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Factors affecting variability in fleshy cone production of *Juniperus macrocarpa*

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A B S T R A C T

Juniperus macrocarpa woodlands represent the mature ecosystem on outer sandy dunes and cliffs of the Mediterranean coasts, and typically show little or no recruitment in degraded coastal habitats. Production of fleshy cones may have strong effects on its recruitment as well as on the populations of animal species that eat the cones and disperse the seeds. In this study, I explore the inter-annual variability in cone production, its relationship with rainfall and twig growth, and the effects of silvicultural works carried out to increase the production of fleshy cones and natural regeneration of the species in Enebrales de Punta Umbría Natural Site. Silvicultural treatments had not a significant effect on the cone production, but microhabitat did. *J. macrocarpa* showed a variable fleshy cone production between years and synchronized fleshy cone production within years among individuals. Precipitation during the period of pollination negatively affected the production of fleshy cones which allow us to classify *J. macrocarpa* as a putative masting species. In clearing plants, twigs that produce many cones grew less than twigs without or with few cones, while cone production in understory plants was lower but increased with twig growth. All results seem to reinforce the fact that pollen is essential for seed cone development in *J. macrocarpa*, and that this is highly dependent on variation in climate (precipitation during the pollination period) and landscape features (pine plantation).

1. Introduction

In the last 80 years, the intensive and consumptive use of coastal dunes has resulted in strong degradation or destruction of them and their habitats (Martínez and Psuty, 2004), especially in the Mediterranean Basin (EEA, 2020). Thus, the European Habitat Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora included some of those habitats as a priority for conservation. This is the case of the 2250* "Coastal dunes with *Juniperus* spp.", particularly those with the coastal juniper *Juniperus macrocarpa* (syn. *Juniperus oxycedrus* subsp. *macrocarpa* (Sm.) Ball), which habitats are widespread on the Mediterranean coasts but are not very common (Picchi, 2008) and are particularly vulnerable to anthropogenic activities because they are confined to an ecologically limited position under the sea influence. Relict juniper populations in the sandy coasts of the Mediterranean Basin, typically present no recruitment (Muñoz-Reinoso, 2003; Sánchez Codoñer, 2008; Kazakis, 2014; Pinna et al., 2014a). Therefore, it is critical to identify the factors that limit juniper regeneration, particularly to predict population viability and to promote conservation measures of *J. macrocarpa* coastal woodlands.

Juniperus macrocarpa is a dioecious, wind-pollinated, long-lived tree with a two-year reproductive cycle. Pollen is dispersed from late November to January. During seed cone receptivity period, ovules exude pollination drops, a mechanism that may extend until February if pollination does not occur. Fertilization takes place in late spring (see Arista et al., 2001). Embryos are mature at the end of the second summer, while seed cones ripen in autumn of the second year. The fleshy cones (galbules) usually contain three seeds, and are relatively large, giving name to the species (*macrocarpa* = large fruit). Fruiting junipers are an important food source for vertebrates such as badgers, foxes, wild boars, and rabbits, which also disperse the seeds (Muñoz-Reinoso, unpublished).

One of the main ecological problems of conifers is a low production of viable seeds (Owens et al., 1990; Arista and Talavera, 1996), although they usually produce many cones. Low seed viability, low germination rate, predispersal seed predation, summer drought, herbivory, and human activities (trampling, off-road vehicle circulation) have been pointed out as responsible for the lack of recruitment in coastal juniper (Juan et al., 2003; Muñoz-Reinoso, 2003; Pinna et al., 2014a, 2014b). Thus, population persistence may relay in the longevity of individuals or

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in scarce recruitment events as pointed for other Mediterranean junipers (García et al., 1999).

Previous studies about the reproductive success of the two-year reproductive cycle of *J. macrocarpa* carried out in Enebrales de Punta Umbría (SW Spain; Ortiz et al., 1998; Juan et al., 2003) reported high seed cone abortion (80–90%), low number of filled seeds per cone (0.45–0.60), and a variable proportion of seeds with an embryo (20.26–56.53%). However, none of those studies have estimated the production of fleshy cones of this juniper and its interannual variability. Production of fleshy cones and viable seeds may have strong effects on the recruitment of coastal juniper as well as on the populations of the species of animals that eat the cones and disperse the seeds (Herrera, 1998a; Koenig et al., 2015).

Several Mediterranean junipers show annual variation in cone and seed production from year to year (García et al., 2002; Herrera, 1998a; Jordano, 1993; Montesinos, 2007). That variable seed production between years and synchronized seed production within years among individuals within a population is known as masting behaviour (Janzen, 1971; Kelly, 1994; Silvertown, 1980). Masting is widespread in long-lived plants, particularly in woody and wind-pollinated species (Herrera et al., 1998). Studies on masting deal with causes, environmental factors, resources (physiological constraints on reproductive processes), and evolutionary benefits (Kelly, 1994; Pearse et al., 2016). This article explores immediate factors that may affect whether a particular year will be a high fleshy cone year (proximate causes; Kelly, 1994).

Several factors may affect the production of fleshy cones in coastal juniper. According to Arista et al. (2001), pollen is essential for seed cone development. However, airborne pollen is affected by rainfalls (Jato et al., 2002), although the pollen of some plant species may be more strongly affected than the pollen of others (Kasprzyk et al., 2014). Therefore, the precipitation during the pollination period may affect the fleshy cone production in *J. macrocarpa*. Fruit production is also dependent on the numbers of flowers formed (Mezquida et al., 2016). Since conifers grow their flowers on twigs from the previous year (Politi et al., 2011), the growth of twigs may be an important factor in the production of flowers and cones.

As the juniper populations that develop in the understory of coastal pine plantations show little or no recruitment (Muñoz-Reinoso, 2003), the implementation of the Conservation Programme of Coastal Juniper Woodlands of the Andalusian Regional Government (Muñoz-Reinoso et al., 2013) made it possible to evaluate the effect of silvicultural treatments for thinning the coastal pine plantations on the production of cones and the regeneration of original coastal juniper communities. These works involved the thinning and pruning of the pine trees in the close vicinity of junipers to reduce competition for resources (light, nutrients, water).

In this study, I explore the inter-annual variability in cone production of *Juniperus macrocarpa* in the Enebrales de Punta Umbría Natural Site. First, I assessed the effects of silvicultural works on fleshy cone production. If the felling and pruning of pines changes the site conditions and cone production increases, other potential causes of variability in fleshy cone production would be compromised. Once the effect of silvicultural work was ruled out, the inter-annual variability of production was studied and related to climatic factors (precipitation during the pollination period). Finally, the cone production was related with the annual growth of twigs.

2. Materials and methods

2.1. Study area

The study was conducted in the *Enebrales de Punta Umbría* Natural Site (37°11′29.20’’N 6°59′42.45’’W), located in the Gulf of Cádiz (SW Spain), southward of Huelva city. This coastal dune area (162 Ha), protected since 1989, harbors one of the westernmost populations of *J. macrocarpa* in the Mediterranean Basin, which co-occur with *Pinus pinea* and Phoenicean juniper (*Juniperus phoenicea* subsp *turbinata*). The climate is Mediterranean with oceanic influences (Csa according to Köppen classification). Average temperature is 17.4 °C and annual precipitation 495.7 mm, with temperate winters and hot, dry summers. Highest precipitation occurs in late autumn-early winter (October–December), with a second, small peak in spring (March–May). Soils contain *ca.* 98% of sand, their pH is 8.5, and have a low nutrient content: 0.27% Organic Matter, 0.01% N, 30.99 ppm P (Muñoz-Reinoso, 1999).

J. macrocarpa population consists of *ca.* 300 mature individuals, with a sex-ratio close to 1:1, without seedlings or saplings (Muñoz-Reinoso, 2003), and without senescent or dead individuals. Junipers are scattered throughout the area, appearing on dune ridges and slacks, in a fringe 2.5 km long and 140 m wide (35 ha), where the pine canopy creates two contrasting microhabitats. Most junipers in the dune valley are below a dense pine tree canopy 7–12 m tall; only a few individuals are found in small clearings (*ca.* 0.1 ha) where pines did not grow. Phoenicean juniper and shrubs such as *Cistus salviifolius*, *Halimium halimifolium*, *H. calicynum*, *Salvia rosmarinus*, *Rhamnus oleoides* and *Pistacia lentiscus* share the habitat with the coastal juniper, making plant diversity relatively high regarding other juniper populations (Muñoz-Reinoso, 2004). The zone is crossed by several wooden footpaths connecting the road with the beach and so the presence of people is frequent, especially in summer.

Silvicultural works were carried out in Enebrales de Punta Umbría at the beginning of 2004, after the pollination season, to restore, at least partially, the physical environmental conditions of the habitat and to increase the natural regeneration of *J. macrocarpa*. Those works involved the thinning and pruning of the pine trees in the close vicinity of the coastal junipers. Thus, the cover of pine trees decreased *ca.* 18% in the dune slack.

2.2. Measures of fleshy cones production and twigs growth

I estimated cone production by counting all mature fleshy cones/tree in the autumns of 2003–2008, in the same 30 individuals (15 per microhabitat, clearings and closed canopy). Although radial growth is an integrative measure about the plant's entire life span growth (Montesinos et al., 2006), the measurement of twig growth gives a more immediate picture of changes in meteorology or land management. Thus, the growth of twigs was estimated in both microhabitats of Enebrales de Punta Umbría (clearings and closed canopy), following the method of Massei et al. (2006). The length of the previous year growth was estimated on 10 twigs from 30 junipers (15 individuals per microhabitat) and related to their fleshy cone production in 2006.

2.3. Statistical analyses

To assess the effects of silvicultural works carried out at the beginning of 2004 in Enebrales de Punta Umbría Natural Site, the differences in cone production between microhabitats and years (before and after pine thinning) were tested with a General Linear Model using microhabitats and crop years as fixed factors. The cone production was log-transformed to meet the assumptions of normality (Shapiro-Wilk's test, $p > 0.05$). As Mauchly's Test of Sphericity indicated that the assumption of sphericity had been violated, $\chi2\ (9) = 36.385$, $p < 0.001$, a Greenhouse-Geisser correction was used. Levene's Test showed that there was homogeneity of variances in all the levels of the independent variable ($p > 0.05$), and Box's M test of the homogeneity of the covariance matrices of the dependent variables across all level combinations of the between-subjects factors was also significant (M de Box = 11.585, $p = 0.860$).

Once the effect of silvicultural work was excluded, to assess annual variability in fleshy cone production and synchrony for the period 2003–2008 (data for 2005 were not available), a population coefficient of variation (CV_P hereafter), a mean within-plant coefficient of variation

($\overline{CV_i}$ hereafter), and Kendall's coefficient of concordance (*W*; Zar 1999) were calculated (Herrera, 1998b) for the total of individuals (n = 30), and separately for the individuals located in clearings and under closed canopy. CV_P was computed as the coefficient of variation of yearly totals of fleshy cone production. $\overline{CV_i}$ was computed as the mean of (individual) within-plant coefficients of variation. Kendall's coefficient measures the overall degree of concordance between individual plants with respect to the temporal pattern of variation of their crop sizes across years, and ranges between 0 (complete discordance) and 1 (perfect synchrony).

A negative binomial mixed model was fitted to relate cone production across years to precipitation during the pollination months (November to February) and individuals' microhabitat (clearings *versus* closed canopy). Individuals and years were included as random effects. R v. 4.2.2 (R Core Team, 2022) and R package glmmTMB (Brooks et al., 2017) were used. GLMM were also fitted for 3- and 2-month periods within the pollination period but, as nested predictor variables, there were no differences among Akaike Information Criterion values; thus, only the model for the whole pollination period (November–February) is shown. Precipitation data comes from the meteorological station of Moguer, located to the East, 15 km away from the study area, and close to the coast.

Finally, the relationship growth-fleshy cone production was studied through regression analysis in both microhabitats. In both cases the relationship was significant (R squared = 0.362, F = 7.362, $p = 0.018$ and R squared = 0.484, F = 12.190, p = 0.004 for clearings and closed canopy respectively), residuals were independent (1.5 < Durbin-Watson values < 2.5) and had a normal distribution (p > 0.05), but in the case of clearings the residuals variance was not constant. Regression analyses were carried out with SPSS v26.0 software package (SPSS, Chicago, IL, USA).

3. Results

3.1. Effect of silvicultural works on cone production

There was a significant effect of the crop year on cone production, $F = 27.210$, $p < 0.001$, but not in the interaction crop year*microhabitat $F = 0.989$, $p = 0.397$. The estimated marginal means showed that the cone production in 2004 was significantly lower than in all other years, and the cone production in 2006 was also significantly higher than in 2007, but there were no significant differences in production in the rest of the cases, i.e., the production of fleshy cones was not significantly higher after the silvicultural works. There was also a statistically significant effect of microhabitat on cone production, $F = 41.540$, $p < 0.001$, being significantly higher in the clearings than under the closed canopy of pine trees (Fig. 1).

3.2. Interannual variability in fleshy cone production

The fleshy cone production for the whole period (2003–2008) ranged between 5,146 (in 2004) and 15,429 (in 2006). Cone production in clearings was much higher compared to those in the understory, ranging from 80 to 94% of total production (Fig. 1). In all cases, the population coefficients of variation (CV_P) were lower than the mean coefficient of variation of the individual plants $\overline{CV_i}$), but especially for the whole sample and for the individuals in clearings (Table 1). In all the cases, plants showed a significant synchrony (Kendall's coefficient of concordance) in cone production (Table 1), which was higher in plants located under the closed pine canopy, which consistently showed a lower cone production over time.

3.3. Relationships precipitation-cone production

Cone production was much larger in clearings than under the closed canopy of pines (Fig. 1, Table 2). Average cone production in an average year was 451 ± 84 for individuals in open microhabitats *versus* 127 ± 27 for individuals growing under closed canopy. Cone production decreased significantly with precipitation (Fig. 2): average cone production per individual was 445 in the driest year *versus* 172 cones in the wettest year (75 *versus* 383 mm of rain, respectively).

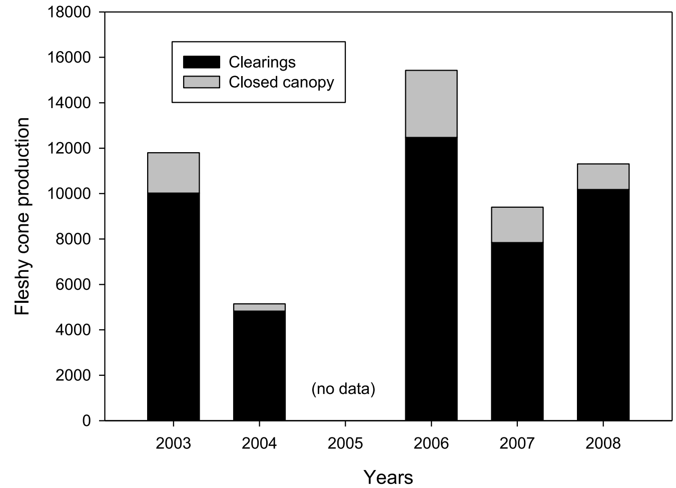

Fig. 1. Annual fleshy cone production showing the contribution of junipers located in clearings and under closed canopy (n = 30, 15 individuals/microhabitat).

Table 1
Annual variability in fleshy cone production for the whole sample of 30 individuals and for each microhabitat. CV_P: population level variation, $\overline{CV_i}$: individual level variation, *W*: Kendall's coefficient of concordance, χ^2 and significance level for *W*.

Sample	CV_P	$\overline{CV_i}$	*W*	χ^2	*p*
Overall	35.4	81.7	0.360	43.21	<0.001
Clearings	31.8	74.5	0.229	13.74	0.008
Closed canopy	62.2	84.6	0.537	32.21	<0.001

Table 2
Results of the negative binomial mixed model relating individual cone production to microhabitat and precipitation during the pollination months (November–February). R^2 = 0.536 (conditional), 0.344 (marginal).

Parameter	Estimate	95% Confidence Interval	p-value
Fixed effects:			
Intercept	4.8	4.4, 5.3	<0.001
Microhabitat Clearings	1.3	0.84, 1.7	<0.001
Log precipitation	−0.58	−1, −0.14	0.01
Random effects:			
Individual	0.47	0.32, 0.69	
Year	0.25	0.11, 0.58	

3.4. Relationship twig growth-fleshy cone production

Regression analysis seems to show that twig growth had a negative effect on cone production in clearings and a positive effect in closed canopies (Fig. 3), although there were no significant differences in mean twig growth between microhabitats (p = 0,359). This means that in clearing plants, twigs that produce many cones grew less than twigs without or with few cones, while cone production in understory plants was lower but increased with twig growth.

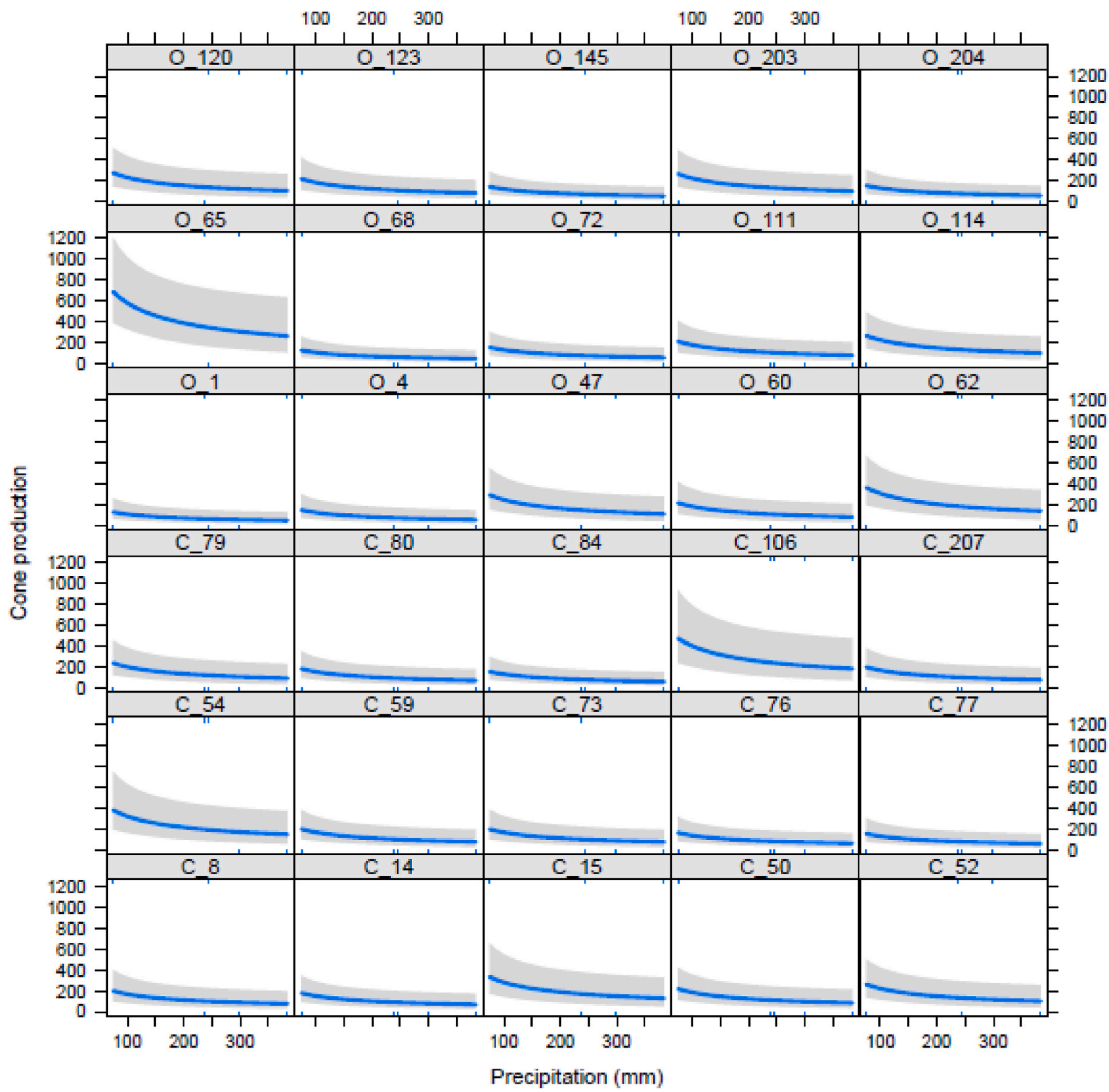

Fig. 2. Estimated individual cone production as a function of precipitation during the pollination months (November to February). Each panel represents an individual (O = clearings, C = closed canopy).

4. Discussion

The results have shown that *Juniperus macrocarpa* is a masting species with synchronous variations in cone production. Further, the cone production was strongly linked to the precipitation during the pollination months. In Enebrales de Punta Umbría, the production of fleshy cones was also related to the microhabitat in which the junipers are located (clearings and closed canopy), which seems to be mediated by the growth of the twigs and the arrival of pollen (Muñoz-Reinoso et al., 2013). Finally, the silvicultural treatments carried out at the beginning of 2004 did not significantly increase the production of fleshy cones in the Natural Site.

4.1. Effect of silvicultural works on cone production

The silvicultural treatments carried out in Enebrales de Punta Umbría Natural Site should have improved conditions for the junipers by reducing competition from the pines for light, water, and soil nutrients, and their barrier effect on pollen movement, thus improving the juniper reproduction. However, the results showed that the thinning carried out in 2004 had no effect on cone production, with only differences in production between microhabitats remaining (Fig. 1). Thinning favored juniper growth by reducing competition for light, water, and soil nutrients, but probably not the arrival of pollen necessary for seed and cone production (Arista et al., 2001). Several authors have shown the detrimental effect of canopy closure on pollen dispersal in wind-pollinated species (Robledo-Arnuncio et al., 2004; Millerón et al., 2012; Rodríguez-García et al., 2017). Heterospecifics such as pines and Phoenicean junipers, and non-reproductive or female conspecifics can still exert a barrier effect to pollen arrival. Thus, more intensive thinning seems to be necessary to facilitate the arrival of pollen to female individuals and to increase cone and seed production.

4.2. Interannual variability in fleshy cone production

The coastal junipers of Enebrales de Punta Umbría showed a variable fleshy cone production between years and synchronized fleshy cone production within years among individuals for the studied period, which allow us to consider *Juniperus macrocarpa* as a masting species, as other Mediterranean junipers (García et al., 2002; Herrera, 1998a; Jordano,

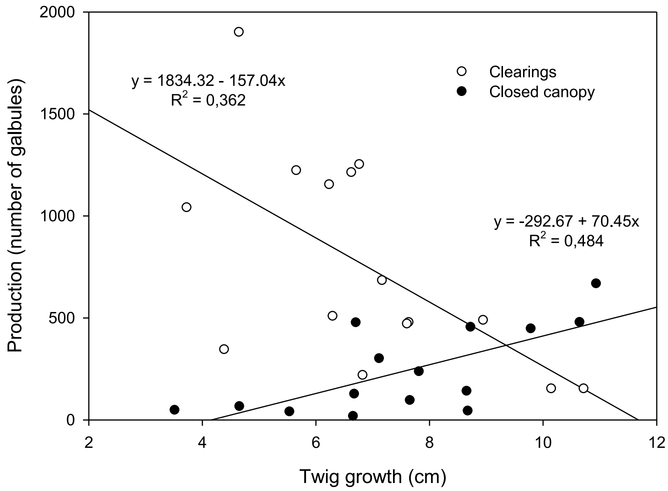

Fig. 3. Relationships between twig growth and cone production in junipers located in clearings and closed canopy. Linear regressions and equations are shown.

1993; Montesinos, 2007).

García et al. (2002) have shown similar values of synchrony to those found in this study but high levels of interannual variation in crop size in *J. communis*. Herrera et al. (1998) also showed high levels of interannual variation in other Mediterranean junipers. In the present study, the population coefficients of variation (interannual variation) were lower than the mean coefficient of variation of the individual plants. According to Buonaccorsi et al. (2003), the observed differences between CVp and $\overline{CV_i}$ values in the whole sample and in the individuals growing in clearings (Table 1) may be due to the discrepancy in crop size between good producers and poor producers. That difference is clear in the whole sample when the cone production of clearing and closed canopy individuals is compared (Fig. 1), but even among individuals located in the clearings there were important differences in production which may be due to the presence of nearby conspecific males.

Fleshy cone production of the individuals sampled in Punta Umbría seems to be very low. The mean production for 2003 was 393.4 ± 94.5 fleshy cones/tree (mean ± s. e.), almost four times lower than that of a sample of 54 individuals of similar size from the mature juniper woodland of Doñana (1530.4 ± 214.0, unpublished). This low fleshy cone production together with low levels of interannual variation in crop size seem to indicate the existence of factors affecting the production of fleshy cones in Enebrales de Punta Umbría. If pollen is essential for seed cone production (Arista et al., 2001) and air pollen density is low under pine canopy (Muñoz-Reinoso et al., 2013), it is possible that juniper air pollen density was relatively low throughout Enebrales de Punta Umbría Natural Site compared to populations such as Doñana (pollen data not available). This would be consistent with the spatial restriction of effective pollen dispersal observed by Robledo-Arnuncio et al. (2004) in dense Scots pine stands, and with the higher pollination failure of *J. thurifera* in mixed forest suggested by Rodríguez-García et al. (2017). That is, landscape features (Koenig et al., 2017) such as pine plantations strongly affect wind-pollinated species such as *J. macrocarpa*. Thus, the low reproductive success reported in previous studies for the Enebrales de Punta Umbría's junipers (Ortiz et al., 1998; Juan et al., 2003) could be due to the site features (pine plantation) and the low number of individuals studied (n = 10) rather than reproductive problems of the juniper.

4.3. Relationship precipitation-fleshy cone production

García et al. (2002) showed that variation in precipitation during the pollination period (June) increased the number of empty seeds, but no the production of cones in *J. communis* of the mountains of southern Spain. In this case, precipitation during the period of pollination negatively affected the production of cones in *J. macrocarpa* individuals (Table 2, Fig. 2). In the 2011 ripening season no mature cones were found in the coastal juniper populations of Punta Umbría and Doñana (pers. observation), which seems to indicate that the event was not local. This was because the precipitation during the pollination period (November 2009–February 2010) was higher than the mean annual rainfall (495.7 mm), which must have impeded the transport of pollen by removing it from the air (precipitation for December, January and February were respectively 219.2, 196.4 and 227.8 mm). Thus, the drier the winters, the higher the production of fleshy cones (Fig. 2). According to Kelly (1994), *J. macrocarpa* would fall under the putative mast species definition because variation in fleshy cone production seems to follow the variation in the environment (precipitation during the pollination season). Parmenter et al. (2018) have also proposed *J. monosperma* as a putative mast species with mast production positively related to current-year late-winter precipitation, combined with negative relationship with current-year summer temperatures in the semiarid woodlands of the American Southwest.

These data support the hypothesis that environmental factors, the Moran effect, are key drivers of spatial synchrony in fleshy cone production at both small and larger spatial scales, as showed by Koenig et al. (2017) in *Quercus lobata*. However, that putative masting behaviour may be happening in coastal juniper populations at the westernmost end of the species' distribution, where the highest annual rainfall coincides with the species' pollination period. To confirm this, therefore, it would be necessary to study the variability in fleshy cone and seed production over a longer period across the whole Mediterranean Basin, considering sites with equinoctial rainfalls.

4.4. Relationship twig growth-production

Shade is a type of stress which limits photosynthesis and plant growth (Valladares et al., 2004), and reduce photosynthate available for allocation to growth and reproduction (Lawton and Cothran, 2000). Although it has been shown that juniper twigs grow less under the closed canopy of pines (Muñoz-Reinoso et al., 2013), in the present case there were no differences in growth between microhabitats. This may be because, in some way, thinning favored greater input of solar radiation and consequently more growth under the closed canopy. However, the relationship between twig growth and cone production showed that, despite the same mean growth, the cone production was higher in plants located in the clearings and it decreased with twig growth (Fig. 3). Conversely, cone production was lower in understory plants and increased with the growth. That may show that there was a trade-off between growth and reproduction (Álvarez-Cansino et al., 2010) at the twig scale. In clearing plants, twigs that produce many cones grew less than twigs without or with few cones as showed by Hoffman and Alliende (1984) in dioecious species of Central Chile. However, although a larger twig growth resulted in a relative larger cone production in understory plants, there does not seem to be a large allocation of resources to reproduction as is showed by an overall low cone production, which could again be due to the lack of pollen (Arista et al., 2001).

Lack of or low natural regeneration is a general feature of *J. macrocarpa* woodlands in the Mediterranean coastal ecosystems (Muñoz-Reinoso, 2003; Sánchez Codoñer, 2008; Kazakis, 2014; Pinna et al., 2014a), which indicates the degradation of those coastal habitats. Habitat degradation affects several of the processes involved in natural regeneration at the local and landscape spatial scales. Thus, coastal pine plantations are a sort of "superimposition" on the dune ecosystem (Bonari et al., 2018) that change coastal landscape features and affects the reproduction of the heliophilous and dioecious wind-pollinated *J. macrocarpa* (Muñoz-Reinoso, 2021). The findings of this work highlight the need for appropriate pollination in coastal juniper to tackle the following processes in the regeneration of the species in these coastal degraded habitats.

Declaration of competing interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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