



Spatial dynamics of cone production in Mediterranean climates: A case study of *Pinus pinea* L. in Portugal

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ABSTRACT

Seed production of trees is key to natural regeneration of forests and to successful conservation management. Despite its importance no spatially explicit analyses of seed production have so far been carried out in this important field. Analyses like these are particularly important in areas with regular summer droughts. We used *Pinus pinea* L. as a model species and analysed a short time series comprising four replicated plots in the Alcácer do Sal region in Portugal. In 2003, all trees in four plots with a size between 0.6 and 1.6 ha were mapped. Crown diameters were established in 2003 and cone weights were measured annually from 2003 to 2005. The marked point patterns formed by tree locations, crown diameters and cone weights were analysed with three second-order characteristics. As expected there was good correlation between crown diameters and coning. We found considerable variability in cone production, which was larger between plots than between years. It was confirmed that there is fairly regular spacing with distances larger than 10 m between mature trees. This is mainly a consequence of a climate with regular summer droughts and of poor soils. The mark correlation function revealed strong mutual stimulation of coning between trees around 10 and 23 m. According to our field observation recruitment of *Pinus pinea* and cork oak mainly occurs in the vicinity of large, mature *Pinus pinea* trees causing negative autocorrelation and benefitting from semi-shade and increased soil moisture. *Pinus pinea* cone production and recruitment are strongly influenced by tree spacing. Depending on the water holding capacity of soils, spacing between mature trees needs to be optimised for successful coning. Local forest owners and managers are aware of this and have developed a system of adaptive management.

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1. Introduction

How forests regenerate naturally has been an important research topic both in natural and in managed forests throughout the world (Schütz, 1990; Oliver and Larson, 1996; Smith et al., 1996). Apart from the fact that the ecology of regeneration processes and the associated patterns are interesting in themselves, the topic also ties into the management concept of sustainability. Therefore factors influencing germination and survival as well as mortality of seedlings and saplings have been studied in many species (e.g. Burschel et al., 1992; Harmer, 1994, 1995; Boyden et al., 2005; Oliver, 2007).

A necessary precondition for natural regeneration is seed production and there is accordingly also a great deal of work that has been dedicated to seed production cycles, to the existence of mast years and to factors influencing seeding (e.g. Koenig et al.,

1994; Mencuccini et al., 1995; Guariguata and Pinard, 1998; Sirois, 2000; Calama and Montero, 2007; Lusk et al., 2007; Ganatsas et al., 2008; Zlotin and Parmenter, 2008; Ganatsas and Thanasis, 2010; Calama et al., 2011; Garcia-del-Rey et al., 2004). A number of papers have been published that investigated spatial seed dispersal, spatial regeneration and species patterns (Bleher et al., 2002; Kunstler et al., 2004; Wiegand et al., 2006; Sagnard et al., 2007), but to our knowledge there has not yet been any attempt to study spatial dynamics of seed production using point process statistics. Temporal regeneration dynamics have been investigated by Nanos et al. (2004), Barbeito et al. (2008), and Ledo et al. (2011). Spatio-temporal dynamics of seed production is particularly interesting in Mediterranean climates with regular summer droughts, as the adverse climatic conditions during the summer months are likely to have a significant influence on these processes. Below-ground competition for water is for example very likely to have a considerable influence on seed production.

As a model species we selected *Pinus pinea* L., because this species is one of the most important forest trees in the summer dry areas of the Iberian Peninsula. *Pinus pinea* is patchily distributed around the northern and eastern Mediterranean, from Portugal to

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Syria (Goes, 1991). The Iberian Peninsula accounts for approximately 75% of *Pinus pinea* stands, Portugal has the second largest area of 130,300 ha (IFN5, 2010) after Spain with an area of 464,000 ha (BDN, 2008).

We observed *Pinus pinea* research forests from 2003 to 2005 and analysed their spatial patterns of cone production with methods from point process statistics as detailed in Diggle (2003) and Illian et al. (2008).

The two-dimensional arrangement of tree locations in a forest can be interpreted as a realisation of a point process. In a point process, the location of each individual tree, i , can be understood as a point or event. The observation window, W , is usually a rectangular or circular area in the forest that is selected to yield representative information on the forest as a whole. Point process analysis can be refined; if additionally quantitative information such as crown diameters and cone weight is available. This type of information is referred to as quantitative marks.

The mark correlation functions, $k_{mm}(r)$, and mark variograms, $\gamma_m(r)$, allow the analysis of marked point patterns, i.e. the location of trees and their attributes whereas the pair correlation function, $g(r)$, describes point patterns only (Penttinen et al., 1992; Stoyan and Penttinen, 2000; Pommerening, 2002; Diggle, 2003; Illian et al., 2008). The three functions used contributed different aspects of spatial plant interaction through their respective test functions.

A good example of an analysis of ecological data with second-order characteristics is Zhang et al. (2010). The authors presented an interesting application of second-order characteristics to the distribution of female and male trees of the dioecious species *Fraxinus mandshurica*. Similar to our paper, this is one of the rare studies on trees that used variables other than species, stem diameters or tree heights as marks. Zhang et al. (2010) found that female and male individuals of this species were not completely randomly distributed in the study areas but showed

different responses to specific microenvironments in the Chinese study area.

The objective of this study is to understand the interactions between spatial structure of parent trees and cone production using the data from four replicated research plots in the Alcácer do Sal region in Portugal. In particular this study intends to answer the following questions: (1) Does coning show the same trend for different site conditions?; (2) Does cone production show variability between years?; (3) Is it possible to identify a mean spacing for the production of pine cones? and (4) How does *Pinus pinea* react to an increase in growing space?

2. Methods

2.1. Model species

Pinus pinea is well adapted to Mediterranean climate, that is to high temperatures and regular summer droughts (Raddi et al., 2009) and due to its ecological plasticity can grow well even in poor and degraded soils (Iovieno et al., 2010). The most important environmental variables determining *Pinus pinea* distribution include the mean temperature of the coldest month and winter precipitation, the former determining plant survival and the latter growth rates, especially in the areas where the main source for groundwater is precipitation (Raddi et al., 2009).

Pinus pinea is a monoecious species and seed production starts at an age of approximately 15–20 years (Franco, 1943; Figueras, 1979; Ferreira et al., 2001). The maturation of *Pinus pinea* cones requires four growing seasons (Goes, 1991; Alpuim, 2002). This species has a monopodial cyclic growth pattern with annual shoots deriving from buds formed at shoots of preceding years. Annual shoots elongate in spring and have lateral buds and female strobili.

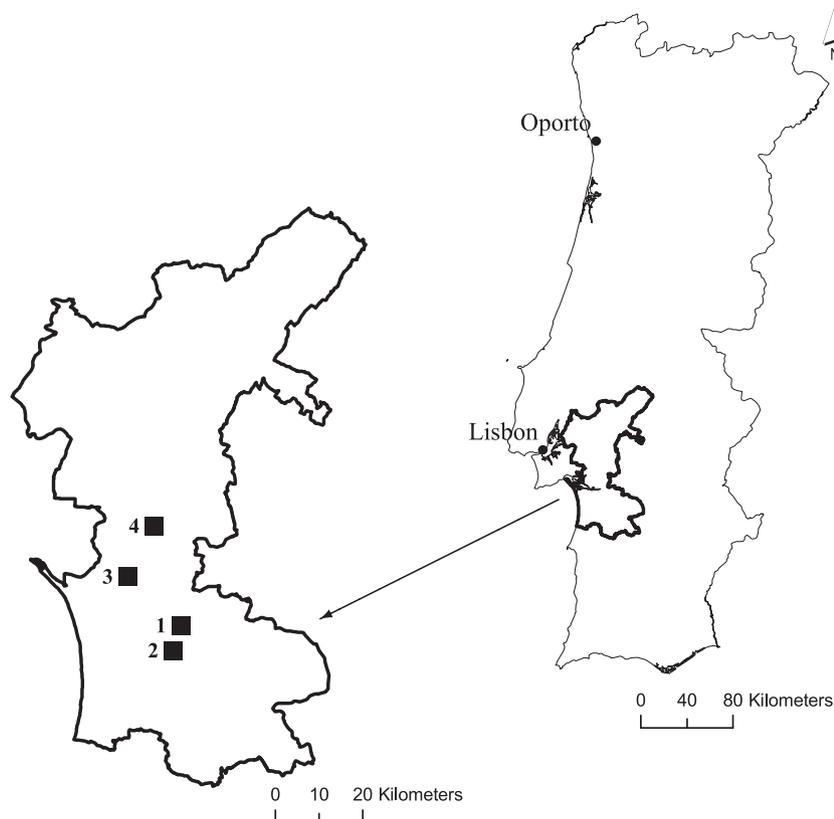


Fig. 1. Location of the replicated research plots in the Alcácer do Sal region (Portugal).

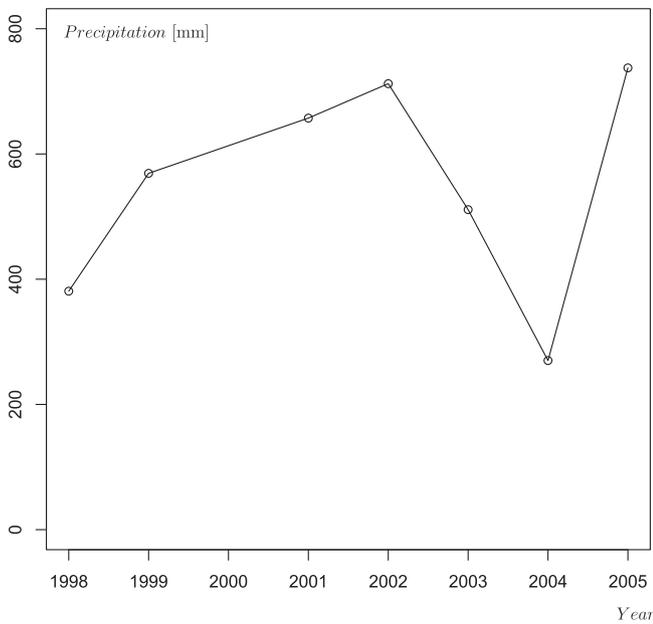


Fig. 2. Mean annual precipitation between 1998 and 2005.

The latter develop for three years and in the third year the main cone growth occurs after fertilisation. Fruit maturation occurs in the winter of the following year. The cones can have a weight between 200 and 500 g (Mutke et al., 2005). According to Agrimi and Ciancio (1994) and Bachiller (1995) *Pinus pinea* fruit production is correlated with crown size, which is why we selected crown diameter and cone weight as main variables in the spatial analysis. Cone production usually shows large variability between years (e. g. Mutke et al., 2005; Calama et al., 2008, 2011; Raddi et al., 2009). Seed dispersal depends much on seed weight; heavy seeds like those of *Pinus pinea* (Costa, 1984; Calama and Montero, 2007; Ganatsas et al., 2008; Ganatsas and Thanasis, 2010) have a comparatively restricted area of dispersal.

2.2. Study site

The time series data were collected in four replicated plots situated in the Alcácer do Sal region of Portugal (Fig. 1). Plot 1 (1.5 ha), Herdade do Pai Sobrado (38° 21' 34" N and 8° 31' 07" W), plot 3 (1.6 ha), Herdade do Monte Novo (38° 29' 35" N and 8° 38' 35" W) and plot 4 (2.0 ha), Quinta de Sousa (38° 33' 55" N and 8° 35' 15" W), in pure even-aged *Pinus pinea* stands with a few cork oak trees (*Quercus suber* L.) as part of a privately owned forest. Plot 2 (0.6 ha), Mata de Valverde (38° 19' 28" N and 8° 32' 36" W) is located in a pure even-aged stand of a state forest originally established for timber production. The stands have a mean age of 60 years (Vacas de Carvalho, pers. comm.), which is in accordance with the results in Ganatsas and Thanasis (2010). The plots are situated on sites of sandy soils, in typical Mediterranean climate with a mean annual temperature of 16 °C, a mean annual precipitation of 600 mm, a mean relative humidity of 75% and a drought period from May to September. The mean annual precipitation shows considerable variability (Fig. 2) with the lowest value in 2004 (270.1 mm) and the largest in 2005 (737.5 mm). In plots 1 and 3, there are chromic regosols (with a soil water retention capacity of 36 mm/m) and in plot 2 there are chromic podzol regosols (with a soil water retention capacity of 15 mm/m). Plot 4 is characterised by cambic podzol regosols (with a soil water retention capacity of 51 mm/m).

The plots were installed in 2003 and surveyed in 2003, 2004 and 2005 (see Fig. 3). The main stand was defined as all individuals

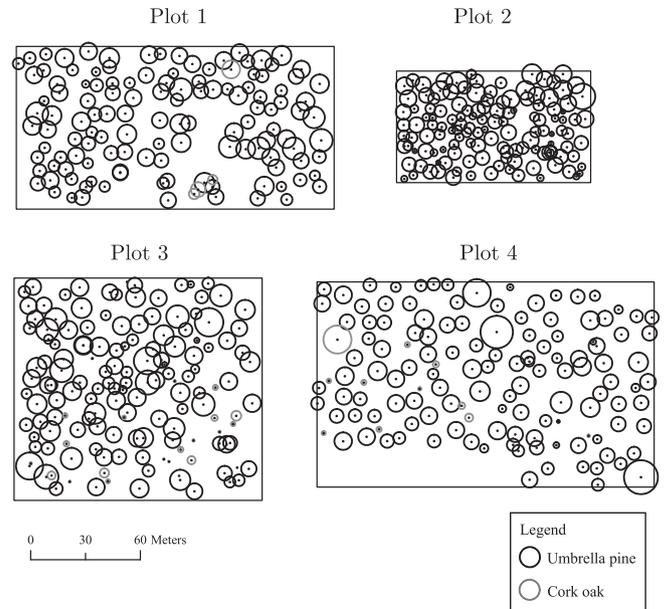


Fig. 3. Detailed tree location maps of the four *Pinus pinea* plots in the Alcácer do Sal region. Crown diameters of 2003 were used to scale the circles representing the trees.

with diameters at breast height larger than 20 cm and recruitment as the individuals with diameters at breast height between 5 and 20 cm. In each plot, tree locations were measured as well as crown radii (cr , four radii measured in North, South, East and West directions) (Avery and Burkhart, 1994). Polar coordinates of tree locations were measured with compass and tape and converted to Cartesian coordinates. For the four crown radii per tree we measured bearing and distance between stem centre and crown periphery with compass and tape, respectively. Crown diameter (cd) was calculated as the quadratic mean of crown radii $cd = 2 \times \sqrt{\frac{1}{n} \sum_{i=1}^n cr_i^2}$, with n , the number of radii, according to Siostrzonek (1958) and Hasenauer (1997). Crown cover was estimated from the relation of horizontal crown projections to total plot area. The cones of all trees were collected in the three surveys, from December to March, and quantified by cone fresh weight (cw) and by the number of cones (cn) per tree. The cones were viable; only a tiny fraction was infested by *Dyorictria mendacella* Stgr., no other pest or diseases were detected.

2.3. Data analysis

First, we checked and quantified the correlation between crown diameter and cone weight using the Spearman correlation coefficient (Maroco, 2007) with SPSS (version 18.0 for Windows) for $\alpha = 0.05$.

The patterns of tree locations were analysed with the pair correlation function, $g(r)$. We used the mark correlation function, $k_{mm}(r)$ and mark variogram, $\gamma_m(r)$ (Diggle, 2003; Illian et al., 2008) to characterise the marked point patterns given by tree locations as points and crown diameter and cone weight per tree, respectively as quantitative marks. Cone weight was used because, as supported by Calama et al. (2011), it is a better indicator of the allocation of resources to fruit production than just the number of cones.

In this study, particular attention was paid to the quantification of mark correlation, since our main tree variable of interest was cone production. Using the framework of second-order characteristics, we decided to apply two different test functions (see Illian et al., 2008, p. 343) simultaneously to develop a better understanding

of the spatial interactions in *Pinus pinea* forests: The analysis of quantitative marks of pairs of trees with inter-tree distance r is usually carried out using a test function $t(m_1, m_2)$ in order to quantify the similarity or dissimilarity of pairs of quantitative tree marks, m_1 and m_2 , (in our case either crown diameters or cone weights). For the mark correlation function, the test function used was $t_1(m_1, m_2) = m_1 m_2$, computing the mark product of pairs of points with inter-tree distance r . For small values of t_1 , both marks are similarly small whilst large values indicate large crown diameters or cone weights of pairs of trees at distance r . For the mark variogram, we applied the test function $t_2(m_1, m_2) = \frac{1}{2}(m_1 - m_2)^2$ characterising the squared differences between the marks of pairs of points with distance r (Illian et al., 2008). In contrast to t_1 , small values of t_2 are the result of similar sized m_1 and m_2 , which can be either both small or large. Large values of t_2 are possible, if m_1 and m_2 are of different size.

The second-order characteristics were estimated using the Epanechnikov kernel (see Illian et al., 2008, p. 481f.). The estimators of the three summary characteristics were denoted by $\hat{g}(r)$, $\hat{k}_{mm}(r)$ and $\hat{\gamma}_m(r)$, Eqs. (1)–(3), respectively.

$$\hat{g}(r) = \sum_{x_1, x_2 \in W}^{\neq} \frac{k_h(\|x_1 - x_2\| - r)}{2\pi r A(W_{x_1} \cap W_{x_2})} \quad (1)$$

$$\hat{k}_{mm}(r) = \sum_{x_1, x_2 \in W}^{\neq} \frac{m(x_1)m(x_2)k_h(\|x_1 - x_2\| - r)}{2\pi r A(W_{x_1} \cap W_{x_2})} \quad (2)$$

$$\hat{\gamma}_m(r) = \sum_{x_1, x_2 \in W}^{\neq} \frac{\left(\frac{1}{2}(m(x_1) - m(x_2))^2\right)k_h(\|x_1 - x_2\| - r)}{2\pi r A(W_{x_1} \cap W_{x_2})} \quad (3)$$

where x_1 and x_2 are arbitrary points of the point pattern in the observation window W , k_h is the Epanechnikov kernel function, $A(W_{x_1} \cap W_{x_2})$ is the area of intersection of W_{x_1} and W_{x_2} , see Illian

et al. (2008, p. 481f. and p. 188). We applied a bandwidth of 4 m and edge corrections following the suggestions in Illian et al. (2008). The mark variogram was used without normalisation term to better account for different levels of mark variability.

Monte Carlo simulations were applied to test complete spatial randomness (CSR) of tree locations and spatial independence of marks (Diggle, 2003; Illian et al., 2008). In each simulation, the same number of randomly distributed tree locations was generated as originally observed and $\hat{g}(r)$ was calculated for the simulated patterns. Then envelopes marking the acceptance regions of the CSR hypothesis were estimated from the maxima and minima of 1000 simulations following the recommendation in Illian et al. (2008, p. 455f.).

We tested the hypothesis of mark independence by using the random labelling test (Diggle 2003, p. 48f; Illian et al., 2008, p. 466ff). In each simulation, observed crown diameters or cone weights were re-allocated randomly through random permutations to the observed, fixed tree locations. For these randomly labelled patterns, we calculated $\hat{k}_{mm}(r)$ and $\hat{\gamma}_m(r)$ and again estimated the corresponding envelopes from the maxima and minima of 1000 simulations following Illian et al. (2008, p. 466ff.).

Any empirical second-order characteristic, which is not completely inside the envelopes of the acceptance region, indicates a significant departure from the CSR hypothesis in terms of $\hat{g}(r)$ or from spatial independence of the respective two marks in terms of $\hat{k}_{mm}(r)$ and $\hat{\gamma}_m(r)$. Since we have used probability density functions, the ranges of the inter-tree distance r , where function graphs happen to be outside the acceptance region, therefore need to be considered as particularly interesting, special cases of tree interactions. The authors are aware of the fact that cumulative characteristics such as Ripley's $K(r)$ function (Ripley, 1977) and Besag's $L(r)$ function (Besag, 1977) should generally be preferred in tests and that envelope tests are not always satisfactory (Loosmore and Ford,

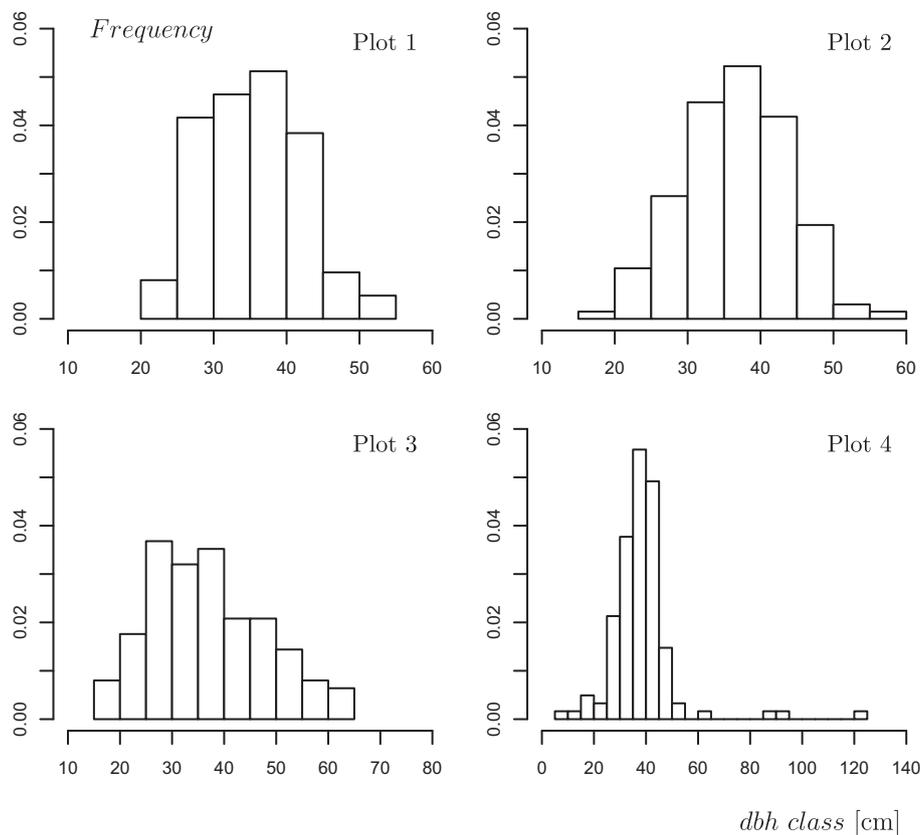


Fig. 4. Diameter distribution of the four *Pinus pinea* plots. Diameters at breast height of 2003 were used.

Table 1

Number of trees per hectare (N), basal area per hectare (G) and ground cover (GC), as well as the mean crown diameter (CD), the mean weight and mean number of cones per tree in 2003 ($cw03$, $cn03$), in 2004 ($cw04$, $cn04$), in 2005 ($cw05$, $cn05$) and standard deviation. $CV\ cw$ and $CV\ cn$ is the coefficient of variation of cone weight and cone number.

Plot	N	G (m^2ha^{-1})	GC (%)	CD (m)	$cw03$ (kg)	$cw04$ (kg)	$cw05$ (kg)	$cn03$	$cn04$	$cn05$	$CV\ cw$	$CV\ cn$
1	95	9.8	51.2	8.3 ± 1.8	10.0 ± 13.6	6.3 ± 6.6	11.6 ± 13.4	43.1 ± 49.0	23.3 ± 21.7	40.2 ± 44.1	0.29	0.30
2	233	25.3	85.9	6.7 ± 2.1	1.5 ± 1.6	4.4 ± 4.0	4.0 ± 5.4	6.6 ± 6.2	15.5 ± 12.8	16.6 ± 22.2	0.48	0.43
3	103	10.7	53.9	8.6 ± 2.4	6.9 ± 7.6	8.2 ± 8.4	15.9 ± 20.2	29.1 ± 32.1	30.0 ± 32.5	52.3 ± 64.1	0.47	0.35
4	66	8.1	32.8	7.9 ± 2.2	15.2 ± 12.9	31.9 ± 36.6	47.1 ± 42.2	52.9 ± 45.6	109.1 ± 131.0	163.4 ± 143.5	0.51	0.51
		CV (spatial)			0.68	1.01	0.96	0.61	0.98	0.96		

2006). However, we felt that diagnostic properties were of greater importance in this study and therefore decided to use density distributions.

3. Results

3.1. Summary characteristics and correlation coefficients

The four stands are even-aged. The histograms of diameter at breast height are shown in Fig. 4. Summary characteristics for the four plots are presented in Table 1. Number of trees per hectare (N), basal area per hectare (G) and ground cover (GC) are highest in plot 2 and lowest in plot 4. Cone weight and cone number per tree shows some variability for the three surveys in 2003 ($cw03$, $cn03$), 2004 ($cw04$, $cn04$), 2005 ($cw05$, $cn05$) and between plots. The mean number of cones per tree is comparable to the results of Ganatsas and Thanasis (2010) where mean annual precipitation is similar (approximately 700 mm in the Strofilia Coastal Area (Georgiadis et al., 1990)) but different to the studies by Barbeito et al. (2008) and Calama et al. (2011) where mean annual precipitation is much lower (370 and 460 mm, respectively). Clearly, judging by the coefficient of variation, the variability of cone production is generally larger between plots than between years.

All trees in the three surveys had cones, except two trees in plot 1 in 2003 and one tree in plot 4 in 2005.

As expected Spearman coefficients in most cases show a clear positive correlation between crown diameter and cone weight for the three surveys and their mean values. The considerable inter-annual production variability may explain the lack of correlation in plot 1 in 2004 and plot 2 in 2003 and 2005 (Table 2). The strongest correlations are found in plot 3 and 4 with comparatively lower tree density. Seed production in these plots probably mainly depends on environmental factors and less on competition, since the latter is insignificant at low densities. The weakest correlations are found in plot 2 where tree density is maximum.

3.2. Pair correlation function

The pair correlation functions, $\hat{g}(r)$, for all plots are shown in Fig. 5. The results were from 2003 and apply for the whole observation period from 2003 to 2005, since there were no dead or removed trees and no new recruitments. In all plots the shapes of the graphs indicate significant repulsion between points at short distances. This usually leads to regular point patterns. The CSR

hypothesis must be rejected for all plots. In plots 1 and 2, $\hat{g}(r)$ shows a maximum at 9 and 8 m, respectively, indicating the most frequent inter-tree distances. Interestingly, the pair correlation functions in plots 3 and 4 show two maxima at 11 and 23 m, and 14 and 24 m, respectively. The kinks in the curves at very short distances, particularly in plot 1, are significant and indicate weak clustering.

3.3. Mark correlation function with crown diameters

There was little change in crown diameters between 2003 and 2005, since the Wilcoxon test showed no significant differences between years for crown diameters for $\alpha = 0.05$. Therefore the crown diameters from 2003 were used in all subsequent years. In general, the mark correlation function, $\hat{k}_{mm}(r)$, (Fig. 6) indicates inhibition for small inter-tree distances and no correlation between crown diameters at larger r . The correlation range, marking in this case the maximum extent of inhibition, is 3 and 10 m in plots 1 and 2. In plots 3 and 4, inhibition can be observed up to an inter-tree distance of 12 m. The correlation range gives the maximum range of spatial correlations between tree locations and their associated marks. There are no correlations at larger distances. There is obviously a tendency that at small inter-tree distances both trees of a pair have smaller crown diameters than the average of the stand. The hypothesis of spatial independence of crown diameters must be rejected for plots 1, 2 and 4 and cannot be rejected for plot 3.

3.4. Mark variogram with crown diameters

The mark variogram, $\hat{\gamma}_m(r)$, using crown diameters of 2003 as marks (Fig. 7) shows similar trends in plots 1, 2 and 4 which can be referred to as positive autocorrelation (Suzuki et al., 2008). This means that crown diameters of pairs of trees up to a distance of 25 m (i.e. the correlation range) in plots 1, 2 and 4 tend to be similar in size. By contrast there is negative autocorrelation in plot 3 up to a distance of 5 m, i.e. the crown diameters of pairs of trees in this distance range are very different. Only in plots 1 and 2 the hypothesis of spatial independence must be rejected because the $\hat{\gamma}_m(r)$ curve is not completely inside the acceptance region in the range $4 < r < 12$ m. For the other two plots the hypothesis of spatial independence of crown diameters cannot be rejected. Crown diameter variance is largest in plot 3 ($\sigma_{cd}^2 \approx 10\ m^2$), followed by plot 4 ($\sigma_{cd}^2 \approx 7\ m^2$). Plots 1 and 2 have the lowest crown diameter variances with $\sigma_{cd}^2 \approx 3\ m^2$ and $\sigma_{cd}^2 \approx 5\ m^2$, respectively.

3.5. Mark correlation function with cone weights

The mark correlation function using cone weights of 2003, 2004 and 2005 revealed again some variability between years and plots (Fig. 8). In plot 1, there is mutual stimulation of cone production for distances between 4 and 11.5 m in 2003 and 2004. This is remarkable since mutual stimulation is very unusual for most tree analyses, because stem diameter is often the main variable used and mutual stimulation is almost impossible for this variable (see also

Table 2

Correlation between crown diameter and cone weight.

	All plots	Plot 1	Plot 2	Plot 3	Plot 4
2003	0.432*	0.384*	0.004	0.581*	0.517*
2004	0.408*	0.053	0.291*	0.740*	0.651*
2005	0.414*	0.299*	-0.036	0.773*	0.597*
Average	0.462*	0.352*	0.220*	0.746*	0.561*

* Correlation is significant at the 0.05 level (2-tailed).

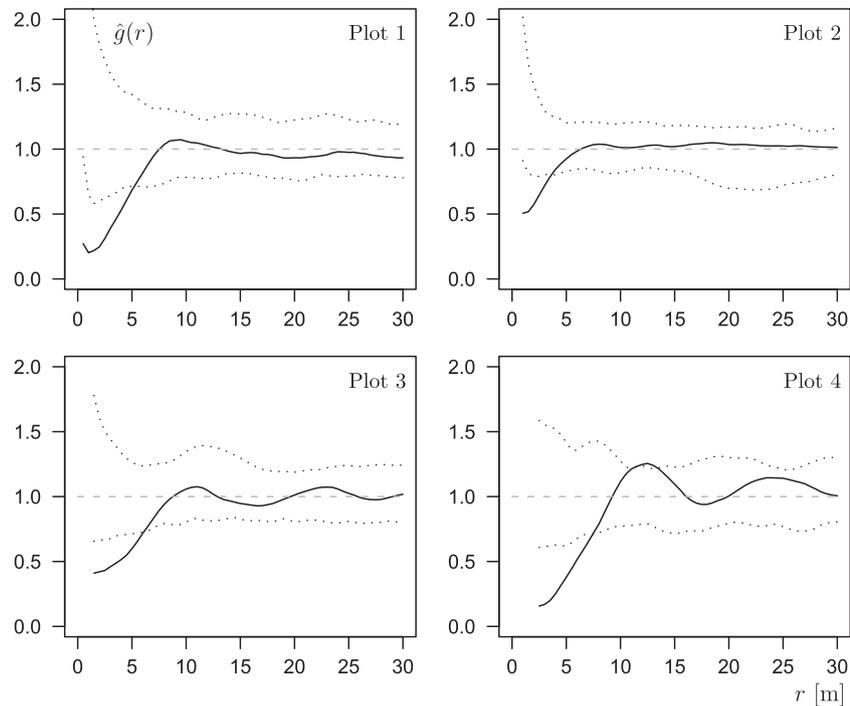


Fig. 5. Pair correlation function, $\hat{g}(r)$, describing the tree location patterns in the four plots in 2003. There were no changes in the point pattern between 2003 and 2005. Envelopes of the acceptance regions of the CSR hypothesis are shown as dotted lines. r is the distance between pairs of trees.

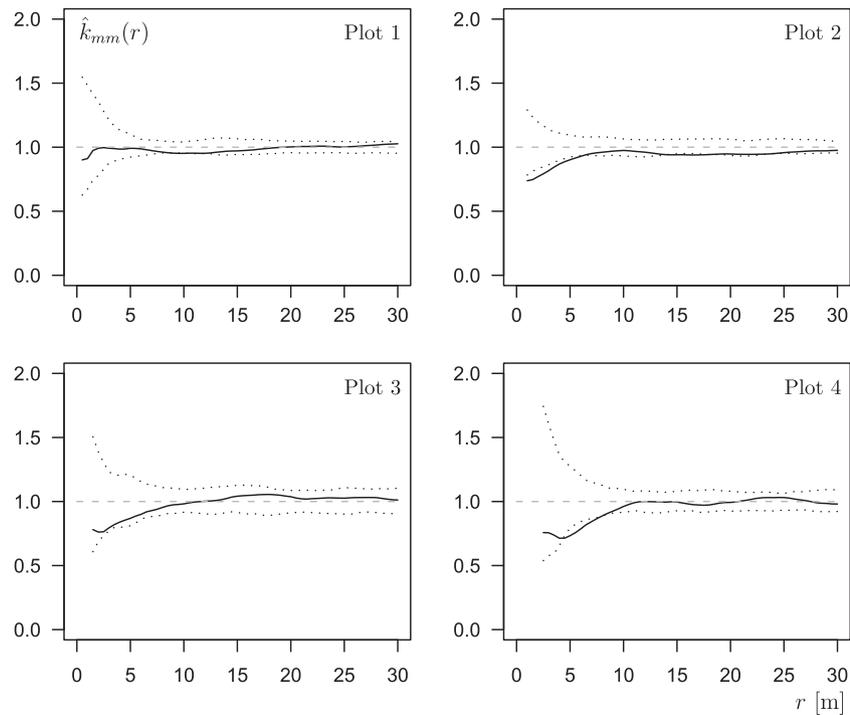


Fig. 6. Mark correlation function, $\hat{k}_{mm}(r)$, using crown diameters of 2003 as marks. Envelopes of the acceptance regions of the mark independence hypothesis are shown as dotted lines. r is the distance between pairs of trees.

Pommerening et al., 2011). Mutual stimulation in this context means that trees benefit from being close together and thus show a tendency of having larger cone weights than the average of the stand. In 2005, mutual stimulation of cone production at very short distances in plot 1 is followed by considerable inhibition of coning for distances smaller than 12.5 m. In plot 2, there is inhibition of

cone production for distances smaller than 11, 9 and 5 m in 2003, 2004 and 2005, respectively. Also in plot 3, inhibition of cone production occurs at distances smaller than 15, 12.5 and 8 m in 2003, 2004 and 2005, respectively. In 2005, pairs of trees in the range $8\text{ m} < r < 15\text{ m}$ in this plot appear to stimulate each other in terms of seed production. In plot 4, there is weak mutual

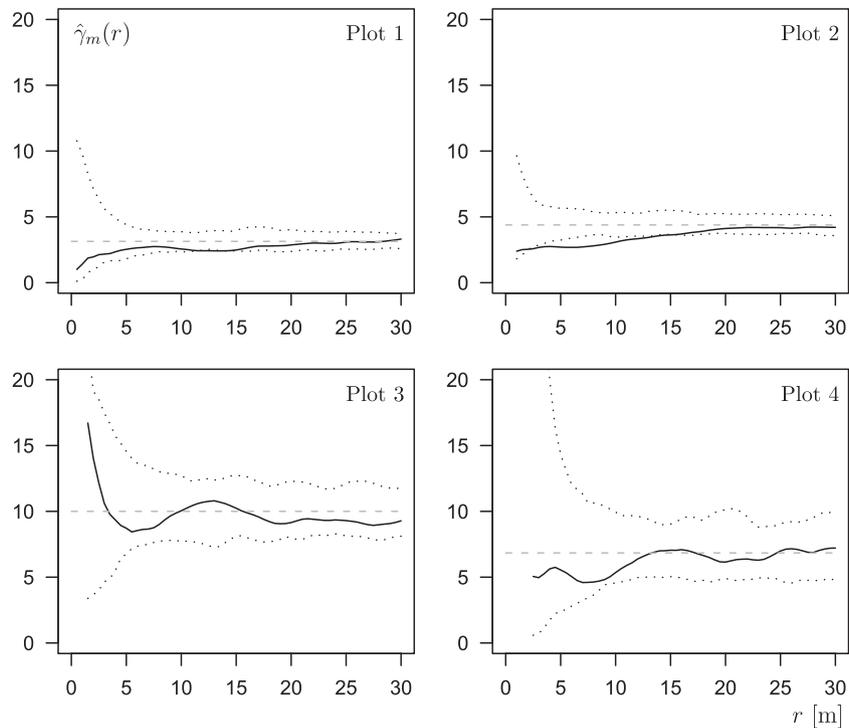


Fig. 7. Mark variograms, $\hat{\gamma}_m(r)$, using crown diameters of 2003 as marks. Envelopes of the acceptance regions of the mark independence hypothesis are shown as dotted lines. r is the distance between pairs of trees. The grey dashed line indicates the variance of crown diameters.

stimulation of coning at very short inter-tree distances up to approximately 5 m followed by inhibition of cone production for distances smaller than 22.5, 20.5 and 21.5 m in the years 2003, 2004 and 2005, respectively. In this plot, the main mutual stimulation of seed production occurs at much larger inter-tree distances than in any other plot, i.e. between 21 and 27 m.

From the results of all plots, we can conclude that there is a trend towards inhibition of cone production at small distances followed by a mutual stimulation of cone production at larger distances. The results of plot 2 (2003) and plot 4 (2003–2005) suggest that the hypothesis of spatial independence of cone weights needs to be rejected. In plots 1 and 3 the hypothesis of spatial independence of cone weights can be accepted.

3.6. Mark variogram with cone weights

Also the shapes of the mark variograms indicate considerable variability between plots and years.

Cone weight variance usually increases in all plots from 2003 to 2005 with the exception of plot 1, where there is a marked decrease in variance in 2004. The most remarkable temporal changes in cone weight variance were observed in plots 3 and 4.

In plots 1 and 2, there is positive autocorrelation in all survey years throughout the distance range. This means that in plots 1 and 2 there is a weak trend of pairs of trees up to 5–10 m to have similar cone production. There is negative autocorrelation in plot 3 throughout the observation period with a considerable increase from 2004 to 2005, which is also reflected by the increase in cone weight variance. This finding implies that the coning of pairs of trees at $r < 5$ m is dissimilar in this plot, particularly in 2005. In plot 4, positive autocorrelation markedly increases along with increasing cone weight variance from 2003 to 2005, whilst the correlation range remains more or less constant. As in plot 1, pairs of trees at short distances have a very similar cone production behaviour, however, this trend is much stronger in plot 4 and also the

correlation range is larger. Interestingly there also seems to be a weak trend of regularity of cone production in plots 3 and 4 (2004/5): Around 12 and 25 m there is often positive autocorrelation in the four plots indicating pairs of trees with similar cone production (Fig. 9).

In all plots, there is never a change from positive to negative correlation or vice versa between the years. Also the correlation range remains constant in all plots from 2003 to 2004. The hypothesis of spatial independence has to be rejected for plot 2 (for all three years), plot 3 (2003) and plot 4 (for all three years), i.e. there is weak spatial interaction of cone production in most plots apart from plot 1.

4. Discussion

Starting with the three predictions made in the introduction, there was indeed considerable temporal and spatial variability in cone production, which interestingly was found to be larger between plots than between years (see the coefficients of variation in Table 1 and the different shapes of $\hat{k}_{mm}(r)$ and $\hat{\gamma}_m(r)$ in Figs. 8 and 9). This is partly also attributed to different soil water retention capacities of the soils involved: Plot 4 has the highest cone production per tree and is located in the soil with higher soil water retention capacity, and plot 2 has the lowest and is located in the soil with the smallest soil water holding capacity. Inter-annual seed production variability has been referred to by various authors (e. g. Mutke et al., 2005; Calama et al., 2008, 2011; Raddi et al., 2009). In contrast to Calama et al. (2011) who reports for *Pinus pinea* forests on the Spanish Northern Plateau a considerable proportion of trees with no cone production, only three trees in the plots of Alcácer do Sal region had no production at all.

The sizes, a little less the locations, of the maxima and minima of the mark correlation functions and the mark variograms are clearly affected by the temporal fluctuations of cone production, see also Table 1. As there were no changes to the spatial forest

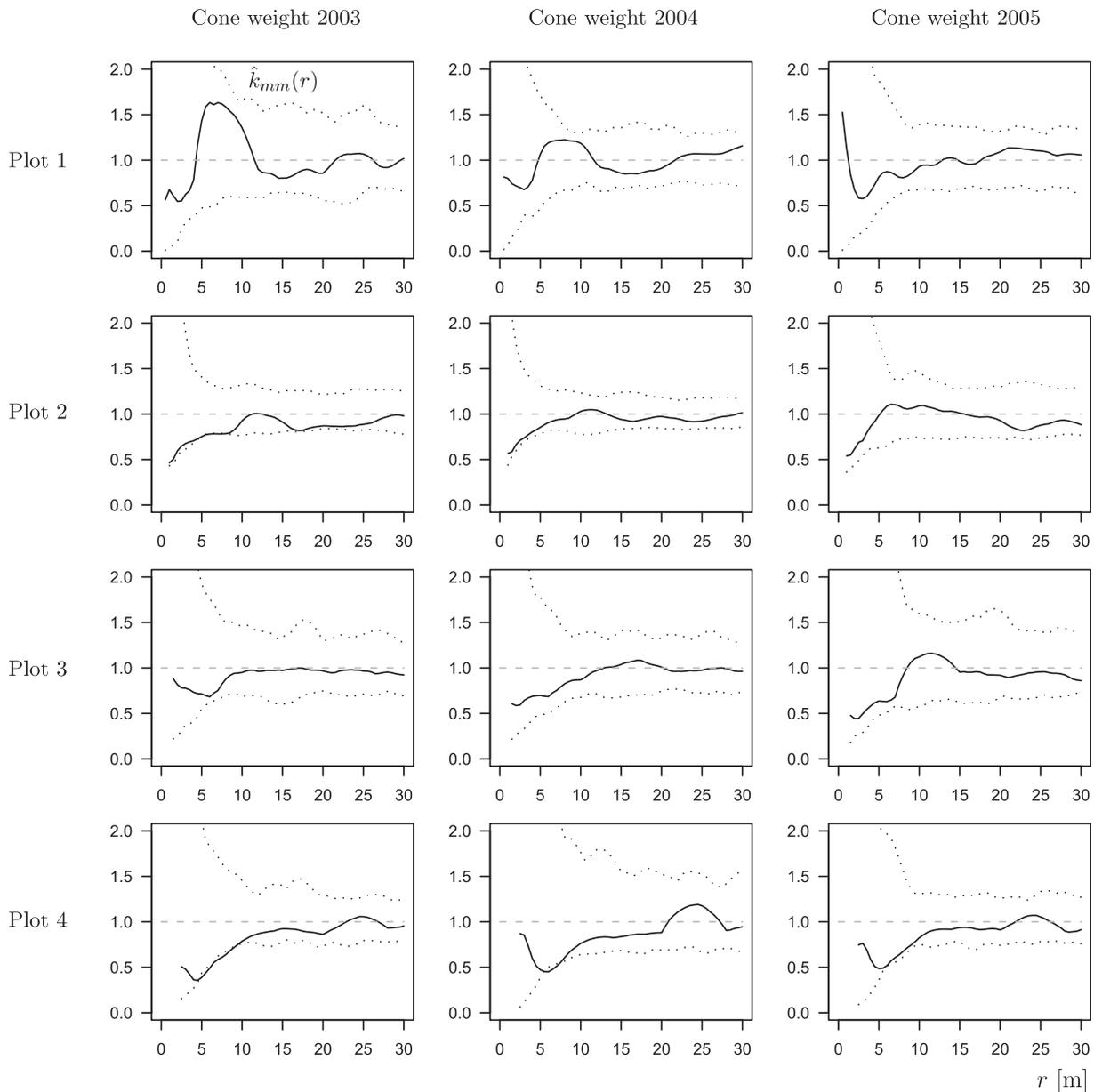


Fig. 8. Mark correlation function, $\hat{k}_{mm}(r)$, using tree cone weights in 2003, 2004 and 2005. Envelopes of the acceptance regions of the mark independence hypothesis are shown as dotted lines. r is the distance between pairs of trees.

structure between 2003 and 2005 these fluctuations are probably mainly caused by localised climatic factors. Calama et al. (2008) emphasised that genetic factors might also be of importance as the individuals are of local seed origin and not genetically improved seeds; see also Sirois (2000). Long-term climate and production data would be necessary for each stand to separate the effects of these factors on coning. On the third question, all second-order characteristics agree that trees with similar crown diameters in the *Pinus pinea* forests of the Alcácer do Sal region in Portugal appear to have fairly regular spacing with a distance larger than 10 m between them. This is mainly the consequence of the light demanding nature of *Pinus pinea* and partly the result of adaptive management. Frequent summer droughts and poor, sandy soils resulting in limited nutrient and water availability have a clear influence on inter-tree competition and are reflected by local management practices as stated in Calama et al. (2008, 2011).

Finally, the local maxima of the $k_{mm}(r)$ curves indicating mutual stimulation (Fig. 8) convey the impression that *Pinus pinea* strongly

reacts to available growing space in terms of cone production. As briefly mentioned before, mark correlation functions with $k_{mm}(r) > 1$ indicating stimulation can hardly be observed for tree data if stem diameters are used as marks. Therefore this finding is quite remarkable. Lancaster (2006) reports a spatial analysis of ragwort plants (*Senecio jacobaea* L.) where the marks were the number of caterpillars of the cinnabar moth (*Tyria jacobaeae* L.) in a particular season. Also in her study there was considerable stimulation with similarly large numbers of caterpillars, however, in this case on immediately adjacent plants. Contrary to this, in our study there was usually first inhibition of cone production between trees close in space followed by stimulation at larger distances. A notable exception is plot 1 in 2005 where we obtained a $k_{mm}(r)$ curve similar to those in Lancaster (2006). Suzuki et al. (2008) also detected stimulation patterns in a coniferous mountain forest in Japan using tree heights as marks. Calama et al. (2008) state that the bigger the number of dominant trees the lower is the density and the higher the site quality the larger is the average

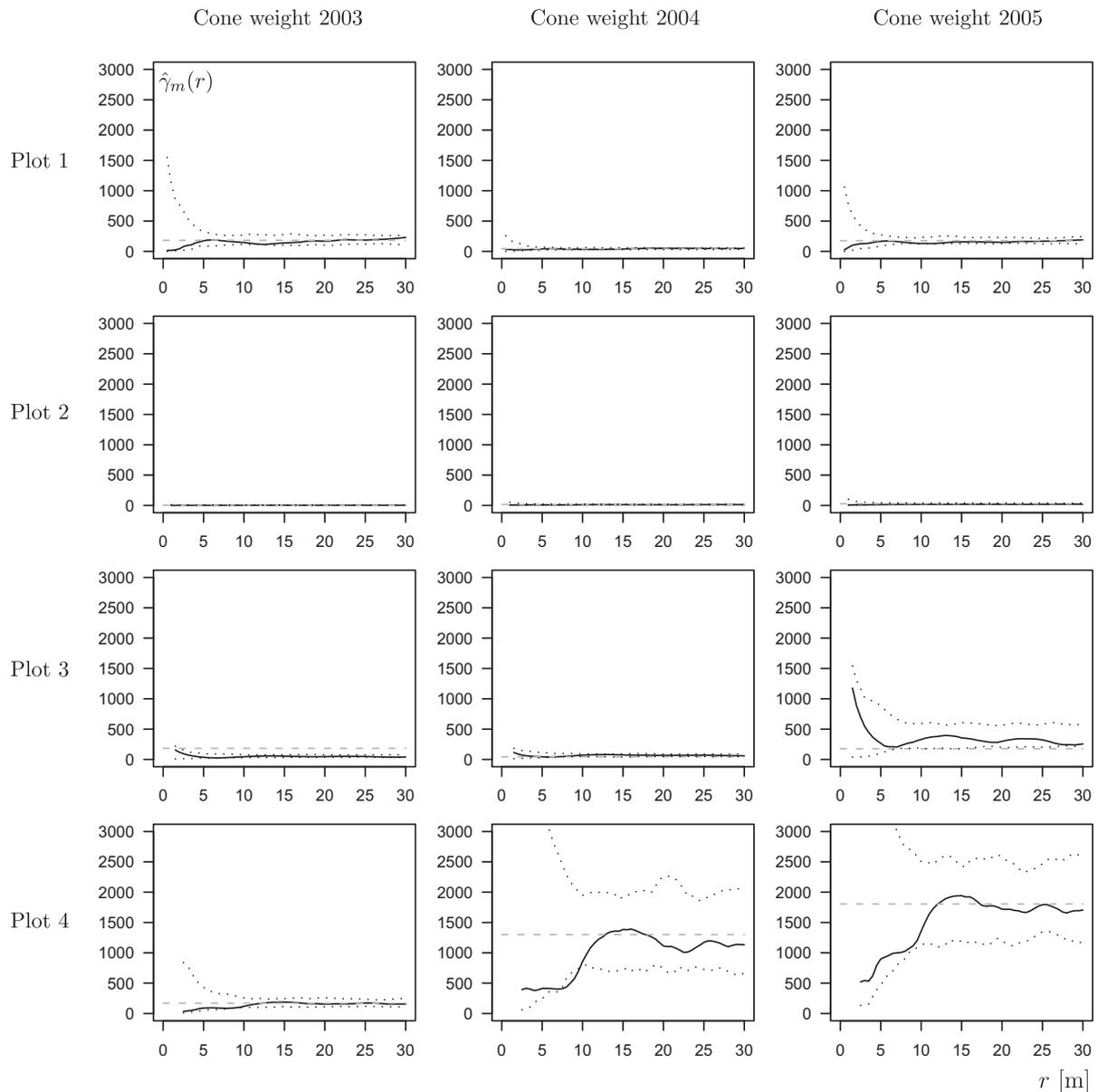


Fig. 9. Mark variograms, $\hat{\gamma}_m(r)$, using tree cone weights in 2003, 2004 and 2005. Envelopes of the acceptance regions of the mark independence hypothesis are shown as dotted lines. r is the distance between pairs of trees. The grey dashed line indicates the variance of cone weight.

cone yield. This is also evident in our observations; especially in plot 4 where the largest production was attained because dominant trees were particularly frequent. Tree density was low in this plot and soil water retention capacity was highest.

In addition we made another interesting observation:

The spatial characteristics also indicate that there is some sparse recruitment (individuals with less than 20 cm of diameter at breast height) of *Pinus pinea* and cork oak in the vicinity of large, mature *Pinus pinea* trees, particularly in plot 3 where they cause negative autocorrelation and large mark variance. Similar to the findings in interior Douglas fir (*Pseudotsuga menziesii* var *glauca* (Mirb.) Franco) (LeMay et al., 2009), according to our observation *Pinus pinea* and cork oak saplings seem to benefit from the semi-shade and from the greater soil moisture in the vicinity of mature *Pinus pinea* individuals. Also *Pinus pinea* seeds are heavy and there is a natural tendency of this species to germinate near parent trees contrary to for example *Pinus halepensis* and *Pinus pinaster* where seed dispersal

and recruitment can be found at larger distances from the parent trees, with greater probability of recruitment between 20 and 30 m for *Pinus halepensis* Mill. (Ganatsas and Thanasis, 2010) and 0–30 m for *Pinus pinaster* Ainton. (Nanos et al., 2004).

In conclusion, *Pinus pinea* cone production is strongly influenced by tree spacing. This is mainly due to the light demanding nature of this pine species and the specific environmental conditions of the Alcácer do Sal region, which are characterised by regular summer droughts and soils with limited water and nutrient availability. Local forest owners and managers are well aware of this and their management aims at providing maximum growing space and thus maximum resources to every single tree leading to regular patterns of tree locations. Despite the similarity of environmental factors and management in the Alcácer do Sal region, the details of microstructure vary more between different forests of the region than between different times in the same forest.

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