Growth phenology and mating system of maritime pine ("Pinus pinaster" Aiton) in central Spain

I. Miguel, Santiago C. González-Martínez, R. Alia, L. Gil

Growth phenology and mating system of maritime pine *(Pinus pinaster* Aiton) in central Spain

I. Miguel Pérez [1], S.C. González Martínez [2], R. Alía Miranda [2], L. Gil Sánchez [1*]

[1] Unidad de Anatomía, Fisiología y Genética, ETSIM.
Ciudad Universitaria, s/n. 28.040 Madrid, España

[2] CIFOR-INIA. Crta. de La Coruña, km 7,5. 28.040 Madrid, España
santiago@inia.es

SUMMARY

The study of the mating systems of forest species is important both in forest management and breeding. In this work, we analyzed the phenology of diameter growth, the phenology of female and male flowering, and the seed yield in a native stand of maritime pine (from Meseta Castellana provenance) during the years 1999 and 2000. Maritime pine showed a long vegetative period in the study area (8.6 months). The male flowering period lasted 15 days whereas the female flowering lasted four weeks. Maximum pollen production occurred when most female strobili reached their maximum receptivity. Individual female strobilus production was medium-high in the studied stand (annual mean about 30 strobili per tree) and there was a remarkable correlation between both years. During the studied period, a high seed yield was observed (300,000 seeds/ha estimated in year 2000) and no limitation to natural regeneration due to mating system is expected.

Key words: stem diameter growth, phenology, seed crop, pinus, Mediterranean forest.

INTRODUCTION

The mating system of a plant species (mainly flowering phenology, flower, fruit and seed production, outcrossing rates and interannual variation of these phenomena) conditions its genetic structure (e.g. the distribution of genetic diversity among and within populations) and has important evolutive consequences (Charlesworth and Charlesworth, 1987). Studies aimed at establishing the basic parameters of the mating system of forest species are considered fundamental in conservation programmes and forest improvement strategies (Boshier, 2000). In spite of that, mating system studies of Mediterranean native conifers in natural

* Autor para correspondencia
Recibido: 3-10-01
Aceptado para su publicación: 11-2-02

populations are scarce, the efforts being concentrated in the study of different species of Iberian pines in seed orchards (Martín and Agúndez, 1992; Rodríguez, 2001, for *P. sylvestris)*, clonal banks (Mutke, 2000, for *P. pinea,* Auñón and Tadesse, 2000, for *P. pinaster)*, and progeny or provenance tests (Prada, 1999, for *P. halepensis)*, that have more or less controlled conditions and a spatial scheme designed to avoid endogamy (seed orchards) or to control experimental errors (progeny or provenance tests).

Maritime pine *(Pinus pinaster* Ait.) is the forest species that has been more extensively used in Spanish plantations in the last forty years (more than 800,000 ha). It is also the widest spread conifer species in Spain nowadays (near 1,200,000 ha). Its wide distribution and variety of sites occupied have made *P. pinaster* a species of high relevance in Iberian forestry (Gil *et al.,* 1990; Costa *et al.,* 1997). Maritime pine populations from the Iberian Peninsula show high levels of genetic diversity and an important genotype-by-environment interaction that favors the existence of adaptations to local ecological conditions (Alía *et al.,* 1995; Alía *et al.,* 1997; Salvador *et al.,* 2000). The existence in the same geographic area of central populations with a great number of trees and marginal populations of high fitogeographic and conservational interest, and very differentiated population dynamics, makes this species ideal for autoecological and genetic studies.

Maritime pine fruit production begins at an early age (normally at 15-20 years old) with a regular recurrence of copious crops every 1 or 2 years and a high seed production (Alía *et al.,* 1999). The seed production and mating strategy of maritime pine are related, generally, to the fire regime (intensity, frequency, size and spatial scheme). Stands suffering recurrent and high-intensity fires show serotinous cones and an important aerial seed bank. On the contrary, serotinous cones are rare in stands where crown fires are not frequent (Tapias *et al.,* 2001). An extreme case is that of Sierra del Teleno (León), where there is a marked incidence of fires and serotinous cone production reaches some years 100 %, with an aerial seed bank larger than 1,000,000 seeds/ha (Tapias, 1998).

The main aim of this study is to analyze maritime pine mating system in a central-range stand of the species. This is the reason why a stand in Coca (Meseta Castellana provenance) has been selected. The specific objectives are (1) to determine the vegetative period and growing pattern of *P. pinaster,* (2) to describe the female and male flowering periods within the stand, and (3) to estimate cone and seed production in the study period.

MATERIAL AND METHODS

Study area

The study area is a native stand of *P. pinaster* situated in the province of Segovia (Meseta Castellana provenance). This stand is located in «Pinar Viejo» forest (Coca, CUP 105) at latitude 41 16' N and longitude 4 29' W. In Allué and Allué (1994) a detailed reference of the management of this forest since 1901 can be found. A circular plot of 25 m radius (1,963 m^2) was selected taking into account: 1) the existence of abundant natural regeneration, 2) the accessibility of the plot, and 3) a low level of forest management within the plot. In fact, in the selected plot, there have been no silvicultural treatments in the last years but for the cutting of dead trees. The plot has twenty *P. pinaster* adult trees and 206 seedlings and saplings (Fig. 1).

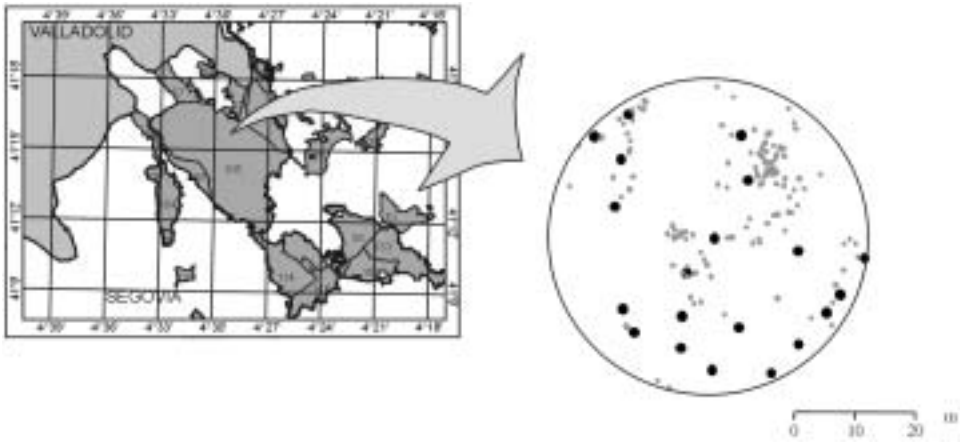

Fig. 1.–Location of the study plot and spatial position of mature trees and natural regeneration

The climate is typically Mediterranean with a mean annual rainfall of 461 mm (65 mm in summer) and a pronounced summer drought. The mean annual temperature is 11.3 C and a four-month frost period is common. A comparison of climatic parameters between the study area and other regions mentioned in the present study is shown in Table 1. The vegetation of the area is a mixture of *Pinus pinaster* and *Pinus pinea* L. trees, with a wide predominance of the first, and a mean density of around 100 trees per ha. The low-density understorey is dominated by scrubland species as *Lavandula pedunculata* Miller., *Retama sphaerocarpa* (L.) Boiss., *Cytisus scoparius* (L.) Link., *Thymus mastichina* (L.) L. and *Helichrisum stoechas* (L.) DC.

Table 1

Comparison of climate parameters

	Coca	Sierra del Teleno	Cabañeros
Mean annual temperature (°C)	11,3	9,7	12,8
Mean annual rainfall (mm)	461	750	800
Altitude (m.a.s.l.)	780	900	1.045

Study design

Growth and flowering phenology

Dendrometers of millimetric precision were placed on 14 adult trees in the stand in order to determine vegetative active periods and diameter growth. Measurements were made over two growing periods, from 17 march 1999 to 31 august 2000. The periodicity

of the measurements ranged between one and three weeks depending on the time of the year.

Male flowering phenology was studied in all the adult trees in the plot. The phenological stages described in Table 2 were distinguished. Observations were made weekly, knocking the branches in different parts of the crown using a long pole. Temperature is an important factor for flowering of pine species (Jackson and Sweet, 1972), so northern and southern exposures have been analyzed separately. Female flowering was monitored in two branches of 19 adult trees in the study plot. A minimum of 5 whorls and 8 buds (although these numbers were generally surpassed) were tracked. Each year of the study different branches in each tree were selected. Weekly observations were made until all female strobili reached their final phenological stage (i.e. stage 4; see Table 2).

Table 2

Phenological stages for male and female flowering (modified from Martín and Agúndez, 1992; Auñón and Tadesse, 2000)

	Male flowering
Stage 0	Male strobili without apparent pollen production.
Stage 1	Male strobili with great pollen production. The branches produce a notable pollen cloud when moved.
Stage 2	Male strobili with residual pollen production.
	Female flowering
Stage 0	Bud covered by protective scales. Bud growth is not apparent.
Stage 1	Growth of female buds starts to be apparent.
Stage 2	The female cones are evident but not fully developed.
Stage 3	Female cones are fully developed. Cones have a bright red colour. Receptivity period.
Stage 4	Postflowering growth of the vegetative bud. The pollination has been completed. Cones have a dark red colour.

Female strobilus, cone and seed production

In the spring of 1999, all female strobili in the phenological stage 3 of half crown and of the whole crown of the stand trees were counted from the ground. Since strong correlation between the number of female strobili in half crown and the whole crown was thus found, ($r = 0.99$), in the next year only the female strobili in half of the crown were counted when calculating the total annual crop. Cone production was estimated by total counts in 1999 and 2000.

In order to determine cone and seed characteristics, 3-4 cones of each tree in the study plot that produced cones in the year 2000 (18 trees) were picked. Total length was measured and the number of pinyons, scales, and percentage of empty seeds were counted following Tapias (1998).

Cone opening

At least four cones, normally developed and mature, were selected and marked for each adult tree in the stand. From march to october 2000 their opening was followed fortnightly. Two phenological stages, open or closed, were distinguished.

Data analysis

Correlations between two variables were computed using Kendall's parameter. This correlation coefficient does not imply normally distributed variables, so it is adequate when the number of observations is low.

RESULTS AND DISCUSSION

Growth and flowering phenology

Growth phenology

Mean stem diameter growth of the trees in the studied period was 0.66 (S.D. 0.21) cm. Three periods in which diameter growth was detected were clearly differentiated (Fig. 2). Two of them were in 1999's and 2000's springs (early april to mid-june) and the other was in 1999's autumn-winter (late august to early october). Around 60 % of the annual growth

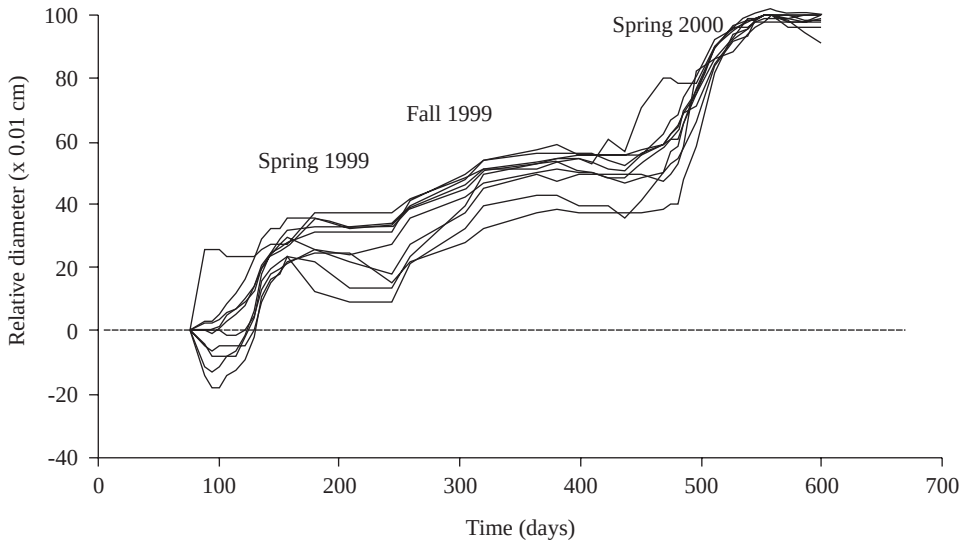

Fig. 2.–Mean relative diameter growth for 10 mature trees in the study plot. Note that a high experimental error is present at the beginning of the study due to the dendrometers adjustment period. Zero corresponds with 01.01.99

occurred in spring and 40 % in autumn. The spring growing period was a month longer in 2000 than in 1999: it began 20 days before and ended 15 days afterwards. Moreover, it was quantitatively double (0.25 cm mean growth in 1999 compared to 0.50 cm in 2000). The higher precipitation during the growing period in 2000 (P_{2000} = 167 mm in contrast with P_{1999} = = 116 mm) and the most favorable mean temperature (T_{2000} = 15.8 C in contrast with T_{1999} = 14.1 C) explain the differences observed in spring growth.

In 1999, the vegetative period lasted 260 days (8.6 months). This result is very similar to the nine-month annual growth obtained by Figueiredo (1992) for *P. pinaster* in Portuguese submediterranean coast, with more favourable precipitation and temperature. In a similar work in Cabañeros (Ciudad Real), Alía and Gil (1992) observed, in relation to our study, an earlier beginning of spring growth and summer stop (around 40 days). An early final stop of growth was also observed (11 september contrasted with 3 october in Coca). According to Alía and Gil (1992), a seasonal variation in diameter growth can be recognized in *Pinus pinaster* that does not correspond to the ecological factors of the provenance origin, as the different provenances essayed in the same site did not show significant differences. The differences observed between the Coca plot and the performance of that provenance in the essay plot studied by Alía and Gil (1992) may be due to location, as the last one is situated in Cabañeros (Ciudad Real), with a mean temperature and number of degrees-day in spring higher than Coca (Segovia).

Male and female flowering phenology

A summary of the male and female flowering phenology in the two years of study is shown in Figure 3. Total length of male flowering period was around 15 days. In both years, the dates of the different phenological stages were similar, with the exception of the beginning of flowering, which in 2000 occurred some days before than in 1999. Rodríguez (2001) found interannual differences of a week in pollen dehiscence for *P. sylvestris* in a seed orchard at Valsaín (Segovia). Mutke (2000) observed for *P. pinea* in a clonal bank in Valladolid dates of pollen dispersion with differences of four days between the first and the last observations (first week in june).

The moment of maximum pollen dispersion (stage 1) matched in date the period of receptivity of female strobili (stage 3) in both years. The success of pollination lies in the synchronization of pollen emission with female flower receptivity. Nonetheless, in the study plot the first female strobili were receptive when there was not any local male flowering yet. This could expose some strobili to desiccation or even death before they are pollinated. Late female strobilus pollination seems guaranteed, as pollen can remain suspended on the air for some days (Bramlett *et al.,* 1993). In general, the male strobili in the part of the crowns facing south matured about a week before than those in the part facing north. This fact is due to a greater sun exposure (Jackson and Sweet, 1972).

The length of the period in which female flowering was completed –from most trees got to stage 1 until they reached stage 4– was around four weeks. A difference of a week in the beginning of flowering between both years was observed. In 1999, most of the trees (more than 80 %) were in stage 1 on day 114 (25 april), on day 121 (2 may) all had reached it. In 2000, almost a 40 % of the trees were in stage 1 on day 121 (2 may) and on day 126 (7 may) all the trees had reached it. In the intermediate flowering stages the week's gap observed between both years at the beginning of flowering was not found. There was a slight delay in 2000 when compared to 1999, but the beginning of stages 2, 3

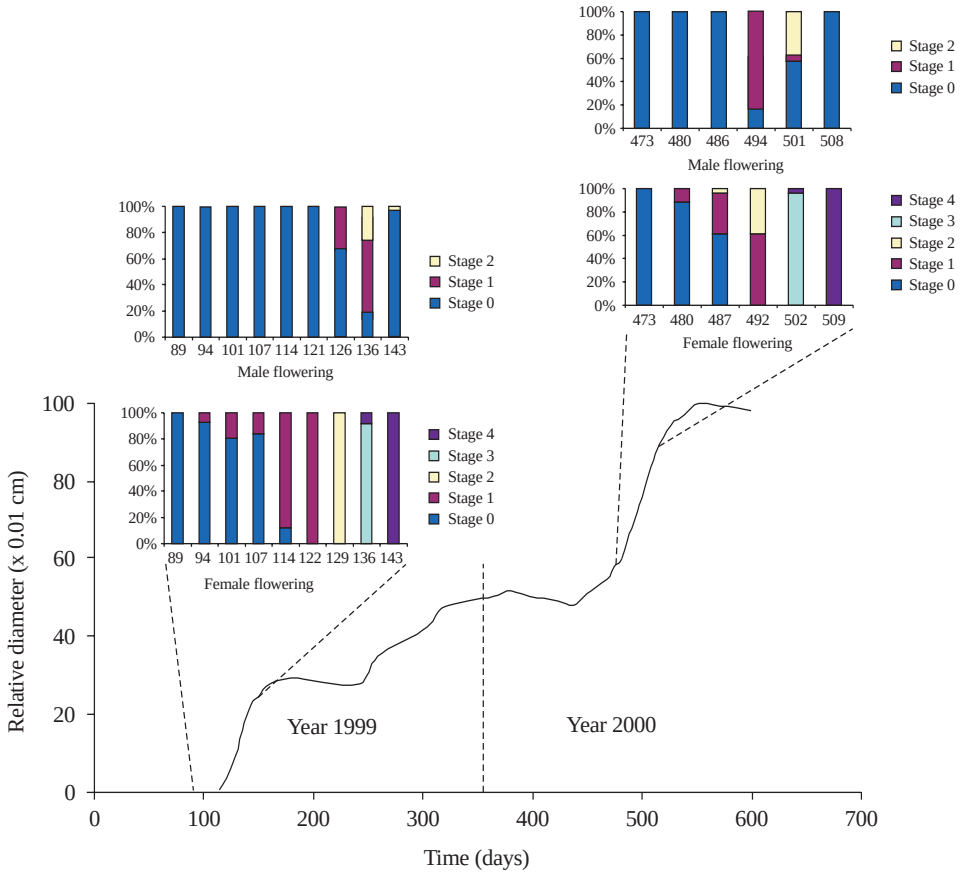

Fig. 3.–Average diameter growth, and male and female flowering phenology. Zero corresponds with 01.01.99

and 4 was very similar in both years. Boes *et al.* (1991) and Rodríguez (2001) found in their interannual flowering studies an important effect of climatic conditions over female flowering phenology in *P. sylvestris* seed orchards.

The length of the male strobilus period of receptivity matches the observations of Auñón and Tadesse (2000), in their phenological study of a *P. pinaster* clonal bank in Carbonero El Mayor (Segovia), 25 km away from our study plot (Fig. 4). The length of the female strobilus period of receptivity depends mainly on pollen availability (Pulkkinen, 1994) as, once the pollen enters the strobilus, it closes (Niembro, 1986). In addition, the two climatic factors that mostly affect the permanence of pollen in the air are wind and rain (Boyer, 1966; Bramlett *et al.*, 1993).

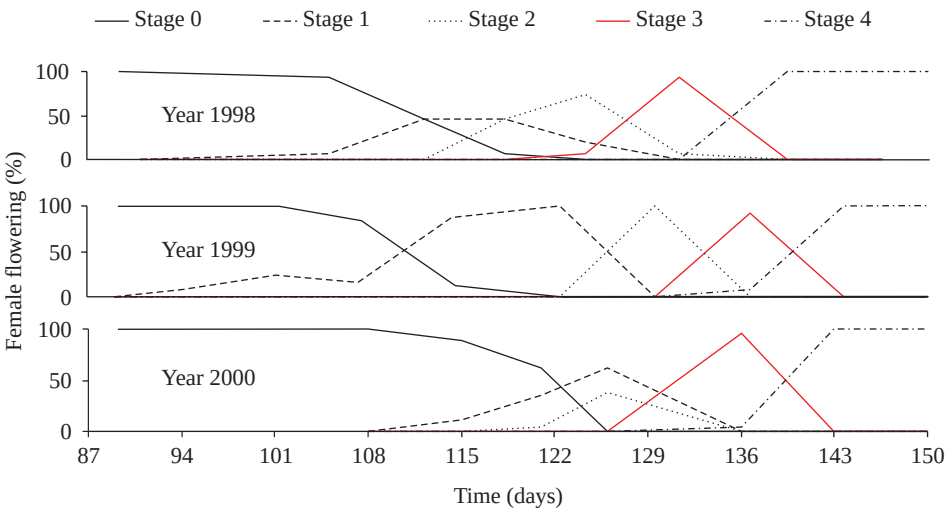

Fig. 4.–Phenological stages in female flowering in 1998 (Auñón and Tadesse, 2000), 1999, and 2000

Production of female strobili, cones and seeds

Production of female strobili and cones

In 1999 the production within the stand of female strobili was double that of 2000's: 774 strobili in contrast with 399 (Fig. 5), which means 39 (S.D. 16) and 20 (S.D. 4) strobili/tree, respectively. The interannual variation may be due to environmental factors such as the lack of precipitation in the moment of differentiation of the meristems. There was a remarkable correlation between 1999's female strobilus production and 2000's (= 0.49; $p < 0.01$), which shows that, in general, individual differences in the production of strobili remain from one year to the next. Cone crop counts showed survival rates from female strobili to ripe cones higher than 90 %.

Cone characteristics and seed production

Total number of scales, cone length, number of pinyons per cone and percentage of empty seeds, as well as the values for these variables obtained by Tapias (1998) in a *P. pinaster* stand in Sierra del Teleno (León), are shown in Table 3. Cones in Coca plot were bigger than those in Sierra del Teleno, and they also showed a greater number of scales but, in spite of that, they contained fewer pinyons. According to Tapias (1998) the number of ovules is similar to the total number of scales in the cone. The number of seeds per cone depends on the number of ovules, on the pollination ratio and on how many of them complete their development. Consequently, in Coca, only 66.7 % of the ovules finally produced seed, in contrast with 87 % in Sierra del Teleno. The mean value observed in

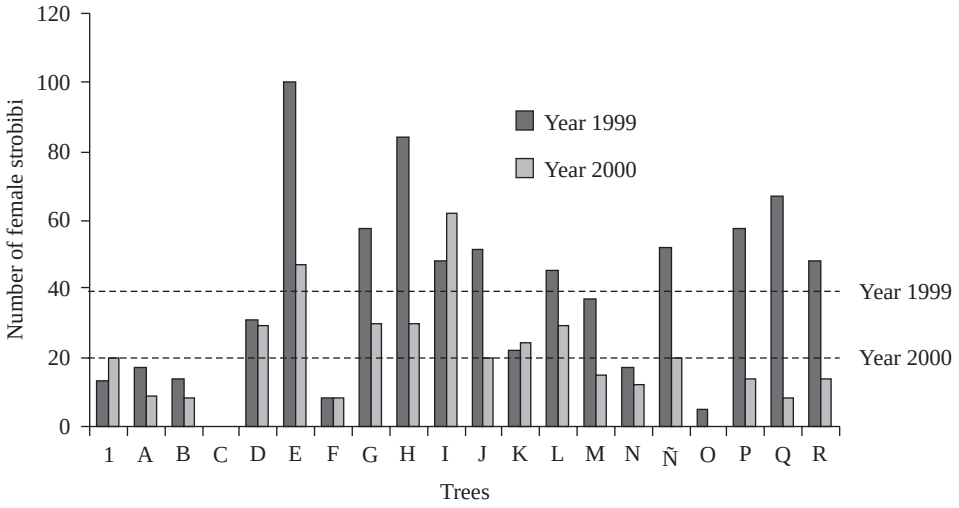

Fig. 5.–Number of female strobili in spring in years 1999 and 2000. Dotted lines indicate the year average

Coca was 155 scales, similar to South African *P. pinaster* stands (153.4 scales) as observed by Siegfried (1986), but the seed/scale rate (0.83 in South Africa and 0.67 in Coca) and, therefore, the number of seeds per cone (127.3 in South Africa and 103.4 in Coca), was much higher in the African stands. On the other hand, the percentage of empty seeds in Coca was smaller than in Sierra del Teleno. In the last case, the study area was a natural regenerated stand produced after a high intensity fire. The production of pollen in these conditions is expected to be scarce due to the low age of the trees, which makes likely a greater number of selfpollinated seeds than in Coca and, therefore, a higher percentage of empty seeds.

Tabla 3

Average values for 54 cones from coca (meseta castellana) and 110 cones from Sierra del Teleno (León)

Provenance	Length (cm)	Scales per cone	Seeds per cone	Empty seeds (%)
Meseta Castellana (Coca)	10.7 (S.D. 1.74)	155 (S.D. 25.1)	103.4 (S.D. 22.4)	16.4
Sierra del Teleno (Tapias, 1998)	7.89 (S.D. 1.4)	137.3 (S.D. 2.1)	119.5 (S.D. 2.6)	23.6

With the results for female strobilus production, percentage of strobilus survival and mean values of pinyons per cone in each tree, an estimation of cone and pinyon production for the year 2000 can be made, obtaining a crop of around 300,000 pinyons/ha. This seed production is considered enough to guarantee the natural regeneration of the stand.

Cone opening

Three serotinous cones were found in the study plot, less than 2 % of the total cone crop. Serotinous cones do not open spontaneously once they are completely mature but remain closed during, at least, the following summer. Cone serotinity, production of a thick bark and production of cones at low ages in *P. pinaster* are considered adaptations to fire (Gil *et al.,* 1990). The main adaptation to fire in the study zone is thick bark in the low part of the tree, as fires are frequent but seldom affect the crowns due to a scarce understorey. On the contrary, Tapias (1998) found in Sierra del Teleno (León), where crown fires are frequent, mean percentages of serotinous cones of 80 %.

All 78 cones monitored during spring-summer 2000 opened and disseminated their seed during this same period. Most of the cones opened in the period between day 178 (28 june) and 239 (18 august). In this period the percentage of open cones remained more or less constant between 50 and 60 % of the total number of cones. The percentage remained constant not because no new cones opened, but because when some opened, others closed once they had disseminated the seed. From day 254 (2 september), most of the cones in the stand were open.

CONCLUSIONS

1. Maritime pine *(P. pinaster* Ait.) in Meseta Castellana shows a double sigmoid diameter growth curve, and a nine-month total vegetative period. Summer and winter resting periods are around one month and a half each. Total growth in diameter is low, around 0.5 cm per year.
2. There is synchronization between the moment of maximum pollen production and the maximum percentage of female strobili in stage 3 (strobilus receptivity). An interannual variation in the beginning and quantity of female flowering was observed, seemingly due to environmental causes.
3. Maritime pine mating in Meseta Castellana observed during the study period seems adequate to guarantee the natural regeneration of the stand. Therefore, difficulties in the regeneration of the stands in this area lie in phenomena affecting the seed once it is disseminated. Bird and rodent predation and the difficulties in the establishment and initial growth of the seedlings in the study zone –Mediterranean with strong summer drought– are the most important among them.

ACKNOWLEDGMENTS

This study was funded by INIA project SC97-118. S. C. González Martínez was supported by a FPU scholarship from MECD (Ministerio de Educación, Cultura y Deporte). Thanks are extended to M. Allué-Andrade who assisted in the selection and installation of the study plot and to F. del Caño and A. Piñera for skillful fieldwork and discussion of a draft of the manuscript. P.C. Grant kindly translated the original manuscript to English.

RESUMEN

Fenología del crecimiento y estrategia reproductora del pino negral (*Pinus pinaster* Aiton) en la Meseta Castellana

El estudio de la estrategia reproductora de las especies forestales proporciona información valiosa para la gestión y mejora de sus masas. En este trabajo se analiza la fenología del crecimiento radial y de la floración tanto masculina como femenina, y la producción cuantitativa de estróbilos femeninos y semilla en un rodal natural de pino negral (región de procedencia Meseta Castellana) durante los años 1999 y 2000. El pino negral presenta un amplio período vegetativo en la zona estudiada (8,6 meses). La duración del período de floración masculina es de 15 días, mientras que el ciclo de floración femenina es de aproximadamente cuatro semanas, estando sincronizados en el tiempo la fase de máxima producción de polen con el momento de máxima receptividad de los estróbilos femeninos. La producción de estróbilos femeninos en el rodal es media-alta (media anual de 30 estróbilos por árbol) y hay una marcada correlación entre los dos años estudiados. Durante el período de estudio se ha observado una producción de semilla elevada (300.000 piñones/ha estimados en el año 2000), indicando una estrategia reproductora de la especie, bien adaptada a las condiciones locales.

Palabras clave: crecimiento diametral, fenología, cosecha de semilla, pinus, bosque Mediterráneo.

REFERENCES

ALÍA R., GIL L., 1992. Ritmo anual de crecimiento en circunferencia de 15 procedencias de *Pinus pinaster Ait.* Montes, 28, 34-35.

ALÍA R., GALERA R., MARTÍN S., AGÚNDEZ D., DE MIGUEL J., IGLESIAS S., 1999. Mejora genética y masas productoras de semilla de los pinares españoles. Monografías INIA: Forestal n.º 1, 239 pp.

ALÍA R., GIL L., PARDOS J.A., 1995. Performance of 43 *Pinus pinaster* provenances on 5 locations in Central Spain. Silvae Genetica, 44, 75-81.

ALÍA R., MORO J., DENIS J.B., 1997. Performance of *Pinus pinaster* Ait. provenances in Spain: interpretation of the genotype-environment interaction. Can. J. For. Res., 27(10), 1548-1559.

ALLUÉ C., ALLUÉ M., 1994. Notes on the managed development of the «Pinar Viejo» pine forest (Coca, Segovia) from 1901 to 1990. Invest. Agr.: Sist. Recur. For., Fuera de Serie 3, 259-281.

AUÑÓN F.J., TADESSE W., 2000. Crecimiento del brote y floración femenina de *Pinus pinaster* Ait. en el banco clonal situado en Carbonero El Mayor (Segovia). Foresta, 9, 30-34.

BOES T.K., BRANDLE J.R., LOVETT W.R., 1991. Characterisation of flowering phenology and seed yield in a *P. sylvestris* clonal seed orchard in Nebraska. Can. J. For. Res., 21, 1721-1729.

BOSHIER D.H., 2000. Mating systems. In: Forest Conservation Genetics: Principles and Practice. Boyle, T., Boshier, D., Young, A., eds. CSIRO Publishing, Australia, 63-79 pp.

BOYER W.D., 1966. Longleaf pine pollen dispersal. Forest Science, 12, 367-368.

BRAMLETT D.L., ASKEW G.R., BLUSH T.D., BRIDGWATER F.E., JETT J.B., 1993. Advances in pollen management. Agriculture Handbook 698, US Department of Agriculture, Forest Service, Washington D.C., 100 pp.

CHARLESWORTH D., CHARLESWORTH B., 1987. Inbreeding depression and its evolutionary consequences. Annual Reviews in Ecology and Systematics, 18, 237-268.

COSTA M., MORLA C., SAINZ H. (eds), 1997. Los bosques ibéricos. Ed. Planeta, 572 pp.

FIGUEIREDO J.P.M., ALMEIDA V.C.V., 1992. La actividad cambial de *Pinus pinaster* y *Pinus pinea* en el litoral submediterráneo portugués. Montes, 28, 40-45.

GIL L., GORDO J., ALÍA R., CATALÁN G., PARDOS J.A., 1990. *Pinus pinaster* Aiton en el paisaje vegetal de la Península Ibérica. Ecología, Fuera de Serie 1, 469-495.

JACKSON D., SWEET G., 1972. Flower initiation in temperate woody plants. Hort. Abs., 42, 9-24.

MARTÍN S., AGÚNDEZ L., 1992. Crecimiento y floración de *P. sylvestris L.* en un huerto semillero clonal. Montes, 28, 46-48.

MUTKE S., 2000. Fenología de *Pinus pinea* L. en un banco clonal (Valladolid). ETSIIAA de Palencia, Universidad de Valladolid. MSc dissertation.

NIEMBRO A., 1986. Mecanismos de reproducción en pinos. Limusa SA, México, 130 pp.

PRADA A., 1999. Mejora genética de *Pinus halepensis* Mill. en la Comunidad Valenciana. ETSI de Montes, Universidad Politécnica de Madrid. PhD dissertation.

PULKKINEN P., 1994. Aerobiology of pine pollen: dispersal of pollen from non-uniform sources and impact on Scots pine seed orchard. Forest Tree Breed., 8, 1-23.

RODRÍGUEZ J.A., 2001. Variabilidad reproductiva y sus implicaciones en el incremento de la producción de semilla en un huerto semillero de *Pinus sylvestris.* ETSI de Montes, Universidad Politécnica de Madrid. PhD dissertation.

SALVADOR L., ALÍA R., AGÚNDEZ D., GIL L., 2000. Genetic variation and migration pathways of maritime pine *(Pinus pinaster* Ait.) in the Iberian Peninsula. Theor. Appl. Genet., 100, 89-95.

SIEGFRIED W.R., 1986. Cone and seed relationships in Cluster pine, *Pinus pinaster* Ait., in the South-Western Cape. Suid-Afrikaanse Bosboutydskrif, 137, 33-36.

TAPIAS R., 1998. Estudio de las adaptaciones al fuego de *Pinus pinaster* Ait. de la Sierra del Teleno. Comparación con otras poblaciones de *P. pinaster, P. halepensis, P. nigra* y *P. pinea.* ETSI de Montes, Universidad Politécnica de Madrid. PhD dissertation.

TAPIAS R., GIL L., FUENTES-UTRILLA P., PARDOS J.A., 2001. Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. Journal of Ecology, 89, 629-638.