootstock species for commercial orchard trees. It has been widely introduced in several countries, becoming invasive in many regions, including the Pampas region of southern Argentina. We studied the reproductive performance of trees spontaneously growing in natural grasslands inside a protected area, estimating age at first reproduction and analysing changes in fruit production, age, canopy volume and basal stem diameter associated with different soil types: rock crevices on hillsides, deep soils in valleys and deep soils in stream-side habitats. Fruit production starts at the age of 3–6 years, and it can be abundant, even for

young plants. We found evidence that fecundity is related to plant size, and that the age at which individuals reach a particular size and begin fruiting differs depending on the soil type where they grow. Trees in the study area show an order of magnitude increase in fruit production on reaching ages from 7 to 10 years for plants growing in deep soils at stream-side habitats and 13–16 years for plants growing in rock crevices. Invasive trees should be felled before they reach a basal stem diameter of *c.* 9 cm to avoid this increase in propagule pressure. Considering that the age at which this stage is reached depends on soil type, the streams could act as dispersal corridors for the spread and invasion of this species.

Keywords: invasive species, *Prunus mahaleb*, fecundity, dispersal, nature reserve, management, allometry.

ZALBA SM, AMODEO MR (2015). Site-specific reproductive performance of an invasive fleshy-fruited tree in remnant grasslands of the Argentinean Pampas. *Weed Research* **55**, 546–554.

Introduction

During their growth, plants allocate biomass to various structures and functions, among them reproduction. The relationship between the accumulation of biomass and its allocation is the core of plant life-history strategies (Weiner *et al.*, 2009). Such allocation strategies are often considered to be genetically determined, and many of them follow allometric trajectories, being therefore a function of plant size (Climent *et al.*, 2008). Because

resources that are allocated to one function or organ are not available to others, allocation implies trade-offs (Weiner, 2004). One such trade-off occurs between size and the age at which the organism reaches sexual maturity. The life-history strategy of an individual is expected to reflect some balance between the benefits of reaching reproductive maturity earlier vs. growing larger before reproducing (Forrest & Miller-Rushing, 2010). Environmental features can obscure this trade-off, with individuals growing in high-quality habitats being larger at

maturity or reaching it earlier than those growing in other habitats (van Noordwijk & de Jong, 1986). If allocation to plant structures involved in resource capture or reproduction is allometric, then any environmental factor affecting plant size will also alter allocation patterns (Weiner, 2004; Hulme, 2008). Through the ontogeny of any individual plant species, the average duration of developmental stages is genetically fixed, but individuals may in fact reach a certain stage at different chronological ages depending on environmental conditions (Gatsuk *et al.*, 1980). While some allocation patterns show plasticity at any given size, others are characterised by relatively fixed allometric trajectories, varying primarily in the speed at which the trajectory is travelled in different environments. Some of the plasticity in resources allocation reported in the literature turns out to be simply a result of the interaction between individual size and environmental conditions (Weiner, 2004). This phenomenon has been called 'apparent plasticity' and can be better understood as allometric growth and changes in growth rate, rather than as a real plasticity in the allocation of resources (Weiner *et al.*, 2009).

A high relative allocation of resources into reproductive output has been cited as one of the features commonly associated with invasive plant species (Pyšek & Richardson, 2007). A small portion of the species that are accidentally or intentionally introduced into areas outside their native range dramatically increases their abundance and distribution, developing what is defined as a biological invasion (Williamson, 1996). Several major hypotheses have been proposed to explain this phenomenon, including greater phenotypic plasticity in invasive species (Richardson & Pyšek, 2006; Jeschke *et al.*, 2012). However, the effect of variations in allometric growth and plasticity on plant invasions remains poorly explored, and data on this issue are scarce for long-lived iteroparous plants (Weiner *et al.*, 2009). More knowledge in this area may enable better management decisions in the context of biological invasions.

Propagule pressure and local dispersal have been shown to increase the chance for an exotic species to successfully establish and invade, even in poor habitats (Sebert-Cuvillier *et al.*, 2009; Simberloff, 2009). For long-lived plants, such as trees, seed production has been usually considered to have a low influence on population growth, compared with other demographic parameters, like the survival of established adult individuals (Silvertown *et al.*, 1993, 1996). Nevertheless, sensitivity and elasticity analyses of matrix population models have suggested that fecundity is more important in affecting the population dynamics in populations with high growth rate (Silvertown *et al.*, 1993). This is often the case for invasive alien species, at least

at the phase of range expansion, when seed production may be a determinant of invasive success. Spatially explicit modelling has helped to identify seed pressure as a key component of invasive plants expansion rates, with seed production, germination capacity and seedling survival as the most sensitive components for explaining the extent of invasion (Sebert-Cuvillier *et al.*, 2008, 2009).

Prunus mahaleb L. (Saint Lucie's or Mahoma's cherry) is a small, deciduous, rosaceous tree, native to central and southern Europe, north-western Africa and west-central Asia (Herrera & Jordano, 1981). Because of its showy flowers, variety of growth habits, fast development, adaptability to a wide variety of soils and climates and resistance to pests, *P. mahaleb* is frequently used as a rootstock for orchard trees, as an ornamental plant and also for wood production (Bass *et al.*, 2006). It has been widely introduced and has become invasive in several countries. In Argentina, it has spread over remnant grasslands at the Ernesto Tornquist Provincial Park, one of the few protected areas of the whole Pampas ecoregion, where individuals are commonly found in dense populations associated with streams and scattered stands can also be found on hillsides (Zalba & Villamil, 2002; Amodeo & Zalba, 2013). The species shows a great adaptability to different types of soils, being found both in deep soils and in crevices on rocky outcrops.

In this study, we studied the development and fecundity of *P. mahaleb* trees invading native grasslands in southern Argentine Pampas using an allometric approach. We expected *P. mahaleb* fecundity to be strongly related with size and the time (the calendar age) that individuals take to reach certain state of development (a given size or fruit crop) and to differ depending on the soil type where a plant grows. We discuss potential implications of variations in reproductive age and fecundity on *P. mahaleb* range expansion and propose specific management strategies to control this invasive tree.

Materials and methods

Reproductive biology of the study species

Prunus mahaleb requires high light intensity and has a prostrate to vertical growth habit (0.5–10 m height), depending on local conditions (Kollmann & Pflugschaupt, 2001). Within its native range, the species can be found growing on shallow and rather poor soils, from the vicinity of streams to dry hillsides at mid-elevations (1250–1900 m asl, Herrera & Jordano, 1981). Corymbs of 3–10 small white flowers, with numerous stamens, are produced by mid-spring

(Gutián *et al.*, 1992; Prada & Arizpe, 2008; Amodeo & Zalba, 2015). Jordano (1993) described *P. mahaleb* populations in south-eastern Spain as functionally gynodioecious, with partial self-compatibility. Within this schema, any given population will include individuals with hermaphroditic flowers (functional hermaphrodites) and others with androsterile flowers (functional females) that require cross-fertilisation to achieve maximum fruit set (Gutián *et al.*, 1992; Jordano, 1993). Bees (Hymenoptera: Andrenidae, Halictidae, Apidae) and flies (Diptera: Calliphoridae, Tachinidae, Syrphidae) are its main pollen visitors within its native range (Gutián *et al.*, 1992; Jordano, 1993; Marañón *et al.*, 2004), while *Apis mellifera* (Hymenoptera: Apidae) and *Astylyus quadrilineatus* (Coleoptera: Melyridae) are the most frequent flower visitors at the study site, followed by others belonging to Lepidoptera, Hymenoptera, Diptera and Coleoptera (MR Amodeo personal observation). Production and ripening of fleshy fruits take place during *c.* 2 months in late spring and early summer, both in Europe and in the Argentine Pampas (Marañón *et al.*, 2004; Prada & Arizpe, 2008; Amodeo & Zalba, 2015). One-seeded drupes, bright black when ripe, 8 mm in diameter and with a sugary water-rich pulp are held in auxiliary clusters of one to ten fruits (Herrera & Jordano, 1981; Jordano, 1995). At least 28 bird species, four mammals and one lizard have been recorded feeding on *P. mahaleb* fruits in its native range of distribution (Jordano, 1995; Jordano & Schupp, 2000). Similar numbers of animals manipulate *P. mahaleb* fruits in our study area: 20 bird species, seven mammal species and one ant species.

Study area

This study was carried out at the Ernesto Tornquist Provincial Park, which covers an area of *c.* 6700 ha of mountain grasslands in the southern Argentine Pampas (38° 3.90'S; 61° 58.33'W). This reserve is recognised as one of the few protected areas of the whole ecoregion that includes remnant grasslands in good conservation status (Zalba & Villamil, 2002; Bilenca & Miñarro, 2004; de Villalobos & Zalba, 2010). The climate is temperate, with a mean annual temperature of 14°C and wide annual and daily fluctuations. The annual precipitation is around 800 mm, mostly concentrated in spring and part of the summer (Burgos, 1968). The park includes 37 endemic species, and a high proportion of the plant diversity present in the Pampas (Long & Grassini, 1997; Zalba & Villamil, 2002; Bilenca & Miñarro, 2004). The vegetation is dominated by steppe (including *Stipa* spp., *Nassella* spp., *Piptochaetium* spp., *Festuca* spp. and *Briza* spp., Long & Grassini, 1997; de Villalobos & Zalba, 2010) alternating with

rocky outcrops. Exotic woody plants can be found growing in small plantations, spontaneous forests or as isolated individuals (Zalba & Villamil, 2002). In particular, humid habitats are located in valleys and canyons, where *P. mahaleb* individuals are commonly found scattered or aggregated in stands of different size. The densest populations are associated with riparian habitats, although smaller stands can also be found on rocky hillsides. Sampled trees were located between 400 and 550 m asl, on foothill valleys and by temporary streams, growing either in deep soils or in rock crevices.

Sampling design and data analysis

Age-size allometry

Linear models were constructed to explore how basal stem measurements relate to canopy size and plant age. We recorded basal stem diameter (*BSD*) in cm, estimated canopy volume (*CNPYVOL*) in m³ and age of the trees (*A*) in years, by counting annual tree rings in cross sections of basal stems, for a sample of 75 *P. mahaleb* trees felled during invasive species control activities. Canopy volume was calculated as an ellipsoid using the difference between maximum height and the height of the first canopy branch as the vertical axis, and the maximum canopy diameter and its perpendicular as the horizontal axes. We recorded the soil type where plants were growing using three categories:

- Rock crevices on hillsides (RC): a plant that grew inside a crevice limiting its stem and root growth.
- Deep soils in valleys (SV): no rocky substrate surrounding the stem or roots and more than 20 m away from the nearest stream.
- Deep soils in stream-side habitats (SS): no rocky substrate and closer than 20 m from the next stream.

The trees were selected at random from sites with specific characteristics, providing equal sample sizes and including the full range of tree sizes in each soil type (*N* = 26, 22 and 26 for RC, SV and SS respectively). We performed regression analyses and ANCOVA to explore the relationship between tree characteristics and soil type. According to normal probability plots of model residuals, variable transformations were applied in order to fulfil homoscedasticity and normality assumptions ($\sqrt{}$ for *CNPYVOL*, decimal logarithm for *BSD* and age).

Fecundity and developmental stages

During early December, when fruits begin to ripen, the total number of ripe and unripe fruits produced per plant (crop size) was estimated from a sample of trees growing in rock crevices (*N* = 59) and in deep soils at

stream-side habitats ($N = 31$). Trees were randomly selected, providing that the full range of tree sizes was included in the sample. For small plants ($BSD < 10$ cm), the number of fruits was recorded by a complete count on all branches, whereas for bigger trees, it was calculated by counting all fruits on a sample of branches representing a portion of the fruited canopy, and then extrapolating to the total crown volume. For each tree, basal stem measurements were registered to estimate its age using *Age*–*BSD* linear models. These models were used separately for trees growing in different soil types. We performed generalised linear models with a negative binomial distribution in order to analyse the relationship of fecundity with respect to basal stem diameter and age (both log-transformed). We used a likelihood ratio test to test the model assumptions, comparing the negative binomial distribution with a Poisson model as a null model. The models included *BSD*, soil type and the interaction between them. The interaction term between soil type factor and *BSD* was also analysed using a likelihood ratio test (Bolker, 2008) for a subsample of under 30-cm *BSD* plants (with an equal representation for both soil types).

Plants were categorised in three different developmental stages: stage 1 (non-reproductive plants), stage 2 (reproductive plants with crop sizes under 1000 fruits), stage 3 (reproductive plants with crop sizes over 1000 fruits). The transition between stages 1–2 was defined as maturity (the start of reproduction). Transition between stages 2–3 was identified with a

remarkable increase in crop sizes exceeding 1000 fruits. We modelled fruit presence–absence data as a function of basal stem diameter and age using logistic regression analysis for a subsample of 35 under 10-cm *BSD* trees for transition 1–2, and for the full sample of trees for transition 2–3. The influence of soil type in the model was compared using a likelihood ratio test. Because small plant sizes were not sufficiently represented for all soil types, we analysed age and size at maturity for the full data set. For each transition period, we established starting, mid (average) and final sizes as the *BSD*/*age* at which the probability of belonging to the next stage (being mature/bearing thousands of fruits) was 10%, 50% and 90% respectively. All analyses and graphics were performed using R (R-Core-Team, 2012) and the package *ggplot2* (Wickham, 2009).

Results

Age–*size* allometry

The basal stem diameter (*BSD*) is a good estimator of canopy size for trees growing in all soil types. Canopy volume and basal stem diameter were strongly related ($\sqrt[10]{CNP\bar{Y}} = 0.5 + 0.33 * \log(BSD)$, $F_{(3,70)} = 377$, $P < 0.0001$, $R^2 = 0.94$), and no significant interaction with soil type factor was detected in ANCOVA ($F_{(68,70)} = 0.369$, $P = 0.693$, Fig. 1A). Basal stem diameter is also a good predictor of plant age (full model $F_{(5,68)} = 110.7$, $P < 0.0001$, $R^2 = 0.88$). In this case, interaction with soil

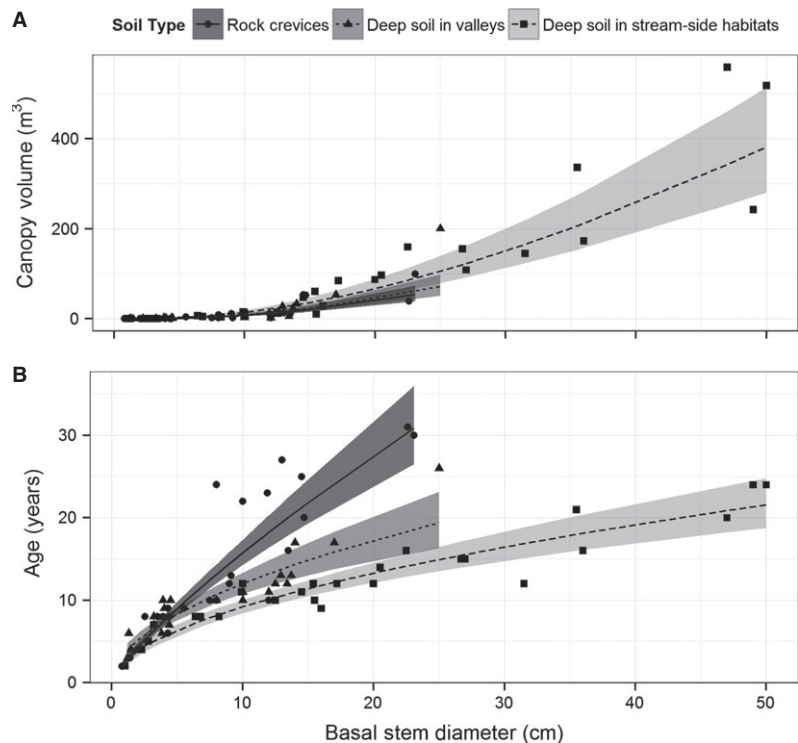


Fig. 1 Relationship between canopy volume (A), age (B) and basal stem diameter for 75 *P. mahaleb* individuals growing in three different soil types at the Ernesto Tornquist Provincial Park, Argentina. Grey areas around curves represent 95% confidence interval.

type was statistically significant in ANCOVA ($F_{(68,70)} = 11.65$, $P < 0.0001$), suggesting a model with different slopes for each soil type (Fig. 1B, Table 1): for plants in rock crevices (RC), $\log(A) = 0.9015 + 0.8056 * \log(BSD)$; for plants growing in deep soils in valleys (SV), $\log(A) = 1.2775 + 0.5248 * \log(BSD)$; for plants growing in deep soils at stream-side habitats (SS), $\log(A) = 1.002 + 0.5289 * \log(BSD)$. Contrasts among model coefficients showed significant differences, except for the slopes corresponding to deep soils (SV and SS models, $t = 0.061$, $P = 0.951$). As with basal stem diameter and plant age, the relationship between canopy volume and plant age was also affected by the interaction with soil type (full model $F_{(5,68)} = 131.4$, $P < 0.0001$, $R^2 = 0.90$, interaction term $F_{(68,70)} = 10.621$, $P < 0.0001$).

Fecundity

The total number of fruits per plant ranged from three to maximum values of 110 100 and 130 560, the last figures corresponding to a 55-cm basal stem diameter tree growing in a rock crevice (estimated age: 62 years) and a 43-cm *BSD* tree in deep soil at a stream-side habitat (estimated age: 23 years). A strong relationship was also detected between the total number of fruits produced by a plant and its basal stem diameter (Table 2, Fig. 2A). The likelihood ratio test indicated that a negative binomial distribution was more appropriate than the Poisson distribution (null model) for this particular data set ($\chi^2_{(3)} = 372099.7$, $P < 0.0001$). We found weak evidence favouring the full model considering *BSD* and soil type as predictor variables (interaction term not significant, LRT = 2.18, $P = 0.14$), thus we chose the simplest model: $\log(\text{Nr. of fruits}) = 0.52 + 2.99 * \log(BSD)$ ($\chi^2_{(88,89)} = 342.73$, $P < 0.0001$).

Interaction with soil type was highly significant in the analysis of the relationship between the total number of fruits produced per plant and its age, ($\chi^2_{(86,87)} = 22.99$, $P < 0.0001$). Thus, in this case, we chose the full model considering different curves for the plants growing in rock crevices or in deep soils ($\chi^2_{(88,89)} = 342.73$, $P < 0.0001$, Table 3). Plants growing in deep

Table 2 Generalised linear model coefficient estimates for a negative binomial distribution relating the total number of fruits produced by plant and their basal stem diameter (*BSD*) for 90 *P. mahaleb* individuals growing in different soil types at the Ernesto Tornquist Provincial Park, Argentina

Coefficient	Estimation	SE	IC(95%) _{inf}	IC(95%) _{sup}
Intercept	0.5215	0.29	-0.114	1.21
Log(<i>BSD</i>)	2.9926	0.115	2.72	3.257

soils reached high crop sizes faster than those growing in rock crevices (Fig. 2B).

Maturity was affected both by basal stem diameter (likelihood ratio test, Res. Dev. = 18.6, d.f. = 33, $P < 0.0001$) and age (likelihood ratio test, Res. Dev. = 16.3, d.f. = 33, $P < 0.05$) showing a good fit. Basal stem diameter at maturity in the model ranged from 1.3 cm ($P = 0.1$) to 4.6 cm ($P = 0.9$) with an average of 2.4 cm ($P = 0.5$). Age at maturity ranged from 3.3 years ($P = 0.1$) to 6.1 years ($P = 0.9$), with an average of 4.7 years ($P = 0.5$). The youngest *P. mahaleb* individual bearing fruits showed a 1.5-cm basal stem diameter and was 3.8 years old, while the oldest plant with no fruits was 5.5 years old. Thus, age at first reproduction could be estimated between 3 and 6 years, considering that all individuals at 6 years old and over were recorded as reproductive.

The size at which plants started bearing crop sizes greater than 1000 fruits was unaffected by the soil type they were growing in (interaction term not significant, likelihood ratio test, Res. Dev. = 14.54, d.f. = 86, $P = 0.33$). For rock crevices and deep soil at stream-side habitats, the basal stem diameter at which plants started to bear thousands of fruits ranged from 7.7 cm ($P = 0.1$) to 10.9 cm ($P = 0.9$), with an average of 9.3 cm ($P = 0.5$). Conversely, the age at which plants started bearing thousands of fruits differed between soil types (soil type term, likelihood ratio test, Res. Dev. = 18.19, d.f. = 87, $P < 0.0001$). For plants growing in rock crevices, it ranged from 13.6 years ($P = 0.1$) to 16.8 years ($P = 0.9$), with an average of 15.2 years ($P = 0.5$). For plants growing in deep soils in stream-side habitats, this age ranged from 6.8 years

Table 1 Coefficient estimates for the linear model relating age (*A*) and basal stem diameter (*BSD*, in cm) for 75 *P. mahaleb* individuals growing in three different soil types at the Ernesto Tornquist Provincial Park, Argentina

Soil type	Coefficient	Estimation	SE	CI _{lower} (95%)	CI _{upper} (95%)
Rock crevices	Intercept	0.9015	0.094	0.714	1.09
	Log(<i>BSD</i>)	0.8056	0.047	0.712	0.9
Deep soil in valleys	Intercept	1.2775	0.1395	0.812	1.743
	Log(<i>BSD</i>)	0.5248	0.07	0.29	0.759
Deep soil in stream-side habitats	Intercept	1.002	0.1513	0.513	1.491
	Log(<i>BSD</i>)	0.5289	0.064	0.307	0.75

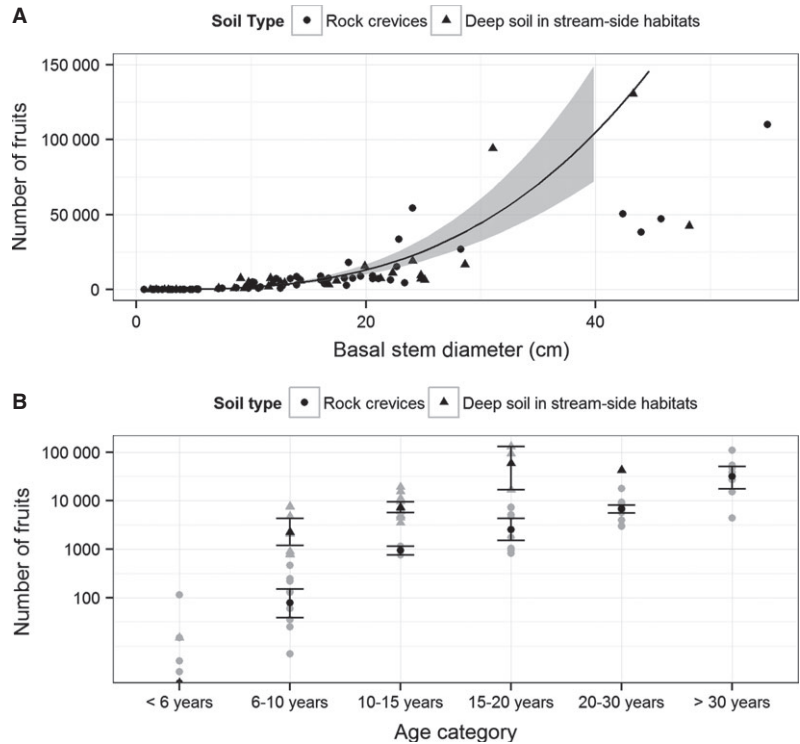


Fig. 2 (A) Relationship between crop size and basal stem diameter for *P. mahaleb* trees invading the Ernesto Tornquist Provincial Park, Argentina. Grey area represents 95% confidence interval. (B) Variation in crop size among plants at different age categories growing in rock crevices and in deep soils in stream-side habitats. Grey shapes indicate original values, black shapes indicate mean values, and bars indicate 95% confidence intervals. The mean fruit production at all age categories older than 6 years differs significantly between soil types (*t* tests, $P = 0.05$).

Table 3 Generalised linear model coefficient estimates of negative binomial model relating the total number of fruits produced by plant and their age for 90 *P. mahaleb* individuals growing in different soil types at the Ernesto Tornquist Provincial Park, Argentina

Soil type	Coefficient	Estimation	SE	IC(95%) _{inf}	IC(95%) _{sup}
Rock crevices	Intercept	-2.5	0.497	-3.52	-1.4
	Log(Age)	3.587	0.174	3.2	3.956
Deep soils in stream-side habitats	Intercept	-9.572	1.162	-14.23	-4.89
	Log(Age)	7.243	0.461	5.419	9.119

($P = 0.1$) to 10.1 years ($P = 0.9$), with an average of 8.5 years ($P = 0.5$). Plants growing in rock crevices showed a mean crop size of 136.6 ± 41.2 fruits at 6–10 years and 970 ± 115.9 fruits at 10–15 years. Plants growing in deep soils at stream-side habitats reached a mean crop size of 3336.9 ± 1042.7 fruits at 6–10 years and 8210 ± 1285.8 fruits at 10–15 years.

Discussion

Our results revealed that basal stem diameter is a good estimator of canopy size and plant age in *Prunus mahaleb*, as has been reported for other fleshy-fruited plants (Kollmann & Pflugshaupt, 2001; Bass *et al.*, 2006; Deckers *et al.*, 2008). The size–age relationship demonstrates that *P. mahaleb* trees increase their size at a different rate depending on the soil type where they grow. This could suggest that some soil types provide optimal conditions for growth and reproduction, while other soil types provide suboptimal conditions, which in

turn could result in different susceptibilities to invasion. Plants growing in deep soils develop larger sizes than plants of the same age growing in rock crevices. The expansion rate of the stem is similar for plants growing in soils either at stream-side habitats or away from water. However, plants growing near a stream seem to develop larger canopies compared with those of similar basal stem diameter growing in other habitats. These results are in accordance with studies reporting a strong effect of local conditions such as light, soil type and water availability on vegetative development and growth habit for *P. mahaleb* (Herrera & Jordano, 1981; Kollmann & Pflugshaupt, 2001) and for other woody plants (Girona *et al.*, 2005).

We found evidence that plant fecundity is related to size and that the age at which individuals reach certain size and fruit crop differs depending on the soil type where they grow. Age at first reproduction is an important determinant of population growth and can have an enormous effect on fitness, especially in invasive woody

plants, which typically have short juvenile periods (<10 years; Williamson & Fitter, 1996). Age at maturity is particularly relevant for expanding populations, because it has a profound effect on the rate of increase (Lewontin, 1965) and is subject to strong selection pressure, which favours individuals that initiate reproduction earlier in the life cycle (Stearns, 1976). *Prunus mahaleb* starts to produce fruit at *c.* 3 years of age in our study area and all individuals over 6 years actively reproduce. Moreover, our analysis of the age–crop size relationship revealed an abundant seed production from an early age. We have not found evidence indicating variation in age at first reproduction between individuals growing in the different soil types. However, trees in the study area show a remarkable increase in fruit production at a certain developmental stage that is reached at different ages for individuals growing in each soil type. For plants growing in deep soils at stream-side habitats, this stage is reached at ages from 7 to 10 years, while for plants growing in rock crevices, it is reached at ages from 13 to 16 years. Most plants at this stage change from producing hundreds of fruits to bear thousands. This difference has clear implications for the spread of *P. mahaleb*. Trees growing in deep soils and along streams may act as propagule sources producing an intense seed pressure on surrounding habitats, and they therefore should be targeted as a priority for control operations.

Nutrient allocation to flower and fruit production in *P. mahaleb* is strongly related to water and nutrient availability and is highly sensitive to shading (Kollmann & Pflugshaupt, 2001). Taking this into account, the increase in fruit crop observed in trees between the ages of seven and sixteen could be related to an increase in the efficiency of resources uptake, as has been described for other woody plant species. For European ash (*Fraxinus excelsior* L.), Gatsuk *et al.* (1980) reported a transition between juvenile and mature plants in which the form of the leaves and the structure of the root system change significantly. These plants adopt a new growth form by developing lateral shoots, changing from a monopodial to a sympodial structure and thus achieving a well-branched crown that increases light absorption by leaves. The authors also reported that the root system of ash changes from a superficial structure, with a tap-root shorter than the second-order lateral roots, to a more developed and deep system, depending on soil conditions. For the desert shrub *Larrea tridentata* (DC.) Coville, crown volume increased gradually during early age classes, after which it increased faster (Chew & Chew, 1965). A similar change inducing higher photosynthesis efficiency in leaves and/or better subterranean water uptake by roots could be the cause that enables larger crop sizes in *P. mahaleb*, with trees growing in

deep soils reaching this stage earlier as a consequence of better conditions for root development and greater water availability.

The increase in fruit production described in this study may have particular implications for the range expansion of *P. mahaleb* at the study area. When a single plant colonises a new site, local dispersion is expected to take some time to occur, because of limited propagule pressure. Age structure analysis in isolated populations from the study site showed the existence of a lag period between the establishment of a founder tree and massive recruitment (Amodeo & Zalba, 2013). It has also been reported that isolated plants experience low rates of visitation by dispersers and consequently a small number of fruits are consumed (Jordano, 1995). Fruit production might need to reach higher levels to promote bird attraction and the recruitment of new individuals in the vicinity of a founder tree. Such a positive relationship between crop size and visitation by potential dispersers has been described for birds feeding on *Prunus serotina* Ehrh. (Deckers *et al.*, 2008) and *P. mahaleb* (Herrera & Jordano, 1981). Once the founder tree reaches significant crown volume and crop size, propagule pressure and bird attraction may greatly increase. It is likely that the increase in fruit production reported in this work could have a strong positive effect on successful recruitment around a single tree and lead to an increase in local expansion and long distance dispersal (*sensu* Moody & Mack, 1988). This situation has clear management implications: invasive *P. mahaleb* trees should be felled before they reach a basal stem diameter of *c.* 9 cm to avoid this increase in propagule pressure. Considering that the age at which this stage is reached depends on soil type, streams could act as dispersal corridors for the spread of trees into uninvaded areas.

Could this high reproductive success be at least in part responsible for the invasive behaviour of *P. mahaleb* in our study area? Does the species show a higher reproductive performance in the Pampas than in its native range? This situation has been proposed for other *Prunus* species. Deckers *et al.* (2005) reported a shortening of the juvenile phase for *P. serotina* invading Central Europe, in comparison with native populations in the USA. Fruit production starts at the age of four in Belgium, where almost all individuals over 7 years old bear fruits, in contrast with the situation observed in the native range of the species, where reproduction starts, on average, as trees approach 10 years of age. To explore this possibility, we made a preliminary comparison of the relationship between crop size and basal stem diameter and a similar model published by Jordano and Schupp (2000) for a sample of trees growing in the species native range (Sierras de Cazorla Natural Park - SCNP, Segura y las Villas, Jaén province, south-eastern

Spain). They reported a similar model constructed by regression analysis: $\log(\text{Nr. of fruits}) = 0.4546 + 2.1981 * \log(\text{BSD})$ ($F_{(1,88)} = 199.2$, $P < 0.0001$, $R^2 = 0.7059$, $N = 90$). Our results suggest that *P. mahaleb* populations invading grasslands in southern Argentina show a much higher reproductive performance than in populations within its native range, reaching larger crop size along the entire range of tree sizes. Nevertheless, these differences in crop size between native and invaded areas must be evaluated carefully, considering that genetic differences, small sample sizes for both native and invasive populations and the possible effects of year-to-year variation in environmental conditions could confound these comparisons. Multiyear data sets from different native and invasive populations of *P. mahaleb* would allow more precise comparisons.

Acknowledgements

This work was funded by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina), CIC (Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Argentina) and Universidad Nacional del Sur, Bahía Blanca, Argentina. We are grateful to Ernesto Tornquist Provincial Park rangers who helped in field work and two anonymous referees that provided helpful comments on earlier versions of the manuscript. No conflicts of interest have been declared.

References

- AMODEO MR & ZALBA SM (2013) Wild cherries invading natural grasslands: unraveling colonization history from population structure and spatial patterns. *Plant Ecology* **214**, 1299–1307.
- AMODEO MR & ZALBA SM (2015) Phenology of *Prunus mahaleb*, a fleshy fruited tree invading natural grasslands in Argentine Pampas. In: *Biological Invasions: Patterns, Management and Economic Impacts* (ed. R WATERMAN), 121–141. Nova Science Publishers, New York, USA.
- BASS D, CROSSMAN N, LAWRIE S & LETHBRIDGE M (2006) The importance of population growth, seed dispersal and habitat suitability in determining plant invasiveness. *Euphytica* **148**, 97–109.
- BILENCA DN & MIÑARRO FO (2004) *Áreas valiosas de pastizal en las pampas y campos de Argentina, Uruguay y sur de Brasil*. Fundación Vida Silvestre Argentina, Buenos Aires, Argentina.
- BOLKER BM (2008) *Ecological Models and Data in R*. Princeton University Press, Princeton, USA.
- BURGOS J (1968) El clima de la provincia de Buenos Aires en relación con la vegetación natural y el suelo. In: *Flora de la provincia de Buenos Aires*, Vol. 4 (ed. A CABRERA), 33–100. Colección científica INTA, Buenos Aires, Argentina.
- CHEW RM & CHEW AE (1965) The Primary productivity of a desert-shrub (*Larrea tridentata*) community. *Ecological Monographs* **35**, 355–375.
- CLIMENT J, PRADA MA, CALAMA R, CHAMBEL MR, DE RONDS & ALIA R (2008) To grow or to seed: ecotypic variation in reproductive allocation and cone production by young female Aleppo pine (*Pinus halepensis*, Pinaceae). *American Journal of Botany* **95**, 833–842.
- DECKERS B, VERHEYEN K, HERMY M & MUYS B (2005) Effects of landscape structure on the invasive spread of black cherry *Prunus serotina* in an agricultural landscape in Flanders, Belgium. *Ecography* **28**, 99–109.
- DECKERS B, VERHEYEN K, VANHELLEMONT M, MADDENS E, MUYS B & HERMY M (2008) Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. *Biological Invasions* **10**, 717–727.
- FORREST J & MILLER-RUSHING AJ (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3101–3112.
- GATSUK LE, SMIRNOVA OV, VORONTZOVA LI, ZAUGOLNOVA LB & ZHUKOVA LA (1980) Age states of plants of various growth forms: a review. *Journal of Ecology* **68**, 675–696.
- GIRONA J, GELLY M, MATA M, ARBONÈS A, RUFAT J & MARSAL J (2005) Peach tree response to single and combined deficit irrigation regimes in deep soils. *Agricultural Water Management* **72**, 97–108.
- GUITIÁN J, SÁNCHEZ JM & GUITIÁN P (1992) Niveles de fructificación en *Crataegus monogyna* Jacq., *Prunus mahaleb* L., *Prunus spinosa* L. (Rosaceae). *Anales Jardín Botánico de Madrid* **50**, 239–245.
- HERRERA CM & JORDANO P (1981) *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs* **51**, 203–218.
- HULME PE (2008) Phenotypic plasticity and plant invasions: is it all Jack? *Functional Ecology* **22**, 3–7.
- JESCHKE J, GÓMEZ APARICIO L, HAIDER S *et al.* (2012) Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* **14**, 1–20.
- JORDANO P (1993) Pollination biology of *Prunus mahaleb* L.: deferred consequences of gender variation for fecundity and seed size. *Biological Journal of the Linnean Society* **50**, 65–84.
- JORDANO P (1995) Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus Mahaleb*. *Ecology* **76**, 2627–2639.
- JORDANO P & SCHUPP EW (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* **70**, 591–615.
- KOLLMANN J & PFLUGSHAUPT K (2001) Flower and fruit characteristics in small and isolated populations of a fleshy-fruited shrub. *Plant Biology* **3**, 62–71.
- LEWONTIN RC (1965) Selection for colonizing ability. In: *The Genetics of Colonizing Species: Proceedings* (eds HG BAKER & GL STEBBINS), 77–94. Academic Press, New York, USA.
- LONG M & GRASSINI C (1997) *Actualización del conocimiento florístico del Parque Provincial Ernesto Tornquist*. Ministerio de Asuntos Agrarios Provincia de Buenos Aires y Universidad Nacional del Sur, Bahía Blanca, Argentina.

- MARAÑÓN T, CAMARERO JJ, CASTRO J *et al.* (2004) Heterogeneidad ambiental y nicho de regeneración. In: *Ecología del bosque mediterráneo en un mundo cambiante* (ed. F VALLARADES), 69–99. Ministerio de Medio Ambiente, EGRAF, S. A., Madrid, Spain.
- MOODY ME & MACK RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* **25**, 1009–1021.
- VAN NOORDWIJK AJ & DE JONG G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist* **128**, 137–142.
- PRADA MA & ARIZPE D (2008) *Manual de propagación de árboles y arbustos de ribera: una ayuda para la restauración de riberas en la región mediterránea*. Conselleria de Medi Ambient, Aigua, Urbanisme i Habitatge, Valencia, Spain.
- PYŠEK P & RICHARDSON D (2007) Traits associated with invasiveness in alien plants: where do we stand? In: *Biological Invasions*, Vol. **193** (ed. W NENTWIG), 97–125. Springer Berlin Heidelberg, Berlin, Germany.
- R-Core-Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- RICHARDSON DM & PYŠEK P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* **30**, 409–431.
- SEBERT-CUVILLIER E, SIMON-GOYHENECHÉ V, PACCAUT F, CHABRERIE O, GOUBET O & DECOCQ G (2008) Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. *Landscape Ecology* **23**, 787–801.
- SEBERT-CUVILLIER E, SIMONET M, SIMON-GOYHENECHÉ V, PACCAUT F, GOUBET O & DECOCQ G (2009) PRUNUS: a spatially explicit demographic model to study plant invasions in stochastic, heterogeneous environments. *Biological Invasions* **12**, 1183–1206.
- SILVERTOWN J, FRANCO M, PISANTY I & MENDOZA A (1993) Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* **81**, 465–476.
- SILVERTOWN J, FRANCO M & MENGES E (1996) Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* **10**, 591–597.
- SIMBERLOFF D (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics* **40**, 81–102.
- STEARNS SC (1976) Life-history tactics: a review of the ideas. *The Quarterly Review of Biology* **51**, 3–47.
- DE VILLALOBOS AE & ZALBA SM (2010) Continuous feral horse grazing and grazing exclusion in mountain pampean grasslands in Argentina. *Acta Oecologica* **36**, 514–519.
- WEINER J (2004) Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **6**, 207–215.
- WEINER J, CAMPBELL LG, PINO J & ECHARTE L (2009) The allometry of reproduction within plant populations. *Journal of Ecology* **97**, 1220–1233.
- WICKHAM H (2009) *ggplot2: Elegant Graphics for Data Analysis*. 0.9.2.1 edn. Springer, New York, USA.
- WILLIAMSON M (1996) *Biological Invasions*. Chapman and Hall, London, UK.
- WILLIAMSON MH & FITTER A (1996) The characters of successful invaders. *Biological Conservation* **78**, 163–170.
- ZALBA SM & VILLAMIL CB (2002) Woody plant invasion in relictual grasslands. *Biological Invasions* **4**, 55–72.