

Annual variability in reproduction of *Juniperus communis* L. in a Mediterranean mountain: Relationship to seed predation and weather¹

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Abstract: The interannual patterns of reproductive output were analysed for a population of *Juniperus communis* in the Mediterranean mountains of southern Spain. Cone production, number of seeds per cone, predispersal seed predation, seed abortion, and final seed set were studied for six consecutive years (1992-1997). Interannual variation in reproduction was assessed in relation to weather conditions during pollination and cone development. All the reproductive components varied strongly among years. Ripe cone production correlated positively to seed set and seed predation but was independent of the percentages of empty and filled seeds. The percentage of empty seeds positively correlated to precipitation during the month of pollination. Interannual patterns in reproductive output proved inconsistent with the predator satiation hypothesis. Mediterranean mountain weather affected juniper reproduction at a local scale, acting in a narrow range of variation, since seed emptiness is governed primarily by factors acting at a broader geographical scale.

Keywords: cone production, southern Spain, predispersal seed predation, seed abortion, seed set, temporal variation.

Résumé : Cette étude analyse les patrons interannuels de reproduction d'une population de *Juniperus communis* dans les montagnes méditerranéennes du Sud de l'Espagne. Pendant six années consécutives (1992-1997), on a étudié la production de cônes, le nombre de graines par cône, la prédation des graines avant la dissémination, l'avortement des graines et la production finale de graines. La variation interannuelle de la reproduction a été mise en relation avec les conditions météorologiques qui ont prévalu au cours de la période de pollinisation et du développement des cônes. Toutes les variables reproductives ont fortement varié entre les années. La production de cônes était positivement corrélée avec la production et la prédation des graines, mais elle était indépendante des pourcentages de graines vides et pleines. La proportion de graines vides était positivement corrélée avec les précipitations pendant le mois de pollinisation. Les patrons interannuels de reproduction du genévrier ne s'expliquent pas par l'hypothèse du rassasiement du prédateur. Les conditions météorologiques des montagnes méditerranéennes affectent la reproduction du genévrier à l'échelle locale et sur une étroite bande de variations, puisque la quantité de graines vides produites est influencée surtout par des facteurs agissant à une échelle géographique plus vaste.

Mots-clés : avortement de graines, prédation de graines avant la dissémination, production de cônes, production de graines, Sud de l'Espagne, variation temporelle.

Introduction

Year-to-year fluctuation in reproductive output is common to many polycarpic plants (Sork, 1993; Kelly, 1994; Herrera *et al.*, 1998; Houle, 1999). Several explanations have been proposed for variations in annual seed production. Proximate causes include climatic factors, which affect resources for reproduction, pollen dispersal, and flower and fruit survival (Sork, Bramble & Sexton, 1993; Koenig *et al.*, 1996; Sperens, 1997; Houle, 1999), as well as endogenous cycles of resource storage and trade-offs between different components of reproduction (Allen & Platt, 1990; Crawley & Long, 1995; Antos & Allen, 1999). Ultimately, evolutionary causes might also explain interannual variation in reproduction, since massive and synchronous flowering can be advantageous for plant fitness by increasing the probability of escaping seed predators (predator satiation hypothesis, Silvertown, 1980; Sork, 1993; Crawley & Long, 1995; Kelly & Sullivan, 1997)

Common juniper, *Juniperus communis* L. (Cupressaceae), is a holarctic fleshy-fruited shrub with relict populations in the mountains of southern Spain. Regeneration is more limited in Mediterranean populations than in the northern European ones, apparently due to lower production of viable seeds and higher seedling mortality (García *et al.*, 1999; García *et al.*, 2000; García, 2001). However, as suggested for other long-lived species (Crawley, 1992; Crawley & Long, 1995), sporadic events of massive propagule production could promote regeneration in Mediterranean mountains. In view of this possibility, the juniper reproductive output in a Mediterranean population over six consecutive years is analysed in an effort to answer the following questions: 1) Do the different components of reproduction vary over time? 2) Are there temporal trade-offs between different components of reproduction? 3) Is the annual variation in reproductive output related to climatic conditions? 4) Does the predator satiation hypothesis explain temporal changes in reproductive output? A negative relationship between fruit or seed production and seed

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predation in a synchronous population would support this hypothesis (Silvertown, 1980; Crawley, 1992; Kelly, 1994).

Methods

STUDY AREA AND NATURAL HISTORY

Juniperus communis, one of the most widely distributed gymnosperms in the Holarctic, has a continuous range in northern Europe but becomes isolated in scattered mountain areas around the Mediterranean Basin. In the mountains of southern Spain, juniper is a dominant woody species above the treeline (1,500-2,500 m a.s.l.), forming Mediterranean high-mountain shrublands (García *et al.*, 1999). This study was conducted during the period 1992-1997 in the locality of Campos de Otero (2,300 m a.s.l., Sierra Nevada, Granada, 37° 06' N, 3° 21' W).

Common juniper is a dioecious and wind-pollinated species (see also García, 1998, for reproductive biology). Pollen dispersal by males concentrates in June. By the same time, females bear axillary conelets that take almost three years to develop into mature fleshy cones. Since female conelets are produced annually, conelets and fleshy cones of two different cohorts appear simultaneously in the same plant. Many conelets suffer abscission during the first summer, after the spring of pollination. Cone and seed growth mostly occurs during the second summer, with many cones aborting before reaching final size. Ripening occurs during the third summer. Ripe cones are ca 6.5 mm in diameter and contain 1-4 seeds per cone. Many seeds within well-developed cones are empty, due to lack of pollination or abortion throughout development. Empty seeds show an undeveloped embryo that does not fill the seed locule, whereas sound (filled) seeds have a white, resinous embryo that entirely fills the seed locule. At the study site, juniper seeds are attacked by the predispersal wasp *Megastigmus bipunctatus* Swed. (Hymenoptera, Torymidae; García, 1998). Ripe cones are consumed by thrushes *Turdus* spp., which disperse seeds in faeces (Jordano, 1993; García, 2001).

ESTIMATES OF REPRODUCTIVE OUTPUT

Reproductive output was estimated by the following variables:

1) Cone production, the number of cones m⁻² of plant surface, distinguishing between one-year (green) and two-year (ripe) cones. Cone production was calculated according to plant surface because *J. communis* has a stunted, prostrate structure in mountain environments. This estimate, independent of plant size, was calculated by counting green and ripe cones in a quadrat of 0.04 m² ($n = 10$ measurements plant⁻¹). For comparisons of our ripe cone-production data with those of Zamora (1987) and Jordano (1993) for the same locality, the number of cones per ha (cones/ha) was calculated by extrapolating the number of ripe cones per plant-surface unit to the total area (coverage of female junipers = 14.5%).

2) Number of seeds per cone (seeds cone⁻¹), by averaging from a sample of 30-40 ripe cones randomly collected for each plant.

3) Percentages of depredated, empty, and filled seeds per plant. Collected seeds were opened under binocular

magnification and assigned to one of the following categories: depredated, showing signs of predation; empty, having an undeveloped embryo; and filled, having an undamaged, well-developed embryo. Empty seeds included mostly unpollinated seeds, but occasionally also pollinated seeds that aborted early in the development, these two types usually being impossible to differentiate. Seed predation was invariably attributable to *M. bipunctatus*, depredated seeds showing the adult exit hole and larval excrement inside. Only filled seeds were considered to contain a living embryo (D. García, pers. observ.).

4) Seed set, the number of filled seeds per m² of plant surface, was calculated for each plant as ripe cone production × number of seeds cone⁻¹ × proportion of filled seeds per plant.

All these reproductive variables were quantified for six years (1992-1997). Cone production was evaluated for 40-75 plants per year (310 plants). Kendall's coefficient of concordance (Zar, 1996) in ripe cone production was calculated from a subsample of 40 plants repeatedly visited each year and was used to assess the degree of supra-annual synchrony among individuals (Herrera, 1998). Number of seeds/cone was evaluated for 10-75 plants per year (239 plants, 8,541 cones), and the percentages of depredated, filled, and empty seeds were evaluated for 6-75 plants per year (205 plants, 19,283 seeds).

CLIMATIC VARIABLES

Monthly values of precipitation (total) and temperature (average) for the period 1980-1997 were obtained from the Albergue Sierra Nevada meteorological station (2,500 m a.s.l.), situated roughly 1,000 m from the study site. Climatic effects on reproductive output were studied by relating reproductive variables to climatic variables corresponding to the year when the crop of ripe cones was sampled (yr), the previous year (yr-1), and two years before (yr-2). This procedure enabled us to identify climatic effects on different stages of cone and seed development, as the number of cones and the number of seeds per cone are determined one or two years before cone ripening when pollination, flower abscission, seed coat growth, and cone abortion occur (for similar procedures, see Houle & Filion, 1993; Sork, Bramble & Sexton, 1993). The percentage of empty seeds was also correlated to the precipitation of the month of pollination of the corresponding crop, that is, June of two years prior to the crop (June yr-2).

Results and discussion

All the reproductive components of *J. communis* varied significantly among years (Figure 1). Despite this variation, the percentage of empty seeds consistently exceeded 68%. This minimum value of seed abortion, however, surpassed the average value for juniper populations in central and northern Eurasia (García *et al.*, 2000). Therefore, the comparatively low seed viability characterising this Mediterranean population of *J. communis* can be considered a consistent trait over time.

Interannual trends in green cone production, the number of seeds per cone, and the percentage of empty seeds were independent of the trend in ripe cone production

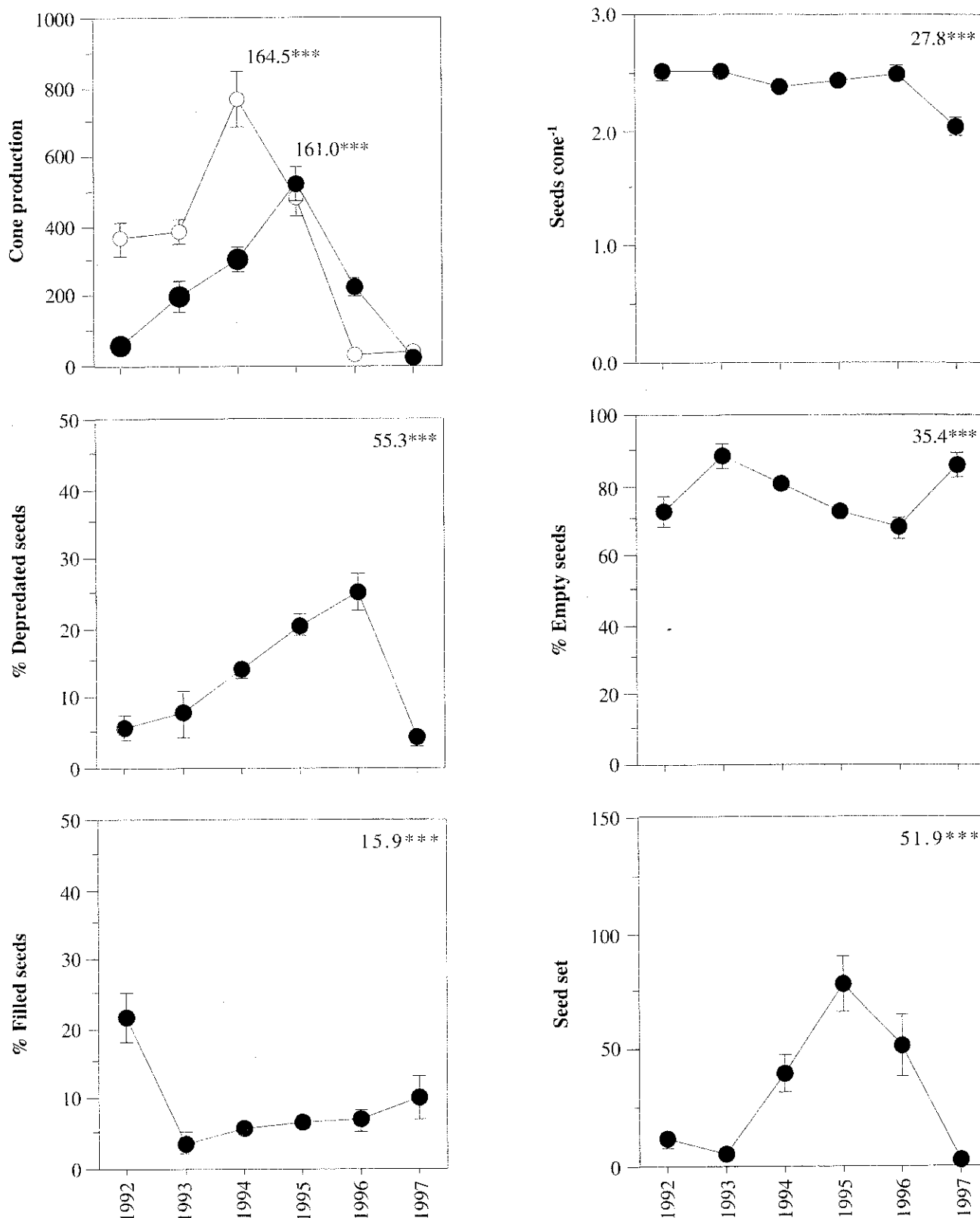


FIGURE 1. Mean values (± SE) of different reproductive variables of *Juniperus communis* in the Campos de Otero population for the period 1992-1997. Cone production (empty circles = green cones; filled circles = ripe cones) and seed set refer to the number of cones and seeds per m² of plant surface, respectively. The result of a Kruskal-Wallis test (*H*) and its significance level (*** = *p* < 0.001), checking for interannual differences, is shown for each variable.

(Spearman rank correlation: $r_s < 0.59$, $p > 0.21$, $n = 6$, for all correlations). Apparently, lower investment in cone production in some years did not translate into more resources for seed production and embryo development in the same years (Lee, 1988). Similarly, younger cone cohorts seem to be unaffected by the current ripening. Therefore, no evidence of trade-offs between different components of repro-

duction, both between-years and within-year, emerged from our data. On the other hand, the independence between seed abortion and cone production also implies that the seed set increased significantly only during years of high production of cones ($r_s = 0.886$, $p = 0.019$, $n = 6$), suggesting a potential demographic effect of masting years (Crawley, 1992; Crawley & Long, 1995). However, the potential of these

sporadic events to offset current reproductive failure in Mediterranean mountains must be very low for two reasons: 1) seed set in masting years is insufficient to compensate for seed and seedling mortalities, and 2) huge cone productions can satiate avian dispersers at the population level, resulting in cone removal rate proportionally decreasing in masting years (as happened in 1995; García, 2001).

Plants showed a significant synchrony in cone production for the period 1992-97 ($W = 0.367$, $\chi^2 = 86.01$, $p < 0.001$, $n = 40$). Despite this synchrony, no evidence of predator satiation was found, either between years (predation did not decrease in years of reduced cone production) or within year (predation was never negatively related to cone crop at plant level). In fact, predation runs parallel to cone production ($r_s = 0.829$, $p = 0.042$, $n = 6$; Figure 1), indicating that *M. bipunctatus* populations track interannual variation in resource availability (see also Turgeon, Roques & De Groot, 1994, for other *Megastigmus* species; Sperens, 1997). Besides this tracking ability, predator satiation at population level might be precluded by the magnitude of change in cone crop between successive years, which was probably weak for promoting satiation (transitions between large and small crops were gradual, as depicted by data from 1984 to 1997, Figure 2). Ultimately, predator satiation might be influenced by the dispersal system of *J. communis* since, for endozoochorous plants, the evolution towards masting depends on the trade-off between the advantages of satiating predispersal seed predators and the disadvantages of simultaneously satiating dispersers (Herrera *et al.*, 1998). This trade-off is especially pressing for plants like *J. communis*, which suffer a specialized seed predator, have avian dispersers that do become saturated in high reproductive years (García, 2001), and despite endozoochory, show relatively high levels of interannual variation in crop size ($CV = 99.9\%$, $n = 11$ years; for comparative values see Herrera *et al.*, 1998).

Some effect of local climate on juniper reproductive output is evidenced by our results, as precipitation during the period of pollination negatively affected seed development. In 1992-1997 almost 90% of seeds in a given crop proved empty if the pollination period of that crop had been especially rainy ($r_s = 0.943$, $p < 0.01$, $n = 6$; Figure 3). This negative effect, probably reflecting failed pollen dispersal from males, would be promoted by the pattern of spring precipitation in Mediterranean mountains, characterized by short but strong storms, as well as by the open structure of juniper shrublands. Similar climatic impact has been suggested for other woody wind-pollinated plants in which an adequate fruit set requires dry conditions during pollination (Sork, 1993; Despland & Houle, 1997). Aside from seed emptiness, no reproductive component was correlated to climate ($p > 0.05$, for all correlations).

In conclusion, this long-term study suggests that the low production of viable seeds in juniper in Mediterranean mountains is affected by climate at two different scales. Locally, seed emptiness varies between years from 70% to 90%, depending on weather. Minimum, but consistent, levels of seed emptiness (*ca* 70%) are better explained at a broader geographical scale and by factors such as environmental stress associated with the Mediterranean climate,

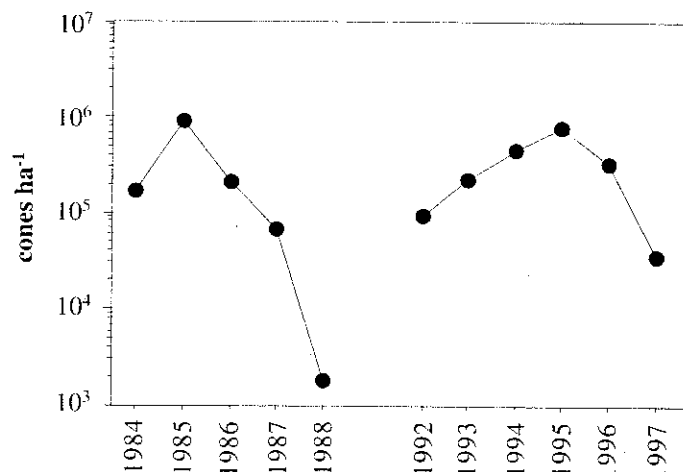


FIGURE 2. Number of juniper cones per ha in Campos de Otero in different years during the period 1984-1997. Data for 1984-1988 are extracted from Zamora (1987) and Jordano (1993). Data for 1992-1997 are calculated by extrapolating the number of cones per plant surface unit to the total area (coverage of female junipers = 14.5%).

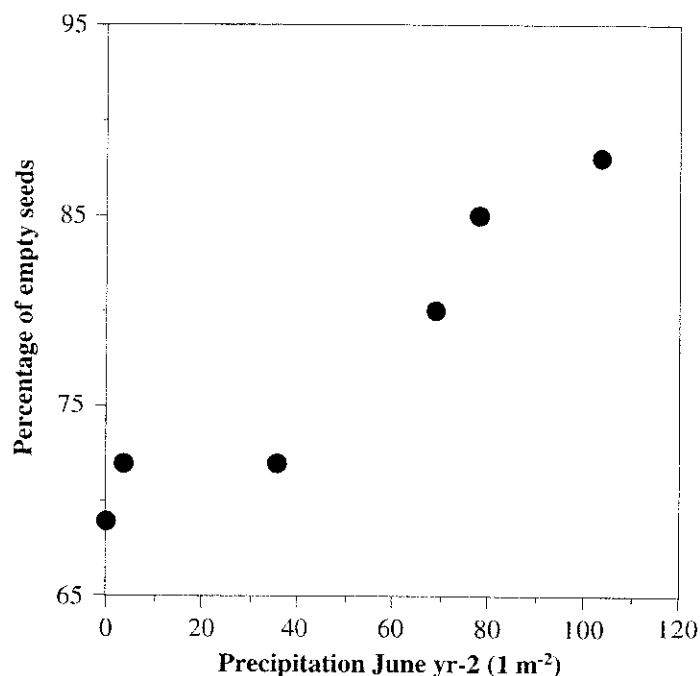


FIGURE 3. Percentage of empty seeds in *Juniperus communis* in relation to precipitation (1 m⁻²) in the month of pollination (June two years before cone crop), for different years (1992-1997).

together with genetic isolation (García *et al.*, 2000). Clearly, the combination of broad spatial and temporal scales is needed to analyse the effect of environmental constraints on plant reproduction.

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